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Biomass allocation of tidal freshwater marsh species in response to natural and manipulated hydroperiod in coastal deltaic floodplains



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ABSTRACT

Deltaic floodplains are highly vulnerable to relative sea level rise (RSLR) depending on the sediment supply from river channels that provides elevation capital as adaptation mechanism. In river channels where levees have restricted sediment supply to coastal deltaic floodplains, river sediment diversions have been proposed as a restoration strategy to increase elevation allowing for marshes to establish and cope with RSLR. The response of coastal wetlands to surface elevation has been well-defined for estuarine marshes, but models for coastal deltaic floodplain marshes have not been resolved. Here we coupled field observations from biomass plots and a mesocosm experiment ('marsh organ') with remote sensing techniques to assess biomass allocation of tidal freshwater marsh species in response to gradients in hydroperiod in Wax Lake Delta (WLD), coastal Louisiana, U.S.A.. We found that, contrary to salt-tolerant species, Colocasia esculenta aboveground biomass (AGB) is strongly positively correlated with percent inundated time (R² = 0.79, P < 0.001), increasing from (mean \pm 1SE) 186 \pm 69 g/m^2 in the supratidal zone to $1422 \pm 148 \text{ g/m}^2$ beyond its natural occurrence range in the lower intertidal zone. Belowground biomass consistently exceeded AGB at 2363 \pm 294 g/m² on average across elevation treatments. We also found that C. esculenta expanded its surface coverage area by 31% in five years consistent with the growth and emergence of WLD's subaqueous platforms, reflecting this species ability to cope with higher inundation time. In contrast to earlier studies conducted in brackish and saline settings, where longer hydroperiods had negative effects on biomass accumulation, our data suggest that tidal freshwater marshes can cope with longer hydroperiods caused by river sediment diversions.

1. Introduction

Coastal deltaic floodplains shelter a disproportionate amount of the global population and provide a wealth of ecosystem services to communities and industry (Edmonds et al., 2020; Tessler et al., 2015). However, these areas are also some of the most vulnerable habitats on Earth due to accelerated sea level rise, particularly along deltaic coastlines where high subsidence rates and reduced sediment supply (from river engineering structures such as dams and levees) result in accelerated loss of floodplain area (Syvitski et al., 2005; Vörösmarty et al., 2003). This vulnerability is defined by a decrease in sediment surface elevation of deltaic floodplains, referred to as a decrease in elevation capital, that determines the hydroperiod of delta wetlands in response to increase in relative sea levels (Cahoon et al., 2019, 2020; Morris et al., 2016). The evolution of delta landscapes is controlled by mineral sedimentation and organic production defining delta succession in the coastal landscape, describing how river flood-pulses, geomorphology and ecological succession are linked to increase elevation capital of coastal deltaic floodplains (Twilley et al., 2016). Understanding the co-evolution of natural and social systems in response to soil vertical dynamics at the land-ocean interface is paramount to informing policymakers and managers about best strategies to address coastal

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management issues under conditions of accelerated relative sea level rise (RSLR) (Jankowski et al., 2017; Törnqvist et al., 2020; Twilley et al., 2016).

In coastal wetlands, long-term soil vertical dynamics depend on feedbacks among vegetation, geomorphology, sea level and climate (Bevington et al., 2017; Day et al., 2008; Ma et al., 2018; Morris, 2007; Rogers et al., 2019). Feedbacks occur when plants at suitable elevations promote soil accretion via belowground (root) productivity and lateral trapping of suspended sediments, increasing soil elevation capital (Cahoon et al., 2019; Nardin and Edmonds, 2014). However, without adequate sediment supply to maintain marsh elevation at or above mean sea level (MSL) many coastal wetland plants cannot tolerate prolonged flooding, leading to conversion to open water and inland migration of coastal waters (Ganju et al., 2020; Morris et al., 2002; Stagg et al., 2020; Twilley et al., 2016). The capacity of coastal marshes to withstand submergence also depends on species-specific abilities to respond to frequency, duration and depth of flooding events (collectively referred to as hydroperiod). Morris (2002) observed reduced production at both short and long durations of flooding. Since then, a multitude of studies have observed disparate responses to hydroperiod across a variety of taxa (Adam Langley et al., 2013; Janousek et al., 2016; Kirwan and Guntenspergen, 2015; Morris et al., 2013; Mozdzer et al., 2016; Mueller et al., 2016; Peng et al., 2018; Schile et al., 2017; Snedden et al., 2014; Voss et al., 2013; Watson et al., 2016, 2017; Wigand et al., 2016; Wong et al., 2015). Prolonged hydroperiods can alter soil conditions beyond levels that wetland plants can tolerate, such as increasing sulfide concentrations when oxygen is depleted (Mendelssohn and McKee, 1988). Understanding species-specific responses to increased flooding is key to developing models that predict the fate of coastal wetlands in response to RSLR scenarios.

The response of wetland vegetation to hydroperiod gradients can be assessed along hydrogeomorphic zones where these communities naturally occur (Bevington and Twilley, 2018) or by manipulating elevation that simulate exposure of wetland platforms to a range of hydroperiods that span from subtidal to supratidal conditions. A common technique for the latter manipulated approach consists of deploying plants in racks with varying elevations relative to mean sea level (MSL) and measuring biomass accumulation in response to changes in platform elevation (i.e., surface elevation capital). This mesocosm experiment, known as the 'marsh organ', can yield relevant information about biomass production and partitioning between plants' above- and belowground compartments (Morris, 2007b), which can vary as a function of soil fertility and stress conditions (Chapin III et al., 1986; Song et al., 2019; Vitousek and Farrington, 1997). For example, excess nutrient loading can disproportionately stimulate plants' aboveground production relative to investment in root tissues, compromising species structural support (Livesley and Andrusiak, 2012) as well as reducing root tensile strength (Hollis and Turner, 2018). Marsh organs have been largely used to assess the response of coastal saltmarshes in transgressive coastal environmental settings to idealized sea level scenarios (e.g., Fagherazzi et al., 2015). However, to our knowledge, it has not yet been used in prograding coastal deltaic floodplains that test vegetation response in tidal freshwater environments.

In this study we combined both natural and manipulated approaches to assess wetland biomass allocation across multiple marsh platform elevations that occur along a chronosequence of deltaic floodplains relative to their exposure to subaerial levels (see Bevington and Twilley, 2018 for details). To test these approaches, we first designed a natural field experiment in the Wax Lake Delta (WLD), a coastal deltaic floodplain in the Mississippi River Delta, to ask how biomass production and allocation vary among dominant wetland plant populations relative to age (chronosequence) and range of marsh platform elevations. Further, to examine the specific response of a tidal freshwater species to hydroperiod gradients, we selected *Colocasia esculenta* (L.) Schott (elephant ear or taro) as a test species for our mesocosm experiment based on this species' accelerated expansion rate in the Atchafalaya river delta

(Shaffer et al., 1992) as well as its response to high river flood pulses and disturbances such as hurricanes, rapidly colonizing newly available subaerial substrates (Bevington, 2016). Using the mesocosm approach, we asked if inundation time had an effect on C. esculenta biomass production and hypothesized that C. esculenta above- and belowground biomass would be higher at intermediate elevations (e.g. upper intertidal zone) and decrease at both higher (supratidal) and lower elevations (lower intertidal) in response to hydroperiod as reported for other brackish and saline species elsewhere (e.g., Kirwan and Guntenspergen, 2012; Morris et al., 2013). We also used remotely-sensed estimates of C. esculenta surface area expansion in WLD for the period 2011–2016 to assess how this species' spatial dynamics reconcile with biomass production across elevation treatments in our mesocosm experiment, in particular those simulating longer hydroperiods. Our findings are applicable to other coastal deltaic floodplains worldwide and should provide wetland scientists and decision makers with a broader understanding regarding the response of tidal freshwater marshes to river sediment diversions used as a strategy to manipulate elevation capital of deltaic wetlands to mitigate high RSLR rates and consequential land loss.

2. Methods

2.1. Study area

The WLD is a jet plume deltaic formation (Fig. 1) that became subaerial in 1973 resulting from a river diversion implemented in 1941 to control the routes of channel flow to the coast reducing the risk of flooding to Morgan City (Wellner et al., 2005). WLD is part of the Atchafalaya River basin complex, which receives approximately 30% of the water discharge from the Mississippi River (Allison et al., 2012). The WLD outlet accounts for 10% of the Atchafalaya River flow (Allison et al., 2012). The constant sediment supply coupled with river floods, hurricanes and cold fronts, and biological processes such as organic matter production, are responsible for the morphological development of the WLD (Bevington et al., 2017). Tidal freshwater wetland species zonation in coastal deltaic floodplains, such as WLD, reflects multiple marsh elevation platforms ranging from subtidal to supratidal hydrogeomorphic zones (Bevington and Twilley, 2018; Carle et al., 2014; Jensen et al., 2019; Ma et al., 2018; Twilley et al., 2019). These geomorphic characteristics make WLD an excellent natural observatory to test hypotheses concerning the trajectory and sustainability (e.g., process-based approach; Naiman et al., 2010) of designed coastal deltaic wetlands as an adaptation strategy to RSLR.

2.2. Natural experiments of biomass allocation

To test the influence of hydroperiod and chronosequence (that is, land age relative to subaerial exposure) on marsh biomass allocation in WLD, we designed our field (natural) surveys based on the classification proposed by Bevington and Twilley (2018). Chronosequence transects were set along the Mike Island longitudinal axis to capture wetlands that have become subaerial earlier, close to WLD's apex (between 1983 and 1998 for transects #1 and #2), relative to the island's southward portion that have emerged later (between 1998 and 2012 for transects #3 and #4) (Fig. 1b, but see Bevington and Twilley, 2018 for details). Along this chronosequence, specific hydrogeomorphic zones are defined by sediment surface elevation ranges relative to mean high water (MHW) and mean low water (MLW): subtidal (<-0.04 m NAVD88), intertidal (-0.04 to 0.30 m) and supratidal (>0.30 m). It should be noted, however, that we subdivided the intertidal class into low intertidal (-0.04 to0.12 m) and high intertidal (0.12-0.30 m) due differences in species dominance with C. esculenta prevailing in high intertidal and supratidal areas and Nelumbo lutea Willd. in low intertidal zones. High intertidal and supratidal zones naturally prevail in transects #1, #2 and #3, subtidal, low intertidal, high intertidal and supratidal zones in transects #2 and #3, and subtidal zone in transect #4 (Fig. 1). Mean sea level

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Fig. 1. Map of the study area showing the distribution of hydrogeomorphic zones and the location of chronosequence transects, biomass sampling sites and the mesocosm experiment (red star) on Mike Island in the Wax Lake Delta, coastal Louisiana (a,b). Yellow and green diamond symbols show *C. esculenta* sampling sites whereas blue-shaded circles show *N. lutea* sampling sites (symbols not to scale). Panel 'c' shows dominant patterns in species composition across hydrogeomorphic zones along transects.

(MSL) and mean tidal range at our study site, based on the NOAA tidal datum at Amerada Pass, are 0.12 m and 0.35 m adjusted to NAVD88, respectively (Shaw et al., 2013). The elevation records used in this study were derived from the U.S. Geological Survey (USGS) Atchafalaya 2 project LiDAR Survey 2012 digital elevation model (U.S. Geological Survey, 2020) 1 m² grid cell resolution (available at https://www.scie ncebase.gov/catalog/item/5ead02a782cefae35a252ccb, accessed on 7/26/21), hereafter referred to as USGS DEM. We used this dataset since it is the most recent and only high-resolution terrain-level DEM measuring marsh surface elevation (and not the canopy) available for this region, as subsequent LiDAR campaigns from the USGS 3DEP program do not include WLD. Noteworthy, the 2012 USGS DEM data acquisition campaign occurred during the month of December when plants were senesced and water levels much lower, fully exposing bare ground, which further reduces errors in elevation measurements associated with standing water overtopping the marsh surface. However, to further improve the accuracy of this elevation dataset, we used 196 observed elevation records retrieved with a Real Time Kinematic (RTK) portable GPS unit (Trimble, R8 GNSS/R6/5800) the same year vegetation biomass was sampled (that is, September 2017) to assess the bias and adjust inconsistencies between the USGS DEM and RTK readings (Table S1). There is a significant and strong correlation between the USGS DEM and RTK readings (y = -0.183645 + 1.029057x; adjusted $R^2 = 0.89$, P = 0.000, df = 194, RMSE = 0.07 m), with the USGS DEM values consistently averaging 0.18 m NAVD88 higher than RTK points measured across a 1-m elevational gradient (-0.64 to 0.34 m) (Fig. S1). To produce a more accurate elevation dataset for the study area, we fitted the original USGS DEM values to the model above and used the corrected elevation values in our analyses, hereafter referred to as adjusted DEM. Noteworthy, while models that couple RTK measurements with remotely sensed vegetation structural attributes (e.g., Normalized Difference Vegetation Index - NDVI) render robust surface elevation predictions (Buffington et al., 2016; Holmquist et al., 2021), NDVI imagery available to date only covers a fraction of our study region preventing us from using such approach.

Biomass sampling took place during September 2017 to capture the peak biomass season in WLD (Carle et al., 2014; DeLaune et al., 2016; Shaffer et al., 1992; Thomas et al., 2019). In each hydrogeomorphic zone defined above we randomly established between one and three 50 m radius sites (Fig. 1, Table 1). The influence of hydrogeomorphic zones on

Table 1

Site characteristics of biomass survey in Wax Lake Delta, coastal Louisiana.

Chronosequence	Hydrogeomorphic zone	Site (N = 2 plots)	Latitude ^a	Longitude ^a	Elevation. m NAVD88 ^b	Dominant Species
T1 (older)	Supratidal	А	29.51506	-91.43826	0.51	Colocasia esculenta
	-	В	29.5122	-91.4434	0.38	
	High intertidal	Α	29.51309	-91.4413	0.27	Colocasia esculenta
		В	29.51169	-91.43781	0.22	
T2	Supratidal	Α	29.50051	-91.44714	0.31	Colocasia esculenta
		В	29.50407	-91.43844	0.33	
		С	29.50452	-91.4471	0.43	
	High intertidal	Α	29.50278	-91.44691	0.15	Colocasia esculenta
	Low intertidal	Α	29.5037	-91.44533	0.09	Nelumbo lutea
	Subtidal	Α	29.50335	-91.44027	-0.27	Nelumbo lutea
		В	29.50267	-91.44097	-0.33	
		С	29.50464	-91.44214	-0.35	
T3	Supratidal	Α	29.49713	-91.44123	0.67	Colocasia esculenta
	High intertidal	Α	29.49156	-91.44089	0.12	Colocasia esculenta
	Low intertidal	Α	29.49027	-91.44128	0.03	Nelumbo lutea
		В	29.49175	-91.44703	0.06	
	Subtidal	Α	29.49075	-91.44631	-0.37	Nelumbo lutea
		В	29.49088	-91.44306	-0.44	
T4 (younger)	Subtidal	Α	29.47922	-91.44053	-0.17	Nelumbo lutea
		В	29.48242	-91.4399	-0.19	
		С	29.48011	-91.44817	-0.64	
		D	29.47917	-91.44345	-0.18	

^a Center coordinates for sampling sites.

^b Marsh elevation retrieved from adjusted USGS DEM.

plant biomass distribution was assessed using elevation values from the adjusted DEM given that percent inundation time is a function of marsh elevation. Two plots were randomly delimited within each site, totaling 44 plots established in the field to harvest vegetation biomass in *C. esculenta*- and *N. lutea*-dominated zones along the range of elevations where these species naturally occur. In supratidal and high intertidal zones, where *C. esculenta* is the dominant species, plots were 1 m^2 due to high plant density, whereas in low-density *N. lutea*-dominated lower intertidal and subtidal zones plot dimensions were 4 m^2 to include a representative number of plants.

Aboveground biomass (AGB) was sampled by clipping all vegetation inside the plots to the sediment surface. Two 15.24 cm diameter 50 cm long PVC belowground biomass (BGB) cores were sampled within each AGB plot. Cores were placed over target plants and inserted into the sediment to a depth of 50 cm to ensure representative collection of root and rhizome mass, particularly for sparse N. lutea root system. For C. esculenta, however, only the top 25 cm of soil was considered for BGB determination since these species have a shallower rooting system based on field observations. Both AGB and BGB samples were separated in the field and stored at 4 °C until processing. In the laboratory, AGB was rinsed with tap water and BGB was washed over 2 mm mesh sieves to separate live roots and live rhizomes from all sediment and necromass. Necromass was not included in our analyses. Stems, roots and rhizomes were dried separately at 60 °C until constant weight and both AGB and BGB were determined on a dry mass basis per unit area (e.g., g/m^2). For high-density C. esculenta-dominated zones, per-area basis BGB biomass values were obtained by dividing the root mass inside the core by the core area (e.g., g/m^2 for the top 0.25 m of soil). For N. lutea-dominated zones, due to more sparse distribution of this species, BGB was standardized to a per-area basis by multiplying the mean BGB per plot by the density of stems within the plot and then dividing it by the area of the plot. Root-to-shoot ratios were calculated dividing the BGB (roots and rhizomes) by the AGB.

2.3. Mesocosm experiments of biomass allocation

We conducted a mesocosm experiment to represent distinct hydrogeomorphic zones in WLD coastal deltaic floodplains as defined above (Fig. 1) to test how *C. esculenta* biomass accumulation (that is, yield at the end of the experiment, from May 23rd to October 3rd 2018) responds to percent inundated time. Although an introduced species in coastal Louisiana, we selected *C. esculenta* to test our hypothesis because this species dominates the higher portion of the intertidal zone (e.g., high intertidal to supratidal) in WLD, allowing us to test effects of increased inundation as a competitive trait to other common species in the floodplain as demonstrated in previous studies (Bevington, 2016; Shaffer et al., 1992).

The mesocosm consisted of an aluminum frame (rack) with four rows that represented treatments to simulate different marsh platform elevations (Fig. S2). Each row had four fixed structural 15.24 cm diameter PVC pipes placed side by side leveled at the same height referenced to the NAVD88: Row #1: lower intertidal (0.06 m), Row #2: high intertidal (0.21 m), and Rows #3 and #4: supratidal (0.47 and 0.77 m, respectively) (Table 2). The total number of plants in the mesocosm was 16, with 4 elevation treatments (fixed factor) and 4 replicates (plants in PVC pipes, random factor). To establish these target elevations in the field we used an RTK portable GPS unit (Trimble, R8 GNSS/R6/5800). We calculated percent inundated time for the mesocosm pipes using a nearby (~2.4 km away) water-level recorder (CRMS0479; www.lacoast. gov/crms) as a proxy. Those water level data were used in a predictive equation derived from regressing deharmonicized tide water-level data at the mesocosm site against water-level data collected at CRMS0479 during previous years (2014–2017) when water-level data were simultaneously collected at both stations (see Supplemental Information for details). Percent inundated times were calculated for the period April 15 to October 15, 2018, encompassing the time period the mesocosm was deployed.

Table 2

Characteristics of the mesocosm experiment deployed between May and October 2018 in Wax Lake Delta, coastal Louisiana.

Simulated hydrogeomorphic zone	Mean elevation treatment ± 1SE (m NAVD88) ^a	Number of plants per elevation treatment	Hours inundated	Percent inundated time
Supratidal 2	$\textbf{0.77} \pm \textbf{0.021}$	4	0	0
Supratidal 1	0.47 ± 0.015	4	134	3.1
High Intertidal	0.21 ± 0.007	4	1900	43.3
Low Intertidal	$\textbf{0.06} \pm \textbf{0.009}$	4	3155	71.8

^a From in situ RTK GPS measurements.

In each row we transplanted four *C. esculenta* plants, one per pipe. Transplanted plants' heights varied from 10.2 to 26.2 cm with mean ($\pm 1SE$) AGB and BGB at 0.73 \pm 0.05 and 8.65 \pm 0.89 grams, respectively, as measured from eight extra plants brought to the laboratory to determine initial values. We started our mesocosm experiment with young C. esculenta plants to better capture the growth response to different flooding regimes over the incubation period. To avoid disturbance due to excessive manipulation we cored over C. esculenta plants using a PVC pipe measuring 15.24 cm in diameter and 40 cm in length. These PVC pipes, now containing undisturbed soil and rooted plants, were then fastened together to the opened-bottom structural fixed PVC pipe sections using PVC couplings such that the elevations of the soil at the top of the pipes where the stems emerged corresponded to the target elevations described above (Table 2). Fixed structural PVC pipes were previously filled up all the way with mostly mineral soil from nearby mudflats and allowed to settle for 15 days prior to transplanting to minimize compaction after deployment. To mitigate the effect of shading mesocosm sets were deployed facing south, with pipe elevations increasing northwards.

In addition, to evaluate the effect of transplantation on plant survival we performed a separate control experiment where we dug out 8 extra cores containing soil and plants using the same sampler (PVC pipe, 15.24 cm diameter, 40 cm length) used to transplant plants into the mesocosm. These plants were immediately placed back in the same hole along the island's levee where they were dug out from, tagged, and monitored for a period of 15 and 30 days to assess survival. Our goal was to certify that eventual mortality in the mesocosm would not be related to the transplanting method, but instead related to elevation treatments.

The experiment spanned the 2018 growing season (May–October 2018). The mesocosm was visited monthly for maintenance purposes including removal of stranded debris and overgrown floating vegetation. At the end of the growing season we retrieved the PVC pipe sections (that is, 15.24 cm diameter, 40 cm length) containing transplanted plants. AGB and BGB samples were separated in the field and stored at 4 °C until processing. Both AGB and BGB samples were processed and determined using methods described above for the natural experiments of biomass allocation.

2.4. Environmental variables and analytical procedures

Water physico-chemical parameters, including conductivity, temperature and nitrate (NO₃) were obtained from sensors deployed at our study site for the period April–October for the years 2014, 2015, and 2016 (Table 3). Total suspended solids (TSS) values were obtained from several distributary channels in WLD and Terrebonne basins, the latter for comparison purposes. While these values are not from the same year that we conducted our field experiment, they reasonably represent the interannual variability of such parameters in the study area.

We also collected three soil samples to characterize the site where the transplanted plants were obtained (Table 3). Soil bulk density was determined on a dry mass basis, dividing the dry mass of soil in a sample by its wet volume (i.e., gDM/cm³). Soil samples were dried at 60 °C until constant weight and homogenized using a grinder. Soil organic matter (OM) content was determined by loss on ignition (LOI) where samples were combusted at 550 °C for 2 h. Soil samples were pre-treated for carbonate removal using 1N HCl fumigation for 6 h prior to total soil organic carbon (SOC) and total nitrogen (N) determination (Harris et al., 2001). Soil organic C and total N contents were obtained by elemental analyses (ECS 4010 elemental analyzer, Costech Analytical Technologies). C and N density were obtained from the product of these elements' contents (i.e., mg/g) and bulk density (g/cm³).

2.5. Statistical and spatial analyses

 $2.5.1. \ \ \text{Peak biomass distribution and response to manipulated hydroperiod}$

We used unbalanced type 'II' ANOVA ('Anova' function in 'car' package in R; Fox and Weisberg, 2019) coupled with least-squared means post hoc comparisons ('Ismeans' function in 'emmeans' package in R; Lenth, 2020) to assess differences in both peak AGB and BGB distributions across the islands chronosequence (transect, fixed effect), hydrogeomorphic zones (elevation, fixed effect) and the interaction between these factors. Since all hydrogeomorphic zones do not naturally occur along all transects, we ran separate ANOVA tests accordingly to assess the interaction effect where possible: 1) high intertidal vs. supratidal between transects #1, #2 and #3; 2) subtidal vs. low intertidal vs. high intertidal vs. supratidal between transects #2 and #3; and 3) subtidal among transects #2, #3 and #4.

We used both the mesocosm pipes elevation values and the water level timeseries recorded at the study area to calculate percent inundated time for each mesocosm elevation treatment over the duration of the experiment (Table 2). Calculations were based on NAVD88 reference system. We used a mixed effects model to fit a nested ANOVA ('lme' function in 'nlme' package in R; Pinheiro et al., 2021) to assess differences in biomass allocation in our mesocosm experiment, with elevation (rows) being treated as a fixed effect and replicates (plants in PVC pipes) as a random effect nested within elevation treatments. We also used linear and non-linear regressions to test the influence of elevation treatments on marsh biomass allocation. All statistical analyses were conducted in R (R Core Team, 2020).

Table 3

Mean (range between brackets) values for water and soil properties measured in central coast Louisiana.

Water parameters								
Period	Conductivity WLD (mS/ cm)	Temperature WLD (°C)	Water Level WLD (m NAVD88)		Nitrate WLD (uM)	TSS WLD (mg/L)	TSS Terrebonne (mg/ L)	
April–October 2014	0.34 (0.12–0.45)	26.08 (9.91–34.05)	0.15 (-0.65-0.8)		18.95 (9.26–43.4)	ND	ND	
April–October	0.34 (0.18-0.51)	26.47 (14.89-32.06)	0.14 (-0.65-0.74)		34.94	70.75	29.12 (13.53–53.14)	
2015					(7.27–184.77)	(59.35-84.67)		
April–October	0.35 (0.17-0.47)	26.76 (12.02-33.92)	0.08 (-0.65-0.82)		13.69	51.82 (22.9–110.4)	ND	
2016					(0.03–179.85)			
Soil parameters WLD								
Core	Depth interval (cm)	Bulk density (g/cm ³)		Carbon (%) Ni		Nitrogen (%)	Organic matter (%)	
1	0–20	0.93		0.81		0.07	2.80	
	20-40	0.85		0.84		0.08	3.25	
2	0–20	0.90		0.70		0.07	2.97	
	20-40	0.80		1.14		0.09	3.87	
3	0–20	0.85		0.90		0.08	3.57	
	20-40	0.63		1.63		0.13	4.52	

WLD: Wax Lake Delta; ND: no data available.

2.5.2. Change in plant surface cover

We used two high-resolution species-level classification maps to examine changes in C. esculenta cover in WLD. As a baseline we used a 2 m resolution map showing this species distribution on October 2011 (Carle et al., 2014). This baseline map was developed using Maximum Likelihood Classification (MLC) on WorldView-2 multispectral data, which distinguished C. esculenta at a high accuracy (100% user's accuracy, 66.67% producer's accuracy). The supervised classification, based on MLC using WorldView-2's eight bands (coastal blue, blue, green, yellow, red, red-edge, near-infrared 1, near-infrared 2), attained an overall vegetation class accuracy of 71.7% and a Kappa of 0.66 (see Carle et al., 2014 for details). To estimate change in C. esculenta cover over time we derived a map for October 2016 using Airborne Visible/Infrared Imaging Spectrometer - Next Generation (AVIRIS-NG) data, with a resolution of 5.4 m, in conjunction with a 1 m 2012 USGS DEM (U.S. Geological Survey, 2020). AVIRIS-NG measures 14-bit radiance from 380 to 2510 nm wavelengths with a \sim 5 nm spectral resolution (Hamlin et al., 2011), and the five flight lines collected over the WLD were corrected to account for atmospheric (Thompson et al., 2015) and bidirectional reflectance distribution function effects (Jensen et al., 2018), producing a surface reflectance mosaic.

Subsequent spatial analyses were performed in ENVI 5.4, including



reducing the 425-band AVIRIS-NG reflectance data via Principal Components Analysis to nine projected component bands, which altogether explained 99.97% of the variance. These component bands were then stacked with the resampled digital terrain model, and an unsupervised ISODATA classification returned unlabeled classes that were subsequently grouped into species or type classes. In addition to C. esculenta, these classes included the dominant species S. nigra, Polygonum punctatum, and N. lutea along with broader type classes of grasses, floating vegetation, and submerged aquatic vegetation (see Jensen et al., 2021 for details). The class interpretation was informed by aerial imagery and in situ pictures and the map attained an overall accuracy of 77.62% and a Kappa of 0.72 (Jensen et al., 2021). C. esculenta formed its own labeled class whose accuracy was validated by collecting a selection of in situ points and recording the map's validity at each point. With both maps compiled, covering a timespan of 5 years, the 2011 map was resampled to the 2016 map's 5.4 m resolution. The 2016 map's user's and producer's accuracy for C. esculenta are 82.61% and 65.55%, respectively. Changes in C. esculenta cover over this period was estimated based on the difference between these two maps (Jensen et al., 2021). While we have not measured net elevation change over time, it has been shown that most of the change on WLD occurs down delta as subaqueous platforms continuously transition into subaerial floodplains towards



Fig. 2. Distribution and response of peak above- (a–c) and belowground biomass (d–f) in *C. esculenta*- (yellow and green-shaded bars and diamond symbols) and *N. lutea*-dominated zones (blue-shaded bars and circle symbols) to distinct hydrogeomorphic zones and marsh surface elevation range in Wax Lake Delta. The hatched pattern in panel 'a' shows *C. esculenta* and *N. lutea* aboveground biomass (AGB) while the solid colors show total AGB within surveyed plots. Small caps letters on top of groups in 'b' and 'e' show statistical differences in peak biomass among hydrogeomorphic zones across all transects (See Supplementary Information for all tests results). In panels 'c' and 'f', only *C. esculenta* and *N. lutea* biomass is used

equilibrium elevation (Shaw et al., 2016; Wagner et al., 2017). Based on this empiric framework, we assumed that *C. esculenta* surface coverage expansion is consistent with the growth of and emergence of WLD's subaqueous platforms, reflecting this species ability to cope with higher inundation time.

3. Results

3.1. Distribution of biomass across hydrogeomorphic zones

Over 92% of total AGB in both high intertidal and supratidal hydrogeomorphic zones was represented by *C. esculenta*, whereas *N. lutea* accounted for 75% of AGB in low intertidal and subtidal sites (Fig. 2a). While it was not possible to fully differentiate BGB between target (e.g., *C. esculenta* and *N. lutea*) and other plant species, we assumed that most BGB biomass at our sites (Fig. 2d) belonged these target species based on respective AGB dominances, including in *N. lutea*-dominated areas where other species present were mostly comprised by shallow-rooted submerged aquatic vegetation.

Chronosequence and the interaction between chronosequence and hydrogeomorphic zone had no significant effect (P > 0.05) on AGB and BGB distributions at both C. esculenta- and N. lutea-dominated zones (See Supplementary Information for all ANOVA tests results). Accordingly, to further investigate the effect of elevation as a main driver of C. esculenta and N. lutea biomass variability, we dropped the chronosequence factor from our analyses and contrasted only hydrogeomorphic zones across all our study sites (Fig. 2b,e). Both AGB and BGB were significantly higher in C. esculenta-dominated high intertidal and supratidal sites relative to N. lutea-dominated low intertidal and subtidal hydrogeomorphic zones (Fig. 2b,e). Mean AGB in C. esculenta plots averaged (mean \pm 1SE) 424.0 \pm 29.6 g/m² (range: 325.4–559.5 g/m²) and 451.5 \pm 30.4 g/m² (range: 260.9-646.3 g/m²) in high intertidal and supratidal zones, respectively (Fig. 2b). Mean AGB in *N. lutea* plots was lower at 176.1 \pm 37.8 g/m² (range: 55.5–289.1 g/m²) and 97.6 \pm 15.7 g/m² (range: 10.1–289.6 g/ m²) in low intertidal and subtidal sites, respectively (Fig. 2b). The distribution of BGB across hydrogeomorphic zones was similar to the pattern observed for AGB. BGB in C. esculenta plots averaged 3374.9 \pm 691.2 g/m² (range: 1085.4–6260.5 g/m²) and 4577.9 \pm 497.0 g/m² (range: 1545.9–6666.1 g/m^2) in high intertidal and supratidal sites, respectively (Fig. 2e). BGB for N. lutea-dominated low intertidal and subtidal hydrogeomorphic zones averaged 105.7 \pm 20.9 g/m² (range: 18.5–167.7 g/m²) and 79.5 \pm 16.7 g/m² (range: 3.1–253.0 g/m²), respectively (Fig. 2e). C. esculenta biomass (AGB and BGB) was not

correlated to marsh elevation (Fig. 2c,f). In *N. lutea*-dominated zones elevation had a marginal effect on AGB distribution (Fig. 2c) while BGB did not change with elevation (Fig. 2f). Mean (\pm 1SE) root-to-shoot ratios for *C. esculenta* between high intertidal and supratidal zones were similar (7.9 \pm 1.6 and 11.3 \pm 1.9, respectively) and higher relative to *N. lutea*-dominated zones with equivalent values at 0.74 \pm 0.2 and 0.96 \pm 0.2 for low intertidal and subtidal zones, respectively.

3.2. Biomass allocation in C. esculenta relative to manipulated hydroperiod

All plants in both our control (designed to assess mortality due to transplanting) and mesocosm experiment survived the end of the study. Contrary to our hypothesis that biomass would peak in intermediate flooding regimes, C. esculenta AGB decreased exponentially with increasing elevation ($R^2 = 0.74$, P < 0.001), decreasing from (mean \pm 1SE) 1422.5 \pm 148.2 g/m² in the lower intertidal zone, where plants were flooded over 70% of the time during experiment's duration, to $185.9 \pm 69.4 \text{ g/m}^2$ in the supratidal ST2 treatment (Fig. 3a). AGB in supratidal ST1 and high intertidal mesocosm treatments ranged from 277.8 to 573.9 g/m² (mean of 421.2 ± 61.5 g/m²) and 503.9–1166.7 g/ m^2 (mean of 840.0 \pm 169.6 g/m²), respectively. BGB was consistently higher than AGB at 2363.1 \pm 294.4 g/m² on average but exhibited no discernible trend across mesocosm elevation treatments (Fig. 3b). Biomass allocation in the mesocosm pipes exhibited similar trends relative to field values, with root-to-shoot ratios increasing from low (1.6) and high intertidal (3.6) to supratidal ST1 (4.6) and ST2 (18.4) treatments (Fig. 3c), reflecting primarily changes in AGB.

3.3. Change in C. esculenta area cover

C. esculenta areal cover in WLD increased from 2.19 km^2 on October 2011 to 2.87 km^2 on October 2016, expanding its coverage by 31% in five years (Fig. 4a and b). Most of the observed changes for this period were driven by losses of *C. esculenta* patches in the apex of deltaic islands and along higher elevation levees coupled with large gains mainly along lower elevation levees on deltaic islands and towards the delta fringes (Fig. 4c).



Fig. 3. Above- (a) and belowground biomass (b), and root to shoot ratios (c) of *C. esculenta* plants incubated in the mesocosm experiment conducted on Wax Lake Delta.



Fig. 4. Change in *C. esculenta* extent in Wax Lake Delta between 2011 and 2016. (a) Baseline October 2011 (modified from Carle et al., 2014) and (b) October 2016 map showing *C. esculenta* distribution for these two time intervals, and (c) net changes in *C. esculenta* distribution for this period based on the difference between the two classifications. In 'a' and 'b', *C. esculenta* surface area cover is shown in green shading. In 'c', Hydrogeomorphic zones are shown in grayscale, and loss, gain and no change in *C. esculenta* surface area cover is shown in red, green and blue shadings, respectively

4. Discussion

4.1. Biomass allocation in response to hydroperiod

Above- and belowground biomass distributions for both C. esculenta and N. lutea, as measured from our natural field experiment, were not correlated with age (e.g., time since subaerial exposure) of coastal deltaic floodplains in WLD. Instead, hydrogeomorphic zones explained these species' biomass variability across all our study sites. WLD coastal deltaic floodplains became subaerial nearly 50 years ago, when submerged and emergent wetland plant species begin to colonize newly intertidal platforms (Elsey-Quirk et al., 2019; Shaffer et al., 1992). These relatively young wetland soils have not yet developed marked gradients in soil nutrient concentration (Aarons, 2019), partly due to constant loading of nitrate-rich waters currently fivefold the concentration in pre-industrial times (Goolsby et al., 2000). Thus, the consistency in soil nitrogen density and nitrogen:phosphorus stoichiometric ratios across the study area (Aarons, 2019) may explain why plant biomass was not associated with marsh platform age. In WLD coastal deltaic floodplains, vegetation biomass was closely related to discrete hydrogeomorphic zones, indicating that dominant plant assemblages reflect shorter erosional and depositional timescale processes (Jensen et al., 2021; Ma et al., 2018) as well as stochastic events (e.g., hurricanes, storm surges, major river floods; Bevington et al., 2017; Tweel and Turner, 2014). These sub-decadal processes and stochastic events can alter the marsh platform elevation from one season (or event) to another, shifting vegetation's composition and dominance reflecting species-specific tolerance to flooding (Bevington, 2016; Bevington et al., 2017; Carle et al., 2015; Jensen et al., 2021).

Regarding our mesocosm experiment, our results differed from other marsh organ studies performed using brackish and saline marsh species. When exposed beyond the elevation range in which C. esculenta thrive in WLD (e.g., high intertidal and supratidal zones), this species showed a higher tolerance to flooding where naturally other species dominate. N. lutea and a myriad of submerged aquatic vegetation species dominates low intertidal and subtidal hydrogeomorphic zones where hydrodynamics and sedimentation are higher, which probably prevent the establishment of C. esculenta and subsequent spread of rhizomes and stolons due to overgrowth and burial in these deeper zones. Our mesocosm results show that C. esculenta AGB increased steadily with percent inundated time as high as 70% (equivalent to 3155 h of submergence during the incubation period; Table 2) while in most other studies of brackish and saline species, biomass either peaked when flooded between 20 and 40% of the time, exhibiting a parabolic relationship or decreased linearly or exponentially with increasing inundation time. For example, parabolic response curves in which biomass decreases once inundation time exceeds ~30% have been reported for the United States (hereafter U.S.) west coast for Juncus balticus Willd., Carex lyngbyei Hornem., Spartina foliosa Trin. and Batis maritima L. (Janousek et al., 2016), and for Schoenoplectus americanus (Pers.) Volk. ex Schinz & R. Keller, Sporobolus alterniflorus (Loisel.) P. M. Peterson & Saarela (formerly Spartina alterniflora Loisel., but see Bortolus et al., 2019) and Sporobolus pumilus (Roth) P. M. Peterson & Saarela (formerly Spartina patens (Aiton) Muhl.) in the east coast (Adam Langley et al., 2013; Kirwan and Guntenspergen, 2015; Morris et al., 2013; Mueller et al., 2016; Watson et al., 2015; Wigand et al., 2016). Other studies have also shown that the same species can respond differently, likely due to site-specific and mesocosm design characteristics. For example, biomass decreased linearly with increased percent inundated time for both Schoenoplectus americanus and Schoenoplectus acutus (Pers.) Volk. ex Schinz & R. Keller in the U.S. west coast, as well as for Sporobolus pumilus in different localities along the east coast (Adam Langley et al., 2013; Kirwan and Guntenspergen, 2015). Moreover, mesocosm experiments using Sporobolus alterniflorus and Sporobolus pumilus conducted in the Mississippi river deltaic plain showed that biomass for both species decreased exponentially with increased inundation time (Snedden et al., 2014).

Similarly, Salicornia pacifica Standl. biomass has also been noted to decrease exponentially with increased inundation time in the U.S. west coast (Janousek et al., 2016). There was one study at the Plum Island Ecosystem Long Term Ecological Research (LTER) site where the biomass response to percent inundated time was similar to our results with Sporobolus alterniflorus AGB increasing with percent inundated time (Morris et al., 2013). However, elevation treatments in this mesocosm experiment were mostly distributed around mean high water level, which led these authors to posit that the productivity in this site will initially increase with percent inundated time but ultimately decline once a threshold flooding depth or duration is exceeded (Morris et al., 2013). Similarly, in spite of the higher tolerance to inundation time relative to other species, C. esculenta response to inundation indicates that our mesocosm design may have not covered the full elevation range of biomass production (e.g., no elevation treatment beyond 70% inundated time).

Despite site- and species-specific physiological constraints, discrepancies in biomass accumulation responses to percent inundated time can be explained in part by disparate elevation ranges used among studies. For example, in certain marsh organ mesocosms the top of tallest pipes exceed mean high water level (MHW) by roughly 20 cm (Snedden et al., 2014) while in other studies this difference between highest pipe elevation and MHW was more than twice that distance (Kirwan and Guntenspergen, 2012). High elevations relative to MHW can cause desiccation, facilitating hypersalinity and inducing osmotic stress as discussed elsewhere (Snedden et al., 2014). In our mesocosm design we included elevations representing the upper boundary of the supratidal hydrogeomorphic zone (that is 0.77 m, NAVD88) based on field observations and ranges reported in the literature (Carle et al., 2014; Ma et al., 2018). Similar to previous studies (Kirwan and Guntenspergen, 2012; Morris et al., 2013), aboveground accumulation in our tallest pipes was the lowest across target elevations (Fig. 3a). We attribute the reduced AGB values in our tallest pipes to water stress as soil wetting could only have occurred by occasional splashing or rainfall since water levels did not exceed this supratidal elevation treatment (e.g., 0.77 m NAVD88) during the experiment's duration. Indeed, during multiple maintenance visits we observed completely dry soil inside tallest pipes in our mesocosm. Surface and porewater salinity is not a stress factor for vegetation in WLD as it varies only from 0 to 0.2 ppt (Table 3) and 0.3–0.4 ppt (Li and Twilley, 2021), respectively. This trend was confirmed during the mesocosm deployment (that is, April-October 2018), with mean salinity at 0.22 ppt, never exceeding 0.3 ppt as measured at a nearby (2.4 km away) data collection platform (Station CRMS0479; www.lacoast. gov/crms).

We believe higher AGB in mesocosm pipes situated lower in the tidal frame could be explained by a combination of three main factors. First, C. esculenta is a pioneer species in coastal deltaic floodplains colonizing newly emergent levees along deltaic islands where hydroperiod is higher relative to older levees in the delta's apex (Bevington, 2016; Bevington and Twilley, 2018). Thus, the response we observed in our mesocosm experiment could be reflecting this species' intrinsic capacity to withstand prolonged inundation time. Second, the WLD is an active coastal deltaic floodplain that receives a much higher sediment load compared to other coastal environmental settings such as estuaries or lagoons, also including inactive deltaic floodplains such as Terrebonne and Barataria coastal basins in central Louisiana. Thus, an increase in AGB with depth could have been triggered by higher concentration of total suspended solids (TSS), which can reach over 110 mg/L in river-dominated WLD relative to river-disconnected Terrebonne basin at 13-53 mg/L (Table 3). The relatively higher TSS in WLD could stimulate plants to grow to compensate for light attenuation in the water column. Among shade-avoiding strategies, aquatic plants have developed morphological adaptations to increase photosynthetic efficiency at or below the light compensation depth, including allocating more biomass to the stem and increasing shoot height and specific leaf area (Fu et al., 2012; Hu et al., 2019; Maberly, 1993). Lastly, unlike brackish and saline wetlands,

coastal marshes in active deltaic floodplains are tidally influenced but often lack the presence of salt in microtidal systems. As noted earlier, salinity levels at our study site never exceeded 0.3 ppt (Table 3). Salt triggers the formation of sulfide in wetland soils, which is amplified with increased flood duration. Sulfide is a stressor to marsh productivity (Mendelssohn and McKee, 1988), reducing the diversity of species and constraining the geomorphological displacement of plants to a narrower range in marsh platform elevations (Day et al., 2011). In contrast, tidal freshwater wetland assemblages are more diverse than saline and brackish marshes, and in the absence of inundation time thresholds associated with soil sulfide formation, can colonize a wider range of marsh platform elevations (Twilley et al., 2019).

Plant biomass accumulation in coastal wetlands is also related to soil fertility (Morris et al., 2013). For example, fertilization experiments with Sporobolus alterniflorus, Schoenoplectus americanus and Phragmites australis (Cav.) Trin. ex Steud. have shown an increase in both AGB and BGB in response to nitrogen addition (Adam Langley et al., 2013; Caplan et al., 2015; Morris et al., 2013). While we have not fertilized our mesocosm experiment, all elevation treatments were exposed to equal water source with nitrate concentration reaching nearly $185 \,\mu M \, \text{NO}_3^-$ at our study site (Table 3), which is at least five times higher than pre-industrial natural concentrations (Goolsby et al., 2000). Therefore, a plausible hypothesis is that AGB development in our mesocosm experiment was not related to gradients in nutrient availability since WLD is not a nutrient limited system. BGB increased consistently but did not vary across elevation treatments, indicating that BGB response to percent inundated time in nitrogen-rich settings differ from AGB. In addition to eutrophic conditions, WLD is a young system without marked gradients in soil nutrient concentrations such as N and P, and in N:P ratios (Aarons, 2019; Twilley et al., 2019). This homogeneity in soil fertility and exposure to equal water source may also be a plausible hypothesis to explain why root growth was similar across elevation treatments in our mesocosm. However, these trends in BGB across elevations may have been partly influenced by high variability in initial root mass when C. esculenta plants were transplanted along with undisturbed soil columns they were rooted into. This consistency in BGB values across elevations can also result from a limited growing time. Our experiment was conducted over one growing season (May-October 2018), which could have limited plants' response to elevated nutrient concentrations in WLD. Although biomass tends to correlate positively with nutrient additions, over time, a decrease in the BGB to AGB ratio is expected under eutrophic conditions (Chapin III et al., 1986; Hollis and Turner, 2018; Song et al., 2019; Turner, 2011; Vitousek and Farrington, 1997). Further, space limitation within cores used in these experiments may constrain root development over extended periods of time. For instance, while new cohorts emerge from prior stolons in natural conditions, it is not known that rhizomes and roots will be viable within mesocosm cores from one year to another. These seem to be artifacts inherent to this type of mesocosm experiment which, combined with the plant's life cycle, may obscure the processes controlling BGB accumulation in response to percent inundated time over short periods of time. Indeed, we observed some degree of root bound forming near the surface of the PVC pipes when we harvested biomass at the end of the growing season. Our study draws attention to plausible mechanisms that can explain variations from one experimental approach to another as seen from published studies, offering relevant design modifications to be considered in future marsh organ mesocosm studies.

4.2. Spatial distribution and expansion of C. esculenta

We find that *C. esculenta* areal cover increased $31\% (0.68 \text{ km}^2)$ between 2011 and 2016 (Fig. 4), consistent with previous descriptions on *C. esculenta* expansion rate in the Atchafalaya river delta (Shaffer et al., 1992). Early vegetation surveys carried out nearly a decade after land submergence indicated no presence of *C. esculenta* (or *N. lutea*) in the Atchafalaya River Delta (Johnson et al., 1985), which is located approximately two miles southeast of WLD. The naturally formed Atchafalaya River Delta is the closest 'design' to WLD, having also become subaerial after the near-record Spring flood of 1973, and currently provides the best available early vegetation succession records to contrast with the unique WLD jet plume formation. Subsequent surveys between 1980 and 1986 registered C. esculenta for the first time in 1982, having since become a dominant species, increasing in abundance through time and stabilizing within higher elevational zones (Shaffer et al., 1992). Forty-five years after land submergence, vegetation assessments in WLD showed that lower elevation subtidal and intertidal N. lutea-dominated communities transition to a dense emergent community dominated by C. esculenta at higher intertidal and supratidal elevations (Bevington, 2016). Our results are consistent with this historical analysis, which altogether suggests that C. esculenta plays an important role in the ecological succession and land aggradation in tidal freshwater marshes in coastal Louisiana. Understanding these trajectories are particularly relevant in the context of possible outcomes to planned river sediment diversions to restore the Louisiana's costal basins sediment budget.

Furthermore, we found a noticeable spatial pattern associated with changes in C. esculenta spatial extent. While in 2011 C. esculenta was more abundant towards the apex of WLD islands, in 2016 much of those areas were replaced by Salix nigra Marshall trees following natural secondary succession processes described for the study sites (Shaffer et al., 1992). There was also a marked increase in C. esculenta along the delta's levees for this period. This evident seaward expansion, with marked loss towards the mouth of the outlet, suggests that sediment accretion over the five-year period examined has built up the elevation in the delta apex, favoring other higher elevation species over C. esculenta. Concomitantly, accretion along the islands' levees has increased creating higher elevation platforms to which other tree species such as S. nigra are better adapted to. Our findings are consistent with previous studies that showed that most of the change on WLD occurs down delta as subaqueous platforms continuously accrete, eventually transitioning into subaerial floodplains towards equilibrium elevation (Shaw et al., 2016; Wagner et al., 2017). This empiric framework provides a reasonable explanation for C. esculenta's aerial expansion tracking the growth of and emergence of WLD's subaqueous platforms, reflecting this species ability to cope with higher inundation time as demonstrated by our mesocosm experiment. This successional pattern is consistent with conceptual and empirical models on the role of vegetation controlling soil elevation change and the formation of deltaic islands (Bevington et al., 2017; Bevington and Twilley, 2018; Carle et al., 2014, 2015; Carle and Sasser, 2016; Nardin and Edmonds, 2014; Osterkamp et al., 2012; Wagner et al., 2017). Overall, our findings highlight the ecological role of C. esculenta in successional processes in deltaic tidal freshwater wetlands, controlling soil elevation change by both accelerating allochthonous sediment deposition and autochthonous organic matter production. Altogether, these process are vital to compensate for land loss due to reduced sediment loads to coastal oceans and accelerated sea level rise (Jankowski et al., 2017; Syvitski et al., 2005). While tidal freshwater wetlands generally host diverse plant communities and further investigation using other species is needed to render safer extrapolations from mesocosm to modeled reality, our findings clarify expected biotic feedbacks of newly emerging over existing marshes in response to river sediment diversions.

5. Conclusions

Our results offer important insight to the current uncertainty about the fate of coastal marshes in response to planned river sediment diversions. To our knowledge, previous marsh organ mesocosm experiments have thus far only examined brackish or saline marsh taxa situated on transgressive coastal environmental settings, which includes inactive delta floodplains such as those in southeastern Louisiana (e.g., Breton Sound, Barataria coastal basin, see Snedden et al., 2014 for details). In general, these studies show that, regardless the target species, biomass decrease with inundation time following linear (Adam Langley et al., 2013; Kirwan and Guntenspergen, 2015; Morris et al., 2013; Schile et al., 2017; Wong et al., 2015), exponential (Janousek et al., 2016; Mozdzer et al., 2016; Snedden et al., 2014), or parabolic (Adam Langley et al., 2013; Alizad et al., 2016, 2018; Janousek et al., 2016; Kirwan and Guntenspergen, 2015; Morris et al., 2013; Mueller et al., 2016; Peng et al., 2018; Watson et al., 2015, 2017; Wigand et al., 2016) trends as reviewed earlier. Here, we innovate by using a non-graminoid species within the context of marsh organ mesocosm experiments to assess the effects of percent inundated time in plant biomass accumulation in active coastal deltaic floodplains. We show how biomass accumulation of C. esculenta, a dominant tidal freshwater wetland species in emerging coastal deltaic floodplains, responds positively to increased inundation time. Our spatial analysis is consistent with earlier field-based assessments that showed that C. esculenta colonizes newly emerging levees, accelerating elevation gain and leading to more stable tree-dominated landscapes (Carle et al., 2015; Shaffer et al., 1992). These ecogeomorphic feedbacks (e.g., plant biomass allocation in response to and as a driver of sediment deposition; see Ganju et al., 2020; Ma et al., 2018; Nardin and Edmonds, 2014) are extremely important to maintaining stable shorelines, particularly in the lower Mississippi river delta, which has lost approximately 500,000 ha of land since 1990 (Shaffer et al., 1992). However, river sediment diversions designed to build wetlands will shift the existing geomorphology from a tide-dominated brackish/saline marsh to newly emerging tidal freshwater wetland communities, with high plant species diversity and higher ability to develop on multiple wetland platform elevations. Our findings are relevant in the context of planned Louisiana coastal restoration activities, supporting the notion that designed ecosystems can be strategic to ensure perpetuity of coastal populations and economic and recreational activities in the land-ocean interface.

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CRediT authorship contribution statement

Andre S. Rovai: Conceptualization, Formal analysis, Writing – original draft. Robert R. Twilley: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. Alexandra Christensen: Writing – review & editing. Annabeth McCall: Writing – review & editing, Conceptualization. Daniel J. Jensen: Formal analysis, Writing – review & editing. Gregg A. Snedden: Writing – review & editing, Formal analysis. James T. Morris: Writing – review & editing. John A. Cavell: Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2022.107784.

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