Inundation and salinity impacts to above- and belowground productivity in *Spartina patens* and *Spartina alterniflora* in the Mississippi River deltaic plain: Implications for using river diversions as restoration tools

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ABSTRACT

Inundation and salinity directly affect plant productivity and processes that regulate vertical accretion in coastal wetlands, and are expected to increase as sea level continues to rise. In the Mississippi River deltaic plain, river diversions, which are being implemented as ecosystem restoration tools, can also strongly increase inundation in coastal wetlands. We used an in situ mesocosm approach to examine how varying salinity (two levels) and inundation rates (six levels) influenced end-of-season above- and belowground biomass of *Spartina patens* and *Spartina alterniflora* during the growing season (March–October) in 2011. Above- and belowground biomass was highest in both species at higher elevations when inundation was minimal, and decreased exponentially with decreased elevation and increased flood duration. This negative biomass response to flooding was more pronounced in *S. patens* than in *S. alterniflora*, and *S. patens* also showed stronger biomass reductions at higher salinities. This salinity effect was absent for belowground biomass in *S. alterniflora*. These findings suggest that even subtle increases in sea level may lead to substantial reductions in productivity and organic accretion, and also illustrate the importance of considering the inundation tolerance of co-dominant species in receiving areas when utilizing river diversions for delta restoration.

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1. Introduction

Eustatic sea-level rise (ESLR; $3 \, \mathrm{mm \, yr^{-1}}$; IPCC, 2007; Ablain et al., 2009) is a critical problem in coastal regions today. This crisis is exacerbated in subsiding deltas where subsidence contributes to relative sea-level rise (RSLR) rates that far exceed ESLR alone. Vertical accretion, the mechanism by which coastal wetlands maintain their vertical position in the tidal frame despite high RSLR rates, can occur either through mineral sediment deposition or organic matter accumulation (Morris et al., 2002). Though the relative importance of these processes varies with hydrogeomorphic setting, both are strongly regulated by the quantity of wetland vegetation present and the rate at which it is produced. Deposition in vegetated settings is largely governed by reductions in flow turbulence and wave dampening by plant stems (Leonard and Luther, 1995; Christiansen et al., 2000; Neumeier and Ciavola, 2004), whereas organic matter accumulation primarily results from the balance between root growth and decomposition (McCaffrey and Thompson, 1980).

Primary productivity of emergent wetland vegetation can be impaired by excessive inundation and salinity regimes (Mendelssohn and McKee, 1988; McKee and Mendelssohn, 1989), which can lead to decreased trapping efficiency aboveground (Leonard and Croft, 2006) and diminished organic matter accumulation belowground (Nyman et al., 1993), ultimately increasing submergence and further diminishing productivity. Unabated, this cycle can lead to peat collapse, erosion, and eventually convert wetland landscapes to open water (DeLaune et al., 1994).

In the Mississippi River deltaic plain, RSLR rates as high as $10 \, \mathrm{mm \, yr^{-1}}$ are not uncommon (Coleman et al., 1998). The fluvial sediment supply that once created and maintained this region has been essentially eliminated for nearly a century due to the construction of containment levees along the river's banks. Additionally, numerous pipeline canals now exist on the deltaic plain and have increased flooding depth and duration of the surrounding marsh due to impoundment associated with dredge spoil placement along canal banks. Canals have also increased marsh salinities by providing conduits for enhanced estuary–ocean

exchange (Turner, 1997). Together, these circumstances have contributed to the loss of nearly 5000 km² of coastal wetlands since 1932 (Couvillion et al., 2011), with over 50% of that loss directly attributed to submergence and increased flooding (Penland et al., 2001).

As part of a comprehensive restoration plan for a sustainable coast (State of Louisiana, 2012), a series of Mississippi River diversions are being implemented to stimulate delta growth through increased sediment supply to coastal wetlands. The effect of existing diversions on the deltaic landscape over the last two decades has been disputed. Some studies have shown diversions to stimulate mineral sediment accretion (DeLaune et al., 2003; Wheelock, 2003) and above- and belowground productivity in emergent vegetation (Day et al., 2013; DeLaune et al., 2013) as a result of increased sediment and nutrient inputs. However these findings are confounded by the devastation brought about by hurricane Katrina in 2005, in which over 100 km² of wetlands were converted to open water in upper Breton Sound (Barras, 2006). This region is the receiving basin of the Caernarvon freshwater diversion, a diversion that has been operational for over 20 years primarily for the purpose of maintaining optimal salinity regimes in Breton Sound for commercial shellfish production and landings (U.S. Army Corps of Engineers, 1984). Other areas much further away from the Caernarvon diversion, but still in the storm's direct path, were much more resilient to storm impacts (Barras, 2006). A variety of mechanisms linking this land loss to river diversions have been put forth, including excessive nutrient loading (Kearney et al., 2011), salinity reduction (Howes et al., 2010), and sulfur accumulation in wetland soils (Swarzenski et al., 2008).

In addition to delivering large quantities of sediment and nutrients, river diversions can also result in elevated water levels and prolonged inundation of marshes (Snedden et al., 2007a,b). Thus, whereas diversions may provide much needed mineral sediments for sustaining deltas, these subsidies may come at the expense of vegetation productivity and actually increase submergence brought about by sea-level rise if diversions induce flooding regimes that exceed physiological tolerances of co-dominant plant species in their receiving basins. A clearer understanding of how wetland plants respond to increased hydroperiod is vital not only for forecasting impacts of sea level rise to coastal wetlands, but also for successfully using river diversions to restore deltas.

We examined how variations in inundation duration influence end-of-season above- and belowground biomass in *S. patens* and *S. alterniflora*, two common marsh vegetation species of the Mississippi River deltaic plain. We conducted a mesocosm experiment in the field to simulate flooding regimes at six different marsh elevations and to allow for natural variations in salinity and sea level, driven by a combination of lunar tides and meteorological events. Our objective was to generate above- and belowground biomass response curves for the two species as a function of inundation duration. We also explored how salinity variation may modify the inundation responses of the two species.

2. Materials and methods

Two sites in the Breton Sound estuary were selected for the study (Fig. 1). One situated in middle Breton Sound (MBS; 29.69°N, 89.76°W), is dominated by *S. patens*; whereas the other, in lower Breton Sound (LBS; 29.66°N, 89.60°W), is dominated by *S. alterniflora*. Mean salinity at LBS exceeded that at MBS during the study, though mean water levels at the two sites were similar (Table 1). Water levels at both sites are strongly meteorologically-driven, and the lunar tide only accounts for around 20% and 50% of total water level variance at MBS and LBS, respectively. The Caernarvon freshwater diversion is situated at the head of basin (Fig. 1). While it is capable of discharging Mississippi River water to
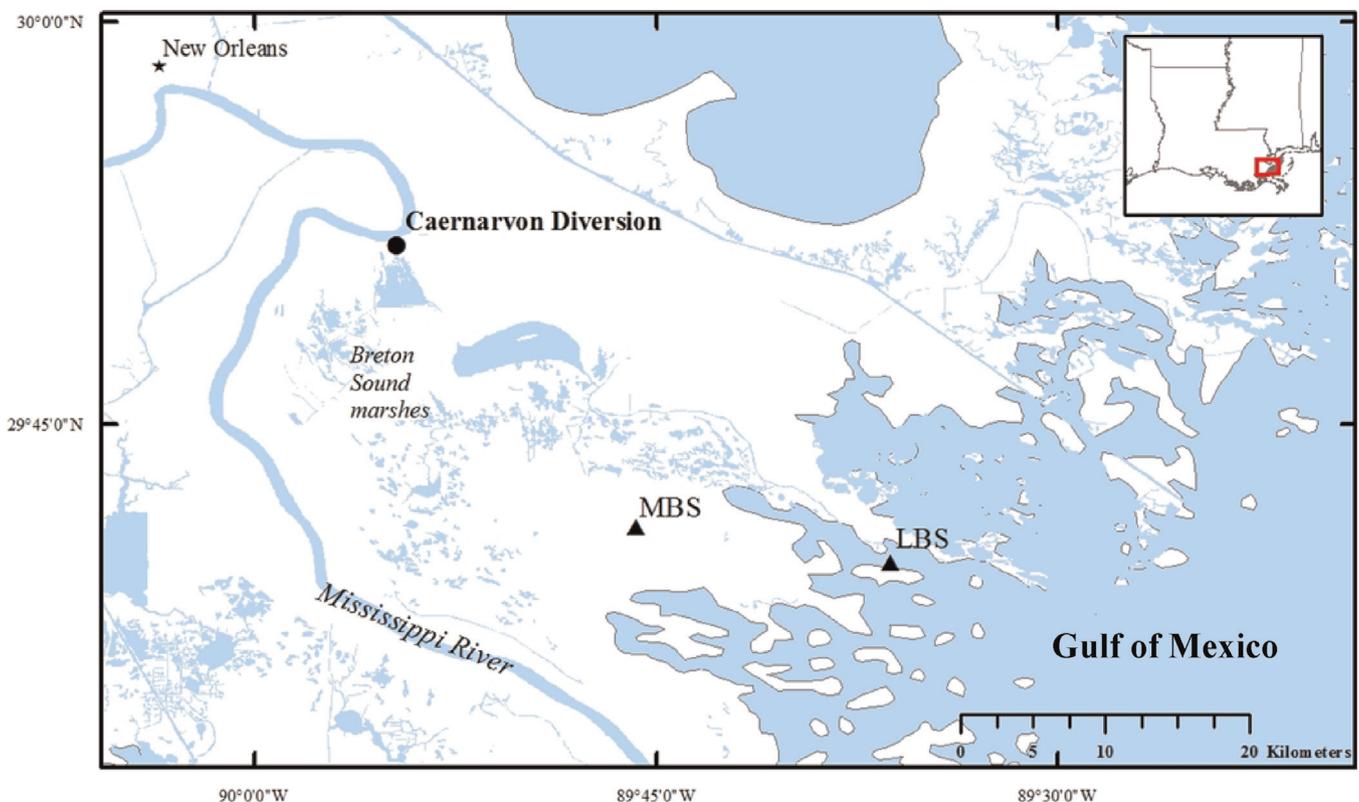
Fig. 1. The location of the Breton Sound estuary, including the middle Breton Sound (MBS) and lower (LBS) Breton Sound sites where marsh organs were deployed, and the Caernarvon freshwater diversion.

Table 1
Hydrographic characteristics of middle Breton Sound (MBS) and lower Breton Sound (LBS) sites.

Site	Mean salinity (psu), ±S.D.	Mean water level (cm NAVD)	Mean high water (cm NAVD)	Local marsh elevation (cm NAVD)
MBS	3.9 ± 2.0	24.9	36.2	24.4
LBS	8.0 ± 2.3	23.4	44.3	26.2

the basin at a rate of $225\,\mathrm{m^3\,s^{-1}}$, MBS and LBS are situated outside the region where the diversion exerts a detectable influence on estuarine water levels (Snedden et al., 2007b).

We constructed four marsh organs (Morris, 2007) to simulate six different flooding regimes. The marsh organs were constructed by fastening together 36 15.2-cm diameter pipes. Each marsh organ consisted of six rows with six pipes in each row. The tops of all six pipes within each row were situated at identical elevations, and the elevations of each row were selected to achieve inundation rates of 90%, 70%, 55%, 45%, 30%, and 10% based on exceedance curves generated from hourly water-level data from the previous growing season (March–October, 2010). Thus, rows with higher elevations experienced less severe inundation regimes than those situated lower. These inundation rates were selected as they span the observed inundation rates for communities dominated by *S. patens* (4.3–100%) and *S. alterniflora* (29–72%; Snedden and Steyer, 2013) across coastal Louisiana.

A pair of marsh organs was deployed in a ponded area at each of the two sites in March, 2011. Each marsh organ was situated such that the tallest pipes were farthest north to minimize shading effects. Bottoms of the pipes were submerged 5–10 cm into the pond bottom and each pipe was filled to the top with sediment from the pond. At each site, all pipes of one marsh organ were planted with locally-harvested, intact sod plugs containing 10 stems of *S. patens*, whereas the second marsh organ was planted with plugs containing three stems of *S. alterniflora*. Marsh organs were visited approximately monthly to re-assess sediment surface elevation in each pipe, as some settling of sediment occurred in the pipes over time (the majority of which occurred during the first month of the study). When settling was observed, holes were drilled in the pipes between the pipe edge and the sediment surface to facilitate drainage. Sediment surface elevations were assumed to settle linearly through time between subsequent monthly surveys. Hourly water level and salinity data were recorded at each site during the field experiment with pressure transducers surveyed to the same elevation datum as the marsh organs, and percent time inundated was calculated for all pipe rows in each marsh organ, taking into account settling described above. By performing the experiment on each plant species at two sites that differed in mean salinity (3.9 psu at MBS; 8.0 psu at LBS), we were able to explore how salinity may also act to control productivity in the two species.

In October 2011, sods were removed from each pipe. Stems were clipped at the soil surface of each sod and stored at 4 °C until processing. Processing aboveground biomass consisted of drying live stems at 60 °C to a constant weight (usually 24 h), and

belowground biomass was processed by washing all roots and rhizomes of all sediment over a 2 mm screen, followed by drying roots at 60 °C to constant weight. After drying, all samples were weighed.

We used an exponential model $y = Ae^{-bx}$ to regress biomass (y) against percent time inundated (x; PROC NLIN; SAS Institute, 1982), where A is an intercept term and b is a "slope" parameter that describes the fraction of existing biomass that is reduced with each unit increase in percent time inundated. In all cases, exponential regressions performed better than linear or quadratic models in terms of maximizing coefficients of determination. For each species, we first fit exponential regressions to data pooled across the two sites, and then tested for differences between site-specific residuals with ANOVA. This procedure is essentially a nonlinear ANCOVA (Waser and Price, 1991; Bosch and Waser, 1999). If no difference between site-specific residuals was detected, the salinity effect was discounted, and data were pooled across sites to examine inundation effects. On the other hand, if differences in residuals existed, regressions to examine inundation effects were performed separately for each site.

3. Results

Elevations of the tops of marsh organ planters ranged from 49 cm (North American Vertical Datum; NAVD) to 8 cm at MBS and 65 cm to 1 cm at LBS (Table 2). During the study, these elevations interacted with water levels to produce inundation rates ranging from 6% to 88% at MBS and 3% to 86% at LBS. In general, observed inundation rates were less than those that were targeted, but still provided a broad range of flooding regimes over which to compare end-of-season biomass for the two species.

Aboveground and belowground biomass decreased with increasing hydroperiod for *S. patens* at both sites. *S. patens* biomass was lower and decreased more rapidly with increased flooding at LBS than at MBS, as indicated by ANOVA performed on site-specific residuals in pooled regressions. This site effect was present both aboveground ($F = 31.6$; $p < 0.0001$) and belowground ($F = 19.22$, $p < 0.0001$). Site-specific exponential regressions fit the biomass data well ($r^2 > 0.7$; Table 2; Fig. 2a and b), and in all cases biomass approached zero as inundation regimes approached 100%.

S. alterniflora biomass also decreased with increasing hydroperiod (Fig. 2c and d), although there was more scatter in the data, particularly aboveground ($r^2 \leq 0.27$). For aboveground biomass, site-specific residuals were higher at MBS compared with LBS ($F = 15.42$; $p < 0.0001$), indicating the presence of a site effect, and separate regressions were used to describe the aboveground

Table 2
Elevations (cm NAVD) and inundation rates (% time inundated) for each row of the four marsh organs deployed.

Row	MBS				LBS			
	Spartina patens		*Spartina alterniflora*		*Spartina patens*		*Spartina alterniflora*	
	Elevation	Inundation	Elevation	Inundation	Elevation	Inundation	Elevation	Inundation
1	49	5.8	48	6.2	64	3.3	65	3.1
2	34	20.6	33	22.3	48	9.4	46	10.9
3	29	31.1	27	37.3	40	17.2	37	22.1
4	25	43.1	24	46.9	34	28.0	30	36.1
5	19	62.3	19	62.3	26	44.5	20	57.5
6	8	87.8	8	87.8	8	77.9	1	86.0
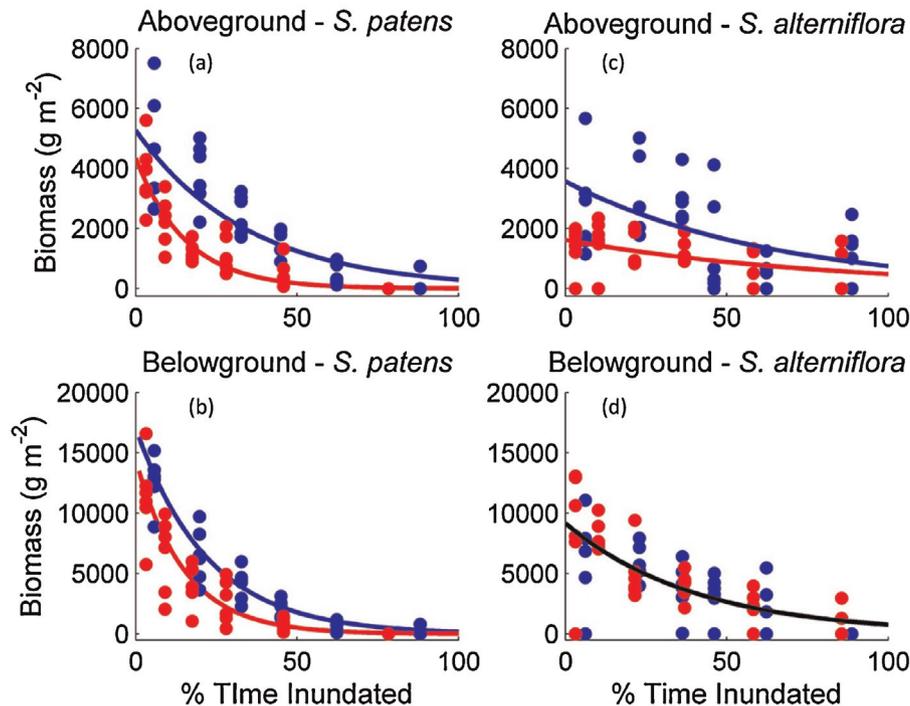
Fig. 2. Aboveground (top) and belowground (bottom) biomass for *Spartina patens* (left) and *Spartina alterniflora* (right) for MBS (blue) and LBS sites (red). Data values are indicated by circles; exponential regressions are represented by lines. Only one line exists for *S. alterniflora* belowground biomass because MBS and LBS data were pooled for that regression. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

biomass response to flooding for each site. This site effect was absent in the belowground response ($F = 0.68$, $p = 0.4166$), and a single regression was used to describe the belowground response to flooding. Similar to *S. patens*, *S. alterniflora* aboveground and belowground biomass trended to zero as permanent flooding was approached.

4. Discussion

The negative biomass response to increased flooding observed in this study was consistent with results of previous investigations of flooding impacts on *S. alterniflora* and *S. patens* biomass and productivity. Visser and Sandy (2009) observed decreases in growth and biomass with increased flooding for both species in mesocosm experiments, and attributed the decreases to soil oxygen depletion and decreased redox potential in the more heavily flooded treatments. In reciprocal transplant studies of *S. alterniflora*, Mendelssohn and McKee (1988) observed decreased aboveground biomass in permanently flooded backmarsh sites as compared with intermittently flooded streamside sites, and suggested that waterlogged soils may lead to the accumulation of toxic sulfides and stress vegetation as soil redox potential drops below critical levels. In mesocosm experiments, Spalding and Hester (2007) showed that increasing flooding depth by 30 cm in *S. patens* could result in nearly a 40% reduction in total biomass. In a broad sense, our results reflect those of numerous studies which demonstrate the critical importance of flooding regime, through its effect on sediment aeration, to wetland plant physiological performance (Mendelssohn and Burdick, 1988; Roberts, 1988; Ernst, 1990; Jackson, 1990).

Though both species in this study exhibited negative biomass responses to increased flooding, the negative response was much stronger in *S. patens*, as indicated by the greater magnitude of the regression coefficients compared with those of *S. alterniflora* at each site (*b*; Table 3). Furthermore, the higher coefficients of determination for the *S. patens* exponential regressions (r^2; Table 3) suggest

that hydroperiod exerts stronger control over productivity for this species than it does over productivity for *S. alterniflora*. Consistent with our findings, Pezeshki and DeLaune (1996) observed that although net photosynthesis decreased for both species as soil redox potential decreased, the reduction in *S. patens* photosynthetic activity was much greater. Likewise, metabolic stress responses such as alcohol dehydrogenase (ADH) production were observed to increase substantially in flooded treatments for *S. patens*, but not for *S. alterniflora* (Naidoo et al., 1992). Our observations of inferior flood tolerance in *S. patens* are also consistent with typical zonation patterns for these two species in estuarine settings, where *S. alterniflora* dominates low marsh settings with high tidal amplitudes and long flood durations, while *S. patens* tends to be found further inland where the marsh platform is higher and the lunar tide is dampened, both which tend to reduce flood duration (Bertness, 1991; Snedden and Steyer, 2013).

Though there were no differences in the belowground biomass response to flooding between the two sites for *S. alterniflora*

Table 3

Regression coefficients (*A, b*), coefficients of determination (r^2), and probability values (*p*; $\alpha = 0.05$) obtained by fitting exponential regressions to relate biomass (g m^{-2}) to inundation rates (% time inundated) for each of the four marsh organs. Regressions take the form $y = Ae^{-bx}$, where *x* is inundation rate and *y* is biomass.

Experiment	A	b	r^2	p
Spartina patens				
Aboveground – MBS	5721	−0.029	0.72	<0.001
Aboveground – LBS	4346	−0.064	0.78	<0.001
Belowground – MBS	16293	−0.045	0.91	<0.001
Belowground – LBS	13480	−0.067	0.77	<0.001
Spartina alterniflora				
Aboveground – MBS	3569	−0.016	0.27	<0.001
Aboveground – LBS	1624	−0.012	0.25	<0.001
Belowground – MBS/LBS[a]	9158	−0.025	0.58	<0.001

[a] Site effect was absent in the *Spartina alterniflora* belowground response, and a single regression was used to describe the belowground response to flooding.

(Fig. 2d), we observed site differences in belowground biomass for *S. patens*, with a more pronounced biomass reduction with increased flooding at the more saline LBS site when compared with the response at the less saline MBS site (Fig. 2b). Gosselink (1970) observed similar salinity impacts on production in greenhouse experiments, where biomass of *S. alterniflora* grown at 10 psu was 92% of that grown at 0 psu, compared with over a 50% reduction in biomass for *S. patens* grown in the higher salinity treatment. Examining metabolic responses to salinity, Naidoo et al. (1992) similarly observed no differences in ADH activity between high and low salinity treatments in *S. alterniflora*, but nearly 50% reductions in ADH activity in their high salinity treatment for *S. patens*, and attributed the treatment effect for *S. patens* to diminished root health and low levels of soluble root protein in higher salinity environments.

All four marsh organs in our study showed a negative response to increase flooding, with highest biomass observed at the highest elevations. Previous marsh organ investigations of *S. patens* (Kirwan and Guntenspergen, 2012) and *S. alterniflora* (Morris et al., 2013) have shown humped-shaped responses, with maximum biomass at intermediate elevations and reduced biomass production at the highest and lowest elevations. This discrepancy may be related to differences in how the elevations of the marsh organ pipes were vertically distributed relative to the tidal frame. In our study, the highest pipes exceeded mean high water (MHW) by only 13 cm and 19 cm at MBS and LBS, respectively, whereas Kirwan and Guntenspergen (2012) situated their highest pipes 30 cm above MHW, and those in Morris et al. (2013) were around 40 cm above MHW. The latter study cited soil desiccation and osmotic stress from hypersalinilty as limiting growth at higher elevations. Our highest pipes were situated much lower in the tidal frame and were inundated more frequently compared to those in previous marsh organ investigations (M. Kirwan, personal communication) Thus, it is likely that desiccation and hypersalinity effects that could lead to decreased productivity at higher elevations, while present, were less severe in our study. In other words, it is plausible that our study only observed the half of the parabolic response below the elevation optima of the previous studies, where biomass decreases as flooding increases.

The strong reductions in belowground biomass associated with increased flooding observed for *S. patens* in this study may provide an explanation for the extraordinarily high land loss rates that occurred within the Caernarvon diversion receiving area within the upper reaches of Breton Sound following the passage of hurricane Katrina in 2005. Prior to hurricane Katrina, *S. patens* was the dominant emergent marsh vegetation species in this region, accounting for over 50% of vegetation cover in the upper basin during monitoring surveys conducted in 2000 and 2003 (Moore et al., 2011). Growing season inundation rates in the upper basin, assessed by a statewide coastal wetlands monitoring network (www.lacoast.gov/crms) and calculated as the number of hours water levels (measured with pressure transducers) exceed marsh elevations divided by the total time assessed (Folse et al., 2012), increased from under 10% in 1997 to over 60% in the 2000–2005 growing seasons (Fig. 3a). Our observations suggest this increased flooding could have brought about a 90% reduction in belowground biomass (Fig. 2b; Table 3), leading to substantial reductions in soil shear strength and erosional resistance (Tengbeh, 1993; Simon et al., 2006; Pant, 2007), reduced organic accretion (Nyman et al., 2006) and, ultimately, to reduced landscape resilience to physical disturbances from hurricanes (Howes et al., 2010).

The increased inundation rates observed in upper Breton Sound from 2000 to 2005 may have resulted in part from more frequent, high discharge events through the Caernarvon diversion (Fig. 3b), which can induce widespread marsh flooding when they exceed
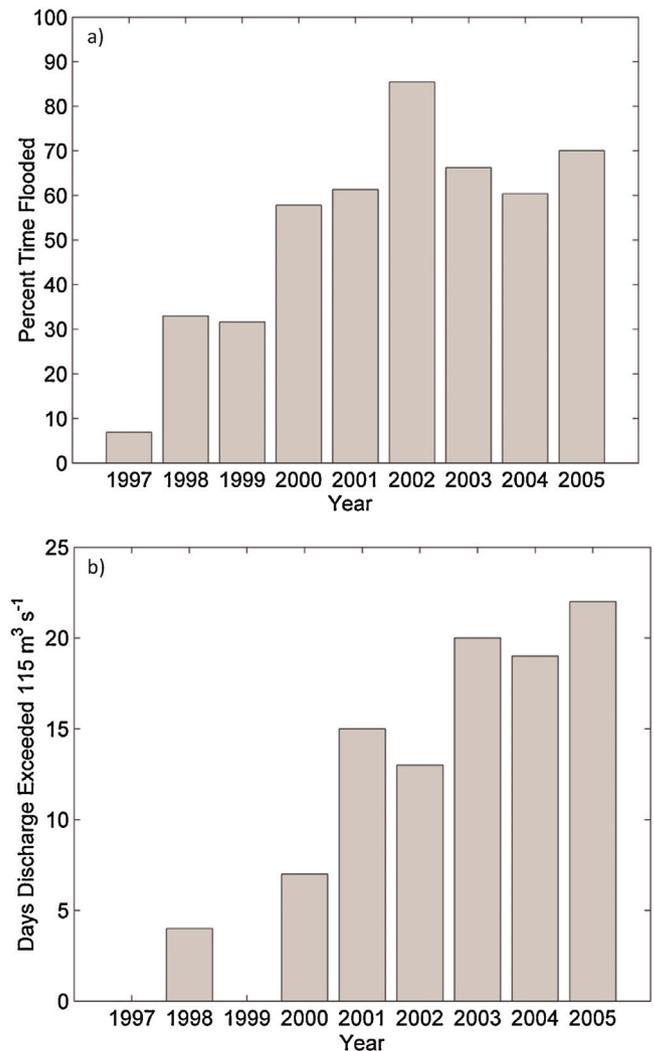

Fig. 3. (a) Growing season (March–October) inundation rates for upper Breton Sound marshes 1997–2005. (b) Number of days during growing season in which Caernarvon diversion discharge exceeded 115 $m^3 s^{-1}$.

115 $m^3 s^{-1}$ (Snedden et al., 2007a). In addition to increased freshwater inflow associated with the diversion, a water management project was completed in 2002 that was designed to restore marshes in the upper basin by increasing water retention times when the diversion is either closed or operating at minimal capacity (Moore et al., 2011). The project, essentially a network of levees and water control structures, was effective at prolonging diversion-induced flooding by trapping river water within the marsh long after water levels in the surrounding waterways naturally began to recede once diversion inflows ceased (Moore et al., 2011).

Whereas our results indicate reductions in belowground biomass occur with increased flood duration for *S. patens* and *S. alterniflora*, other common emergent wetland plant species in the MRDP have been observed to be much more flood-tolerant. Willis and Hester (2004) found no significant differences in belowground biomass for *Panicum hemitomon* when comparing saturated with permanently flooded treatments. A similar lack of response to flooding was observed in *Sagittaria lancifolia* in both laboratory (Martin and Shaffer, 2005) and field experiments (Howard and Mendelssohn, 1995). Thus, the potential for diversion-induced flooding to impair belowground productivity, similar to what may have occurred prior to hurricane Katrina in the upper Breton Sound

marshes dominated by *S. patens*, may be absent in other settings dominated by more flood-tolerant species.

In addition to delivering volumes of water sufficient to cause widespread inundation to wetlands in their receiving basins, river diversions can, in some cases, also deliver sediments in sufficient quantities to build new land in shallow, open-water coastal settings (Roberts and Coleman, 1996; Kolker et al., 2012). Thus, as they pertain to river diversions, the strategies of (1) maximizing sediment delivery to facilitate mineral accretion and (2) creating hydrologic conditions to maximize belowground productivity and subsequent organic accretion can become conflated. A variety of stages of deltaic development and ecological succession exist across the wetlands of the Mississippi River delta plain (Roberts and Coleman, 1996; Nyman, 2014), with each stage relying on different relative contributions of mineral and organic matter to accrue and maintain elevation capital (Cahoon et al., 2011). In the early stages of delta development (active delta), tremendous amounts of mineral sediment infilling occur in shallow, open-water areas to give rise to subaerial mudflats that are subsequently colonized by vegetation. In contrast, the later stages (inactive delta) are characterized by higher elevations with more infrequent flooding, reduced mineral sediment delivery, and a reliance on the belowground productivity of a dense vegetation community for soil production, organic accretion, and maintenance of elevation capital (Cahoon et al., 2011). Many large (1500–7000 $m^3 s^{-1}$) sediment diversions (engineered to build land by delivering large amounts of sediment and mimicking hydrologic conditions in an active delta setting; Nyman, 2014) are planned in coastal Louisiana in the coming decades (State of Louisiana, 2012). The Caernarvon diversion, on the other hand, is a small (225 $m^3 s^{-1}$) freshwater diversion, typically introducing modest quantities of sediment (1×10^5 t yr^{-1}; Snedden et al., 2007a) to the inactive deltaic marshes of upper Breton Sound, but with the primary goal of maximizing commercial shellfish production and landings through estuarine salinity management throughout the receiving basin (U.S. Army Corps of Engineers, 1984). Viewed within the context of delta development and ecological succession, delivering relatively small quantities of sediment to inactive portions of the delta plain while simultaneously inducing prolonged inundation to marsh vegetation communities dominated by flood-intolerant species may not be an effective restoration strategy.

Results from this study provide a step forward toward more effectively modeling the response of marsh vegetation productivity to various sea-level rise scenarios. Additionally, they also provide insight regarding how to optimally manage freshwater inflows to subsiding deltas to facilitate growth and maintenance of coastal wetlands. Relations put forth here can be applied to previously developed wetland sustainability models (e.g., Morris et al., 2002) to make them more suitable to a river-dominated, microtidal landscape such as the Mississippi River delta plain. Our results can also provide better-informed targets for more effective adaptive management of coastal ecosystems. Future investigations should examine how inundation variability influences productivity in other dominant species in the northern Gulf of Mexico, particularly those associated with lower salinities and greater inundation such as *S. lancifolia* and *P. hemitomon*, to provide a more thorough understanding of how wetlands may respond differently depending on where along the estuarine gradient a river diversion is placed. Additionally, other effects such as nutrient loading and seasonality, as well as a more thorough investigation of salinity effects, should be incorporated into future marsh organ studies to better understand how hydroperiod interacts with other edaphic factors. Such studies, along with the results put forth here, will help provide a better understanding of the hydrologic niches of important species and facilitate more effective modeling, restoration and management of coastal ecosystems.

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