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ORIGINAL PAPER

Response of tidal marsh vegetation to pulsed increases in flooding and nitrogen

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Abstract Worldwide, human activities have modified hydrology and nutrient loading regimes in coastal wetlands. Understanding the interplay between these drivers and subsequent response of wetland plant communities is essential to informing wetland management and restoration efforts. Recent restoration strategies in Louisiana proposes to use sediment diversions from the Mississippi River to build land in adjacent wetlands and reduce the rate of land to open water conversion. In conjunction with sediment delivery, diversions can increase nutrient loads and water levels in the receiving basins. We conducted a greenhouse mesocosm experiment in which we exposed three common tidal freshwater and brackish marsh plants (*Panicum hemitomon, Sagittaria lancifolia,* and *Spartina patens*) to two nitrate loading rates [high (35 g N m^2 $year^{-1}$) and low (0.25 g N m^2 $year^{-1}$)], and two flooding treatments (with and without diversion pulsing). Experimental units were set at two different elevations within the treatment tanks to simulate both a healthy and degraded marsh. Plant growth metrics and soil physicochemical properties were measured monthly. Final total biomass was determined at the study's conclusion. Growth responses differed between species but were not significantly influenced by the treatments. Soil redox potential decreased significantly following the increase in flooding associated with the diversion pulse, but recovered to pre-diversion levels after a 3-month recovery period. Our study suggests short flooding pulses with a recovery period may be key for maintaining healthy marshes, however there remains a need for longer-term empirical studies to understand marsh response to pressures associated with river sediment diversions over time.

Keywords Flooding · Louisiana · Nitrate · Nutrient loading · River diversion

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Introduction

The wetlands of the Mississippi River Delta originally formed as a result of sediments deposited by the river, which formed deltaic lobes and a network of natural levees and barrier islands which functioned to further trap river sediment, contributing to the formation of the modern deltaic system (Roberts 1997). These surface wetlands continue to be sustained through a combination of accretion of riverine sediments and biomass production. The marshes of the Mississippi River Delta provide numerous important ecosystem services, including improvement of water quality, sequestration of atmospheric carbon, storm surge protection, and support of economically important markets such as fisheries (Costanza et al. 2008, 2014; Day et al. 2016). Unfortunately, since the mid-twentieth century, these wetlands have been in a state of decline.

Of the multiple threats that Louisiana's coastal wetlands face, some of the most critical issues include high rates of relative sea-level rise (RSLR) caused by the subsidence of compacting deltaic sediments (Day et al. 1995; Spalding and Hester 2007), and reduction in sediment-rich freshwater pulse events (i.e. a discrete, but reoccurring, input of water and sediment into marsh systems) caused by levee construction along the Mississippi River and modification to river hydrology and sediment load caused by upstream dams (Day et al. 1995; Spalding and Hester 2007; Wang et al. 2014; Day et al. 2016). Additionally, there are many other factors that contribute to high rates of coastal wetland loss in this region, including salinity intrusion, water quality deterioration, decreased biological production, severe weather related disturbances, erosion, canal dredging, and geologic faulting (Day et al. 1995; Kennish 2001; Day et al. 2009; Kolker et al. 2012; Visser and Peterson 2015; Day et al. 2016). Since the 1930's, these combined factors have contributed to approximately 4833 km^2 of land loss, with current loss rates reaching approximately 28 km^2 per year (Peyronnin et al. 2013; Wang et al. 2014; Couvillion et al. 2017). Louisiana's coastal industries, economies, communities, and government are now challenged with taking definitive action to reduce or reverse the state's rapid rates of land loss to recover the essential functions provided by deltaic wetland ecosystems.

Current restoration plans in Louisiana focus on re-establishing the natural processes of delta formation with the primary goal of rebuilding land and reducing the rate of land loss. Establishment of connections between the sediment-rich Mississippi River and its flanking wetlands via river sediment diversions is idealized to build land (Ialeggio and Nyman 2014) and limit the extent of saltwater intrusion associated with rising sea levels that may negatively impact glycophytes (Day et al. 2009; Visser and Peterson 2015; Day et al. 2016; van der Deijl et al. 2017). Although reintroduction of the sediment-rich Mississippi river water into flanking marshes is expected to provide improved sediment capacity for land building, this process is also expected to change the hydrology and nutrient load in the receiving basins. Concerns have been raised over ecosystem responses to stressors associated with increased flooding, decreased salinity, and nutrient additions that accompany river sediment diversions (Slocum and Mendelssohn 2008; Visser and Peterson 2015; Day et al. 2016).

Construction of new river sediment diversions along the Mississippi River will affect a range of marsh types (including fresh, intermediate, brackish, and salt). Marshes can respond to the associated increased flooding and heightened nutrient availability in a variety of ways; for example, in a mesocosm study Langley et al. (2013) found that N fertilization stimulated *Spartina patens* productivity under increased inundation duration up to a level where this species was unable to survive. Nitrogen fertilization under extended tidal flooding duration may shift the entire plant community toward more flood-tolerant species, such as *Schoenoplectus americanus* (Langley et al. 2013). Both of these species are native to Louisiana but typically occupy different positions in the marsh platform. Visser et al. (1999) documented a decrease in the dominance of *P. hemitomon* in Louisiana's coastal zone driven by changes in water level and water quality. Swarzenski et al. (2008) observed that long-term influx of river water resulted in degraded root mats and enhanced decomposition in a *P. hemitomon* marsh in coastal Louisiana. Responses may also include changes in species richness, species composition, and lower marsh surface elevation due to a decrease in productivity (Day et al. 2009; Kearney et al. 2011; Roy et al. 2016; Wasson et al. 2017). Furthermore, a shift from high salinity marsh species to more freshwater wetlands may reduce overall wetland resilience to hurricanes, as low salinity marshes in Louisiana's coastal plain tend to have weak soil shear strength at $\sim$ 30 cm depth, at the base of rooting (Howes et al. 2010). Studies on the response of marsh macrophytes to elevated nutrient input have shown varied results. In some cases, increased nutrient input to freshwater marshes resulted in root and rhizome biomass decline, whereas in other studies, there was an increase in soil organic matter and litter decomposition rates (Valiela et al. 1976; Kearney et al. 2011; Turner 2011). Previous field studies in Louisiana reported that freshwater input, in conjunction with increased nutrients, had a positive effect on biomass production for *Spartina patens* with increases in both live and total cover (DeLaune et al. 2005; Meert and Hester 2009). Other studies, spanning more species across larger biogeographic ranges, found that responses can be variable, displaying a decrease or no change of aboveground biomass, and a decrease in the belowground:aboveground biomass ratio (Slocum and Mendelssohn 2008; Wasson et al. 2017). Under nutrient enrichment, plant communities have higher rates of degradation and decomposition rates by anaerobic microbes may increase (Swarzenski et al. 2008; Deegan et al. 2012; Bodker et al. 2015). Additionally, high nutrient loading rates reduce both soil shear strength and marsh platform stability, consequently contributing to marsh collapse (Turner 2011; Deegan et al. 2012). These combined environmental alterations can lead to increased submergence of the marsh surface and may create a negative feedback that continues to lower productivity of the marsh (Snedden et al. 2015).

When excessive flooding occurs, productivity of wetland vegetation may decrease, thus reducing belowground organic matter accumulation and altering plant community composition (Casanova and Brock 2000; Snedden et al. 2015). Flooding can also reduce soil redox potential, creating stressful conditions for both aboveground and belowground plant structures (Blom and Voesenek 1996; Lessmann et al. 1997; Dat et al. 2004). Although many wetland plant species have adaptations that enable them to survive flooding events, (i.e., etiolation, increased aerenchyma formation to facilitate gas flow, and adventitious root growth) (Blom and Voesenek 1996; Dat et al. 2004; Sloey et al. 2016), these physiological coping mechanisms may decrease the amount of energy allocated to biomass production. Eventually, waterlogging may result in plant death, marsh deterioration, and marsh submergence (McKee and Mendelssohn 1989; Schuyler et al. 1993; Blom and Voesenek 1996; Lessmann et al. 1997; Snedden et al. 2015).

The response of freshwater and brackish marsh plant species to increased flooding is of particular concern, as the marshes located in receiving basins of the proposed Mid-Barataria river sediment diversion project in coastal Louisiana are dominated by freshwater and brackish marsh vegetation (*Spartina patens*, *Sagittaria lancifolia*, and *Panicum hemitomon*). Several studies have previously addressed the ecology and stress response of these important species. For example, *Spartina patens* declined in total biomass with increased flooding (Spalding and Hester 2007; Visser and Sandy 2009; Snedden et al. 2015). *Sagittaria lancifolia* exhibited an inverse relationship between flooding duration and biomass production and a negative growth response to increased salinity (Spalding and Hester 2007; Visser and Sandy 2009). Flooding duration had no significant effect on total biomass production in *P. hemitomon*, though longer durations of flooding did result in greater adventitious root biomass (Willis and Hester 2004; Spalding and Hester 2007). Understanding plant responses to flooding regimes may be especially critical in Louisiana's coastal restoration efforts as diversions will likely result in longer periods of flooding and increased inundation durations.

Although the effects of permanent flooding on marshes has been studied extensively, our understanding of the effects of flood pulses and presses is more limited (Blom and Voesenek 1996; Dat et al. 2004; Visser and Peterson 2015). Furthermore, the majority of these studies have focused solely on either flooding or salinity, or they have included combined effects of the two but only considered static water levels (Lessmann et al. 1997; Visser and Sandy 2009; Merino et al. 2010; Ialeggio and Nyman 2014; Visser and Peterson 2015). Few studies have investigated the interactive effects of nutrient loading in conjunction with flooding, and these studies are likely to be instrumental in modulating the response of wetlands to river sediment diversions. Many uncertainties remain regarding ecosystem response to such a large-scale environmental alteration (Slocum and Mendelssohn 2008; Visser and Peterson 2015; Day et al. 2016).

Our greenhouse study examines the response of three key freshwater to brackish marsh plant species

(*Panicum hemitomon*, *Sagittaria lancifolia*, and *Spartina patens*) to hydrologic regime, nutrient enrichment, and marsh surface elevation. A 7-month long mesocosm study was used to determine the responses of vegetation and soil physicochemical characteristics to pulsed flooding and nutrient enrichment anticipated based on a pre-established scenario for operation of proposed river diversions in Louisiana (Meselhe et al. 2015). Our mesocosm study focused on nitrate enrichment, though it should be noted that river diversions may introduce numerous other elemental compounds in a variety of ratios. We hypothesized that (1) the addition of nutrients, both independently and in combination with different hydrologic regimes, will promote aboveground plant growth, but responses will vary by species, and (2) soil redox potential will shift towards a more reduced state in response to increased flooding duration and nutrient enrichment. By enhancing the understanding of plant and soil responses to alterations of water and nutrient regimes, we can aid coastal wetland ecologists, engineers, land managers, and policy makers in making informed decisions on how river sediment diversions may influence marshes in the proposed receiving basins.

Materials and methods

Plant species selection and collection

Species selected for this study (*Panicum hemitomon*, *Sagittaria lancifolia*, and *Spartina patens*) are all native to Louisiana and are found in freshwater (0.00–0.5 ppt), intermediate (0.5–5.0 ppt), and brackish (4.5–10.00 ppt) marshes. They commonly occur within the projected receiving basins of newly proposed Mississippi River sediment diversions. *Panicum hemitomon* makes up 25% of the vegetation in Louisiana's fresh marshes and is considered a good shoreline stabilizer due to its rapid growth rate, ability to form dense stands, and a root network capable of anchoring soil and trapping sediment (Chabreck 1972; Newman and Gates 2009). *Panicum hemitomon* sometimes co-occurs with *S. lancifolia,* a common species that composes 15.2% and 6.5% of the vegetation cover in Louisiana's fresh and intermediate marshes, respectively (Chabreck 1972). *Spartina patens*, also valued for shoreline protection and marsh restoration, makes up 55.2% of the vegetation in Louisiana's intermediate to brackish marshes (Chabreck 1972; Leif 2013).

Plants were obtained by collecting marsh sods from areas where the target species was dominant in Lake Salvador Wildlife Management Area (WMA) and Jean Lafitte National Historical Park and Preserve, both of which are located in the Barataria Basin of southeast Louisiana. Sod collection areas were selected based on overall health of the target species present and similarity in the number of live stems, however some sods included the presence of other non-target species. Sods were extracted to a depth of 35 cm from the field throughout August and September of 2016. After extraction from the field, intact sods were immediately placed in 16.9 L plastic containers with five cm of pea gravel at the bottom to facilitate drainage. These units were transported to a greenhouse at the U.S. Geological Survey Wetland and Aquatic Research Center in Lafayette, Louisiana (30.304206 N, − 92.009775 E). An evaporative cooling system along one wall of the greenhouse maintained air temperatures below 35 °C. Containers were perforated along the sides and top to facilitate water uptake and drainage. All sods were standardized to a belowground soil depth of 30 cm and dead stems were removed. The containers with sods, hereafter referred to as experimental units, were placed in tanks (60 cm deep × 122 cm diameter) with roughly 15 cm of fresh tap water and allowed to acclimate to greenhouse conditions for 4 months.

Experimental design

The study is a split plot on a randomized block design consisting of three plant species (*S. patens, S. lancifolia,* and *P. hemitomon*), two hydrologic regimes (normal diurnal microtidal and simulated diversion pulse), two relative soil surface elevations (representing a healthy marsh and a degraded marsh), and two nitrate loading rates [high (35 g N m^2 $year^{-1}$) and low (0.25 g N m^2 $year^{-1}$)]. There were three replicate treatment tanks (91 cm deep × 122 cm diameter) for each of the four following treatment combinations: (1) normal tidal hydrology with low nitrate treatment (TLN), (2) normal tidal hydrology with high nitrate treatment (THN), (3) diversion hydrology with low nitrate treatment (DLN), and (4) diversion hydrology with high nitrate treatment (DHN). Each treatment tank contained two experimental units of each species, with one unit designated as healthy marsh and the other as degraded marsh, as determined by elevation within the tank (see below for details). The 12 treatment tanks maximized available space in the greenhouse and were arranged in three blocks perpendicular to the east/west light gradient. The duration of this study was 7 months, from February 2017 until the end of the growing season in August 2017.

Hydrology treatments

Six experimental units, two for each of the three species, were placed in the cylindrical treatment tanks. Two soil surface elevations were applied within the tanks to represent either healthy or degraded marsh conditions, and were achieved using cinderblocks and PVC spacers to raise healthy marsh elevation units + 15 cm above degraded marsh elevations. Hydrology treatments were applied at the tank level. A diurnal tidal regime was engineered to represent normal conditions in coastal Louisiana, and was characterized by a 30-cm tide (Gosselink and Pendleton 1984; Coastal Protection and Restoration Authority 2016). Because of elevation differences within the treatment tanks, healthy marsh units were inundated 35% of the time (average water level − 5 cm below the soil surface) and degraded marsh units were inundated 85% of the time (average water level +10 cm above the soil surface) (Fig. 1). Using aquarium pumps (Lifeguard Aquatics Quiet One Pro Series 1200) and gravity drainage, we achieved a continuously moving tidal system. Pumps, connected to an automated timer, transferred water from an adjacent reservoir tank (60 cm deep × 122 cm diameter) into the treatment tank over the course of a 12-h period, then pumps turned off to allow the tanks to drain for 12 h. Tidal cycles for each of the blocks were set 5 min apart to prevent an overload to the electrical system. Water levels in the treatment tanks subjected to normal diurnal hydrology were 38 cm deep at low tide and 68 cm deep at high tide. All 12 tanks were treated with the normal tidal regime for the first 4 weeks of the experiment to allow for initial establishment of all vegetation.

After the initial 4 weeks, half of the treatment tanks (6) were subjected to a simulated diversion hydrology treatment. To apply this hydrology, water levels were elevated to a depth of 89 cm (adding + 25 cm of water above soil surface of the healthy marsh elevation units and + 45 cm of water above degraded marsh units) for a 4-week period starting in February and April of 2017 (Fig. 1). Both marsh elevation treatments were flooded 100% of the time for the continuous 4-week diversion period as per Louisiana

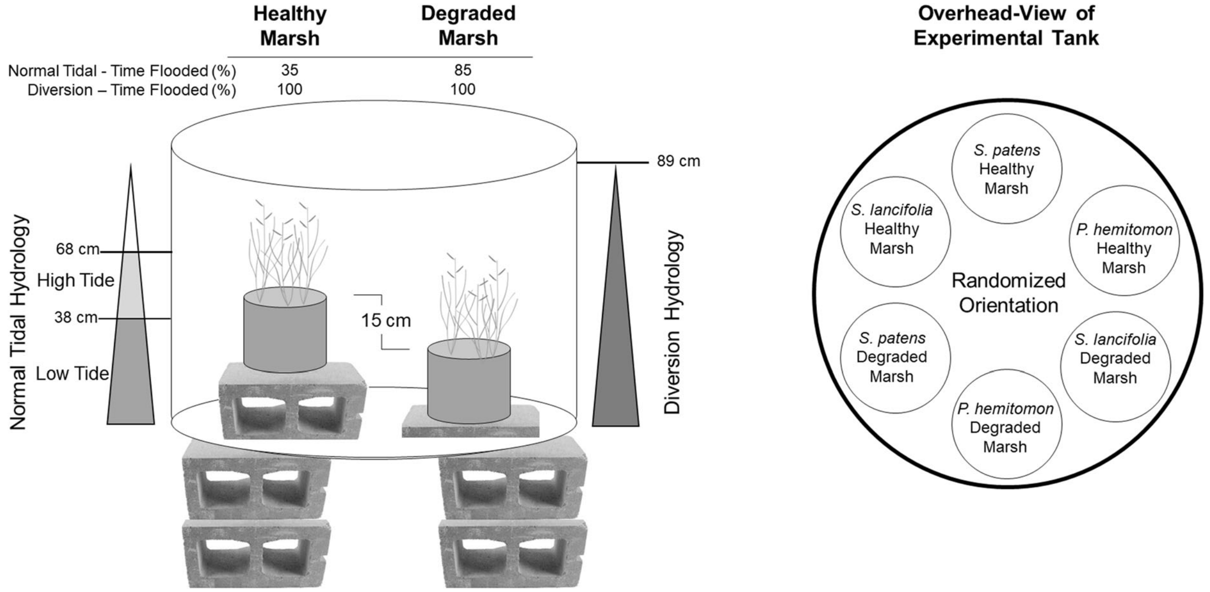

Fig. 1 Representation of experimental set up showing tidal regime, elevation, and percent flooding differences between Healthy Marsh Elevation treatments and Degraded Marsh Elevation treatments subjected to either Normal Tidal Hydrology or Diversion Hydrology

river diversion scenarios (Meselhe et al. 2015). Diversion treatment tanks had no tide during the diversion regime as we assumed that a tidal signature would not be noticeable while a diversion event was taking place in situ. However, diversion treatment tanks were outfitted with a pump that operated for 12 h each day to circulate the water and prevent stagnation. The first 4-week diversion treatment was initiated on Feb. 27, 2017. After 4-weeks of elevated flooding, hydrology was returned to a normal 30-cm tidal regime for another 4-weeks (recovery period) before a second 4-week diversion treatment was initiated on April 22, 2017. At the conclusion of the second diversion event, hydrology was again returned to normal tidal conditions for the remaining weeks of the study, through August 2017.

Nutrient enrichment treatments

Two nutrient enrichment treatments were applied at the tank level. Half of the tanks received background nutrient levels (0.25 g N m^{-2} $year^{-1}$) while the remaining half received high nitrogen loading (35 g N m^{-2} $year^{-1}$). The background nitrate loading rate was measured from the well water used to fill the tanks. High nitrogen loading rates were based on water quality data collected from the Caernarvon river diversion into the Breton Sound estuary in Louisiana (Lane et al. 1999). We believe this to be a representative value as nitrate concentration in the lower Mississippi River has remained relatively constant since 1980, with the exception of regional heterogeneity and weather-related abnormalities (Sprague et al. 2011). High nitrogen loading was accomplished by adding dissolved sodium nitrate ($NaNO_3$) to the treatment tanks twice during the study, simultaneously with the diversion hydrology treatment to simulate the nutrient pulse that would accompany a diversion.

Measured metrics

Plant growth metrics, including number of live and dead stems and average stem height of both target and non-target species, were measured monthly. On a monthly basis, soil redox potential was measured in each experimental unit (modified from Spalding and Hester 2007). Soil redox potential was measured at 1 cm and 10 cm depths, utilizing ORP electrodes (Thermo Orion 9179BN, Thermo Electron Corporation, Wisconsin); a correction factor of 200 mV was added to all redox potential measurements prior to analysis.

At the end of the experiment, aboveground material was clipped at the soil surface and stored at 4 °C until processing. Stems were separated into target and non-target species, sorted into live and dead, and final stem counts recorded. Once sorted, all leaf tissue was dried in a convection oven at 60 °C for 2 weeks until all moisture was removed, and aboveground biomass for each target species was determined. A subsample of dried leaf tissue was collected from each experimental unit target species and ground to a homogenous mix using a Wiley Mill with a 60 micron mesh sieve. An additional dried leaf subsample was collected and used for total carbon (TC) and total nitrogen (TN) analysis via dry combustion utilizing an elemental analyzer (ThermoFinnigan Flash 112 Series) (Carter and Gregorich 2006).

At the end of the study, soil cores and soil shear strength values were collected from each experimental unit. Belowground biomass was estimated by taking a 10-cm diameter core from the center of each unit, for the entire depth of the sod (~ 30 cm) (Farnsworth and Meyerson 2003). Cores were washed thoroughly using a 2-mm mesh sieve placed over a 0.05-mm mesh sieve to prevent loss of dead and fine root material (Darby and Turner 2008a). The roots were sorted into live and dead by inspection of turgor and color (Farnsworth and Meyerson 2003). All plant biomass was dried for 2 weeks at 60 °C and dry weight was recorded (Spalding and Hester 2007).

Soil shear strength was measured by using a handheld shear strength meter (Geovane Model 49, Geotechnics, Auckland, NZ), with a 33-mm blade. Triplicate soil strength measurements were taken at 5 cm soil depth and averaged for each experiment unit. Soil cores were taken using a stainless steel split corer (diameter of 4.7 cm with a piano hinge to facilitate opening and closing). After collection, cores were immediately placed into pre-weighed sample bags, wet weight was recorded, and then cores were placed into a drying oven to be dried at 60 °C, until a constant weight was achieved (Wang and Li 2011). Cores were pulverized using a mortar and pestle and then filtered through a 2 mm sieve before being analyzed for bulk density and percent soil moisture. Bulk density was calculated using a simple dry weight to volume ratio and percent soil moisture was determined using the weight difference after drying. For soil organic matter (SOM), total nitrogen (TN), and total carbon (TC) analyses, soil cores were first run through a planetary mill (Fritsch Pulverisette 6, Pittsboro, NC, USA) to achieve a fine homogenous mill. Soil organic matter was determined by loss on ignition in a muffle furnace at 475° for 5 h (modified from Wang and Li 2011). TN and TC was calculated via dry combustion utilizing an elemental analyzer (ThermoFinnigan Flash 112 Series) (Carter and Gregorich 2006).

Data analysis

Analyses were conducted separately for each species-elevation combination. All analyses were conducted in R (R Core Team 2018; Version 1.1.442). For variables measured on monthly intervals (stem counts, and average stem height), a regression framework was used to analyze the effects of time, block, and each treatment (tidal hydrology-low nitrate (TLN), tidal hydrology-high nitrate (THN), diversion hydrology-low nitrate (DLN), and diversion hydrology-high nitrate (DHN). The interaction between treatment and the time factor was examined for each response variable, however, insufficient degrees of freedom prohibited examination of all time factors by treatment interactions, so individual treatments were graphed over time to examine differences between treatments. Model selection was carried out using AICc values (due to small sample size) and single deletion of non-significant terms. Data that were heteroscedastic in nature were log transformed prior to regression analysis. Because of zero dead stems values for *P. hemitomon* and *S. patens*, a constant of one was added to all values to allow for log transformation. An additional sum of squares test was utilized to determine if omitted terms from sub-models were significantly different than zero. Post-hoc analysis was conducted using the multcomp package (Version 1.4-8) in R and Tukey HSD test of pairwise comparisons were used to determine significant differences between means (Hothron et al. 2008). Monthly soil redox potential measurements at 1 cm and 10 cm were analyzed using an analysis of variance (ANOVA) framework to test for a discrete effect of time (month). Month, hydrology treatment, nitrogen treatment, elevation, and all two-way interactions were analyzed as categorical variables within each species separately due to limited degrees of freedom. Three- and four-way interactions could not be conducted due to lack of statistical power and limited replication. If two-way interactions were found to be insignificant, the interaction was removed from the model.

All variables measured at harvest (aboveground and belowground biomass, soil shear strength, SOM, TN, TC, bulk density, and soil moisture) were analyzed using an ANOVA framework with treatment type (TLN, THN, DLN, DHN) as our independent variable. Post-hoc analysis using Tukey HSD test of pairwise comparisons to determine significant differences between means were utilized. Data were analyzed for normality and homogeneity of variance prior to all analyses.

Results

Plant metrics

The number of live stems in *P. hemitomon*, *S. lancifolia*, and *S. patens* (healthy marsh elevation) showed a statistically non-linear relationship with respect to time across all hydrology and nutrient treatments, whereas *S. patens* (degraded marsh elevation) showed a stable linear relationship with respect to time, as the number of live stems remained consistent throughout the duration of the study (Fig. 2, Tables S1–S6). There was not a significant effect of treatment on above- or belowground biomass (Tables S7–S9), or the number of live stems for any species, except for *S. patens* at degraded marsh elevations (Fig. 2, Tables S3 and S6). Degraded marsh *S. patens* subjected to the DHN treatment had significantly fewer live stems throughout the study compared to the live stem number in the TLN treatment (Fig. 2, Table S6). The number of dead stems of *P. hemitomon* and *S. lancifolia* did not vary between treatments (Fig. 3, Tables S1 and S2). However, *S. patens* in the TLN treatment had a higher number of dead stems compared to the DHN treatment at degraded marsh surface elevations (Fig. 3, Tables S3 and S6). All species increased in the number of dead stems over time as would be expected with normal seasonal growth (Fig. 3, Tables S1–S3). Although species were analyzed separately due to limited degrees of freedom, it should be noted that the

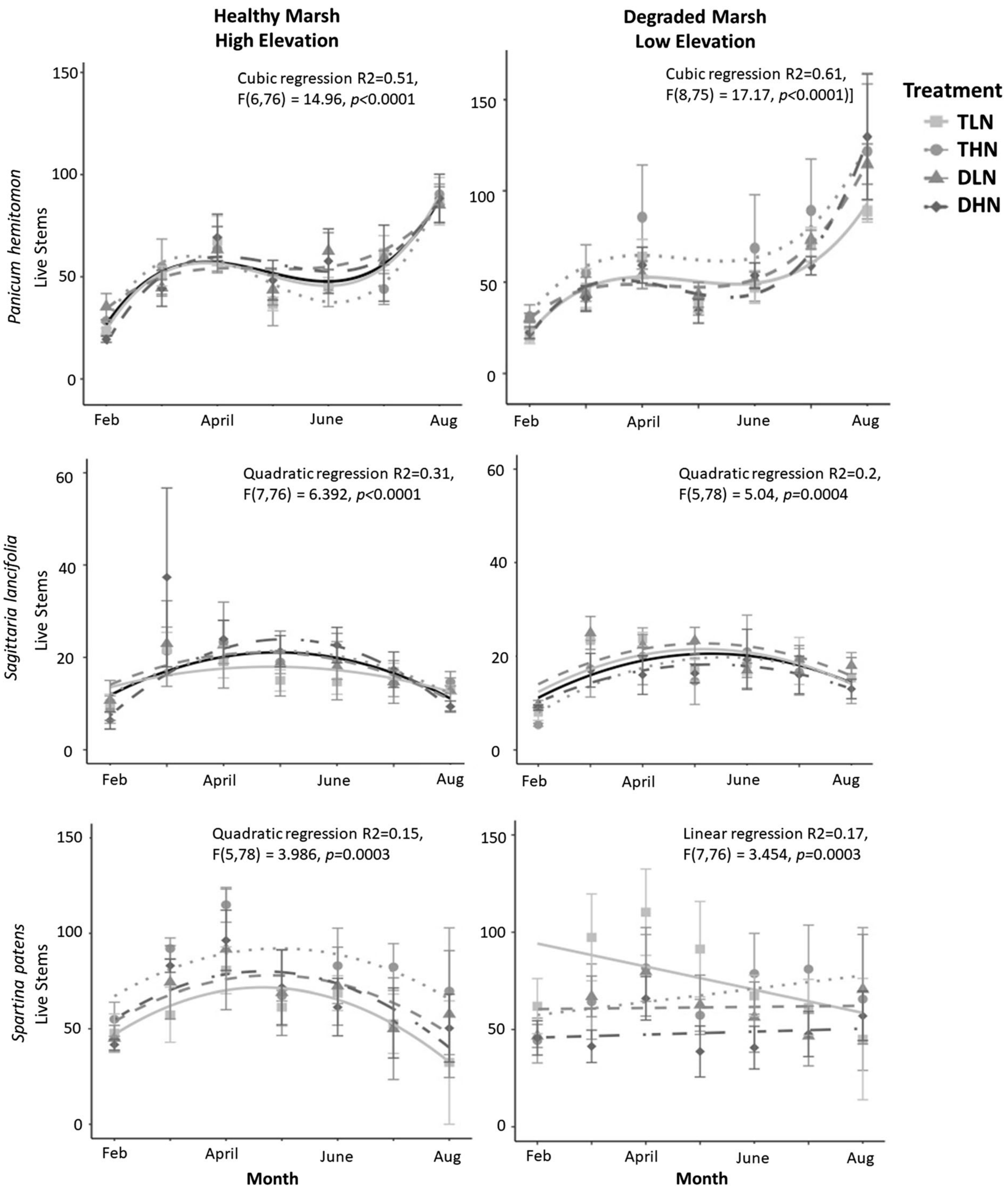

Fig. 2 Relationship between time and number of live stems for *P. hemitomon, S. lancifolia,* and *S. patens* at Healthy Marsh soil surface elevation (left column), and Degraded Marsh soil surface elevation (right column). Treatments are as follows: TLN (tidal hydrology-low nitrate), THN (tidal hydrology-high nitrate), DLN (diversion hydrology-low nitrate), DHN (diversion hydrology-high nitrate). Diversion treatments were implemented for 4 weeks starting on Feb 27 and April 22, 2017. Solid black line represents mean of all treatments. Points represent the mean (± standard error) for all treatments and regression statistics provided are for the overall regression model

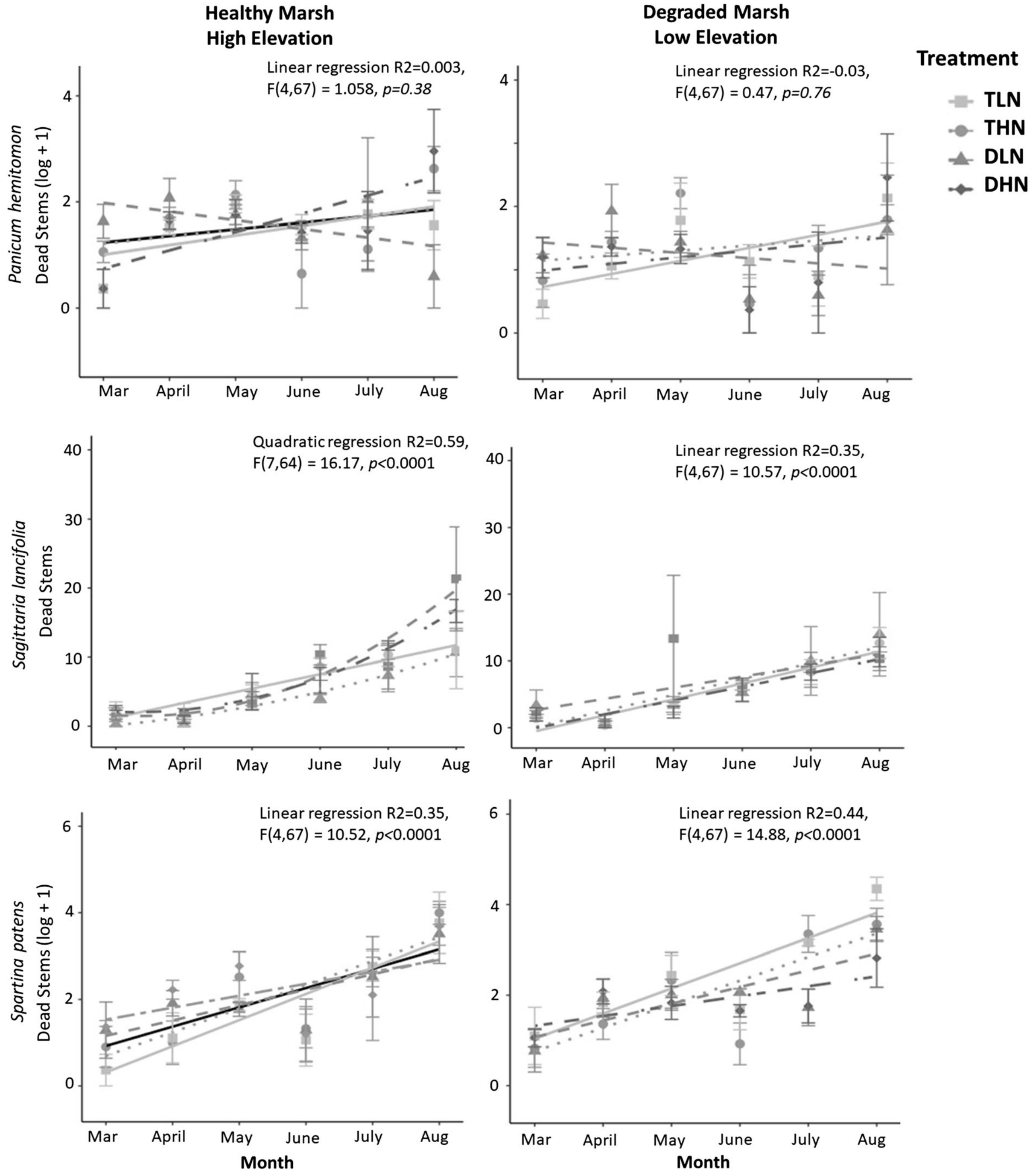

Fig. 3 Relationship between time and the number of dead stems for *P. hemitomon, S. lancifolia,* and *S. patens* at Healthy Marsh soil surface elevations (left column), and Degraded Marsh soil surface elevation (right column). Treatments are as follows: TLN (tidal hydrology-low nitrate), THN (tidal hydrology-high nitrate), DLN (diversion hydrology-low nitrate), DHN (diversion hydrology-high nitrate). Diversion treatments were implemented for 4 weeks starting on Feb 27 and April 22, 2017. Solid black line represents mean of all treatments. Points represent the mean (± standard error) for all treatments and regression statistics provided are for the overall regression model

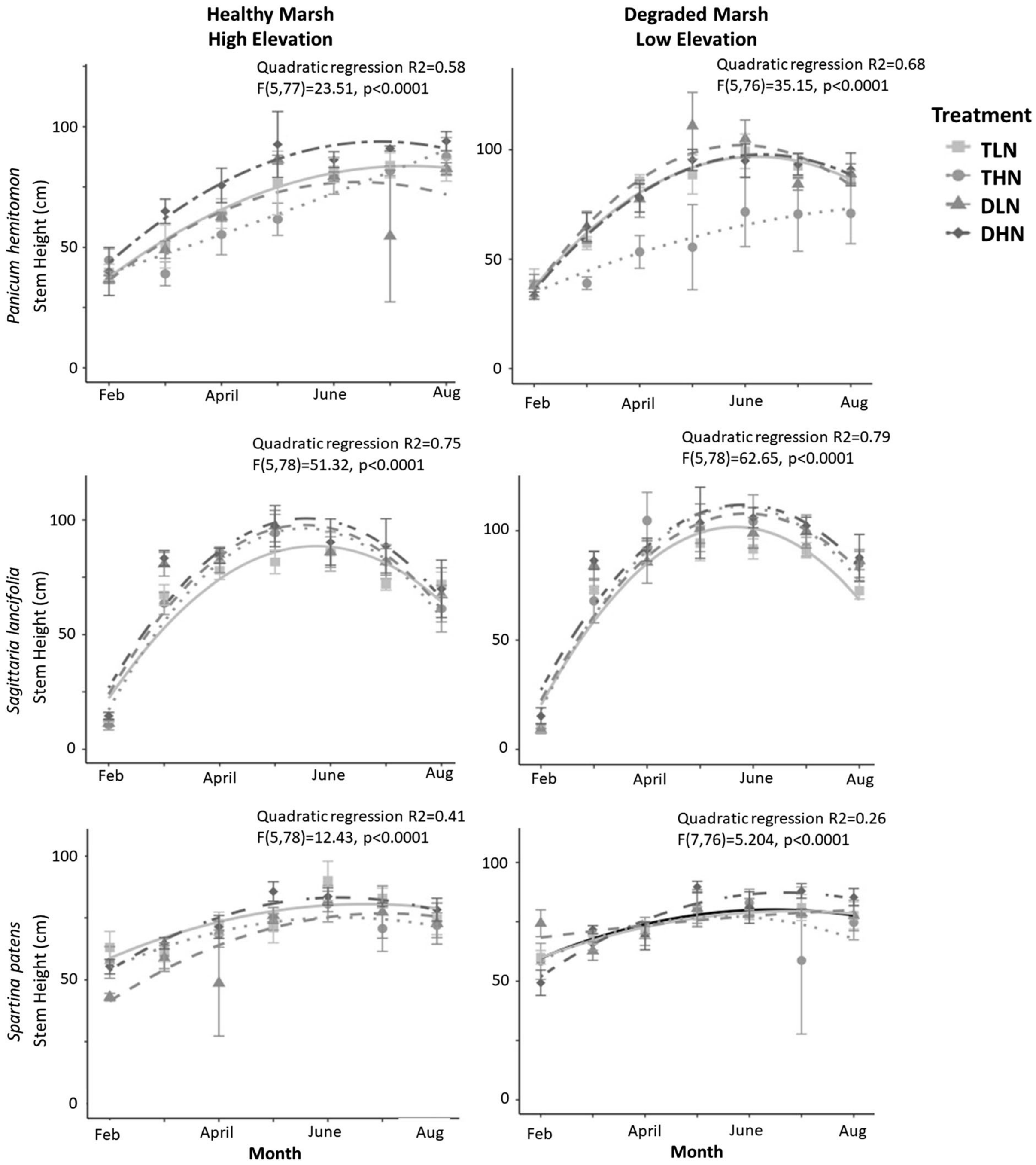

Fig. 4 Relationship between time and average stem height for *P. hemitomon, S. lancifolia, and S. patens at* Healthy - Marsh soil surface elevations (left column), and Degraded Marsh soil surface elevation (right column). Treatments are as follows: TLN (tidal hydrology-low nitrate), THN (tidal hydrology-high nitrate), DLN (diversion hydrology-low nitrate), DHN (diversion hydrology-high nitrate). Diversion treatments were implemented for 4 weeks starting on Feb 27 and April 22, 2017. Solid black line represents mean of all treatments. Points represent the mean (± standard error) for all treatments and regression statistics provided are for the overall regression model

number of both live and dead stems varied greatly between species.

The stem height of *P. hemitomon* at healthy marsh surface elevation in the DHN treatment was greater compared to the THN or DLN treatments (Fig. 4, Tables S1, S4). *Panicum hemitomon* at degraded marsh elevation units subjected to the THN exhibited a slower rate of increase in stem height, when compared to the DLN treatment (Fig. 4, Tables S1, S4). All species showed non-linear changes in average stem height with respect to time (Fig. 4, Tables S1–S6). Analyses of plant tissue chemistry did not show statistically significant results (Tables S10–S11) between treatments except for *S. patens* units growing at the degraded marsh elevation, in which leaf tissue TN of the DHN units was significantly greater than other TLN or THN units (Table 1).

Soil physico-chemical parameters

Soil redox potential measured at 1 cm and 10 cm depths showed significant effects of hydrology, month, and elevation, though differences varied by species, which were analyzed individually (Tables 2, 3). The effect of nitrogen on soil redox was not significant. Soil redox potential measured at 1 cm depth (Table 2) in *P. hemitomon* units showed a significant interaction between hydrology and month [$F_{(6,152)} = 2.668$, $p = 0.017$] as well as elevation [$F_{(1,152)} = 14.37$, $p = 0.0002$] as redox was significantly lower in units placed at the degraded marsh elevation and redox levels fell in response to diversion treatments. Within the *S. lancifolia* units, soil redox at 1 cm was significantly lower in units exposed to diversion hydrology [$F_{(1,158)} = 9.791$, $p = 0.00209$], during the month of diversion treatment [$F_{(6,158)} = 3.897$, $p = 0.00117$], and was lower at degraded marsh elevations [$F_{(1,158)} = 6.225$, $p = 0.01362$]. Soil redox measured at 1 cm depth in *S. patens* units was also lower in units placed at degraded marsh elevation [$F_{(1,152)} = 10.813$, $p = 0.00125$] and a significant interaction between hydrology and month [$F_{(6,152)} = 2.906$, $p = 0.0103$] indicated soil redox rose and fell with the diversion treatments.

Soil redox potential at 10 cm depth displayed similar trends across species in response to hydrology, elevation, and time (Table 3). Soil redox values in *P. hemitomon* units showed a significant interaction between hydrology and elevation [$F_{(1,157)} = 5.86$, $p = 0.0166$] as values were lower in units exposed to the diversion treatment and were consistently low in degraded marsh elevations. Additionally, redox levels were lower in months that followed the diversion treatment [$F_{(1,157)} = 6.558$, $p < 0.0001$]. Soil redox at 10 cm in *S. lancifolia* units was lower at degraded marsh elevation [$F_{(1,158)} = 4.269$, $p = 0.0405$] and decreased after a month of diversion treatment followed by an increased after the recovery [$F_{(6,158)} = 5.534$, $p < 0.0001$]. Similarly, *S. patens* units showed a significant interaction between hydrology and month [$F_{(1,152)} = 2.263$, $p = 0.0403$], and elevation [$F_{(1,152)} = 29.392$, $p < 0.0001$]. Soil redox values were lower following diversion treatments and

Table 1 Leaf and stem total nitrogen and total carbon analysis for *Spartina patens*

	Treatment	TN %	TC %
S. patens (healthy marsh)	TLN	0.7 ± 0.00^{A}	45.3 ± 0.00^{A}
	THN	0.7 ± 0.06^{A}	45.0 ± 0.8^{A}
	DLN	0.8 ± 0.02^{A}	45.4 ± 0.8^{A}
	DHN	0.7 ± 0.11^{A}	44.1 ± 0.7^{A}
S. patens (degraded)	TLN	0.7 ± 0.03^{B}	45.3 ± 0.5^{A}
	THN	0.6 ± 0.01^{B}	46.0 ± 0.2^{A}
	DLN	0.8 ± 0.05^{AB}	45.2 ± 0.6^{A}
	DHN	0.9 ± 0.04^{A}	45.1 ± 0.5^{A}

Total nitrogen (TN %) and Total Carbon (TC %). Treatments are as follows: *TLN* tidal hydrology-low nitrate, *THN* tidal hydrology-high nitrate, *DLN* diversion hydrology-low nitrate, *DHN* diversion hydrology-high nitrate. Different letters indicate significant differences, within species-elevation ($p < 0.05$). Values represent the mean ± standard error

Table 2 Soil redox potential (mV) measured at 1 cm depth (mean ± se) for all units

		24 Feb.	24 March	21 April	25 May	23 June	19 July	23 Aug.
Normal hydrology	*Panicum hemitomon* (healthy)	$369 \pm 37_{a}$	$225 \pm 59_{a}$	$348 \pm 61_{a}$	$256 \pm 20_{b}$	$304 \pm 31_{a}$	$281 \pm 37_{a}$	$343 \pm 69_{a}$
	Panicum hemitomon (degraded)	$223 \pm 32_{a}$	$201 \pm 61_{a}$	$222 \pm 32_{a}$	$193 \pm 25_{a}$	$222 \pm 38_{a}$	$225 \pm 58_{a}$	$206 \pm 36_{a}$
Diversion hydrology	*Panicum hemitomon* (healthy)	$331 \pm 36_{a}$	$189 \pm 70_{b}$	$364 \pm 52_{a}$	$89 \pm 28_{c}$	$359 \pm 30_{a}$	$229 \pm 33_{a}$	$321 \pm 37_{a}$
	Panicum hemitomon (degraded)	$348 \pm 36_{a}$	$70 \pm 17_{c}$	$333 \pm 69_{a}$	$140 \pm 51_{b}$	$311 \pm 20_{a}$	$179 \pm 31_{a}$	$239 \pm 60_{a}$
Normal hydrology	*Sagittaria lancifolia* (healthy)	438 ± 45	316 ± 41	359 ± 86	331 ± 36	216 ± 33	248 ± 52	272 ± 27
	Sagittaria lancifolia (degraded)	273 ± 48	277 ± 20	258 ± 66	306 ± 54	230 ± 15	223 ± 28	371 ± 48
Diversion hydrology	*Sagittaria lancifolia* (healthy)	359 ± 47	234 ± 38	318 ± 30	204 ± 23	220 ± 37	232 ± 39	295 ± 23
	Sagittaria lancifolia (degraded)	266 ± 35	187 ± 63	275 ± 31	$109 _{=} 35$	234 ± 57	190 ± 37	257 ± 36
Normal hydrology	*Spartina patens* (healthy)	$361 \pm 51_{a}$	$327 \pm 44_{a}$	$315 \pm 35_{a}$	$207 \pm 22_{c}$	$289 \pm 53_{a}$	$228 \pm 34_{bc}$	$292 \pm 58_{a}$
	Spartina patens (degraded)	$287 \pm 51_{a}$	$266 \pm 53_{a}$	$298 \pm 79_{a}$	$102 \pm 35_{c}$	$257 \pm 63_{a}$	$135 \pm 33_{bc}$	$222 \pm 75_{a}$
Diversion hydrology	*Spartina patens* (healthy)	$362 \pm 35_{a}$	$90 \pm 41_{c}$	$276 \pm 33_{ac}$	$110 \pm 51_{bc}$	$310 \pm 57_{a}$	$242 \pm 16_{ac}$	$253 \pm 58_{ac}$
	Spartina patens (degraded)	$341 \pm 81_{a}$	$95 \pm 27_{c}$	$229 \pm 65_{ac}$	$-4 \pm 10_{bc}$	$214 \pm 43_{a}$	$160 \pm 31_{ac}$	$227 \pm 42_{ac}$

Redox measurements were obtained monthly. Differing subscript letters indicate significant differences for the interaction between month and hydrology. Diversion treatments were implemented for 4 weeks starting on Feb 27 and April 22, 2017

Table 3 Soil redox potential (mV) measured at 10 cm depth (mean ± SE) for all units

		24 Feb.	24 March	21 April	25 May	23 June	19 July	23 Aug.
Normal hydrology	*Panicum hemitomon* (healthy)	$343 \pm 34_{a}$	$300 \pm 22_{a}$	$279 \pm 57_{a}$	$283 \pm 52_{a}$	$214 \pm 32_{a}$	$238 \pm 20_{a}$	$304 \pm 32_{a}$
	Panicum hemitomon (degraded)	$301 \pm 41_{b}$	$115 \pm 56_{b}$	$190 \pm 45_{b}$	$167 \pm 22_{b}$	$220 \pm 45_{b}$	$131 \pm 59_{b}$	$243 \pm 64_{b}$
Diversion hydrology	*Panicum hemitomon* (healthy)	$305 \pm 34_{ab}$	$167 \pm 32_{ab}$	$301 \pm 41_{ab}$	$119 \pm 43_{ab}$	$229 \pm 33_{ab}$	$239 \pm 33_{ab}$	$242 \pm 27_{ab}$
	Panicum hemitomon (degraded)	$300 \pm 83_{ab}$	$178 \pm 46_{ab}$	$254 \pm 67_{ab}$	$107 \pm 39_{ab}$	$269 \pm 51_{ab}$	$189 \pm 40_{ab}$	$288 \pm 10_{ab}$
Normal hydrology	*Sagittaria lancifolia* (healthy)	379 ± 44	273 ± 39	288 ± 18	187 ± 24	281 ± 41	235 ± 28	269 ± 33
	Sagittaria lancifolia (degraded)	249 ± 54	207 ± 70	303 ± 61	215 ± 45	206 ± 52	211 ± 33	296 ± 20
Diversion hydrology	*Sagittaria lancifolia* (healthy)	257 ± 66	176 ± 57	353 ± 50	170 ± 34	258 ± 38	259 ± 40	310 ± 36
	Sagittaria lancifolia (degraded)	270 ± 23	100 ± 14	270 ± 40	161 ± 27	262 ± 46	221 ± 27	273 ± 22
Normal hydrology	*Spartina patens* (healthy)	$385 \pm 39_{a}$	$317 \pm 28_{a}$	$293 \pm 55_{ab}$	$258 \pm 41_{ab}$	$269 \pm 53_{ab}$	$200 \pm 77_{c}$	$258 \pm 48_{ab}$
	Spartina patens (degraded)	$167 \pm 96_{a}$	$239 \pm 44_{a}$	$169 \pm 45_{ab}$	$106 \pm 29_{ab}$	$174 \pm 39_{ab}$	$106 \pm 22_{c}$	$156 \pm 47_{ab}$
Diversion hydrology	*Spartina patens* (healthy)	$305 \pm 55_{a}$	$170 \pm 68_{b}$	$342 \pm 74_{a}$	$91 \pm 50_{b}$	$300 \pm 70_{ab}$	$221 \pm 28_{ab}$	$306 \pm 35_{ab}$
	Spartina patens (degraded)	$221 \pm 69_{a}$	$99 \pm 40_{b}$	$227 \pm 45_{a}$	$80 \pm 29_{b}$	$196 \pm 43_{ab}$	$130 \pm 40_{ab}$	$197 \pm 52_{ab}$

Redox measurements were obtained monthly. Differing subscript letters indicate significant differences for the interaction between hydrology and elevation in *P. hemitomon* and month and hydrology in *S. patens*. Diversion treatments were implemented for 4 weeks starting on Feb 27 and April 22, 2017 consistently lower in units placed at the degraded marsh elevation. Other soil metrics measured (shear strength, bulk density, percent soil moisture, soil organic matter, total nitrogen, and total carbon) displayed no differences between treatment types regardless of species or elevation treatment (Table S12).

Discussion

Short term changes to hydroperiods, nutrient availability, and freshwater availability may not adversely affect growth or productivity in one growing season, but forced perturbations that occur on an annual schedule could have negative impacts on the long-term sustainability of the ecosystem. Results from empirical studies that evaluate soil and plant response to increased flooding duration and nutrient enrichment are key to accurately predicting outcomes of proposed river sediment diversions in Louisiana. Our manipulative mesocosm experiment helps to fill a critical data gap by demonstrating, at a small scale, the potential effects of large-scale ecosystem modifications.

In the majority of our experimental units, soil redox potential exhibited sharp declines following the onset of the diversion flooding cycles, which increased immediately after hydrology was returned to normal. Low oxygen conditions are characterized by Eh values ranging between + 400 and − 300 mV (Pezeshki and DeLaune 2012). Studies have demonstrated that reduction in plant biomass was concurrent with a reduction in redox potential over time (less than 200 mV) (Spalding and Hester 2007, Visser and Sandy 2009). In our study, redox levels averaged 250 mV, with some values dipping lower (− 19 mV) and some peaking higher (474 mv).

We hypothesize that the lack of observed statistical differences between our treatments over time for several response measures was due to the lack of statistical power in this experimental design. Because of limited greenhouse space, low treatment replication may have reduced the ability to detect response differences. Also, it is important to note that in our study, soil redox potential measured before the start of the study and at harvest were not significantly different. Our observations indicate that soil conditions are capable of recovering when exposed to brief periods of flooding (4 weeks) followed by a recovery period. Managers of river diversion projects would benefit from additional studies to observe the effects of a longer flooding press event.

Within *P. hemitomon*, stem height differed between healthy and degraded marsh surface elevations. *Panicum hemitomon* at healthy marsh surface elevations had increased stem growth under the diversion hydrology-high nitrate treatment, whereas degraded marsh surface elevation units experiencing normal tidal hydrology with increased nitrate had a decreased rate of stem growth. Rapid stem elongation may be evidence of etiolation (Blom and Voesenek 1996), a physiological stress response of the plant to flooded or shaded conditions. Differences in average stem height did not translate to differences in biomass, therefore not impacting important services of the marsh like nutrient assimilation. However, etiolated stems may be weaker, making the marsh more susceptible to wind and wave forces (Sloey et al. 2016).” Our findings suggest that *P. hemitomon* stem height may increase in response to heightened flooding levels, similar to previous reports by Kirkman and Sharitz (1993) and Mayence and Hester (2010). *Sagittaria lancifolia* growth, however, was not influenced by flooding duration in our study, similar to findings by Visser and Sandy (2009). Previous studies have found a variety of responses of *S. patens* to flooding, including no response (Visser and Peterson 2015) and increased growth (Broome et al. 1995). Our study, however, found reduced live stem production in units exposed to the diversion hydrology-high nitrate treatment.

Despite differences in growth responses within species, we found no significant differences between aboveground or belowground biomass for any species in response to treatments. Our findings differ from other studies that have investigated the effects of flooding or nitrate additions on a variety of marsh macrophytes (Kirkman and Sharitz 1993; Spalding and Hester 2007; Visser and Sandy 2009; Visser and Peterson 2015). Many studies that have addressed the effect of flooding on *P. hemitomon, S. lancifolia,* and *S. patens* documented changes in biomass in response to flooding, both positive (McKee and Mendelssohn 1989; Kirkman and Sharitz 1993; Willis and Hester 2004; Visser and Peterson 2015) and negative (Howard and Mendelssohn 1995; Spalding and Hester 2007; Visser and Sandy 2009; Visser and Peterson 2015). Studies on the effects of nitrate amendments on marshes remain inconsistent in their findings. Existing studies range from one-time fertilization applications (nitrogen in combination with phosphorus) on the marsh surface, to bi-weekly fertilizer application, to multi-year nitrate addition into natural marshes (Valiela et al. 1976; Darby and Turner 2008b; Deegan et al. 2012). These studies have found aboveground biomass increases with fertilization, but belowground biomass typically decreases (Valiela et al. 1975, 1976; Darby and Turner 2008b Deegan et al. 2012). In fertilization studies that encompassed an entire growing season, treatments generally lasted the full season with fertilization occurring every other week (Valiela et al. 1976) or occurred over multiple years (Deegan et al. 2012). Our study, however, found no significant influence of hydrology or nitrate amendment on biomass production.

Our results indicating that relatively short pulse events have little impact on plant growth are consistent with Visser and Peterson's (2015) findings that both aboveground and belowground biomass for *P. hemitomon* and *S. patens* was not affected by flood duration, when flooded for short durations (daily, weekly, or monthly). However, the majority of studies that have addressed the effects of long-term flooding on these common marsh plant species do find significant impacts (McKee and Mendelssohn 1989; Howard and Mendelssohn 1995). Spalding and Hester (2007) found that *S. lancifolia* and *S. patens* growing in ambient conditions exhibited greater biomass production when compared to flooded counterparts. Many other studies have observed decreases in both aboveground and belowground biomass with increased flooding duration (Visser and Sandy 2009; Visser and Peterson 2015).

Although our 7-month study did not indicate significant effects of our treatments, results may differ after cumulative effects from multiple years of repeated pulse events. Long term exposure to stressors associated with diversions may have detrimental effects on Louisiana's marshes, making them more vulnerable to disturbances and exacerbating the conversion rates of marsh to open water (Casanova and Brock 2000; Holm 2006; Slocum and Mendelssohn 2008; Meert and Hester 2009; Snedden et al. 2015). Additionally the nature of our mesocosm study only allowed for observation of soil and root dynamics to ~ 30 cm depth, and impacts of these influences on the marsh may extend deeper. There remains a need for additional empirical studies that can closely simulate conditions associated with river sediment diversions to gain a better understanding of ecosystem response to such a large-scale change. Future research on this topic should be encouraged to build on our initial research through the following: (1) adjusting the duration of flooding/nutrient pulses and subsequent recovery time, (2) experimenting with more combinations of nutrients at various concentrations (e.g., N, P, K, etc.), and (3) continuing the study for a longer time period. Whenever possible, more replication and larger mesocosms would help improve the scalability and transferability of this research to inform wetland restoration or management projects that involve introduction of nutrient-laden freshwater. Understanding marsh response to long-term and short-term changes in abiotic conditions through controlled mesocosm experiments can be informative for a variety of ecosystems and restoration applications, but it is important to anticipate that results may differ in situ.

Conclusion

The coast of Louisiana is in dire need of restoration techniques that can restore a range of deltaic freshwater and brackish coastal marshes to preserve ecosystem functions. These coastal marshes require freshwater input to support healthy and resilient plant communities that can contribute to soil accretion through organic matter production, thereby helping to offset the stressors associated with rising sea levels. The detrimental effects of long-term flooding and nutrient additions on plant growth may be reduced with shorter flooding cycles during diversion operations. River diversions may be important tools for the restoration of Louisiana's marshes, but there is a need to further investigate if shorter flood durations with recovery or "drawdown" periods between cycles could be a viable method to mitigate the detrimental effects of long-term flooding and excess nutrients along with aiding recovery of degraded marshes.

Ultimately, the response of marshes to inputs from river diversions will depend on the operation parameters of the diversion and the species composition of the marsh communities in the diversion outfall area. Understanding marsh vegetation response to these stressors is key to projecting the success of using river diversions to mitigate land loss. Our study provides insight into ecosystem response to brief diversion pulses; however, many uncertainties remain that warrant additional research, particularly regarding marsh response to longer durations of diversion treatments and response of other common marsh species.

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