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ORIGINAL RESEARCH

Sea Level Rise Impacts to Coastal Marshes may be Ameliorated by Natural Sedimentation Events

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Abstract

Coastal wetland sustainability in the future will likely depend on the extent to which increases in sea level drive flooding duration, plant submergence, and higher salinities, and how wetlands respond to these changes. Coastal wetlands will need to grow vertically to cope with rising seas, and sedimentation, often observed following hurricane passage, could play a role. A greenhouse mesocosm experiment was conducted to investigate if the impacts of sea level rise (SLR) and elevated salinity on the productivity and resilience of *Spartina alterniflora* marshes could be mediated by simulated hurricane sedimentation. Overall, sedimentation ameliorated the negative impacts of moderate SLR on plant productivity and resilience. Sedimentation improved growth conditions at current and moderate increases in sea level by reducing flooding duration, which in-turn, increased soil Eh, and lowered porewater sulfide. This led to greater productivity of vegetation above- and belowground and improved plant resilience. However, at the highest sea levels, inundation stress was too great for the benefits of added sediment to be realized. Thus, it is likely that the sustainability of coastal marshes will be improved by hurricane-generated sedimentation under moderate SLR scenarios, but will see no improvement with more extreme SLR.

Keywords Sea level rise · Marsh resilience · Sedimentation · Hurricanes · Coastal marsh · *Spartina alterniflora*

Introduction

Rising sea levels may cause coastal wetlands worldwide to experience increased loss by the end of the twenty-first century (Nicholls and Cazenave 2010; Spencer et al. 2016). Coastal wetlands have a high ecological value and provide numerous ecosystem services, so their loss is of global concern, especially to coastal nations (Costanza et al. 1998; Keddy 2000; Barbier et al. 2011). Currently, eustatic sea level rise is occurring at an average rate of 3.2 mm yr.$^{-1}$ globally (IPCC 2013) and relative sea level rise (RSLR), which includes both eustacy and isostacy, can exceed 5× the eustatic rate in some regions of the world. In the Mississippi River Delta Ecosystem (MRDE) of coastal Louisiana, high rates of subsidence have resulted in RSLR rates estimated between 3.6 and 17.7 mm yr.$^{-1}$ based on tide gage data (Penland and Ramsey 1990), but may be higher or lower depending on the method of measurement (Dokka et al. 2006; Törnqvist et al. 2006; Zou et al. 2016; Jankowski et al. 2017). Regardless of the exact rate, high RSLR in the MRDE has contributed to a dramatic land loss problem (Morton et al. 2005; Barras et al. 2008), similar to other deltaic coastlines world-wide (Ibanez et al. 2014). Louisiana's MRDE, which contains nearly 40% of the coastal wetlands in the contiguous United States, has lost more than 4877 km^2 of coastal wetlands since 1932 (Couvillion et al. 2011). Coastal wetlands around the world may experience similarly high rates of loss if global sea levels continue to rise at an increasing pace (Day et al. 2008; IPCC 2013; Kintisch 2013; Spencer et al. 2016).

The degradation and loss of coastal wetlands in response to rising seas is largely attributed to a greater duration and depth of inundation, reduced substrate aeration, increased hydrogen sulfide concentrations and, in some wetland-types, higher salinity; all of which negatively affect wetland vegetation

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(Lamers et al. 2013; van Dijk et al. 2015). For marshes to remain viable, the effects of rising sea level must be offset by positive marsh elevation change. Coastal marshes gain elevation through the accumulation of organic and inorganic materials (Redfield and Rubin 1962; Morris et al. 2002; Nyman et al. 2006), so one, or both, of these processes will need to increase if coastal marshes are to keep pace with relative sea level rise, assuming all else equal.

Organic accumulation in coastal marshes is generated internally through root, rhizome and stem production, while inorganic sediment accumulation is governed primarily by external processes such as tides, floods, and storm-overwash (Nyman et al. 1993; Turner et al. 2001; Nyman et al. 2006) in association with positive biotic feedbacks from vegetation (Baustian et al. 2012). Inorganic sedimentation further benefits coastal marshes by delivering nutrients that improve vegetation growth, as well as iron and manganese that precipitate hydrogen sulfide and improve soil physico-chemical condition (Mendelssohn and Kuhn 2003; Lamers et al. 2013). Tropical cyclonic storms are known to deposit inorganic sediment over large areas of marsh (Cahoon 2006; Turner et al. 2006; Bianchette et al. 2015). This sedimentation has been shown to have a positive effect on marsh primary production and resilience (Baustian and Mendelssohn 2015; Walters and Kirwan 2016), although the detrimental impacts of hurricanes on coastal erosion have been well documented (Guntenspergen et al. 1995; Barras 2009; Stockdon et al. 2012).

Tropical cyclonic storms contribute to the structuring of coastal systems around the world by altering vegetation cover, local hydrology, nutrient cycling, and sedimentation and erosion rates (Michener et al. 1997; Barras et al. 2008; Tweel and Turner 2014). Climate change models predict an increase in frequency of strong storms (Knutson et al. 2010; Emanuel 2013), and consequently, hurricanes may play an increasingly important role in structuring coastal systems in the future. The benefits of hurricane-induced sedimentation, and the detriments of hurricane-induced erosion, have been highlighted in recent years (Barras 2009; Howes et al. 2010; Baustian and Mendelssohn 2015). For example, in a field-based companion study to this research Baustian and Mendelssohn (2015) showed that 2–12 cm of sedimentation from hurricanes in 2008 improved primary production and resilience of brackish and salt marshes in Louisiana; while Howes et al. (2010) documented 527 km^2 of marsh erosion from hurricanes in 2005. However, in a future world characterized by higher sea levels and more intense tropical cyclones, will greater storm-induced sedimentation offset, at least in part, the negative impacts of higher sea levels on coastal wetlands?

Here we utilized natural marsh mesocosms (intact marsh soil and vegetation) in a controlled greenhouse environment to investigate if, and to what extent, simulated hurricane sedimentation alters marsh ecological response to increases in sea level and salinity. To simulate future sea levels and salinity, we first subjected marsh mesocosms to the interactive effects of future sea levels and higher salinity for four months. We then simulated hurricane-induced sedimentation and measured various ecological responses for nearly 2-years to determine if sedimentation could ameliorate the impacts of sea level rise and elevated salinity.

Methods

Experimental Setup

This experiment was conducted over a two-year period beginning in November 2008 in a greenhouse in Baton Rouge, LA, USA (30.4111°N, 91.1731°W). Greenhouse temperatures ranged from 21 to 29 °C between November and April, and 26 to 35 °C between May and October. The greenhouse contained eight fiberglass-lined wooden tanks (440 cm long, 45 cm wide, 100 cm deep). Each tank was connected to a 1000-l plastic water storage tank. Tides were simulated in the tanks by pumping water in-to, and out-of, the storage tanks. Tides were diurnal and had a range of 30 cm, the average tidal range in Louisiana. Water levels rose/fell at a rate of 3 cm hr.$^{-1}$ with low tide occurring between 7 and 9 am and high tide from 7 to 9 pm. The water control system was fully automated, but was monitored daily to ensure water levels and flow rates remained within specification. Water was added to the tanks as needed to compensate for evaporation.

Plant tanks were arranged as four pairs, or blocks, and nine pots were randomly assigned to each tank. Each block contained one tank with a salinity of 18 psu and the other at 36 psu, a range in which *S. alterniflora* may dominate in coastal Louisiana. Tidal range was the same in all tanks, so elevation of the pots within each tank was altered to simulate various sea level rise (SLR) endpoints. Pots (three per elevation in each tank) were randomly assigned one of three SLR endpoints: 0, 15, or 35 cm, similar to those used to estimate wetland loss by Nicholls et al. (1999) and predicted from Hadley Center general circulation models (Table 1 in Nicholls et al. 1999). Tides fluctuated around these SLR endpoints ±15 cm each day.

After the experiment was run for six months, and the effects of salinity and SLR became measurable, sediment was added to the pots to simulate hurricane deposition. The experiment was conducted in this way because it was important to first induce the SLR stressors of salinity and flooding so that we could then test the ability of hurricane-simulated sedimentation to ameliorate these impacts. The sediment was collected from a mudflat in a salt marsh creek in coastal Louisiana, and sieved to remove shells and macro-organic matter prior to use in the greenhouse. The sediment was a silty clay (9% sand, 50% silt, 41% clay), and had a bulk density of 0.43 g cm^{-3}. Three levels of sediment were applied to the pots: 0, 6, or

Table 1 Vegetation and physicochemical response to sea level rise prior to sediment addition. Data means ±1 SE, and means sharing a superscript letter are not significantly different

Sea level endpoint (cm)	Cumulative stem height (cm)	Stem density (m^{-2})	Mean stem height (cm)	Photosynthetic rate*	Leaf elongation rate*	Elevation change (mm)	Redox (mv)	Sulfide (mM)	NH_4-N (mM)
0	1999 ± 89^{b}	397 ± 18^{a}	45 ± 1.5^{a}	10.3 ± 0.7^{a}	0.77 ± 0.08^{a}	2.3 ± 0.2^{a}	-24 ± 22^{a}	0.1 ± 0.0^{a}	0.5 ± 0.02^{a}
15	2186 ± 91^{a}	414 ± 18^{a}	47 ± 1.4^{a}	9.1 ± 0.6^{b}	0.56 ± 0.07^{a}	3.4 ± 0.2^{b}	-85 ± 14^{b}	0.6 ± 0.1^{b}	0.6 ± 0.03^{a}
35	1724 ± 140^{c}	265 ± 18^{b}	59 ± 1.8^{b}	8.3 ± 1.0^{c}	0.30 ± 0.03^{b}	3.7 ± 0.3^{b}	-118 ± 10^{b}	1.6 ± 0.2^{c}	0.8 ± 0.05^{b}
p-value	0.01	<0.01	<0.01	0.04	<0.01	<0.01	<0.01	<0.01	<0.01

*Photosynthesis rate in (μmol CO_2 m^{-2} s^{-1}) and the leaf elongation rate in (mm cm^{-1} d^{-1})

12 cm (sedimentation field-quantified after Hurricanes Katrina and Gustav [Baustian and Mendelssohn 2015]), so that each sea level and salinity combination received all levels of sedimentation in each tank.

Sod Collection

Sods of *Spartina alterniflora* were collected from a coastal marsh near Port Fourchon, LA (29.1307°N, 90.1497°W). Seventy-two sods, 30 cm deep and 38 cm in diameter, were cut from the marsh and placed into plastic pots 38 cm in diameter and 44 cm deep. The pots were brought back to the greenhouse complex and the dead stems and leaves were removed. Pots were kept at a constant water level for 2 months prior to initiation of tidal action and flooding treatments. During this time. Salinity was slowly raised until the target salinity, 18 or 36 psu, was reached. Salinity was raised using a natural sea salt product (Red Sea Salt, Houston, TX, USA).

Vegetation Measurements

Stem lengths and stem counts were used as a non-destructive measurement of vegetation vigor during the experiment. Every stem was counted and stem height was measured to the nearest millimeter by lifting the upper most leaf vertically and measuring from the tip of the leaf to the soil surface. The length of all stems in each pot was summed to yield a single value for cumulative stem length.

Measurements of the net photosynthesis rate (μmol CO2 m^{-2} s^{-1}) were made using a portable infrared gas analysis system (LI-6400, LiCor Biosciences, Lincoln, NE, USA). Measurements were made on the second or third healthy leaf from three plants in each pot, and measurements were taken between 9:00 am and 2:00 pm on days with full sun.

Leaf elongation measurements were made on the youngest leaf from three plants in each pot to assess how the plants were responding to their growing conditions (Ewing et al. 1995). The length to the tip of the leaf above a fixed point was measured, and re-measured three days later to determine elongation rates. The rates were converted to relative leaf elongation rates (RLER) to standardize for differences in initial leaf length by subtracting the natural log of the initial leaf length from the natural log of the final leaf length and dividing by the number of days between measurements.

At the end of the experiment aboveground biomass was harvested, stems were counted, measured, sorted into live and dead fractions, washed, dried, and weighed. Vegetation resilience was estimated by measuring the regrowth of aboveground biomass after 71 days (Slocum and Mendelssohn 2008). Resilience was expressed as a percentage (by weight) of the live end-of-experiment biomass that re-grew after clipping.

Belowground production was measured using a modified ingrowth core technique (Gallagher et al. 1984). Ingrowth bags (5 cm diameter, 24 cm length) were constructed of plastic mesh material and packed densely with a commercial peat moss (Berger Superfine Peat Moss, Quebec, Canada). Ingrowth bags were inserted, 1 per pot, into holes vacated of the surrounding substrate to allow for ingrowth of roots and rhizomes. Ingrowth bags were inserted after sediment was added, and harvested approximately one year later. After removal, each core was washed over a 2 mm sieve to separate the peat from the roots and rhizomes that grew into the bag, and the material that remained on the sieve was dried and weighed.

Soil Measurements

Soil redox potential was measured 2 cm below the surface using bright platinum electrodes (Patrick et al. 1996). Redox potential was calculated by adding the potential of the calomel reference electrode (+244 mv) to each reading. Two redox probes were inserted and allowed to equilibrate for at least four hours before measurements were taken when the tide inside the plant tanks was at its midpoint.

Elevation change in the pots was measured using a miniature surface elevation table (Cherry et al. 2009). An aluminum arm was locked into place across the rim of each pot in two distinct positions. Nine fiberglass pins were lowered from the arm at each position to the soil surface, and the height of the pin that remained above the arm was measured to the nearest millimeter. Elevation change after sediment addition was calculated by determining the difference between the first post-sediment addition reading and the final reading.

To measure decomposition, canvas strips (Tara Materials Inc. style 548) 10 cm wide × 30 cm long were inserted vertically into each pot in November 2010 and removed after ten days. Reference strips were also inserted in each pot, and were immediately removed. Upon removal, all strips were washed, dried, and cut into 2 cm sub-strips. Tensile strength of the sub-strips was determined with a Dillon Quantrol Snapshot tensometer as described in Slocum et al. (2009).

Soil shear strength was measured at 6 cm increments in the top 24 cm of soil using a Geotechnics Geovane (model H-4221, Humboldt Manufacturing, Chicago, IL, USA) with a 33 mm wide by 50 mm tall vane attached. The Geovane was inserted into the soil and twisted until the soil sheared, and the force required was recorded. The shear strength measurements were taken at the end of the experiment after vegetation had been harvested from the pots.

Interstitial Water

Interstitial water was sampled from 10 to 20 cm below the soil surface using a 60 ml syringe attached to a perforated plastic tube (3 mm inside diameter) (McKee et al. 1988). To measure porewater sulfide concentrations, 3 ml of the unfiltered interstitial water was immediately injected into a 7 ml scintillation vial containing 3 ml of Sulfide Antioxidant Buffer (Thermo Scientific). The sulfide concentration was measured using a Thermo Silver/Sulfide electrode within 24 h. Filtered interstitial water (0.45 μ filter) was used for measuring NH_4 concentrations, and samples were analyzed with a segmented flow autoanalyzer (Flow Solution IV AutoAnalyzer, O-I Analytical, USA). All interstitial water sampling took place when the tide was at its midpoint.

Statistical Analysis

The greenhouse experiment was a completely randomized block design with a split plot arrangement of treatments. The salinity treatment was the whole plot and the subplot contained the flooding x sedimentation treatment-levels. Analysis of Variance (ANOVA) was used to determine differences between treatments with salinity, sea level, and sediment-addition as the fixed effects. The analyses of soil shear strength and cotton strip decomposition data included depth as a repeated measure. All statistical analyses were done using SAS version 9.1, and data were checked for normality and homogeneity of variance prior to analysis. Post-hoc Tukey adjusted *p*-values were used for comparisons between treatments, and a significance level of 0.05 was used unless otherwise noted.

Results

Impacts of SLR and Salinity Prior to Sediment Addition

The effects of simulated SLR on plant productivity, soil physicochemical condition, and surface elevation were already evident following the initial 4-months of sea level and salinity treatments. The largest increase in sea level (35 cm) significantly reduced photosynthetic rates, leaf elongation rates, stem density, and cumulative stem height, but significantly increased mean stem height (Table 1). A moderate increase in sea level (15 cm) significantly reduced photosynthetic rates, but had no statistically detectable impact on leaf elongation rates or stem density (Table 1). Also, moderate increases in sea level led to significantly higher cumulative stem heights, while mean stem height significantly increased only at the highest sea level of 35 cm (Table 1). An increase in salinity

Table 2 Vegetation and physicochemical response to the interaction of salinity and sea level rise prior to sediment addition. Data means ±1 SE, and means sharing a superscript letter are not significantly different

Salinity	Sea level endpoint (cm)	Cumulative stem height (cm)	Stem density	Mean stem height (cm)	Photosynthetic rate*	Leaf elongation rate*	Elevation change (mm)	Redox 2 cm (mv)	Sulfide (mM)	NH_4-N (mM)
18	0	2258 ± 118	450 ± 18	45 ± 2	9.7 ± 0.98	0.74 ± 0.03	2.2 ± 0.3^{b}	2 ± 40	0.1 ± 0.0^{a}	0.50 ± 0.02
	15	2412 ± 127	459 ± 18	47 ± 2	9.5 ± 1.0	0.64 ± 0.01	3.1 ± 0.3^{ab}	−61 ± 21	0.5 ± 0.1^{b}	0.51 ± 0.04
	35	2014 ± 191	300 ± 26	61 ± 2	7.4 ± 0.84	0.36 ± 0.04	4.5 ± 0.5^{a}	−120 ± 16	1.9 ± 0.2^{d}	0.74 ± 0.04
36	0	1740 ± 87	344 ± 18	45 ± 2	11.0 ± 1.0	0.82 ± 0.01	$2.4 \pm .3^{b}$	−50 ± 17	0.1 ± 0.0^{a}	0.47 ± 0.02
	15	1959 ± 97	379 ± 18	46 ± 2	8.7 ± 0.49	0.49 ± 0.06	3.7 ± 0.3^{ab}	−110 ± 18	0.7 ± 0.1^{bc}	0.64 ± 0.03
	35	1434 ± 175	229 ± 35	57 ± 3	9.3 ± 1.7	0.25 ± 0.05	2.9 ± 0.3^{b}	−117 ± 13	1.3 ± 0.2^{cd}	0.79 ± 0.09
p-value		0.88	0.65	0.55	0.14	0.34	<0.01	0.41	0.04	0.11

*Photosynthesis rate in (μmol CO_2 m^{-2} s^{-1}) and the leaf elongation rate in (mm cm^{-1} d^{-1})

Table 3 Percent time flooded each day (A) and (B) water levels (cm) relative to the mesocosm soil surface at low tide (LT) and high tide (HT)

A Percent time flooded				**B** Sediment level (cm)					
	Sediment level (cm)			0		6		12	
Sea level rise (cm)	0	6	12	LT	HT	LT	HT	LT	HT
0	46	29	13	-15	+15	-21	+9	-27	+3
15	88	71	54	0	+30	-6	+24	-12	+18
35	100	100	100	+20	+50	+14	+44	+8	+38

from 18 to 36 psu significantly reduced cumulative stem height (2228 ± 88 cm and 1711 ± 80 cm, respectively: $p = 0.049$) and stem density (397 ± 18 stems m^{-2} and 317 ± 18 stems m^{-2}, respectively; $p = 0.03$), while having no significant impact on leaf elongation ($p = 0.31$) or photosynthetic rates ($p = 0.64$).

Increases in sea level had significant effects on the soil physicochemical environment. Higher sea levels led to more reduced soils and increased porewater sulfide and ammonium concentrations (Table 1). Salinity had no significant impact on redox ($p = 0.1701$), porewater sulfide ($p = 0.3973$) or ammonium concentrations ($p = 0.3726$), however, there was a significant salinity by sea level interaction on sulfide concentrations ($p = 0.04$). At 18 psu sulfide was significantly higher with each increase in sea level, while at 36 psu sulfide was equally high at both higher sea levels (Table 2).

Higher sea levels altered marsh surface elevation change as well. A 15 cm increase in sea level caused the marsh surface to rise at a rate 48% higher than under reference conditions, while 35 cm of SLR produced a 60% higher elevation-gain rate compared to reference conditions (Table 1). Although the main effect of salinity did not significantly affect elevation change, there was a significant salinity by sea level interaction (Table 2). At 18 psu changes in surface elevation increased with SLR, but at 36 psu elevation change was not significantly impacted by SLR.

Impacts of SLR and Salinity after Sediment Addition

Flooding Duration

Sedimentation reduced duration of flooding in mesocosms subjected to 0 and 15 cm of SLR, but not 35 cm of SLR (Table 3A). Surface elevation in mesocosms with 35 cm of SLR was not high enough, even with the addition of sediment, to relieve the constant flooding stress, which was 100% at this sea level endpoint. Low and high tide water levels after initial sedimentation are shown in Table 3B.

Aboveground Response

Sedimentation alleviated the impact of moderate SLR on end-of-experiment live aboveground biomass, but had no significant effect at high or reference sea levels (significant sea level by sediment interaction, $p = 0.01$, Fig. 1a). When sea level was increased 15 cm, sedimentation increased live aboveground biomass 80%, but when sea level was increased 35 cm, sedimentation decreased live aboveground biomass

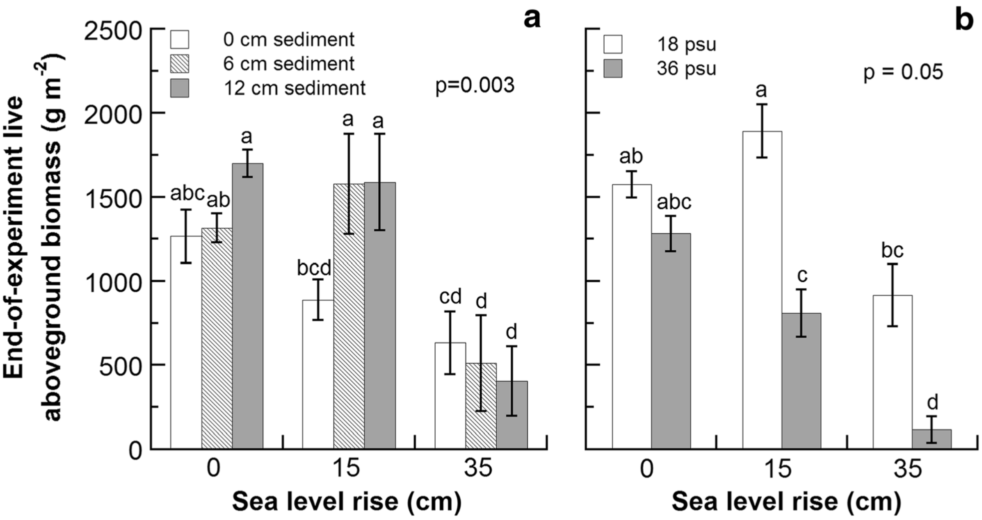

Fig. 1 End-of-experiment live aboveground biomass in response to the interaction of SLR and sedimentation **a** and the interaction of SLR and salinity **b**. Data are means ±1 SE, and bars with a common letter are not significantly different

Table 4 Vegetation and physicochemical response to the interaction of sea level rise and sediment addition

Sea level endpoint (cm)	Sediment level	Cumulative stem height (cm)	Stem density (m^{-2})	Mean stem height (cm)	Photosynthetic rate*	Leaf elongation rate*	Elevation change (mm)	Redox 2 cm (mV)	NH$_4$-N (mM)
0	0	3543 ± 428^{a}	600 ± 62^{ab}	52 ± 2^{ab}	13.4 ± 2.6	0.25 ± 0.03	1.4 ± 1.3	−7 ± 33^{bc}	1.2 ± 0.3^{a}
	6	3457 ± 208^{a}	635 ± 35^{ab}	48 ± 2^{ab}	12.3 ± 2.1	0.20 ± 0.04	−2.6 ± 1.4	125 ± 50^{a}	0.8 ± 0.1^{a}
	12	4129 ± 154^{a}	723 ± 26^{a}	51 ± 1^{ab}	12.4 ± 3.1	0.20 ± 0.03	−4.4 ± 1.8	85 ± 51^{ab}	1.0 ± 0.2^{a}
15	0	2963 ± 418^{a}	503 ± 62^{b}	51 ± 3^{ab}	14.2 ± 3.4	0.18 ± 0.03	1.0 ± 0.8	−164 ± 23^{e}	6.4 ± 2.4^{cd}
	6	3995 ± 650^{a}	635 ± 79^{ab}	53 ± 3^{ab}	11.9 ± 1.9	0.25 ± 0.03	−6.2 ± 1.6	−15 ± 33^{bcd}	4.1 ± 1.0^{bc}
	12	4028 ± 688^{a}	644 ± 88^{ab}	53 ± 3^{ab}	13.1 ± 2.2	0.25 ± 0.03	−6.3 ± 2.4	12 ± 36^{abc}	2.4 ± 0.6^{ab}
35	0	1435 ± 378^{b}	176 ± 44^{c}	66 ± 10^{a}	10.7 ± 2.6	0.11 ± 0.02	0.5 ± 1.4	−152 ± 21^{e}	12.2 ± 1.6^{de}
	6	1090 ± 553^{b}	141 ± 62^{c}	42 ± 13^{ab}	8.7 ± 3.1	0.09 ± 0.02	−6.4 ± 1.4	−104 ± 25^{cde}	19.3 ± 3.9^{e}
	12	810 ± 398^{b}	106 ± 53^{d}	35 ± 13^{b}	6.3 ± 2.7	0.08 ± 0.02	−8.4 ± 1.5	−133 ± 24de	12.1 ± 2.7^{de}
p-value		0.04	0.06	0.07	0.69	0.09	0.34	0.06	0.04

*Photosynthesis rate in (μmol CO$_2$ m^{-2} s^{-1}) and the leaf elongation rate in (mm cm^{-1} d^{-1})

by up to 36% (Fig. 1a). Under reference sea levels, the addition of 6 cm of sediment did not increase live aboveground biomass, but 12 cm of sedimentation caused a non-significant 30% increase. Elevated salinity significantly reduced live aboveground biomass, but this effect was dependent on sea level (significant salinity by sea level interaction, $p = 0.05$, Fig. 1b). At reference sea levels, elevated salinity had no significant effect on live aboveground biomass, while at moderate and high sea levels, higher salinities significantly and dramatically reduced live biomass (Fig. 1b). Neither the interaction of salinity with sediment nor the 3-way interaction of salinity, sea level, and sediment were statistically significant ($p = 0.262$ and 0.378, respectively).

The effects of sedimentation on cumulative stem height, stem density, and mean stem height were dependent on sea level (significant sea level by sediment interactions, Table 4). These parameters tended to decrease with increasing sedimentation at the highest sea level, but were little affected or even increased at lower sea levels (Table 4). Sedimentation tended to negate the impact of SLR on cumulative stem length and stem density at moderate sea levels. This interaction was not significant for leaf elongation ($p = 0.09$) or photosynthesis ($p = 0.69$), although, on average, higher sea levels significantly reduced both (leaf elongation: 0, 15 and 35 cm = 0.22 ± 0.02 mm cm^{-1} d^{-1}, 0.23 ± 0.02 mm cm^{-1} d^{-1}, 0.09 ± 0.01 mm cm^{-1} d^{-1}, respectively; photosynthesis: 0, 15 and 35 cm = 12.7 ± 1.4 μmol CO$_2$ m^{-2} s^{-1}, 13.1 ± 1.4 μmol CO$_2$ m^{-2} s^{-1}, 8.6 ± 1.6 μmol CO$_2$ m^{-2} s^{-1}, respectively; $p = <0.0001$ for both). In addition, the effect of higher sea levels was dependent on salinity (Table 5). For cumulative stem height and stem density, the negative effects of higher sea level were much greater at 36 psu than 18 psu (Table 5). In contrast, the effect of higher sea levels on mean stem height, photosynthesis, and leaf elongation were relatively unaffected at 18 psu, but all tended to decrease at 36 psu (Table 5). There were no significant interactions between salinity and sedimentation for any of these growth variables or any significant 3-way interactions.

Table 5 Vegetation and physicochemical response to the interaction of salinity and sea level rise following sediment addition

Salinity	Sea level endpoint (cm)	Cumulative stem height (cm)	Stem density (m^{-2})	Mean stem height (cm)	Photosynthetic rate*	Leaf elongation rate*	Elevation change (mm)	Redox 2 cm (mv)	Sulfide (mM)
18	0	4030 ± 217^{ab}	670 ± 35^{ab}	54 ± 1^{a}	12.4 ± 1.8^{a}	0.23 ± 0.03^{a}	2.8 ± 0.8^{a}	−25 ± 25^{b}	0.4 ± 0.1^{a}
	15	4987 ± 276^{a}	750 ± 44^{a}	59 ± 1^{a}	12.2 ± 1.9^{a}	0.22 ± 0.02^{a}	−0.04 ± 1.1^{ab}	−61 ± 35^{bc}	1.4 ± 0.3^{a}
	35	1915 ± 345^{d}	238 ± 35^{c}	64 ± 6^{a}	12.1 ± 2.2^{a}	0.15 ± 0.02^{a}	−6.2 ± 1.5^{b}	−139 ± 25^{c}	2.6 ± 0.4^{b}
36	0	3390 ± 239^{bc}	635 ± 44^{ab}	47 ± 1^{ab}	13.0 ± 2.3^{a}	0.21 ± 0.02^{a}	−6.5 ± 1.0^{b}	160 ± 32^{a}	0.1 ± 0.0^{a}
	15	2337 ± 321^{cd}	441 ± 53^{b}	46 ± 1^{ab}	14.0 ± 2.1^{a}	0.23 ± 0.03^{a}	−7.6 ± 1.5^{b}	−50 ± 34^{bc}	2.2 ± 0.5^{ab}
	35	308 ± 181^{e}	44 ± 18^{d}	30 ± 11^{b}	5.0 ± 1.9^{b}	0.03 ± 0.01^{b}	−3.3 ± 1.3^{ab}	−120 ± 12^{bc}	3.1 ± 0.8^{c}
p-value		0.01	<0.01	0.03	<0.01	0.01	<0.01	<0.01	<0.01

*Photosynthesis rate in (μmol CO$_2$ m^{-2} s^{-1}) and the leaf elongation rate in (mm cm^{-1} d^{-1})

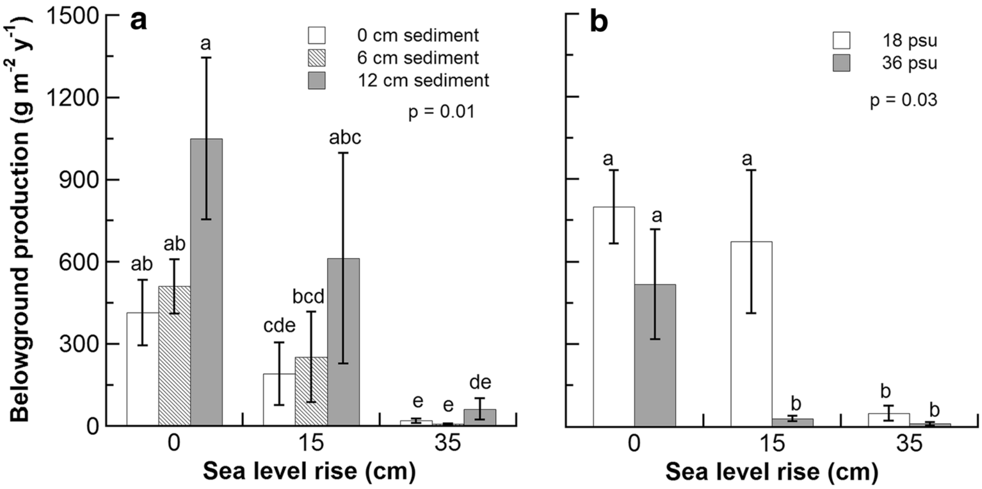

Fig. 2 Belowground biomass production in the top 24 cm of soil measured by the ingrowth method in response to the interaction of SLR and sedimentation **a** and the interaction of SLR and salinity **b**. Data are means ±1 SE, and bars sharing a letter are not significantly different

Belowground Production

Overall, as sea level increased, belowground production significantly decreased ($p < 0.0001$). Sea level was such a strong control that production was reduced by 50% when sea levels were raised 15 cm, and nearly no belowground production occurred when sea level was raised 35 cm (0, 15, and 35 cm sea levels = 694 ± 126 g m^{-2} y^{-1}, 381 ± 148 g m^{-2} y^{-1}, 35 ± 14 g m^{-2} y^{-1}, respectively). However, sedimentation did ameliorate the impact of moderate increases in sea level (significant sediment by sea level interaction, $p = 0.01$, Fig. 2a). Belowground production more than doubled in response to the addition of 12 cm of sediment at both reference and 15 cm sea levels, while the addition of 6 cm of sediment had no significant effect (Fig. 2a). Further, sedimentation had no effect on belowground production with 35 cm of SLR. Elevated salinity also had an impact on belowground production that was dependent of sea level (significant salinity by sea level interaction, $p = 0.03$, Fig. 2b). The negative impact of moderate (15 cm) SLR was significantly greater at 36 psu than at 18 psu, while belowground production was minimal with 35 cm of SLR regardless of salinity level (Fig. 2b).

Resilience

Sedimentation improved vegetation resilience, but the effect varied with sea level (significant sedimentation by sea level interaction, $p = 0.0008$, Fig. 3). Sedimentation increased aboveground biomass regrowth at reference sea levels and with 15 cm of SLR, but had no effect with 35 cm of SLR. Under reference sea level conditions,

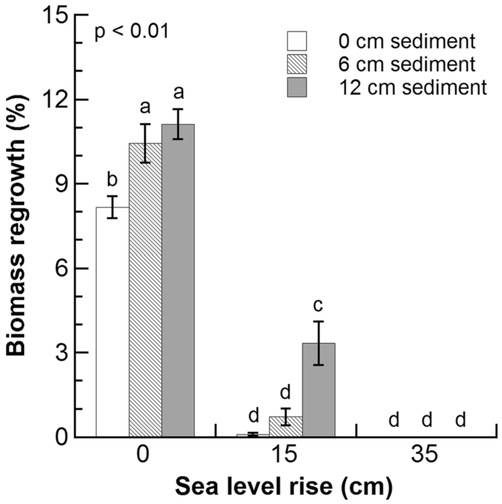

Fig. 3 Resilience (i.e., aboveground biomass regrowth 71 days after harvest) as a percentage of the pre-harvest biomass in response to the interaction of SLR and sedimentation. Data are means ±1 SE, and bars with a common letter are not significantly different

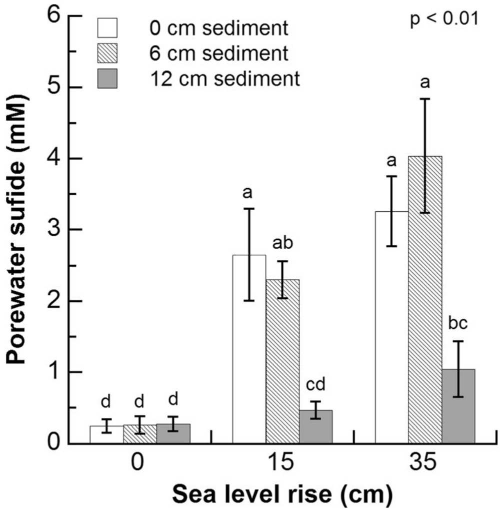

Fig. 4 Porewater sulfide concentrations in response to the interaction of SLR and sedimentation. Data are means ±1 SE, and bars with a common letter are not significantly different

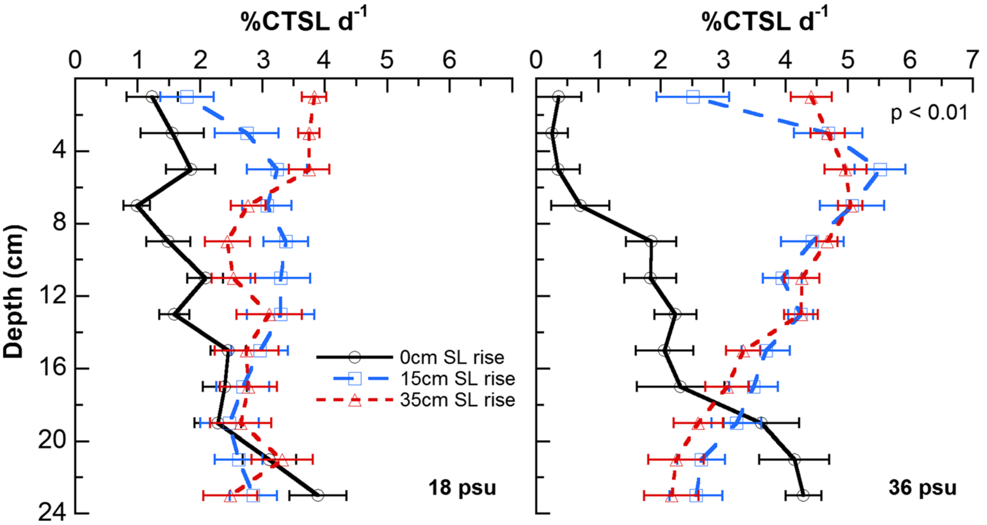

Fig. 5 Percent cotton tensile strength loss per day (% CTSL d^{-1}) in the top 24 cm of soil in response to the interaction of salinity and SLR. Data are means ±1 SE

adding 6 and 12 cm of sediment significantly increased resiliency by 28% and 37%, respectively; while only 12 cm of sedimentation significantly increased regrowth with 15 cm of SLR (Fig. 3). When sea levels were increased by 35 cm there was no regrowth of vegetation, regardless of sedimentation. Neither salinity, as a main effect, nor its interactions with sedimentation and sea level had any statistically significant impact on resilience.

Porewater Chemistry

Porewater sulfide concentrations were lowest at current sea levels and significantly increased with higher sea levels (sea level main effect, $p < 0.0001$), but sedimentation mediated the response (Fig. 4). The addition of 12 cm of sediment significantly reduced porewater sulfide concentrations at 15 and 35 cm of SLR, but 6 cm of sediment had no significant effect. Sulfide was low and constant at the reference sea level, and did not vary with sedimentation. A significant salinity by sea level interaction ($p = 0.0004$) indicated that the increase in sulfide with higher sea levels was greater at the higher salinity treatment-level (Table 5). Porewater ammonium concentrations increased overall with increases in sea level (sea level main effect, $p < 0.001$), but sedimentation controlled the extent of increase (Table 4). At both current conditions and 35 cm of SLR, sediment had no significant impact on ammonium concentrations, but with 15 cm of SLR the addition of 12 cm of sediment significantly reduced ammonium concentrations.

Redox Potential

Sedimentation increased redox potential 2 cm below the soil surface under current sea levels and when sea level was increased 15 cm, but had no impact when sea level was increased 35 cm (significant sea level by sediment interaction, $p = 0.057$, Table 4). Salinity also had an effect on redox potential 2 cm below the soil surface, but this effect varied with sea level (significant salinity by sea level interaction, $p = 0.0004$, Table 5). At 18 psu only the highest sea level significantly reduced redox, while at 36 psu both increases in sea level led to more reducing conditions.

Decomposition

Decomposition rates were highly dependent on sea level. Cotton strip decomposition increased with SLR, but this effect was more pronounced at 36 psu compared to 18 psu and in the top 15 cm of soil (significant sea level by salinity by soil depth interaction, $p = 0.0006$, Fig. 5). With greater sedimentation, cellulose decomposition increased, but this effect also varied with sea level and soil depth (significant sea level by sediment by soil depth interaction, $p = 0.004$, Fig. S1, Supplemental information).

Soil Shear Strength

Sedimentation impacted soil shear strength, but was dependent on sea level and soil depth (significant sea level x sedimentation x soil depth interaction, $p < 0.0001$, Fig. 6). Elevated sea levels reduced soil shear strength compared to the reference condition, and sedimentation did not ameliorate this effect. Shear strength at the soil surface was significantly lower when sediment was added at higher sea levels compared to the no sediment treatment (Fig. 6). When sediment was added at the reference sea level (0 cm), shear strength of the surface soil was equivalent to the reference soil that received no sediment. Neither the main effect of salinity nor its interactions with sediment, sea level, or soil depth significantly affected soil shear strength.

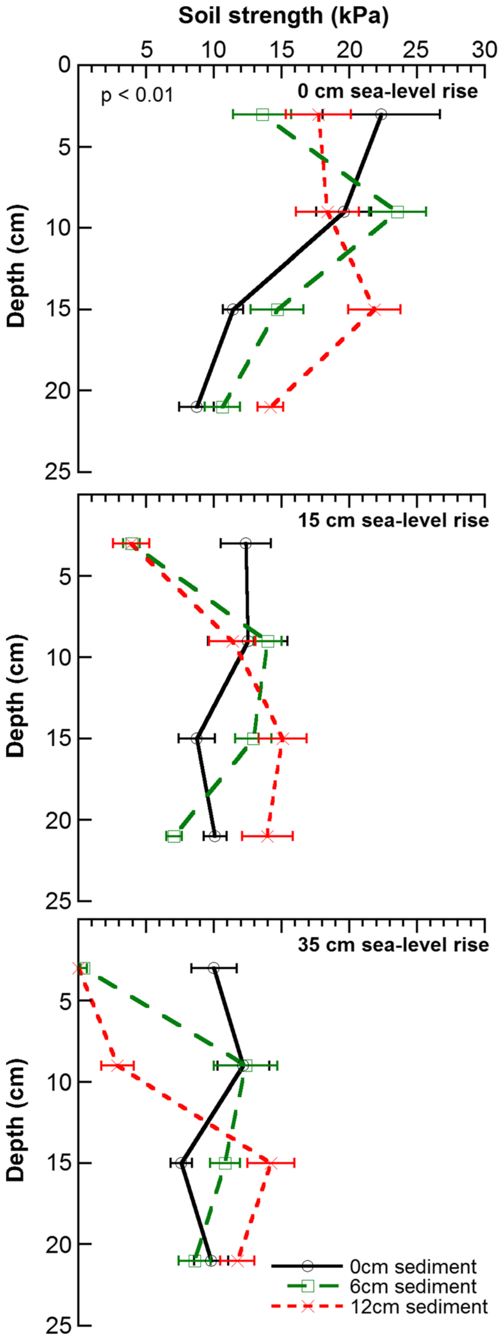

Fig. 6 Soil shear strength by depth in response to the interaction of SLR and sedimentation. Data are means ±1 SE

Surface Elevation Change

The effect of sedimentation on elevation change was complex and depended upon both salinity and sea level, as evidenced by a significant 3-way interaction between these three treatments ($p = 0.047$, Fig. 7). Sedimentation, of course, led to an immediate increase in surface elevation, however, in the months following sedimentation the dominant force acting on surface elevation was compaction of the added sediment. Only at 18 psu and 0 cm of SLR did the added sediment result in positive elevation change (Fig. 7). Additionally, at 36 psu both the 15 and 35 cm SLR treatments with no sediment added increased in elevation.

Discussion

To remain viable over the next century, coastal marshes must be able to raise their surface elevation to offset sea level rise, and sediment deposition from hurricanes may aid in this matter. Overall, our results support this assertion with one caveat. Hurricane-simulated sedimentation ameliorated the effects of moderate SLR on plant productivity and on resiliency; however, at the highest sea levels evaluated, inundation stress was so great that the positive effect of sedimentation was negated. Thus, it is likely that the sustainability of coastal marshes will be improved by hurricane-generated sedimentation under moderate SLR scenarios, but will see no such improvement with more extreme SLR.

Sedimentation has been widely shown to improve growing conditions and increase aboveground productivity in coastal marshes (Pezeshki et al. 1992; Ford et al. 1999; Slocum et al. 2005; Baustian and Mendelssohn 2015; Walters and Kirwan 2016). We found this to be true under current sea levels and with 15 cm of SLR. However, plants subjected to 35 cm of SLR were already stressed from the continuous flooding and high porewater sulfide concentrations they had been experiencing, and, thus, the addition of sediment did not increase productivity. In fact sedimentation had the opposite effect, and growth (stems density, stem length, photosynthesis, and biomass) actually decreased in the 35 cm SLR treatment.

Measurements of aboveground growth parameters are not always good indicators of ecosystem health in coastal wetlands that rely on the accumulation of organic matter belowground to maintain their position in the intertidal zone (Turner et al. 2004). This became apparent here when sedimentation ameliorated the effects of 15 cm of SLR on aboveground biomass, total stem length, leaf elongation, and photosynthesis rates, but did not counter the impact of SLR on vegetation resilience. Vegetation resilience was more closely related to belowground production than to any of the vegetative measures aboveground. In other words, vegetation appeared healthy aboveground, but flooding stress reduced belowground production to such an extent that the plants did not have enough reserves stored belowground to generate new growth following disturbance. Slocum and Mendelssohn (2008) documented similar findings in a submerging Louisiana salt marsh experiencing prolonged flooding.

The importance of inorganic sedimentation in a marshes vertical growth may increase in the future as inputs of iron and manganese may be required to help temper the accumulation of porewater sulfides which can occur with excess

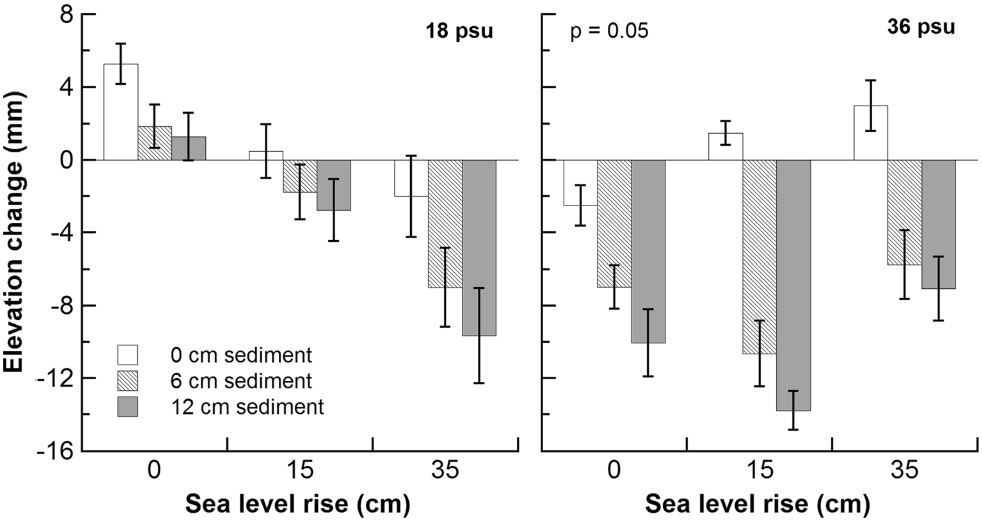

Fig. 7 Surface elevation change following sedimentation in response to the 3-way interaction of salinity, SLR, and sedimentation. Data are means ±1 SE

flooding and reduced plant productivity (Mendelssohn and Morris 2000). Sedimentation (12 cm only) reduced sulfide accumulation when sea levels were increased in this study, although, it is unclear whether inputs of iron and manganese led to the decrease or if it was simply a result of surface elevation being raised which in-turn led to less reducing conditions. These results are similar to findings that sedimentation following Hurricanes Gustav and Ike in 2008 reduced porewater sulfide and increased vegetation vigor (Baustian and Mendelssohn 2015).

Hurricanes have the potential to add significant amounts of sediment to a marsh (Turner et al. 2006; Bianchette et al. 2015), but the same sediments can be easily removed by passage of frontal systems (Cahoon et al. 1995; Bevington et al. 2017) unless roots grow into the added sediment, connecting it to the underlying substrate. Hurricanes can also cause significant erosion in organic-rich coastal marshes with low soil shear strength (Howes et al. 2010), although sediment added to the surface of these types of marshes can reduce erosion potential (Graham and Mendelssohn 2013). Prior to the passage of Hurricane Ike in 2008, Graham and Mendelssohn (2013) added 2 to 20 cm of dredged sediment to a brackish marsh in the MRDE, and as the storm passed, a 3-m storm surge eroded significant portions of the surrounding marsh. In contrast, the sediment-amended plots remained largely intact. Furthermore, in a study investigating the impacts of sediment slurry application to a salt marsh in the MRDE, Stagg and Mendelssohn (2011) found that 15 years after application of 2–11 cm of sediment resilience was enhanced compared to natural marshes. If hurricanes in the future continue to deposit sediment over wider areas of coastal marsh than they erode (Turner et al. 2006; Bianchette et al. 2015), the resilience of the remaining marshes may be enhanced, as we demonstrated here and in the companion field study [where higher levels of sedimentation led to higher resilience (Baustian and Mendelssohn 2015)] and the marshes may become more resistant to erosion from future storms.

The impact of sedimentation on soil shear strength in this study was largely dependent on the amount of root growth into the newly deposited soil. Soil bulk density, texture, structure, organic content, and organic particle size can all impact soil shear strength (Zimbone et al. 1996; Swarzenski et al. 2008), and a soil with more, large plant organs, i.e. roots, rhizomes, and stem-bases, will typically have higher shear strength than one with smaller organic fragments (Swarzenski et al. 2008). The sediment added in this experiment had no measureable shear strength until roots and rhizomes grew into it. For example, sedimentation at the current sea level (0 cm) led to robust root growth, and shear strength in the added sediment increased accordingly. However, increased sea levels hindered root growth, and shear strength of the added sediment there remained low.

Belowground production also played a key role in surface elevation change. Following sediment application, a general decrease in surface elevation, as the added sediments consolidated, was apparent. But under current sea levels root growth into the added sediment was enough to increase surface elevation. The importance of belowground production in maintaining surface elevation in organic coastal marshes is well understood (Hatton et al. 1983; Morris et al. 2002; Nyman et al. 2006; Turner et al. 2006; Cherry et al. 2009), so whether or not a marsh can survive SLR may depend heavily on how belowground production responds to changing conditions. However, predicting that response can be difficult because marsh response to flooding depends on the plant community, current elevation, hydroperiod, and availability of sediment. Marshes dominated by more flood tolerant species can thrive when flooded and increase surface elevation, while less flood tolerant species can languish under flooding pressure (Cherry et al. 2009). In some locations *S. alterniflora* dominated salt marshes may be positioned too high in the tidal prism for optimal growth, so increasing sea levels may lead to increased production (Morris 2007). More flooding can also increase surface accretion because of a greater depth of sediment-laden water and a greater time available for sedimentation to occur. Enhanced sedimentation can boost productivity and increase the chances of surviving rising seas (Leonard and Croft 2006; Morris 2007).

In addition to the influence of sedimentation on soil shear strength and belowground production, soil organic matter decomposition may also be affected. We found that soil cellulose decomposition generally accelerated with increased flooding. Cotton strip decomposition has been shown to increase when soil nutrient concentrations are elevated (Feller et al. 1999; Laursen 2004; Turner 2011), and pots subjected to 35 cm of sea level rise had the highest porewater ammonium concentrations in our study. This large pool of readily available nitrogen likely boosted decomposition of the cotton strips, which are mostly comprised of labile carbon (Slocum et al. 2009). Interestingly, the enhanced decomposition took place in spite of the biochemically reduced soil conditions, which can potentially slow decomposition rates (Mendelssohn et al. 1999; Sahrawat 2003).

In this experiment, we subjected marsh sods to an immediate increase in sea level, not the gradual increase that would be likely to occur with predicted sea level rise. With a more gradual increase in sea level, the vegetation may have reacted in a different manner to sedimentation. For example, Kirwan et al. (2010) found that coastal marshes will likely be able to adapt to slow increases in sea level as long as there is adequate suspended sediment in the water. Longer duration flooding increases the time available for sediment to fall out of suspension, and vegetated marshes decrease the turbulence of floodwaters, which further promotes sedimentation (Morris 2007; Mudd et al. 2010). However, in this study our simulated tides contained no sediment, so there was no mechanism for longer duration flooding to promote increased sedimentation.

These results show the potential benefit sedimentation may have in supporting plant growth and improving resilience in the face of sea level rise. Sedimentation ameliorated the negative effects moderate sea level rise had on plant productivity and soil chemistry. More importantly, sedimentation improved marsh resilience at the moderate sea level endpoint, although not at high sea levels. Hence, a threshold likely exists such that the importance of hurricane-generated sedimentation in promoting plant productivity, resilience and sustainability is dependent on the magnitude of future increases in sea level. This is significant in that even relatively small reductions in future sea level could be enough to stay below this threshold. In some areas, the intensity of sea level rise may prove too great for coastal marshes to overcome, and the long-term stability of coastal marshes in those areas may depend on their ability to migrate inland (Kirwan et al. 2016). However, in many areas marshes are increasingly running out of room to migrate upgradient as hard structures are built to protect human infrastructure from rising seas. In these areas, the long-term stability of coastal marshes will depend on the system's ability to expand vertically. Thus, as we have shown here, enhanced sedimentation from hurricanes, or restoration methodologies that apply sediments, may play a role in determining the future sustainability of coastal marshes.

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