

Submergence, nutrient enrichment, and tropical storm impacts on *Spartina alterniflora* in the microtidal northern Gulf of Mexico

Jennifer M. Hill^{1,*}, Peter S. Petraitis², Kenneth L. Heck Jr.³

¹Louisiana Tech University, Ruston, LA 71270, USA

²University of Pennsylvania, Philadelphia, PA 19104, USA

³Dauphin Island Sea Lab, Dauphin Island, AL 36528, USA

ABSTRACT: Salt marshes face chronic anthropogenic impacts such as relative sea level rise and eutrophication, as well as acute disturbances from tropical storms that can affect the productivity of these important communities. However, it is not well understood how marshes already subjected to eutrophication and sea level rise will respond to added effects of episodic storms such as hurricanes. We examined the interactive effects of nutrient addition, sea level rise, and a hurricane on the growth, biomass accumulation, and resilience of the saltmarsh cordgrass *Spartina alterniflora* in the Gulf of Mexico. In a microtidal marsh, we manipulated nutrient levels and submergence using marsh organs in which cordgrasses were planted at differing intertidal elevations and measured the impacts of Hurricane Isaac, which occurred during the experiment. Prior to the hurricane, grasses at intermediate and high elevations increased in abundance. After the hurricane, all treatments lost approximately 50% of their shoots, demonstrating that added nutrients and elevation did not provide resistance to hurricane disturbance. At the end of the experiment, only the highest elevations had been resilient to the hurricane, with increased above- and below-ground growth. Added nutrients provided a modest increase in above- and belowground growth, but only at the highest elevations, suggesting that only elevation will enhance resilience to hurricane disturbance. These results empirically demonstrate that *S. alterniflora* in microtidal locations already subjected to submergence stress is less able to recover from storm disturbance and suggests we may be underestimating the loss of northern Gulf Coast marshes due to relative sea level rise.

KEY WORDS: Wetland · Salt marsh · Sea level rise · Hurricanes · Multi-stressor impacts · Coastal restoration · Cordgrass

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1. INTRODUCTION

Coastal wetlands are important carbon sinks and among the most productive ecosystems in the world (Mitsch & Gosselink 1993, Chmura et al. 2003). These ecosystems not only provide an impressive array of ecosystem services, such as storm protection and water filtration, but also function as nursery grounds that are critical to many commercial and recreational fisheries (Zedler & Kercher 2005, Barbier et al. 2011). However, the structure and function of coastal eco-

systems worldwide have been adversely affected by increases in air and water temperatures, changes in precipitation patterns, and rising sea levels (Michener et al. 1997, Scavia et al. 2002). Further anthropogenic impacts such as increases in eutrophication and pollution are also influencing nearshore ecosystems with mostly unknown consequences (Pinckney et al. 2001, Islam & Tanaka 2004). In addition to these relatively more chronic stresses, there have also been changes in sporadic, high intensity events such as the frequency and intensity of storms, which also present

additional periodic stresses to wetlands (Knutson et al. 2010). Understanding the mechanisms and consequences of the interaction between gradually changing and periodic disturbances is essential for accurately predicting the future condition of coastal ecosystems and for their management and restoration.

Estuarine salt marshes are sensitive to rising sea levels, but the effects of changes in sea level can be enhanced by subsidence. The combined effects of rising water and land subsidence provide a chronic stress that threatens to drown marsh plants and turn highly productive marshes into less productive submerged mudflats. While low to moderate submergence can increase depositional processes and facilitate marsh building, higher amounts of submergence can stress marsh plants and reduce aboveground and belowground production (Gleason & Zieman 1981, Bertness 1991, Broome et al. 1995, Morris et al. 2002). Lower aboveground and belowground production subsequently promotes further decline by altering depositional and marsh building processes (Leonard et al. 2002, Turner et al. 2002) that allow marshes to keep pace with changing sea levels, and ultimately can lead to marsh loss (Reed 1995, Morris et al. 2002, Craft et al. 2009). At higher intertidal elevations, high salinity stress and soil dryness reduce production (McKee & Patrick 1988, Morris et al. 2002), resulting in a parabolic production curve where marsh plant production peaks at intermediate elevations (Morris et al. 2002).

The amount of time marsh plants are submerged is a function of several factors, including elevation and tidal range, which can vary both across and within geographic regions. Importantly, much of our knowledge of how North American marshes respond to submergence comes from Atlantic Coast macrotidal marshes, where the tide can range from 1–3 m. On the Gulf Coast, tides are microtidal (0.1–0.5 m) and are typically driven more by wind than by lunar cycles. The larger tidal range of the Atlantic coast increases the elevational range of marsh plants, such as *Spartina alterniflora*, often resulting in higher intertidal growth limits (McKee & Patrick 1988). Tidal range can also impact sediment supply (Reed 1988) and plant production (Steever et al. 1976), suggesting that the differing tidal ranges on the Gulf and Atlantic coasts differentially affect plant production (Orson et al. 1985). To date, few experimental studies have examined plant production in response to submergence on the Gulf Coast (but see Snedden et al. 2015). Rates of relative sea level rise, in combination with differing tidal cycles, are likely to differentially affect submergence regimes and marsh production.

Therefore, it is necessary to determine the extent to which growth patterns observed in Atlantic coast studies are predictive of those in microtidal Gulf marshes.

Eutrophication provides an additional threat to the stability and resilience of coastal marshes, but diagnosing the impacts of eutrophication on marsh vegetation has proven difficult. Excess nutrients can flow into marsh environments from a variety of sources, such as agricultural runoff and sewage effluent (as reviewed by Smith et al. 1999). Several studies have demonstrated salt marsh decline with increasing nutrient inputs (Darby & Turner 2008a, Deegan et al. 2012). For instance, studies on the US east coast have shown that nutrient enrichment increases *S. alterniflora* aboveground biomass and reduces belowground root production (Valiela et al. 1976, Darby & Turner 2008b, Deegan et al. 2012). Reductions in belowground root production can result in higher soil fracture rates in marsh creeks and enhance marsh erosional processes (Deegan et al. 2012). Yet other studies have documented increases in both above- and belowground production or have found no changes with nutrient enrichment (Anisfeld & Hill 2012, as reviewed in Wong et al. 2015, Graham & Mendelssohn 2016). These differing conclusions about the effects of eutrophication have important consequences for understanding how eutrophication and sea level rise will interact to influence marsh growth and stability. For example, if nutrient enrichment enhances plant production and results in increased marsh elevation, marshes subject to eutrophic waters may be more resilient to sea level rise. In contrast, if eutrophication promotes marsh collapse, eutrophic waters in combination with sea level rise will accelerate marsh loss.

In addition to understanding the impacts of multiple chronic stresses, we must also examine how these stresses interact with large acute disturbances common to coastal systems. Tropical storms represent acute, low frequency, and often severe disturbances that are predicted to increase in frequency and severity as climate changes (Knutson et al. 2010). These storms contain high winds and can inundate coastal marshes with high salinity storm surge and produce large amounts of precipitation and wave energy that can cause significant negative impacts to marshes (as reviewed by Michener et al. 1997). Erosion damage caused by winds and storm surge can scour vegetation and deposit mats of wrack and debris on marshes (Guntenspergen et al. 1995, Morton & Barras 2011). Although storms can initially damage saline marshes, causing vegetation cover to decline by as much as

35%, marsh vegetation can return to pre-storm levels within 1–2 yr (Chabreck & Palmisano 1973). Marshes may also benefit from overwash, in which sediments and nutrients deposited by storms can increase plant production and elevation (Mendelssohn & Kuhn 2003, Walters & Kirwan 2016). Other evidence suggests that storm disturbances are likely to interact with sea level differences to influence marsh loss. Low lying estuarine marshes are susceptible to storm erosion, and ponds within marshes often expand in response to storm disturbance (Morton & Barras 2011). Periods of time with a paucity of hurricanes have been linked to a slowdown of marsh loss on the Louisiana coast (Couvillion et al. 2017). To date, however, little empirical data exist to show how storms interact with other factors to influence plant production and marsh erosion. This lack of data is understandable given our inability to experimentally mimic hurricane conditions or to insert an experiment into the path of a hurricane.

Here, we examined the effects of nutrient enrichment and submergence on the growth of *S. alterniflora* on a receding shoreline in the northern Gulf of Mexico. Living shorelines comprised of oyster shell breakwaters built at this location to reduce wave action had little success in reducing the retreat of the seaward marsh edge (Scyphers et al. 2011, Moody et al. 2013), suggesting that the loss of *S. alterniflora* on the seaward edge may be due to other factors such as changes in elevation. Thus, the *a priori* goals of our experiment were to examine if the duration of submergence, as determined by changes in sea level and subsidence, was contributing to the retreat of the shoreline; and to determine if nutrient enrichment would promote or reduce marsh susceptibility to submergence. During the experiment, a Category 1 hurricane struck our study site, thereby allowing us to examine the role of acute hurricane disturbances on marsh plants already affected by submergence and eutrophication.

2. MATERIALS AND METHODS

2.1. Study site

We conducted the experiment on the east side of Point Aux Pins, Alabama, USA (30° 22' 46.13" N, 88° 18' 12.74" W). The mean tidal range in this area is approximately 0.5 m and salinity averages around 23‰ (Heck et al. 2001, Scyphers et al. 2011). The seaward marsh edge at Point Aux Pins is dominated by *Spartina alterniflora* (hereafter referred to as *Spartina*)

with interspersed *Distichlis spicata*. The shore consists of a gradually sloping band of *S. alterniflora* that gives way to *S. patens* and *Juncus roemarianus* at higher elevations. In some areas, the shoreline has steep erosional escarpments (Moody et al. 2013, J. M. Hill pers. obs.). Oyster-shell living shoreline breakwaters were constructed near the study site between 2007 and 2009 in an attempt to reduce wave induced erosion (Moody et al. 2013).

2.2. Experimental design and setup

We used marsh organs (Kirwan & Guntenspergen 2012) to manipulate the impacts of submergence (i.e. elevation) on marsh plant productivity. Marsh organs contain a series of PVC pipes that serve as planters and are set at different elevations to maintain plants at different tidal heights. A marsh organ, with its step-like appearance, looks like a pipe organ and thus is so named. We built 2 marsh organs containing 5 elevation levels of PVC pipes (15 cm diameter) with each level representing a 10 cm difference in sea level. Each elevation had 6 pipes for a total of 30 pipes per marsh organ (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m644p033_supp.pdf).

Although we had planned to install marsh organs in early June for a complete summer and fall growing season, we were challenged by weather which promoted wave action in our site as well as obstacles associated with first-time construction and design. In total, 2 marsh organs (labeled A and B and situated approximately 5 m apart) were finally installed on 3–13 July 2012 on the east side of Point Aux Pins at a location where reef breakwaters were not present. The 2 marsh organs were constructed as smaller organs, which were easier to build than a single large marsh organ. The estimated ground elevation of marsh organ sites according to North American Vertical Datum of 1988 (NAVD 88) was –0.37 and –0.32 m NAVD 88, and the *Spartina* on the seaward edge behind the marsh organs was estimated at approximately –0.20 m NAVD 88. These elevations were determined by comparing organ sites to the elevation at a nearby known transect point determined previously by real-time kinematic (RTK) GPS (R. M. Moody unpubl. data). However, as elevation may have changed since RTK measurements were taken and actual sea levels are relative to the hydroperiod experienced at the site, our elevations are estimates. We installed the marsh organs so that the lowest elevation of the organ corresponded to the lowest elevation of naturally

occurring *Spartina* directly onshore. We refer to the lowest elevation as lowest grass level (estimated at -0.20 m NAVD 88) and the other 4 steps up as +10, +20, +30, and +40 cm. At the lowest grass level, plants emerged from the water only during low spring tides, whereas at the highest elevation level (+40 cm), plants were submerged only at peak high tides.

The marsh organs were hammered into place with approximately 20 cm of each pipe below the sediment surface. The bottoms of the pipes were open to allow drainage. Each pipe was filled to 20 cm of its top with subtidal sediment. A wooden brace was fixed to the back of each marsh organ for support (similar to Kirwan & Guntenspergen 2012). *Spartina* planter cores (15 cm diameter; 20 cm deep) were taken from the nearby marsh and placed in each pipe so that the top of the sediment of the planter core was flush with the top of the pipe. Once the planter core was secured, we measured live shoot abundance, shoot heights, and the number of live leaves per shoot. Of the original 60 planter cores, 21 were damaged by storms and/or stress from transplanting and were replaced 1 wk after initial planting. The difference in planting time did not significantly affect aboveground metrics 1 mo later, and therefore we did not consider planting time as a covariate in the analyses.

To limit the possibility of nutrients bleeding into neighboring unenriched pipes, nutrient levels were manipulated with fertilizer plugs, which were added randomly to 3 replicate planters at each elevation. Fertilizer plugs consisted of fiberglass mesh screening bags filled with 10 g of slow release Osmocote (19:6:12 N, P, K: 10% ammonia; 9% nitrate; 6% phosphoric acid; 12% potash). As Osmocote dissolves slowly over a 2–3 mo period within marsh sediments (J. M. Hill unpubl. data), this enrichment corresponded to $126\text{--}190$ kg N ha⁻¹ mo⁻¹ and was within the enrichment range used by previous studies (Pennings et al. 2002, Darby & Turner 2008a, Langley et al. 2013). There was no sign of burning on any plants during the experiment. Placement of the plugs was done by taking a small core from each planter and replacing the core with a fertilizer plug. Sediment from the core was then packed around the fertilizer plug to secure it. To control for the disturbance of coring, we took similar cores in unenriched controls and then re-packed the core sediment. We also measured belowground biomass by placing an ingrowth bag of screen mesh (25 cm long; 6.4 cm diameter) filled with commercially available peat moss (Gallagher et al. 1984) in each planter. To

insert ingrowth bags, we took a core (4 cm diameter; 20–25 cm depth) from each planter and replaced the core with the ingrowth bag.

2.3. Hurricane Isaac

Hurricane Isaac, a Category 1 event, made landfall in the USA near the mouth of the Mississippi River on 28 August 2012, then moved offshore, and finally moved onshore just west of Port Fourchon in southeastern Louisiana on 29 August 2012. For 4 d, tides ran approximately 0.5–1 m above predicted levels (mean \pm SE: 0.48 ± 0.03 m) with a peak tidal height of approximately 1.28 m above mean lower low water (MLLW; NOAA data, Dauphin Island Station). This storm also brought ~ 35.5 cm of precipitation locally (Grand Bay, Alabama; Berg 2013). Although both experimental marsh organs survived Hurricane Isaac, 8 *Spartina* planters lost all of their live aboveground biomass (e.g. shoots were sheared off and/or remaining shoots were dead) and never recovered. A total of 10 other planters (mostly in Marsh Organ B) were lost due to a partial collapse of the marsh organ assembly, which occurred weeks after Isaac due to sediment scoured from underneath the structure (see Table S2). All planters lost during Hurricane Isaac or due to structural collapse were removed from the analysis.

2.4. Experimental monitoring and sampling

Data on shoots, leaves, root growth, and above- and belowground biomass were collected. We measured the number of live shoots, height of each shoot, and number of live leaves per shoot in each planter 3 times: (1) at the start of the experiment (17 July), (2) just before the arrival of Hurricane Isaac (26 August), and (3) a final sampling when the experiment was concluded (20 October). We also sampled the number of shoots only 12 d after Isaac (11 September). For clarity, the 4 sampling times will be referred to as initial (I), prior to Isaac (P), after Isaac (A), and final (F). Measurements for the first 3 dates (I, P, and A) were done *in situ*. For F, all aboveground biomass was clipped at the sediment surface, frozen, and later processed in the lab.

Above- and belowground biomasses were determined from the frozen final samples. For aboveground biomass, dead leaves were removed and all live stems and leaves were dried to a constant weight in an oven at 70°C. Belowground biomass was deter-

mined from roots in the ingrowth bags. Roots on the interior of ingrowth bags were removed, rinsed of peat, and then dried at 70°C to a constant weight.

2.5. Statistical analyses

The original experiment was envisioned as a balanced design having 2 fixed effects and a random blocking effect to control for spatial variation. The fixed effects were submergence (5 levels of elevation), nutrient levels (ambient condition versus addition), and the interaction of elevation and nutrients. There were 6 replicates of each elevation × nutrient combination. The 6 replicates were equally divided into 2 spatial blocks so that blocking was crossed with the fixed treatments. The df for the balanced model were planned to be 1 for nutrients, 4 for elevation, 4 for the interaction of the fixed effects, 1 for blocking, and 49 for the residual error. However, because the hurricane resulted in the loss of several planters and missing observations, we were unable to decompose the residual error and estimate the contribution of interactions of the fixed effects with blocking (df = 9) and the remaining residual error (i.e. df for the balanced design = 2 nutrient levels × 5 elevations × 2 blocks × [3 replicates – 1]). Note that our design, in which random effects are only decomposed into the main effect of blocking and a single estimate of error, is the same design proposed by Snedecor & Cochran (1967, p. 361–364).

We undertook 4 separate analyses of percent changes in leaves and shoots: (1) prior to Isaac (i.e. $[P - I] / I$); (2) immediately following Isaac (i.e. $[A - P] / P$); (3) during the month following Isaac (i.e. $[F - P] / P$); and (4) throughout the entire experiment (i.e. $[F - I] / I$). For the data collected on the last sampling date, we also analyzed the average number of shoots, leaves, and height, and the total aboveground and belowground biomass. The sample size for each variable depended on plant condition. For example, for analysis of percent change in shoot abundance, replicates with a 100% loss were included as –100%, which indicated plant death (total n = 40). However, for analyses of leaf and shoot height, replicates with 100% loss were treated as missing values and dropped from the analysis (n = 26 samples analyzed).

Analyses were done both with a general linear model (GLM) in SPSS and several R packages (R version 3.2.1; R Core Team 2015). Mixed model ANOVAs were analyzed using the 'lmer' function in the 'lme4' R package (version 3.2.5; Bates et al. preprint <http://arxiv.org/abs/1506.04967v2>) and the 'anova' function

in the 'car' package (version 3.2.1; Fox & Weisberg 2011). Type III tests were used in the ANOVAs.

In some cases, data were very unbalanced and/or did not meet parametric assumptions, so permutation tests were also carried out to check for agreement with parametric tests. Permutation tests were done using the sample function in conjunction with the 'lmer' and 'anova' functions; the total number of permutations per test was set to 999. Wald test chi-squared values from the parametric tests were used as the cut-off values for the permutation tests. There was close agreement between the results of the parametric and permutation tests, but any differences are fully described.

Finally, we used a multinomial logistic regression to examine how elevation, enrichment, the position of the marsh organ, and various covariates significantly affected the final state of *Spartina* in each planter. Each replicate was categorized as being in 1 of 5 states: (1) alive at the end of the experiment (26 planters); (2) died prior to Hurricane Isaac (2 planters); (3) destroyed during Hurricane Isaac (8 planters); (4) destroyed by structural collapse of the marsh organ (10 planters); and (5) dead at the end of the experiment (14 planters). Multinomial logistic regressions were done using the 'multinom' function in the 'nnet' package (version 7.3.12; Venables & Ripley 2002) and significance tests were done using the 'anova' function in the 'car' package (version 3.2.1; Fox & Weisberg 2011; Type III sums of squares for categorical variables). The model was initially run as a 3-way design that included marsh organs, elevation, and nutrients as main effects and all possible interactions and with change in abundance, average leaves, total leaves, or shoot height prior to the storm as continuous variables. For ease of presentation, a final model included only marsh organs and elevation as main effects because the effects of nutrients and interactions were not significant. Dropping variables from the model did not substantially change the significance levels.

3. RESULTS

3.1. Changes prior to and following Hurricane Isaac

Approximately 1 mo after the experiment started and prior to the arrival of Hurricane Isaac, there were significant percent changes in number of shoots and leaves, but not in height. Both shoots and leaves showed a change from a percent loss at low elevations to a percent gain at higher elevations (for

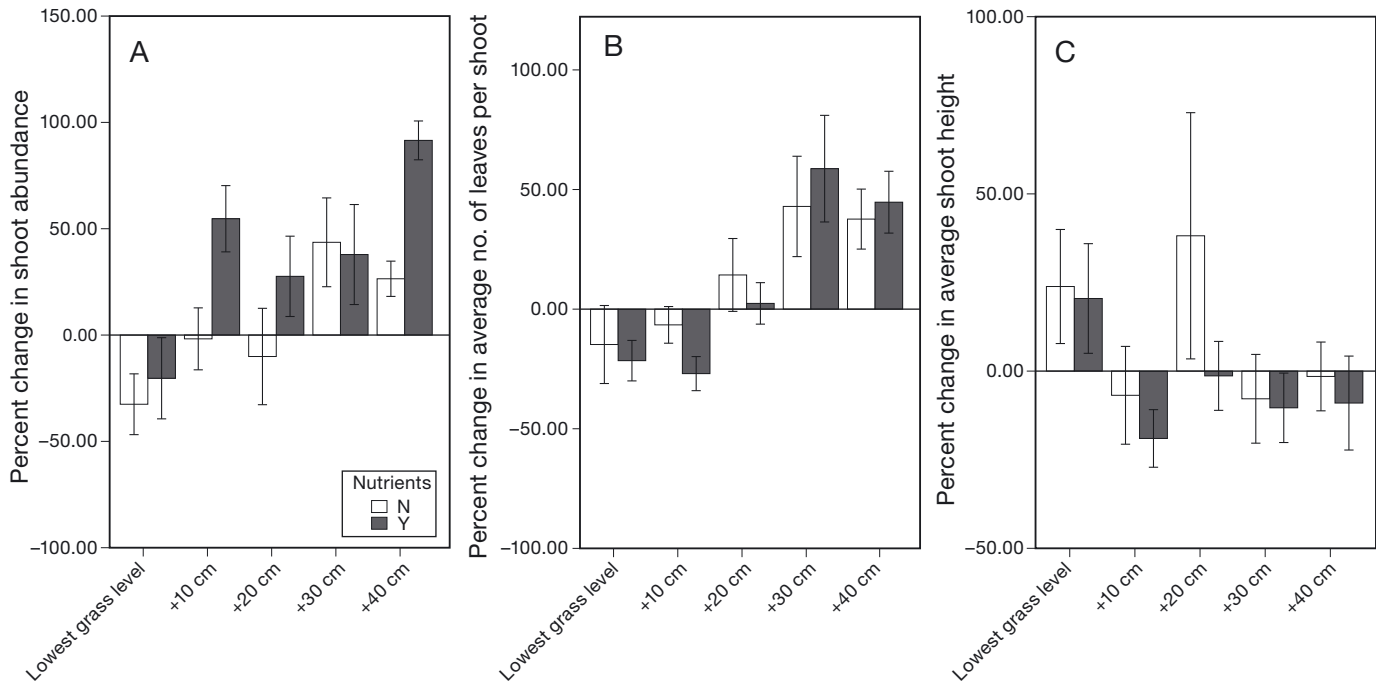


Fig. 1. Mean (\pm SE) percent change in *Spartina alterniflora* aboveground metrics after 1 mo and prior to the arrival of Hurricane Isaac. Change in (A) number of shoots per planter, (B) number of leaves per shoot, and (C) average plant height. Open bars: unenriched planters; grey bars: planters enriched with Osmocote fertilizer; N: no; Y: yes

shoots: $F_{4,48} = 7.05$; $p < 0.001$; for leaves: $F_{4,48} = 10.05$, $p < 0.001$; Fig. 1). There were mean (\pm SE) losses of 2.54 ± 1.12 shoots planter⁻¹ and 0.5 ± 0.17 leaves planter⁻¹ at the lowest elevation and average gains of 5.92 ± 1.34 shoots and 1.07 ± 0.23 leaves planter⁻¹ at the highest elevation (Table S1). Average shoot height per planter tended to increase at the lowest grass elevation levels and decline at higher levels ($F_{4,48} = 2.32$, $p = 0.07$), likely indicating the death of small shoots (<10 cm) at low elevations and the production of new shoots at higher elevations.

Fertilizer enrichment caused a significant percent increase in average shoot abundance ($F_{1,48} = 9.246$, $p = 0.004$), but not in average shoot height or average number of leaves per shoot (height: $F_{1,48} = 1.87$, $p = 0.178$; leaves: $F_{1,48} = 0.126$, $p = 0.724$). On average, fertilizer increased shoot abundance by 3.83 ± 0.96 shoots compared to unfertilized planters, which gained an average of 0.24 ± 0.77 shoots. There were no significant interaction terms for percent changes in aboveground met-

rics (shoots: $F_{4,48} = 1.53$, $p = 0.209$; height: $F_{4,48} = 0.494$, $p = 0.740$; leaves: $F_{4,48} = 0.527$, $p = 0.716$).

Immediately after Hurricane Isaac, not only did shoot abundance decline, but differences in abundance due to elevation and nutrients disappeared (Fig. 2A). The hurricane resulted in an average loss of

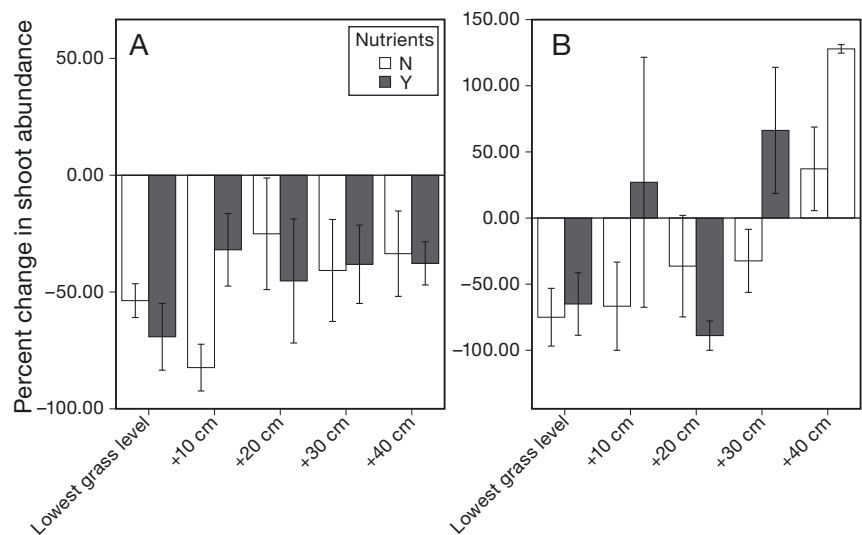


Fig. 2. Mean (\pm SE) percent change in *Spartina alterniflora* shoot abundance (A) immediately following Hurricane Isaac and (B) during the month following Hurricane Isaac. Open bars: unenriched planters; grey bars: planters enriched with Osmocote fertilizer; N: no; Y: yes

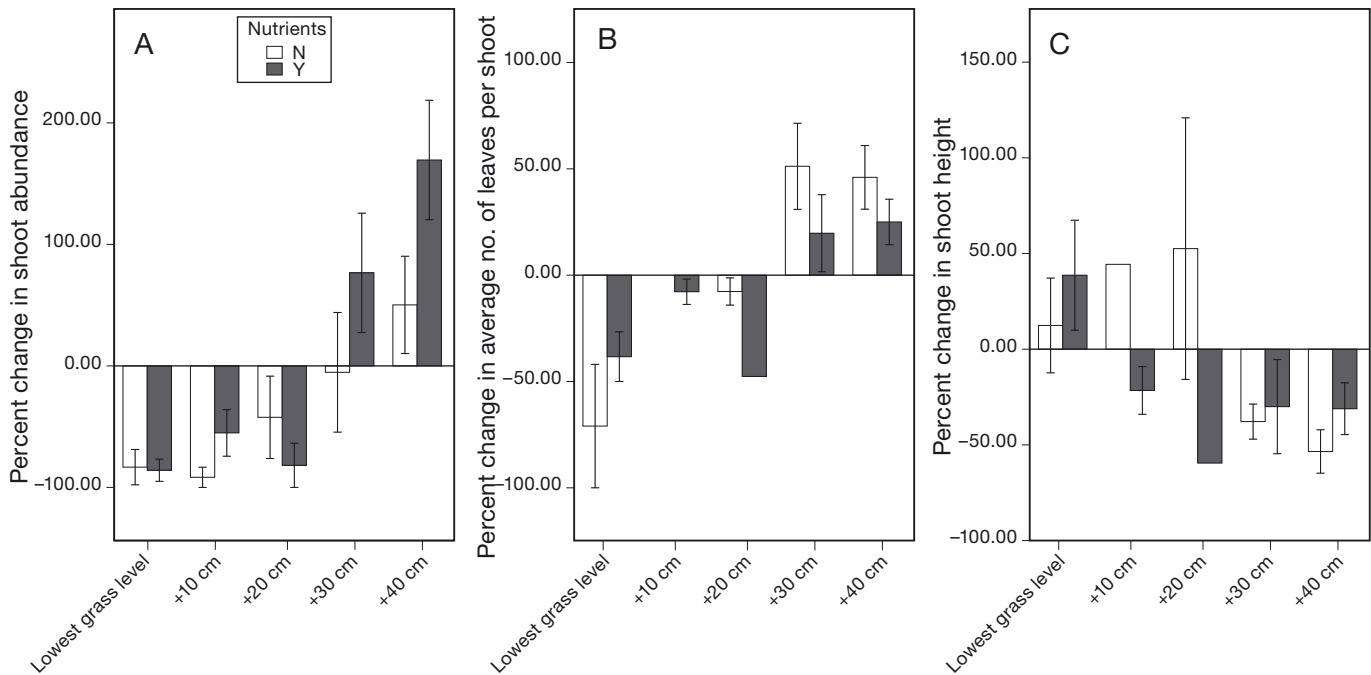


Fig. 3. Mean (\pm SE) percent change in *Spartina alterniflora* aboveground metrics over the course of the entire experiment, showing change in (A) number of shoots, (B) average number of leaves per shoot, and (C) average plant height. Open bars: unenriched planters; grey bars: planters enriched with Osmocote fertilizer; N: no; Y: yes

4.85 ± 0.605 shoots planter⁻¹. There was no significant effect of elevation ($F_{4,39} = 1.19$, $p = 0.329$), fertilizer treatment ($F_{1,39} = 0.064$, $p = 0.802$), or their interaction ($F_{4,39} = 1.68$, $p = 0.174$). This decline in plant abundance continued after Hurricane Isaac in all but the highest 2 levels (+30 and +40 cm; Fig. 2B); however, neither elevation nor enrichment significantly impacted changes in shoot abundance by the final October sampling period (permutation test; elevation, $p = 0.469$; fertilizer, $p = 0.203$; elevation \times fertilizer, $p = 0.592$).

3.2. Overall change and final *Spartina* metrics

Three measures of percent change and 5 measures of absolute amounts were tallied at the end of the experiment. The percent change measures included changes in the number of shoots, average number of leaves per shoot, and average plant height per planter (Fig. 3, Table 1). The 5 absolute measures included total number of shoots, total number of leaves, average plant height (Fig. 4, Table 1), and above- and belowground biomasses (Fig. 5, Table 1).

Elevation had the most consistent significant effect on these metrics, with the exception of percent change in plant height and belowground biomass (Table 1). In general, planters at the lowest elevations

Table 1. Permutation p-values for elevation, nutrients, elevation \times nutrient interactions for all final *Spartina alterniflora* metrics. Where parametric and permutation tests disagreed, p-values for parametric tests are in parentheses

Final metric	Elevation	Nutrients	Interaction
% Δ Shoot number	0.016	0.104	0.38
% Δ No. leaves shoot ⁻¹	0.001	0.207	0.471
% Δ Average plant height	0.078 (0.021)	0.899	0.176
Final shoot number	0.015	0.03	0.163 (0.077)
Final no. leaves shoot ⁻¹	0.001	0.88	0.249
Final average height	0.013	0.899	0.614
Aboveground biomass	0.033	0.024	0.091 (0.019)
Belowground biomass	0.116 (0.04)	0.206	0.869

with the most submergence declined in both the percent change over time and the final total number of shoots and leaves (Figs. 3A,B & 4A,B; permutation test $p = 0.016$ for percent shoots, $p = 0.001$ for percent leaves, $p = 0.015$ for total shoots, and $p = 0.001$ for total leaves; Tables 1 & S2). Changes in final shoot number mirrored the percent changes, and final

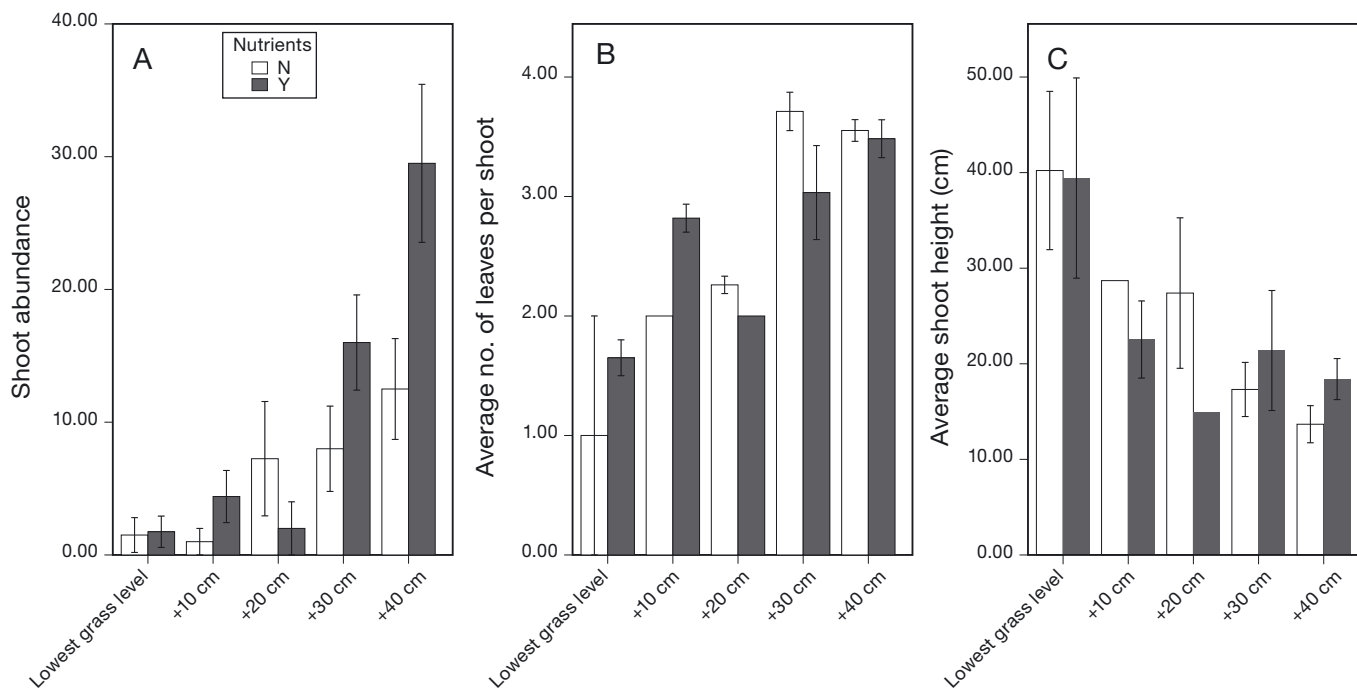


Fig. 4. Mean (\pm SE) impacts of submergence level and enrichment on final *Spartina alterniflora* aboveground metrics on the final sampling date, showing average (A) number of shoots, (B) number of leaves per shoot, and (C) shoot height per planter. Open bars: unenriched treatments; closed bars: fertilizer-enrichment treatments; N: no; Y: yes

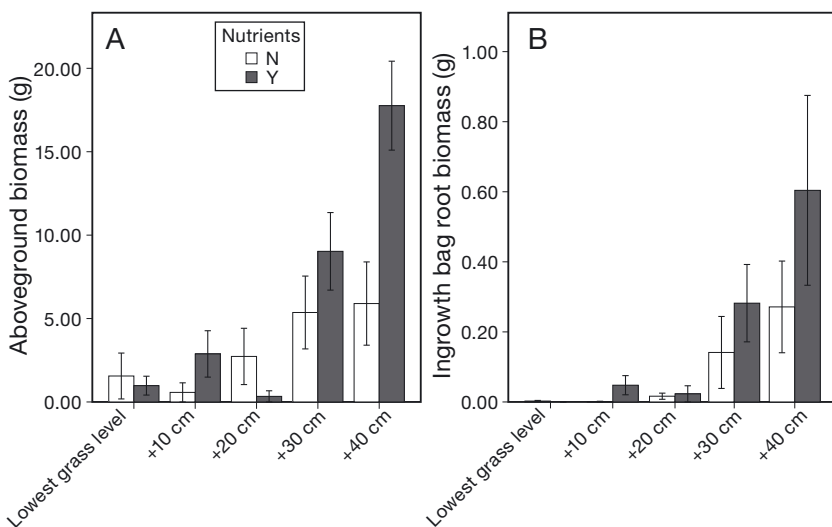


Fig. 5. Mean (\pm SE) impacts of submergence and enrichment on *Spartina alterniflora* (A) aboveground and (B) belowground biomass. Open bars: unenriched planters; grey bars: planters enriched with Osmocote fertilizer; N: no; Y: yes

shoot number was often at least 10 times greater in the higher elevation planters (Fig. 4A; $p = 0.015$). Leaf number showed increases at the highest 2 elevation levels, gaining an average of 0.85 ± 0.19 (+40 cm) and 0.34 ± 0.52 (+30 cm) while the other levels lost leaves at an average of 0.74 ± 0.55

(+20 cm), 0.19 ± 0.14 (+10 cm), and 1.62 ± 0.46 SE (lowest grass level). These changes significantly impacted the final average number of leaves per shoot (Fig. 4B; $p = 0.001$). Overall, planters at higher elevations typically averaged 3–4 leaves shoot⁻¹ while lower elevations averaged 1–2 leaves shoot⁻¹ (Fig. 4B). Lower elevations often had dead or dying leaves, but because dead/brown leaves were not included in leaf counts, these numbers reflect grass health. These changes also resulted in significantly taller final shoot heights at lower elevations (Fig. 4C; $p = 0.013$) and less total live aboveground and belowground biomass at lower elevations (Fig. 5A; $p = 0.033$; Fig. 5B; $p = 0.04$ for parametric test; $p = 0.116$ for permutation test), with the lowest 3 elevation levels often possessing less than 5 g of live biomass.

Nutrient enrichment had a significant effect on only the final number of shoots and total aboveground biomass. Enrichment caused significant increases in final shoot abundance (Fig. 4A; $p = 0.03$),

especially at the highest 2 elevations (elevation \times fertilizer: $p = 0.077$ for parametric test; $p = 0.163$ for permutation test). Aboveground biomass was also significantly increased by fertilizer addition ($p = 0.024$). Fertilizer effects were most apparent at the highest elevations where the biomass was almost double that of unenriched planters (elevation \times fertilizer: parametric = 0.019; permutation $p = 0.091$). None of the metrics showed significant interactions between elevation levels and nutrient enrichment.

3.3. Multinomial logistic regression

The multinomial logistic regression showed significant effects of marsh organs ($p < 0.002$). The structural collapse after Hurricane Isaac affected planters at higher elevations in Marsh Organ B (Table S2). Elevation was also a significant predictor of final plant condition ($p < 0.0012$). Replicates scored as dead at the end of the experiment were confined to the lowest 3 elevations: 6 in the lowest grass level, 4 at +10 cm, and 4 at +20 cm. The changes in shoot height and abundance prior to the storm were not significant predictors of *Spartina* final condition. However, the change in average leaf number was a significant predictor of the final state ($p < 0.022$).

4. DISCUSSION

Setting targets for marsh restoration and management in the face of sea level rise requires identifying the optimum elevation for emergent marsh grasses. Overall, we found that only the highest elevations (+30 and +40 cm) with the lowest frequencies of submergence showed consistent increases in shoot abundance and other metrics and demonstrated resilience to hurricane effects. Lower elevation led to declining grass production, few increases in shoot abundance, and little resilience to hurricane disturbance. In general, fertilizer addition increased *Spartina* shoot abundance, especially at higher elevations, but interactions between submergence and fertilizer were typically not significant.

4.1. Comparisons with other *Spartina* studies

To date, most knowledge of how *Spartina* responds to submergence comes from studies on the US Atlantic coast, with few studies done to determine if production patterns in macrotidal Atlantic Coast are

consistent with the microtidal portion of the Gulf of Mexico. Consistent with previous studies in macrotidal areas (Morris et al. 2002, Kirwan et al. 2012, Voss et al. 2013, Snedden et al. 2015, Hanson et al. 2016), we documented the decline of *Spartina* above- and belowground production with increasing submergence. Prior to the hurricane's arrival, the lowest elevation showed consistent declines in all aboveground metrics (Fig. 1), and at the conclusion of the experiment after Hurricane Isaac, the lower 3 elevations contained little or no live above- or belowground biomass. In contrast, the 2 highest elevations consistently appeared to be at a favorable elevation, with increased production noted across all metrics and high above- and belowground biomass at the experiment's conclusion. Other studies in macrotidal marshes have documented limited, mixed, or no support for a parabolic shaped production curve with increasing elevation (Kirwan et al. 2012, Voss et al. 2013, Snedden et al. 2015, Hanson et al. 2016). We did not observe a peak in *Spartina* production in either above- or belowground biomass at intermediate elevation as proposed by Morris et al. (2002). Instead, plants at higher elevation with infrequent submergence were often in better condition with higher numbers of live leaves than lower elevation plants, which is consistent with another microtidal study (Snedden et al. 2015). Production at higher elevations was primarily driven by the emergence of new shoots, which lowered the average plant height and increased shoot number. These patterns are consistent with Voss et al. (2013) but differ from those of Hanson et al. (2016), who found the largest increase in shoot counts at intermediate elevations. Hanson et al. (2016) also reported that increased *Spartina* production at higher elevations was driven by increases in *Spartina* height rather than shoot number.

The lack of consistency between our results and those of others from macrotidal marshes could have arisen from methodological and/or biogeographic, genetic, or biogeochemical differences (Mendelssohn & Morris 2002, Proffitt et al. 2003, McCall & Pennings 2012, Bernik 2015). Understanding how such differences could impact the growth and production of *Spartina* over its large geographic range remains a significant challenge. Without direct measurements of submergence time, we cannot isolate tidal regime as the only factor that may have influenced plant production in our study. While measurements of submergence would improve the ability to compare results across sites, common garden experiments will likely be necessary to fully examine if geographic differences in plants, soils, or submersion patterns

are responsible for observed differences in plant responses.

Consistent with other studies (Darby & Turner 2008a, Deegan et al. 2012), nutrient enrichment generally stimulated aboveground production of *Spartina* shoots. Enrichment did not increase shoot leaf counts or plant height (Figs. 1 & 3), indicating that increased aboveground biomass was driven primarily by increasing the number of shoots. In contrast, our results indicated that enrichment did not facilitate belowground production, as nutrients caused only modest, non-significant increases in belowground biomass at higher elevations. Previous work has found that nutrient enrichment generally lowers *Spartina* belowground production at most elevations in other marsh organ studies (Watson et al. 2014, Hanson et al. 2016, but see Graham & Mendelssohn 2016).

4.2. Responses to hurricane and restoration implications

Despite increases in aboveground production in planters at higher elevations and with nutrient enrichment, these planters were not more resistant to hurricane disturbance and lost just as many shoots as unenriched planters at lower elevations (Fig. 2A). The low resistance to hurricane disturbance in all planters may have resulted from the short acclimation period prior to the hurricane's arrival. However, plants within our experiment acclimated for at least 1 mo prior to the hurricane. Just before the hurricane, plants appeared healthy and measurements demonstrated that most plants were increasing in shoot number (Fig. 1A) and number of leaves (Fig. 1B), indicating that these plants were growing and therefore had overcome any transplant stress. The exception to this growth pattern was at the lowest elevation, which is more likely indicative of the impacts of submergence on the plants rather than transplant shock. Baldwin & Mendelssohn (1998) suggested allowing 1 mo to overcome transplant shock and another month to alter salinity and submergence regimes, yet a slow acclimation to flooding is not possible in field experiments. The equal impacts of disturbance across elevation could also have been an artefact caused by the marsh organ setup. Within the marsh, higher elevation vegetation is often protected by the lower vegetation in front of it. However, similar losses of aboveground vegetation after hurricanes have been documented in *Spartina* as well as in higher elevation plants such as *Juncus* spp., suggesting elevation does not always confer resistance to

hurricane damage (Chabreck & Palmisano 1973, Meert & Hester 2009). After the hurricane, higher elevation plants were more likely to recover, demonstrating that disturbance can interact with submergence to change the resiliency of marsh grasses. This interaction is supported by Baldwin & Mendelssohn (1998), who found *S. patens* to be generally resistant to flooding when undisturbed, but unable to recover within 1 yr after aboveground vegetation was clipped and then flooded. However, unlike Baldwin & Mendelssohn (1998), our plants were likely further impacted by the hurricane disturbance and we cannot isolate flooding from the impacts of vegetation removal. Yet Meert & Hester (2009) also demonstrated that *S. patens* only recovered from multiple storms and flooding disturbances when elevation was increased due to hurricane sediment deposits. These lines of evidence suggest that elevation does not necessarily protect marshes from hurricane disturbance, but increases in elevation can aid in their recovery. Further experiments must be performed to isolate the impacts of scouring, aboveground vegetation loss, and submergence, as well as their combined impacts, to fully elucidate the impacts of hurricane disturbances on marsh recovery.

The results from our short-term study suggest that we may be underestimating the impacts of climate change on coastal marsh loss because the infrequent and catastrophic effects of tropical storms and hurricanes and their interactions with submergence are not considered in most models. Longer term studies examining the combined impacts of submergence and the loss of aboveground production due to disturbances by storms should be performed to confirm our conclusions. In general, although many recent studies have examined the effects of climate-related impacts on marsh production, few studies have experimentally examined how these impacts might interact with the loss of aboveground vegetation and other acute disturbances associated with tropical storms under field conditions. Some models have estimated that a gradual rise in sea level will cause a global loss of 10 to 62% of coastal wetlands by 2080, depending on the magnitude of sea level rise (Nicholls 2004, McFadden et al. 2007). However, it is not always clear how an increase in the frequency and severity of tropical storms will increase marsh vulnerability at regional scales (but see Meert & Hester 2009, Baustian & Mendelssohn 2015). As sea level rises subject marshes to increased submergence, microtidal marshes may be less resilient to storm disturbance unless those disturbances deposit enough sediment to increase elevation.

4.3. Climate change and management implications

The impacts of increases in submergence and disturbance have important implications for marsh restoration and recovery. Presently, field surveys and experiments are used to determine the elevation of peak marsh production. These elevations can then be used to identify marshes that will be lost to sea level rise as well as to identify elevational targets for marsh restoration projects, which add sediment to increase marsh elevation (Schrift et al. 2008). If submergence stress and the loss of aboveground vegetation due to disturbance synergistically interact to reduce the likelihood of marsh recovery, predicting optimum production with only submergence may be insufficient for coastal management and restoration needs. Instead, we may need to identify the elevation that can both withstand submergence and recover from the storm-related loss of aboveground biomass. Elevation optima may need to be more conservatively set at a level where grasses can recover after 50% shoot loss, which may closely mimic the impacts of storm disturbance. Importantly, it is not clear from current research whether optimum elevations and disturbance resilience converge on the same elevations. We cannot determine this information from our experiment, as we cannot isolate the impacts of the hurricane from submergence. However, prior to the hurricane, the highest *Spartina* elevation demonstrated the largest increase in growth, and this trend remained after the hurricane, suggesting the 2 optima are similar.

Prior to the hurricane, one of our *a priori* motivations for this study was to determine if submergence was contributing to the continued shoreline retreat at this site. Oyster reef breakwaters serving as living shorelines at this site have had little impact on slowing shoreline retreat (Moody et al. 2013). As our lowest planters matched the elevation of the seaward *Spartina* edge, our results indicate that *Spartina* exists well below its optimum elevation. Consequently, living shorelines or other barriers that reduce wave action had little impact in preventing marsh loss. Living shorelines and other shoreline protection methods are currently employed in a variety of regions to help reduce marsh loss (Piazza et al. 2005, Swann 2008) and require significant financial and personnel investment. While in many cases these barriers successfully result in marsh protection and restoration (Piazza et al. 2005, Scyphers et al. 2011), we should be aware that eroding marshes in seemingly wave impacted areas may actually be succumbing to submergence associated with relative sea level rise.

In conclusion, higher elevation and low submergence frequency were consistently significant factors that promoted above- and belowground production and provided resilience to hurricane disturbance, while nutrients typically promoted recovery only at higher elevations. The inability of lower elevation plants to recover after disturbance suggests that we may be underestimating the impacts of climate change on marsh loss and overestimating the resilience of marshes at moderate elevation levels. Thus, we need to assess both regional and site-specific plant responses to submergence and local disturbance in order to accurately predict wetland loss and improve restoration and management efforts.

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