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Plant Community Response to the Combined Effects of Elevation, and Simulated Nutrient and Sediment Loading in Sagittaria Lancifolia-Dominated Wetlands

Donnie Day
Louisiana State University and Agricultural and Mechanical College

PLANT COMMUNITY RESPONSE TO THE COMBINED EFFECTS OF ELEVATION, AND SIMULATED NUTRIENT AND SEDIMENT LOADING IN SAGITTARIA LANCIFOLIA-DOMINATED WETLANDS

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ABSTRACT

Coastal wetlands are experiencing threats to their long-term sustainability brought about by the combined effects of relative sea-level rise and human modifications to hydrology, sediment delivery and nutrient loading. Restoration and management strategies can include adding sediment to the surface of deteriorating marshes to facilitate positive feedbacks among elevation, plant productivity, sediment trapping, and accretion; however, if delivered using nitrate-enriched river waters, belowground biomass and soil organic matter pools may be negatively affected, resulting in the acceleration of wetland loss. Overall, there is limited information on the combined effects of nutrient loading, sedimentation, and flooding dynamics in regulating feedbacks among marsh plant community composition, productivity, and soil organic matter accumulation. For this study, we tested the hypothesis that elevation, sedimentation, and nutrient-enrichment interact to affect wetland community composition and plant productivity. Plant productivity was generally predicted to be greater with a combination of less flooding, greater sedimentation and nutrient-enrichment. To test these hypotheses, 96 marsh soil plugs were collected from a *Sagittaria lancifolia*-dominated oligohaline marsh and placed them into a greenhouse mesocosm. Plugs experienced a simulated diurnal tide of 15 cm and were subjected to a combination of three treatments for two growing seasons (n = 8): 1) an elevation treatment of low (20 cm below MHW) or high (5 cm below MHW) 2) sediment deposition treatment of 0 (control), 5, or 10 cm and 3) no nutrient-enrichment (control) or a nutrient-enriched treatment of 2.0 mg/L N as $(CaNO_3)_2$ and 0.3 mg/L P as PO_4. Measurements included water column and porewater nutrient concentrations, species richness, species-specific stem densities and heights, aboveground biomass, root ingrowth, soil organic matter content, and bulk density. We found that wetland plant productivity and communities are limited by flooding dynamics, but sediment

and nutrient enrichments can improve soil environmental conditions that stimulate plant growth. Interaction between reduced flooding and nutrient enrichment generally increase aboveground productivity but did the opposite when flooding durations increase. Interestingly, reduced flooding regimes interacted with nutrient enriched conditions to created positive effects on ingrowth fine and large roots at specific soil depths. To our knowledge this is the first study to describe this interaction with soil deposition. While no three-way interaction was observed, this study provides valuable information on how flooding, sediment deposition, and nutrient loading affects wetland plant community dynamics.

INTRODUCTION

Coastal wetlands provide a variety of important ecological services of high economic value including habitat for recreational and commercial species of fish and wildlife, water filtration including the sequestration of pollutants such as carbon and nutrients, flood and storm protections, and groundwater recharge (Reddy et al., 2010; Barbier et al. 2011). Constanza et al. (1997) estimate that the total global value of these goods and services is approximately $15.5 trillion representing 46% of the estimated total value of goods and services provided by all ecosystems worldwide. Coastal wetlands are unique in that they rely on a combination of plant production and sediment input to maintain their structure, ecological functions, biodiversity, and soil stability (DeLaune et al. 1981, White and Howes 1994, Drake et al. 2009). Therefore, marsh morphology is strongly influenced by local environmental conditions that influence plant productivity and sediment supply including hydrologic regime, sediment and nutrient availability, and salinity. Yet rapid environmental change from the combined effects of sea-level rise, human modifications to river and tidal hydrology, sediment deprivation, and anthropogenic nutrient loading may threaten their long-term sustainability and associated ecosystem services. It is therefore imperative to assess the factors in greenhouse mesocosm studies to better understand the complex feedbacks among plant community composition, productivity, and soil properties to better inform coastal wetland restoration and management.

Like in many of the world's river deltas, the Mississippi River deltaic wetlands were formed by vegetation established on river sediment deposits (Roberts, 1998). The Mississippi River historically flowed through distributaries, overflowing banks and natural levees creating delta lobes. Over time, as the river changed course, a complex of several hydrologic basins separated by active or abandoned distributary ridges were formed (Day et al., 2000). Currently,

however, river flow is restricted by human modified flood control structures, such as upstream dams and artificial levees, resulting in an overall reduction in river water and sediment supplied to the delta (Boesch et al., 1994). Moreover, the river delta has been further modified for navigation, oil and gas exploration, and development over the years (Keddy et al., 2007). It is predicted that approximately 5,640 km^2 of wetlands have been lost since the early 1930's as a result of these modifications and concurrent geologic subsidence and sea-level rise (Gagliano et al., 1987; Couvillion et al., 2017). Wetland loss in the Mississippi River delta continues at an approximate rate of 28 km^2 yr^{-1} due to a combination of natural processes such as delta abandonment, subsidence, sea level rise, wave erosion, herbivory, hurricanes, geologic faults, in addition to human activities including levee building, hydrologic isolation, land reclamation for agriculture and industry, canal dredging, resulting in salt water intrusion, boat-induced shoreline erosion, herbivory by invasive species, and pollution (Boesch et al., 1994; Turner 1997; Day et al., 2000). It has been predicted that unless allochthonous inorganic sediment is re-introduced to the coast, an additional 10,000-13,500 km^2 will be submerged by the year 2100 (Blum and Roberts 2009). One proposed method for reducing coastal land loss is to reconnect the Mississippi River to its delta through river sediment diversions (Mitsch et al. 2001, CPRA 2017). Sediment diversions will be designed and engineered to transport river water and sediment from the Mississippi River to deteriorating wetland basins through managed openings in the levee with the goal of reducing wetland loss by increasing sediment deposition and stimulating plant growth and accretion (Day et al. 2007). A concern, however, is that diversions will also introduce high nutrient loads via Mississippi River water to existing marshes, which may cause a reduction in root productivity (Valiela et al., 1976; Darby and Turner, 2008a, b; Hines et al., 2006; Davey et al., 2011; Ket et al., 2011; Deegan et al., 2012; Graham and Mendelssohn, 2014,

2016) and increase soil organic matter decomposition through nitrate-reduction (Anisfeld and Hill, 2012; Deegan et al., 2012). In order to offset deltaic wetland losses, river diversions designed to introduce sediment to deteriorating coastal wetland basins are being planned (CPRA 2017). The response of wetland plants to sediment addition through river diversions is predicted to be generally positive yet may depend on species-specific tolerances to inundation and river-borne nutrient-loads (Elsey-Quirk et al. 2019). Therefore, informed predictions of complex wetland plant and soil responses to restoration require examining potential interactions of multiple environmental conditions simultaneously.

Wetlands are recognized for their importance in sequestering and transforming land-based nutrients (Nixon, 1980; Reddy et al., 1999). Over recent decades, anthropogenic change brought about by agriculture and wastewater run-off has increased the supply of available nitrogen (N) and phosphorus (P) to coastal areas around the globe. Coastal wetlands can be sensitive to excess nutrient loading, especially N, because plant growth is generally N-limited (Sullivan and Daiber 1974; Valiela and Teal 1974). Positive relationships between nutrient enrichment and aboveground plant productivity have been shown in variety of field and greenhouse studies around the globe, ranging from tidal freshwater, intermediate, brackish, and salt marshes (Valiela and Teal 1974; Broome et al., 1983; Elser et al. 2007; Morris et al., 2013; Graham and Mendelssohn, 2010; Shaffer et al., 2015). Belowground plant production; however, has exhibited variable response to nutrient-enrichment likely due to different nutrient applications, environmental conditions and species (Graham and Mendelssohn 2015). In a salt marsh in Plum Island Estuary, MA, nitrate enrichment of 10 times that of ambient concentrations resulted in a decrease of bank stabilizing roots and an increase of organic matter decomposition, which led to the collapse of marsh edges (Deegan et al., 2012). In low salinity marshes,

productivity responses to nutrient-enrichment may depend on changes in plant species composition. Often nutrient-enrichment results in an overall decline in community diversity (Tilman 1987; Huenneke et al. 1990, Schlesinger 1994) with variable consequences for primary productivity (Bowman et al. 1993; Verhoeven et al. 1993; Morris et al., 2013). In low salinity marshes under nutrient-rich conditions, species such as *Phragmites* spp. and *Typha* spp. can displace native species resulting in a loss of biodiversity (Rickey and Anderson 2004). In relatively species-diverse and lower salinity marshes, nutrient-enrichment may lower species richness (Smith et al. 1999, Bobbink et al. 2010), resulting in the dominance of a few highly productive species (Suding et al. 2005).

Tidal wetland hydrology and therefore marsh elevation plays a major role in wetland stability, as productivity and survivorship of marsh macrophytes tend to decline with prolonged inundation (Voss et al., 2013). Diversions will introduce freshwater, reduce salinity, and shift species composition in places away from species typical of salt or brackish water habitats to less salt tolerant species (Morris et al., 2013). Plants are strongly influenced by inundation with species-specific responses in avoiding or tolerating anoxic conditions (Burdick and Mendelssohn 1987). Soil waterlogging can severely limit root respiration affecting plant metabolism and growth of even highly adapted species (Kozowski 1984, Mendelssohn and Burdick 1988). For example, *Spartina alterniflora,* a dominant low elevation salt marsh plant, showed significant declines in shoot density when inundated duration increased to 24% more than its normal inundation time (Voss et al., 2013) and an overall decrease in above and belowground biomass (Snedden et al., 2015). Likewise, total biomass of *Spartina patens* was reduced by 40% when flooding deposition increased to 20 cm above soil surface when compared to 5 cm (Spalding and Hester 2007). Unlike salt and brackish marshes, freshwater marshes have greater species

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diversity and potential variability in species-specific responses which may increase or decrease

aboveground production (Howard and Mendelssohn 1995; Martin and Shaffer 2005). For

example, at varying water levels (i.e., -10, 5, and 20 cm above the soil surface), *Sagittaria*

lancifolia increased production by 450 g under low flooding (e.g -10 cm), however as water level

increased (i.e. 5 and 20 cm), so did the production of a co-dominant freshwater marsh species

Panicum hemitomon (Spalding and Hester 2007). Species-specific studies have identified species

responses to increased inundation, yet, many systems have complex plant community dynamics.

Therefore, there is a need to understand how different drivers interact to influences changes in

composition and ultimately primary productivity in order to reverse the trajectory of marsh loss,

increase soil surface elevation, and promote plant productivity.

The stability of coastal wetlands is largely a function of the balance between organic

matter and sediment accretion, marsh subsidence, and sea-level rise (Mitsch and Gosselink

2000). The direct supply of river sediment through diversions has the potential to increase marsh

elevation, soil aeration in the root zone, plant productivity, and soil accretion (DeLaune et al.

1990; VanZomeren et al., 2018). Previous research suggests that sediment deposition through

thin layer sediment placement improves conditions for plant growth and marsh resiliency by

promoting physical stability through increased soil bulk density, and vegetation establishment

(Wilber 1992 b, c; Baustian and Mendelssohn 2015; Berkowitz et al., 2019). However, sediment

deposition influences whether existing plants will be smothered or grow through the

depositional layer with high sediment loads potentially resulting in soils becoming relatively dry,

oligotrophic, and more saline, in which can cause vegetation stress, sparse plant cover, and low

productivity (Slocum et al., 2005; Stagg and Mendelssohn 2010). Sediment depositions of 8, 15,

and 23 cm enhanced total biomass of *S. alterniflora,* but, when in excess of 30 cm, total biomass

was reduced and above 60 cm, burial caused complete plant mortality (Reimold et al. 1978). In freshwater wetlands, sediment deposition can be detrimental even at modest deposition s (LaSalle 1992). Conversely, in other studies, sediment additions of 1-5 cm showed no effect on emergent species productivity in a mesocosm studies containing 25 herbaceous plant species (Geho et al., 2007; Kercher and Zedler 2004). Presumably, too little sediment does not provide sufficient positive effects on elevation and soil physiochemistry to counter the negative effects of excessive flooding (Jurik et al. 1994; Wang et al. 1994). Overall, disturbance due to burial, has the ability to disrupt ecosystem functioning, resulting in a structural change of the plant communities (Ray 2007; Berkowitz et al., 2019).

The input of fresh water, mineral sediment, and nutrient run-off will likely change plant community composition in fresh or brackish peat-dominated wetlands resulting in a complex cascade of events (Morris et al., 2013). For example, nutrient enrichment increases flood tolerance in some wetland species like *Taxodium distichum* (Effler and Goyer 2006) and increases productivity in others (Langley et al. 2013). To examine the effects of inundation, sediment deposition, and nutrient enrichment and their interaction on species community composition, above and belowground production, and soil organic matter content, a controlled greenhouse mesocosm study was conducted focused on oligohaline *S. lancifolia*-dominated wetlands. We hypothesize that lower elevations, and therefore greater flooding depths and duration, will alter species composition in favor of lower marsh species thereby resulting in an overall decrease in net above-and belowground primary production as compared to higher elevations. We expect that nutrient enrichment will alter allocation patterns in favor of aboveground productivity, while sedimentation will favor belowground production. We also predict that nutrient-enrichment and sedimentation will reverse some of the impacts of low

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elevations on species richness and composition and productivity. Thus, by simultaneously

examining the potentially interactive effects of multiple environmental conditions brought on by

river diversions, we can generate improved predictions of responses and recovery in these

complex natural systems.

METHODS

Site description and experimental design

Oligohaline marshes are a dominant wetland type in coastal Louisiana, representing 26% (422,000 ha) of the total wetland area (1.65 million ha) and are most likely to be influenced by the diversions (Field et al. 1991, Sasser et al. 2008). Unlike salt marshes and mangrove forests that contain relatively few plant species, oligohaline wetlands are diverse (Visser et al. 1998). *Sagittaria lancifolia*, a dominant species occupying freshwater marshes in the southeastern United States, is a perennial herb that grows in dense stands and can extend into intermediate marshes (Pezeshki et al. 1987). Leaves of *Sagittaria lancifolia* are arranged in basal rosettes and, presumably, the leaf primordium is responding at least partly to environmental conditions within the range of plasticity within a given genotype (Wooten 1986). Freshwater inputs from diversions can increase flooding, which may stress existing vegetation and select for more flood-tolerant species, confounding nutrient effects. In recent long-term studies, *Sagittaria lancifolia* was able to adapt to increased inundation of 15-cm and 30-cm, which did not affect the standing crop, as indicated by aboveground and total belowground biomass making it ideal for marsh restoration (Howard and Mendelssohn 1995; Martin and Shaffer 2005).

In March 2018, 96 marsh soil plugs removed by polyvinyl chloride (PVC) core barrels (15.24 cm diameter by 40 cm height) were collected in a *Sagittaria lancifolia*- dominated oligohaline marsh in Barataria Basin, Louisiana (Figure 1). The sampling areas were located randomly along a 1-km transect on the east and west sides of the canal (Figure 1). According to the nearest Coastwide Reference Monitoring System (CRMS) Station (4245; Lat, Long: 29.67202, -90.13549) *Sagittaria lancifolia* and *Panicum repens* were the dominant species with

Vigna luteola, Polygonium punctatum, Spartina patens, Eleocharis macrostachya and others present throughout the marsh.
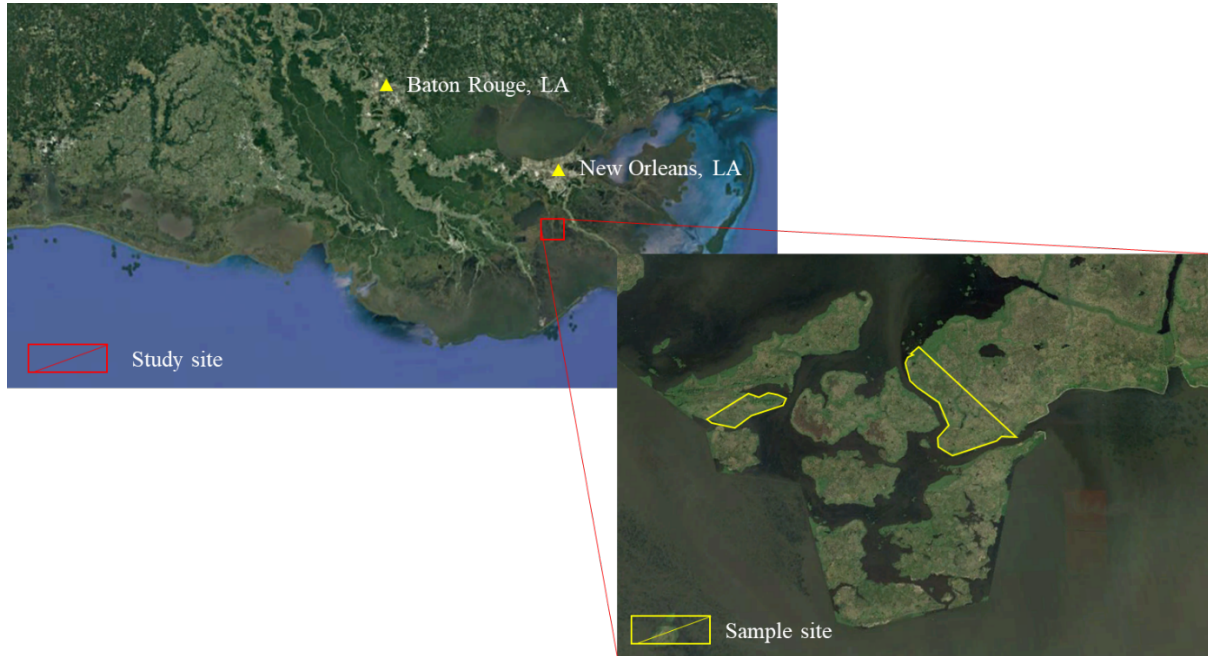
Figure 1. Location of study site (red) in upper Barataria Basin, LA showing sample areas (yellow polygons) of plug extraction in a *S. lancifolia*-dominated oligohaline wetland.

Each plug was collected such that *S. lancifolia* was centered in the middle of the core. All aboveground plant material was clipped before plug extraction. Plugs were extracted and sealed at the bottom using a flexible PVC cap and transported to the Louisiana State University greenhouse facility in Baton Rouge, LA. Core barrels were designed with 42 evenly space, 1 mm holes to allow for lateral water flow once in mesocosm. Each plug was fitted with a 2 mm fiberglass screen (Phifer, Inc), secured to limit sediment loss, and allowed to acclimatize to greenhouse conditions for approximately two months from March to May 2018. Plugs were placed in a series of eight 1502 L mesocosm mesocosm tanks (4.39 m length x 0.46 m width x 0.89 m height), which were each plumbed to a reserve carboy to create a closed system for each

paired tank-carboy. In a split-plot experimental design, one of two nutrient treatments (ambient or nutrient enriched), were randomly assigned to each mesocosm (whole plot factor), within which plugs were assigned to one of two flooding treatments through elevations (low and high), and one of three sediment treatments (0, 5, or 10 cm; Figure 2). Using a tidal control system (Aquabiotech, Inc.), we simulated a semi-diurnal tide with a 15 cm tidal range in each tank. Water was added periodically throughout the study period to counter loss through evapo-transpiration.
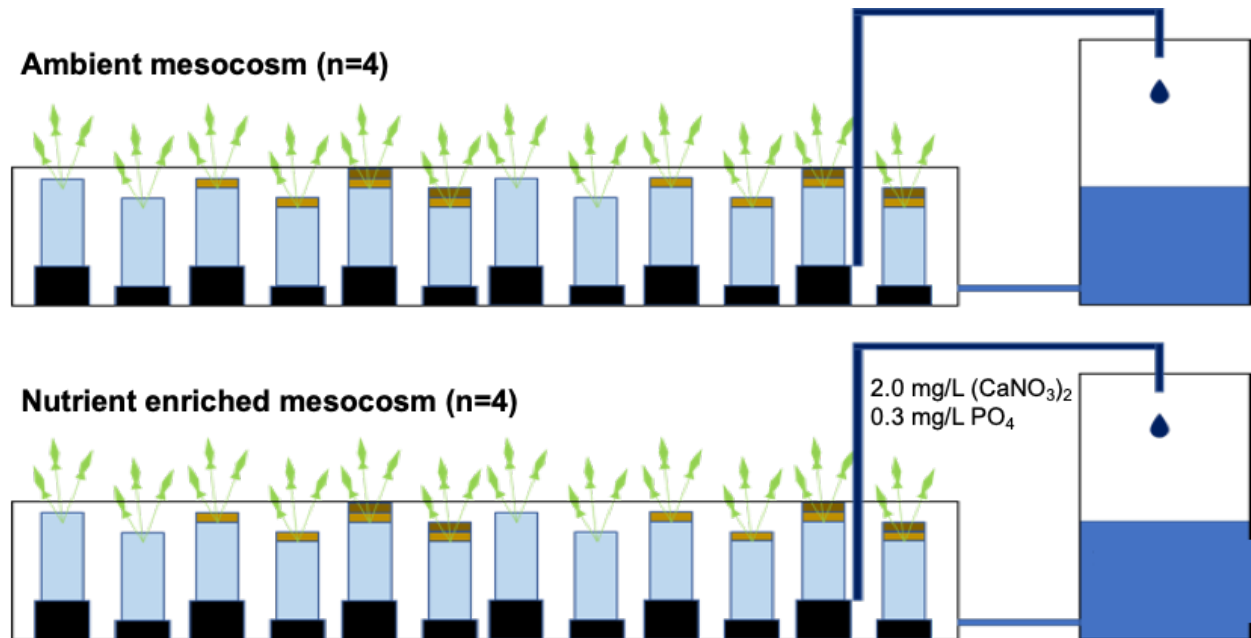
Figure 2. Full factorial experimental design of greenhouse mesocosms including elevation (black boxes), sediment deposition amount (brown layers), and nutrient enrichment treatments (n=4 mesocosm tanks). Nutrient enrichment was applied at 2.0 mg/L Nitrate (N) and 0.3 mg/L Phosphorus (P).

Treatments

Elevation-For the duration of the experiment each plug was subjected to one of two flooding treatments through elevation differences: low (20 cm below MHW) or high (5 cm below MHW). Elevation treatments were established using modified milk crates that were 15 cm different in height (Figure 3). There were six elevation treatment replicates per mesocosm tanks.

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Sediment deposition- Only in the first year were plugs subjected to one of three sediment applications; 0 (control), 5 cm, 10 cm with sediment applied at a rate of 1 cm/14 days until target deposition of either 5 cm or 10 cm was reached (Figure 3). Each sediment treatment was replicated two times per elevation treatment in a single mesocosm.

Nutrient-enrichment- In May 2018 and 2019 of the experiment mesocosm tanks (n=4) were enriched with a nutrient-enriched treatment of 2.0 mg/L (32.25 uM) N as $(CaNO_3)_2$ and 0.3 mg/L (3.15 uM) P as PO_4. Nutrients in granular form were added directly to the water column to mimic the nutrient pathway from dissolved inorganic forms in the water column. These nutrient concentrations were slightly above the nutrient concentrations measured through a freshwater diversion of the Mississippi River in 1997 (1.28 mg/L mg N, and 0.05 mg/L P) (Roy et al. 2013). Ambient mesocosm tanks received no nutrient enrichment and were replicated in four mesocosm tanks (n=4) as controls.
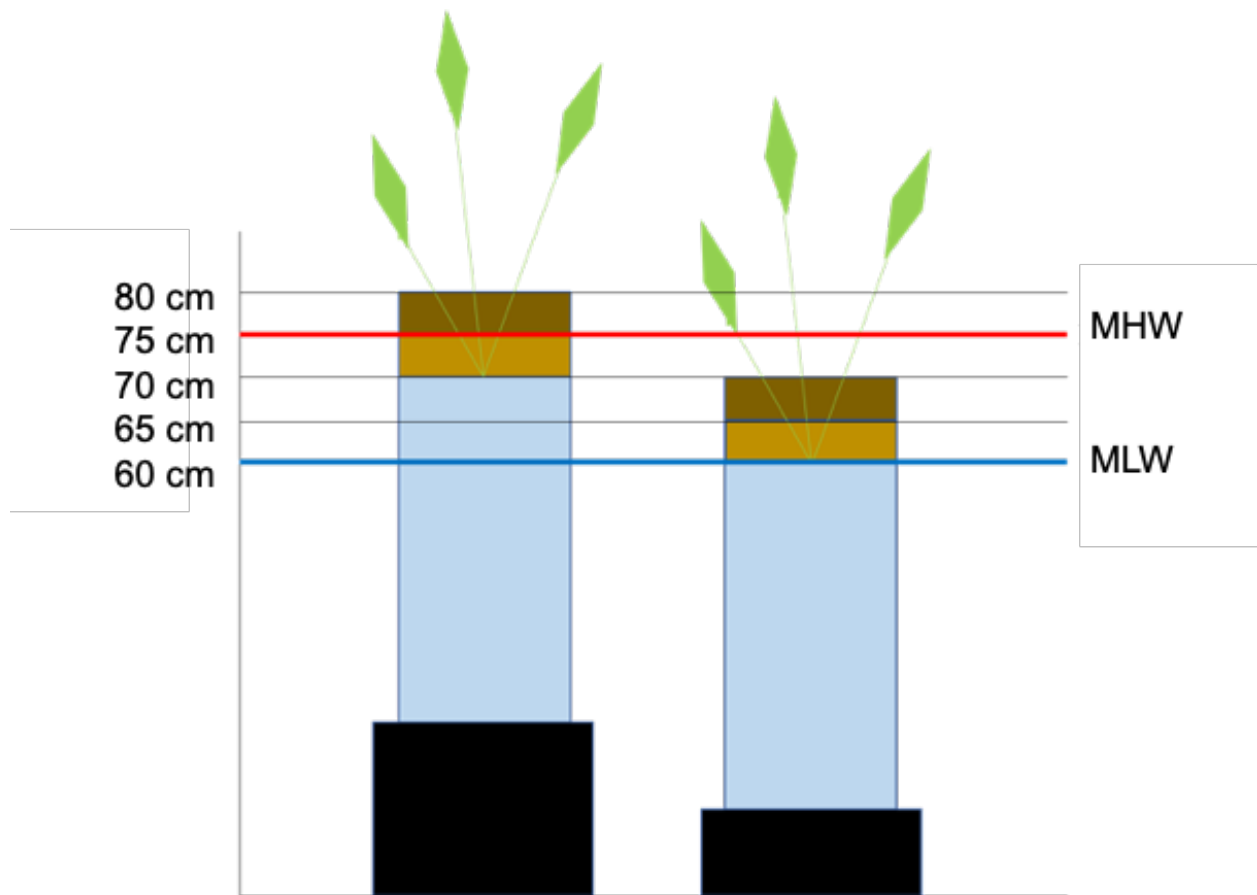
Figure 3. Diurnal tidal heights relative to elevation treatments (5 cm and 20 cm **(--)** below mean high water (MHW), and -10 cm and 5 cm **(--)** below mean low water or MLW), and sediment treatments at 5 and 10 cm sediment additions (brown layers).

Measurements

Water chlorophyll-a and nutrient concentrations- Water column nutrient concentrations in each

tank were measured every three months over the course of the first growing season following

nutrient enrichment. Tank water was collected by stirring the water column and collecting 0.25 L

of water in a cubitainer. Water samples (500 mL) were then filtered through a 25 mm Whatman

GF/F and frozen prior to analysis. Samples were processed using an autoanalyzer for

nitrite+nitrate-N, ammonium-N and phosphate-P concentrations. (OI Analytical Flow Solutions

IV model #). Chlorophyll-a concentrations were measured in the water of each tank bi-monthly

over the first growing season following nutrient enrichment to examine nutrient enrichment

impacts on algal biomass. Tank water was collected by stirring the water column and collecting

0.25 L in a cubtainer. Water samples (500 mL) were then filtered through a 25 mm Whatman

GF/F glass microfiber filter.

Porewater nutrient concentrations- Porewater samples were extracted using two sippers that were

installed in August of 2018 for each plug and inserted at 10 and 20 cm deposition s. Porewater

nutrient concentrations were measured once for each treatment per tank (n=4) at the end of the

first growing season (January 2019). Water samples were then centrifuged for 10 minutes at

1100 g, supernatant was filtered through a 25 mm Whatman GF/F microfiber filter and frozen

prior to analysis. Samples were processed using an autoanalyzer for nitrite+nitrate-N,

ammonium-N and phosphate-P concentrations. (OI Analytical Flow Solutions IV model #).

Plant species richness, composition and relative dominance- Species richness was recorded in

each plug bi-monthly from 2018 May - 2019 January and monthly from 2019 May- 2019

October. Species composition was determined from stem densities measurements. Species-

specific stem densities were determined by counting the number of stems present in each core

per species. A combination of foliar and basal coverage was used to determine percent cover for

each species. Average heights were measured to the nearest centimeter by measuring the longest

two stems and the smallest two stems for each species.

Aboveground biomass- To measure total productivity aboveground, dead senesced biomass was

collected periodically from each plug and summed along with harvested biomass for a

cumulative quantity of aboveground production. After 540 days in the treatments, on October 30,

2019, vegetation was clipped at the soil surface and sorted by species. Plant material was then

dried to a constant mass at 60°C and weighed. As all vegetation was clipped at the beginning of

the study, aboveground productivity was calculated as grams dry weight per year based on the 540-day study period.

Ingrowth rate -Root productivity was measured using in-growth bags with a 1 mm mesh size (2.57 cm diameter x 15.24 cm height) Fig. 4. In-growth bags placed in plugs without sediment additions were filled with 71.48 g of root and rhizome-free marsh soil (organic) collected from the oligohaline study site. The 5 and 10 cm sediment deposition treatments received 47.65 g and 23.82 g of root and rhizome free marsh soil and 23.82 and 47.65 g of Mississippi River silt (mineral) which, mimic sediment treatments. To prevent contamination and ensure the organic and mineral sediments were homogenized, the in-filled material was pasteurized using an autoclave (model# 2540M Tuttmoner Brinkman) at 121 °C for 25 minutes. The material was then sieved through a 2 mm mesh screen and stored in 2-gallon zip-lock bags until bag construction. Ingrowth bags were inserted into each plug in April 2019 by extracting a 2.5 cm x 6 cm PVC soil core from the center of each sample. Ingrowth bags were harvested in October 2019. In the lab, ingrowth bags were rinsed, trimmed of external roots, and material was then gently washed over a 2 mm mesh sieve, separated into categories of live (fine roots, large roots, rhizomes) or dead (fine), and dried to a constant mass at 60° C and weighed. Fine organic matter was distinguished from larger root material by size fractionation; all material that washed through 2.0 mm and retained on 0.71 mm mesh was considered fine.

Figure 4. Ingrowth sediment treatment bags with mineral and organic sediment infill for control (C), 5 and 10 cm sediment additions treatments.

Soil bulk density and organic matter content- All soil cores were sectioned into 2 cm sections to 16 cm, 4 cm sections to 20 cm, then 5 cm sections to 35 cm. Bulk density was measured by removing a 2.5 diameter cylinder from each section. Bulk density samples were dried to a constant weight at 60° C. Bulk density was calculated as the dry weight divided by the volume of the cylinder subsample (g cm³). The dry sediment samples were split in half, re-weighed, then placed in a muffle furnace at 550° C for four hours and re-weighed upon cooling to room temperature to determine the proportion (Wt%) of sample lost on ignition (LOI), a proxy for organic matter content.

Data Analysis

To test the main effects and interactions of elevation, sedimentation deposition and nutrient enrichment on water column nutrients, porewater nutrients, species richness, species-specific responses (stem densities, stem height, and aboveground biomass), total stem densities, stem heights, aboveground biomass, loss on ignition, bulk density, and ingrowth (fine, large,

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rhizome, total live, and dead), a split-plot nested design was constructed using JMP version 15.1, SAS Institute Inc. The mesocosm tanks were a random effect nested within nutrient treatment. A full factorial three-way analysis of variance (ANOVA) was performed using the nested nutrients by tank, elevation (low and high), and sediment (0 cm, 5 cm, 10 cm). A repeated measures ANOVA was used on continuous data (i.e., species-specific stem densities and height) collected throughout the two study. Data averaged over two months during peak stem density (September and October) of Years 1 and 2 where used to determine treatment effects and interactions on species richness, species-specific responses, stem densities, and stem heights. Data were tested for normality and transformed by either log or logit functions when necessary to meet the assumptions of ANOVA. Post hoc differences were analyzed using Tukey's honestly significant difference test.

Treatment effects on vegetation community in Years 1 and 2 were tested using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; Anderson and Ter Braak 2003) using the package PRIMER 6.1.15 (Clarke and Gorley 2006). Relative abundance of species was based on species stem density in June of each year. The PERMANOVA model was constructed using the previously described split plot model. BrayCurtis (1957) similarities were used to calculate compositional dissimilarity between treatments and species using stem density abundance data. Euclidean distances were used to calculate the dissimilarity matrices. Plant community data (species identified) for each treatment were assessed with non-metric directional scaling (nMDS) ordination (McCune et al. 2002). Species with a Pearson Correlation Coefficient of greater than 0.5 were overlaid on the ordination plots as vectors. Data were transformed using a square root transformation prior to analysis. All statistical analyses were tested based on $p < 0.05$.

RESULTS

Tank water- Nutrients were added to enriched mesocosm tanks in concentrations of 32.3 μM $(CaNO_3)_2$ and 3.2 μM PO_4 in May 2018 and 2019. Nutrient and chlorophyll-a concentrations were measured in tank water four times from June to February 2018 (Fig. 5 a-d). By June 2018, the nitrate + nitrite-N (NO_x) and ammonium (NH_4) concentrations averaged 4.99 and 3.15 μM respectively in enriched mesocosm tanks, which were approximately two times greater than in control mesocosm tanks. Concentrations of nitrate-N and ammonium-N in enriched mesocosm tanks declined to levels similar to or less than control mesocosm tanks by December (210 days; Fig. 5 ab). Phosphate (PO_4) concentration was similar between enriched and control mesocosm tanks during the measurement period averaging 3.20 μM in June 2018, indicating efficient assimilation of available PO_4 (Fig. 5c). Algal biomass, measured as chlorophyll-a, mesocosm tank water was stimulated by nutrient-enrichment and was 1.25 times greater than in control mesocosm tanks until December 2018 (Fig. 5d).
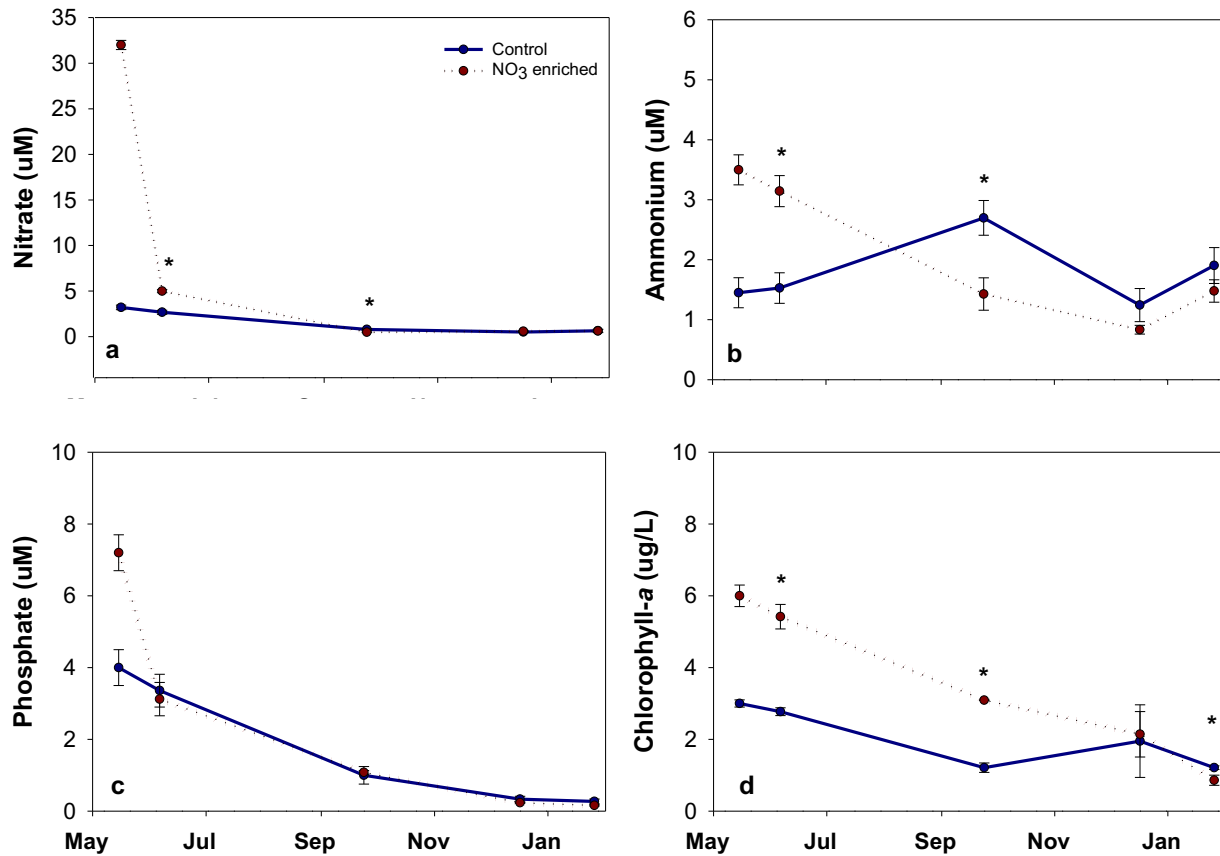
Figure 5. Concentrations of nitrate-N (a), ammonium-N (b), phosphate (c), and chlorophyll-a (d) over time in control and enriched mesocosm mesocosm tanks from June 2018 to February 2019. Nutrients in the form of $(CaNO_3)_2$ and PO_4 at concentrations of 32.25 µM and 3.16 µM respectively, were added in May 2018. Values are means ± standard errors and significant differences between control and enriched mesocosm tanks are shown by * ($p < 0.05$) ($n = 4$).

Porewater nutrient concentrations- Porewater was collected from each plug in January 2019 at

10 and 20 cm depths, approximately eight months following the first nutrient addition in 2018

and four months prior to the second enrichment. In January 2019, mean porewater concentrations

of NO_x were 0.30 µM lower than in tank water, while NH_4 and PO_4 concentrations were 1.30

and 0.03 µM greater than tank water, respectively (Table 1). Elevation and sediment treatments

affected porewater nutrient concentrations mainly at the 10 cm deposition. At 20 cm, porewater

nutrient concentrations were similar among treatments. NH_4 concentrations at a deposition of 10

cm averaged 1.5 µM lower when 5 and 10 cm of sediment was deposited on the surface ($F_{2, 30}$ =

6.39, P=0.0049; Fig 6a). Porewater PO_4 concentration at 10 cm deposition was affected by a significant interaction between elevation and sediment deposition treatment ($F_{2, 83} = 3.61$, P=0.0313; Fig. 6b). At low elevations, PO_4 concentrations with 10 cm of sediment were greater than those without sediment. At high elevations, PO_4 concentration was similar across sediment treatments.

Table 1.Tank and porewater concentrations of nutrients under control and nutrient enrichment. Values are means ± standard error (SE) taken in January 2019.

	Tank water column (µM)				Porewater (µM)			
Nutrient	Control	± SE	Enriched	± SE	Control	± SE	Enriched	± SE
NO_x-N	0.63	0.15	0.62	0.18	0.34	0.02	0.34	0.02
NH_4-N	1.90	0.29	1.48	0.18	2.99	0.24	3.05	0.21
PO_4	0.27	0.06	0.15	0.01	0.26	0.01	0.31	0.018
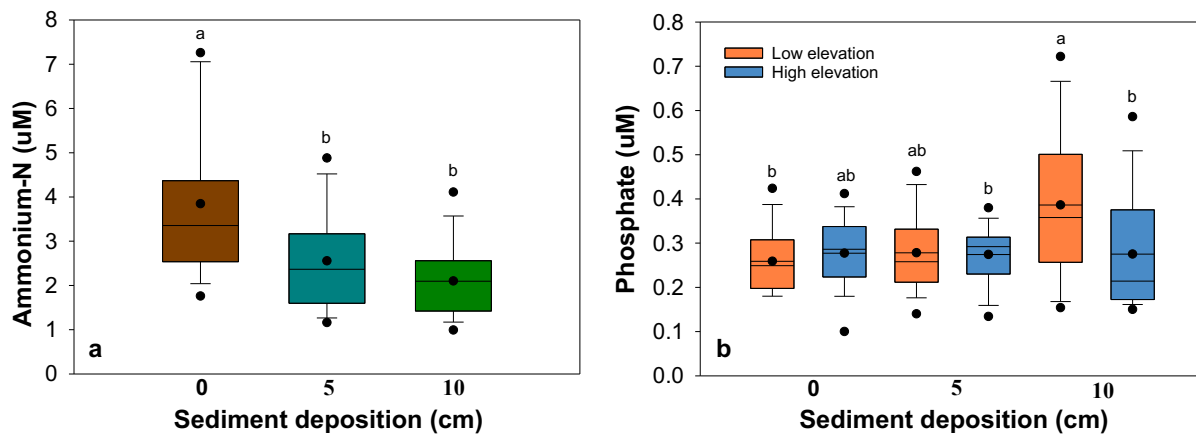
Figure 6. Porewater ammonium- N concentration in response to sediment deposition treatment (a) and porewater phosphate concentration in response to elevation and sediment deposition treatment (b). Porewater was extracted from 10 cm deposition. Values are means ± standard error (n = 4).

Total stem density- Total stem density across species was similar among treatments at the start of the experiment, averaging 20 ± 5 stems/plug (Fig. 7ab). Stem density changed seasonally among

treatments over the two-year period (Fig. 7 cd). Generally, stem densities were relatively high in September 2018 and October 2019. Stem density with 0, 5, and 10 cm of sediment deposited was 37 ± 2, 46 ± 4, and 72 ± 6 stems/plug, respectively in Year 1 and 62 ± 5, 78 ± 8, and $100 \pm 1 0$ stems/plug, respectively in Year 2. High elevation treatments had an average stem density that was 30 stems/plug greater than those at low elevations by the end of the study.
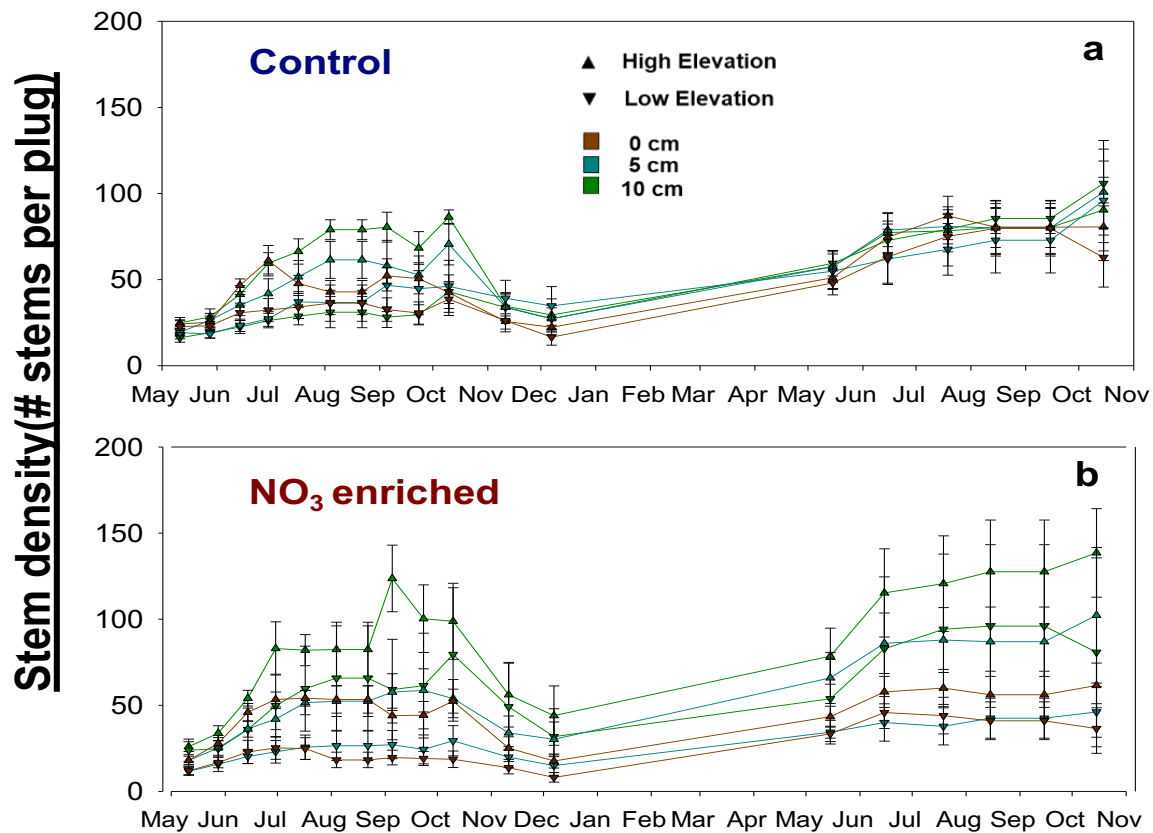
Figure 7. Stem density over time (May 2018- October 2019) by elevation (up and down triangles) and sediment treatment (0, 5, and 10) in control conditions (a) and nutrient-enriched conditions (b). Values are means ± standard error.

In Year 1, stem densities were on average 33 stems /plug greater at high elevations than at low elevations (Fig. 8a) and nutrient enriched plugs receiving 10 cm of sediment had approximately double the stem density of those receiving less sediment (Fig. 8b). Under ambient nutrient conditions, sediment deposition had no effect on stem densities ranging between 41 ± 3

and 53 ±5 stems /plug (Fig. 8b). In Year 2, stem density was an average of 23 ± 5 stems/ plug

greater than in Year 1. Elevation did not affect densities in ambient nutrient conditions, but under

enriched conditions, plants growing at low elevations had 30 fewer stems/ plug than those at

higher elevations. Across elevation and nutrient treatments, stem density increased with sediment

deposition in Year 2.
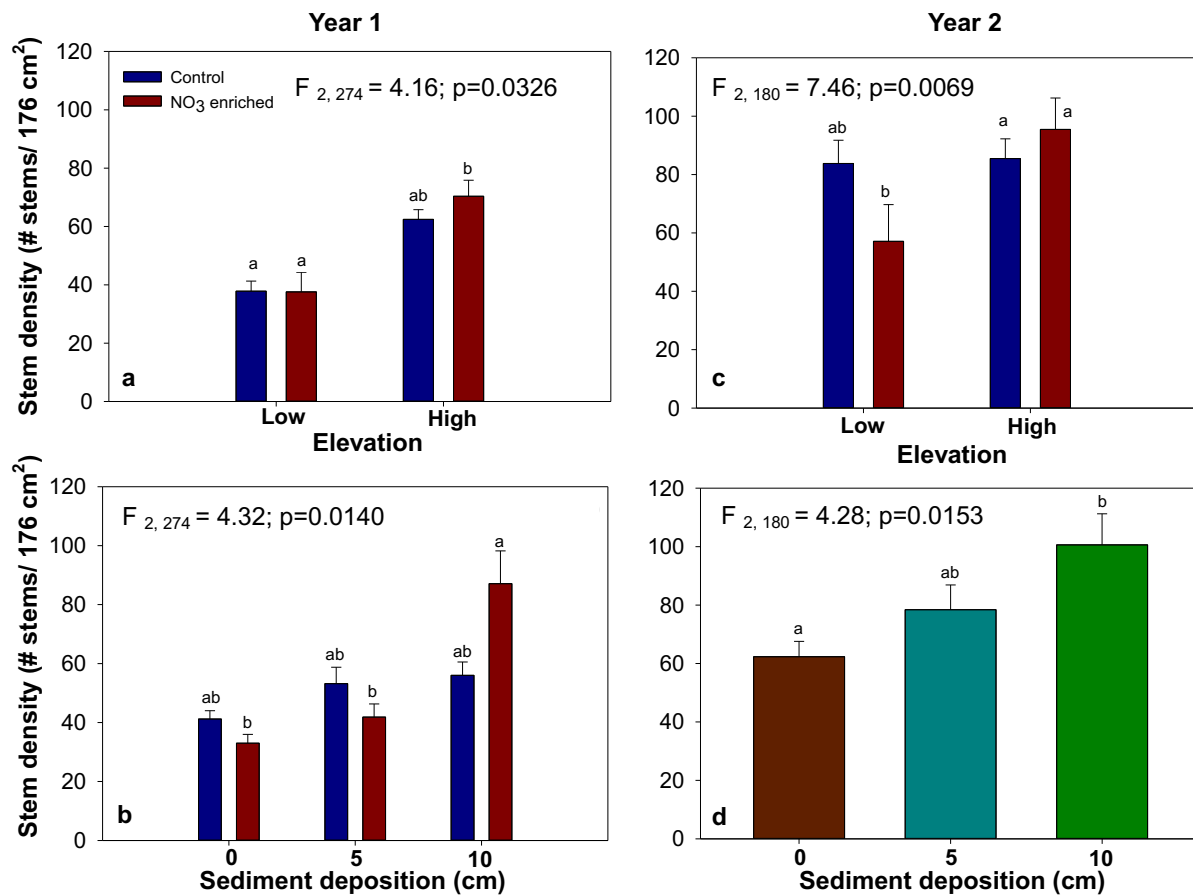
Figure 8. Stem density in response to nutrient-enrichment and elevation (a) and nutrient-enrichment and sediment deposition (b) in Year 1 (September-October 2018) and nutrient-enrichment and elevation (c) and sediment deposition (d) in Year 2 (September-October 2019). Values are means ± standard error.

Stem heights- In Year 1, stem height was lower in 10 cm sediment deposition treatments than

those without added sediment (Fig.9a). This sediment effect disappeared by Year 2, when

heights were greater at low elevation than at high elevation (Fig.9b). Throughout both growing

seasons, nutrient treatments did not significantly influence plant height.
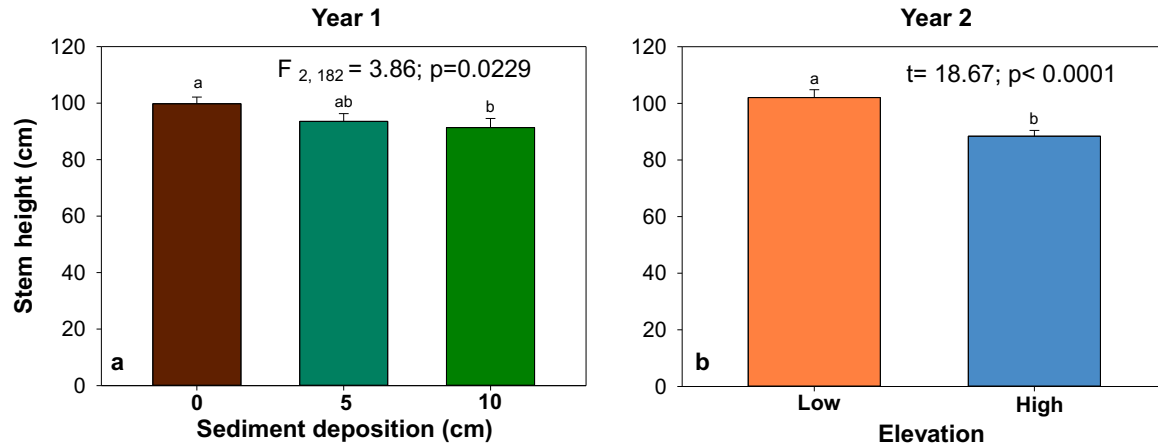
Figure 9. Average stem height (across species) in response to sediment deposition in Year 1 (September-October 2018; a) and Year 2 (September-October 2019; b). Values are means are ± standard error.

Aboveground biomass- Total aboveground biomass (species combined) was over 30 g/plug

greater at high than at low elevations (Fig. 10a). Aboveground biomass with the 10 cm sediment

deposition was an average of 37 g/plug greater than with no sediment and 5 cm of sediment (Fig.

10b). Throughout both growing seasons, nutrient treatments did not significantly influence plant

aboveground biomass.
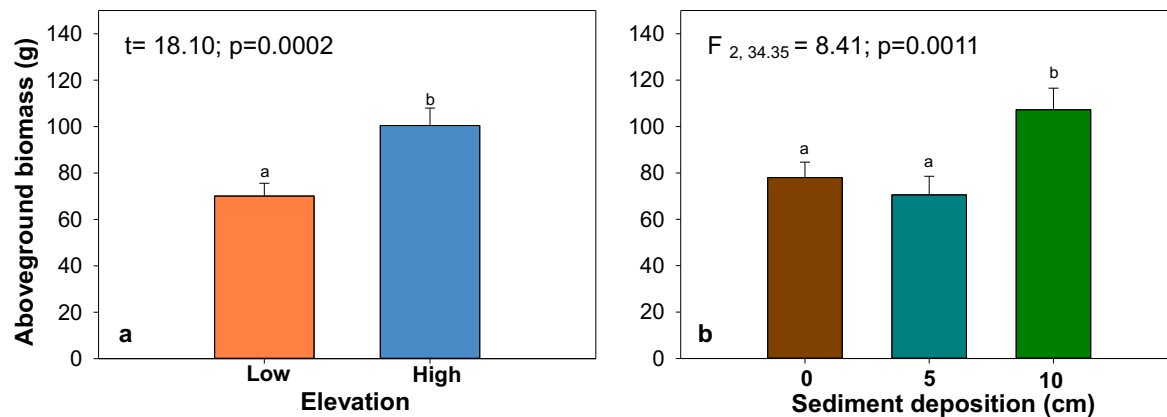
Figure 10. Total aboveground biomass in grams per 176 cm^2 in response to elevation and sedimentation deposition. Values are means ± standard error.

Species richness and frequency distribution- Species richness increased from thirteen species in Year 1 to twenty species in Year 2 across treatments. *Sagittaria lancifolia*, *Panicum repens*, and *Eleocharis macrostachya, Vigna luteola,* and *Polygonum punctatum* were the most frequent species based on their presence in each sample (Table 2). From Year 1 to Year 2, the frequency of *S. lancifolia and V. luteola,* decreased by 5 and 15%, while *P. repens, P.punctatum,* and *E. macrostachya* increased in frequency by 11, 9, and 3%, respectively. Species frequency and distributional changes from Year 1 and 2 can be observed by elevation, sediment deposition, and nutrient treatments in Table 3 and 4.

Table 2. Plant species frequency in mesocosm experiment in Years 1 and 2.

Species	Common name	Family	Duration	Habit	Frequency (%) Yr. 1 2018	Frequency (%) Yr. 2 2019
Sagittaria lancifolia	Bulltongue arrowhead	Alismataceae	Perennial	Forb/herb	100	95.83
Panicum repens	Torpedo grass	Poaceae	Perennial	Graminoid	42.36	53.12
Eleocharis macrostachya	Pale spikerush	Cyperaceae	Perennial	Graminoid	36.45	38.54
Vigna luteola	Hairy cowpea	Fabaceae	Perennial	Herb/vine	49.30	35.93
Polygonum punctatum	Dotted smartweed	Polygonaceae	Annual/ Perennial	Forb/herb	20.13	29.16
Alternanthera philoxeroides	Alligatorweed	Amaranthaceae	Perennial	Forb/herb	16.66	10.41
Paspalum virgatum	Talquezal	Poaceae	Perennial	Graminoid	5.20	5.72
Ipomoea sagittata	Saltmarsh morning-glory	Convolvulaceae	Perennial	Herb/vine	11.11	3.12
Symphyotrichum divaricatum	Annual saltmarsh aster	Asteraceae	Annual/ Biennial	Forb/herb	9.72	3.12
Paspalum vaginatum	Seashore paspalum	Poaceae	Perennial	Graminoid	2.08	2.60
Panicum hemitomon	Maidencane	Poaceae	Perennial	Graminoid	--	2.60
Spartina patens	Saltmeadow cordgrass	Poaceae	Perennial	Graminoid	--	2.60
Setaria viridis	Green bristlegrass	Poaceae	Annual	Graminoid	--	2.08
Crinum asiaticum	Spider lily	Liliaceae	Perennial	Forb/herb	--	1.54
Iva frutescens	Jesuit's bark	Asteraceae	Perennial	Herb/shrub	--	1.04
Spartina alterniflora	Smooth cordgrass	Poaceae	Perennial	Graminoid	--	1.04
Schoenoplectus americanus	Chairmaker's bulrush	Cyperaceae	Perennial	Graminoid	1.04	1.04
Cyperus odoratus	Fragrant flatsedge	Cyperaceae	Annual/ Perennial	Graminoid	2.08	0.52
Eupatorium capillifolium	Dogfennel	Asteraceae	Perennial	Forb/herb	--	0.52
Hydrocotyle umbellata	Marsh pennywort	Apiaceae	Perennial	Forb/herb	1.04	0.52

Table 3. Plant species frequency in mesocosm experiment by nutrient, sediment deposition, and elevation treatments in Year 1. Species not observed (--).

Treatments	Ambient (non-enriched)						Nutrient Enriched					
Sediment Deposition (0, 5, 10 cm)	0	0	5	5	10	10	0	0	5	5	10	10
Elevation (high, low)	H	L	H	L	H	L	H	L	H	L	H	L
Species	Frequency (%) Year 1											
Sagittaria lancifolia	100	100	100	100	100	100	100	100	100	100	100	100
Panicum repens	100	43.75	37.5	18.75	43.75	50	37.5	31.25	25	18.75	62.5	25

(table cont'd.)

Eleocharis macrostachya	6.25	50	75	37.5	50	37.5	12.5	25	37.5	25	37.5	37.5
Vigna luteola	81.25	31.25	75	6.25	87.5	6.25	87.5	6.25	68.75	12.5	75	50
Polygonum punctatum	50	0	37.5	12.5	37.5	0	25	0	12.5	0	56.25	0
Alternanthera philoxeroides	43.75	25	12.5	0	18.75	37.5	12.5	12.5	12.5	0	12.5	12.5
Paspalum virgatum	0	0	25	0	0	0	25	0	0	0	12.5	0
Ipomea sagittata	18.75	12.5	6.25	6.25	12.5	0	25	6.25	0	0	12.5	0
Symphyotrichum divaricatum	0	0	18.75	12.5	12.5	0	18.75	12.5	12.5	18.75	6.25	0
Paspalum vaginatum	0	0	0	0	25	0	0	0	0	0	0	0
Panicum hemitomon	0	0	0	0	0	0	0	0	0	6.25	12.5	0
Spartina patens	--	--	--	--	--	--	--	--	--	--	--	--
Setaria viridis	--	--	--	--	--	--	--	--	--	--	--	--
Crinum asiaticum	--	--	--	--	--	--	--	--	--	--	--	--
Iva frutescens	--	--	--	--	--	--	--	--	--	--	--	--
Spartina alterniflora	--	--	--	--	--	--	--	--	--	--	--	--
Schenoplectus americanus	0	0	0	0	0	0	12.5	0	0	0	0	0
Cyperus odoratus	25	0	0	0	0	0	0	0	0	0	0	0
Eupatorium capillifolium	--	--	--	--	--	--	--	--	--	--	--	--
Hydrocotyle umbellata	0	0	0	0	12.5	0	0	0	0	0	0	0

Table 4. Plant species frequency in mesocosm experiment by nutrient, sediment deposition, and elevation treatment in Year 2.

Treatments	Ambient (non-enriched)						Nutrient Enriched					
Sediment Deposition (0, 5, 10 cm)	0	0	5	5	10	10	0	0	5	5	10	10
Elevation (high, low)	H	L	H	L	H	L	H	L	H	L	H	L
Species	Frequency (%) Year 2											
Sagittaria lancifolia	93.75	93.75	100	100	93.75	87.5	93.75	100	100	100	93.75	93.75
Panicum repens	81.25	50	62.5	43.75	43.75	75	56.25	50	50	31.25	68.75	25
Eleocharis macrostachya	12.5	50	62.5	50	50	43.75	25	37.5	37.5	25	43.75	25
Vigna luteola	43.75	31.25	43.75	18.75	31.25	31.25	43.75	6.25	56.25	37.5	56.25	31.25
Polygonum punctatum	62.5	37.5	68.75	25	12.5	12.5	31.25	37.5	31.25	0	25	6.25
Alternanthera philoxeroides	12.5	6.25	6.25	18.75	12.5	37.5	6.25	0	6.25	0	0	18.75
Paspalum virgatum	12.5	0	6.25	6.25	0	18.75	6.25	6.25	6.25	0	0	6.25
Ipomea sagittata	0	0	0	0	12.5	0	6.25	6.25	12.5	0	0	0

(table cont'd.)

Symphyotrichum divaricatum	0	0	0	0	12.5	0	6.25	0	12.5	6.25	0	0
Paspalum vaginatum	0	0	0	0	25	0	0	0	0	0	6.25	0
Panicum hemitomon	0	0	6.25	0	0	0	0	0	0	6.25	18.75	0
Spartina patens	0	0	12.5	0	0	0	12.5	0	0	0	6.25	0
Setaria viridis	6.25	0	0	0	0	0	0	0	6.25	6.25	6.25	0
Crinum asiaticum	0	0	12.5	0	0	0	0	0	6.25	0	0	0
Iva frutescens	0	0	0	0	0	0	12.5	0	0	0	0	0
Spartina alterniflora	12.5	0	0	0	0	0	0	0	0	0	0	0
Scrmschoenoplectus americanus	0	0	0	0	0	0	12.5	0	0	0	0	0
Cyperus odoratus	0	0	6.25	0	0	0	0	0	0	0	0	0
Eupatorium capillifolium	6.25	0	0	0	0	0	0	0	0	0	0	0
Hydrocotyle umbellata	0	0	0	0	6.25	0	0	0	0	0	0	0

Species richness was greater at high elevation than low elevation in both years by an average of approximately two species (Fig. 11 ab). In Year 1, under nutrient-enriched conditions, species richness was lower with 5 cm than 10 cm of sediment (Fig 11b). Under ambient nutrient conditions, species richness was similar among sediment deposition treatments.
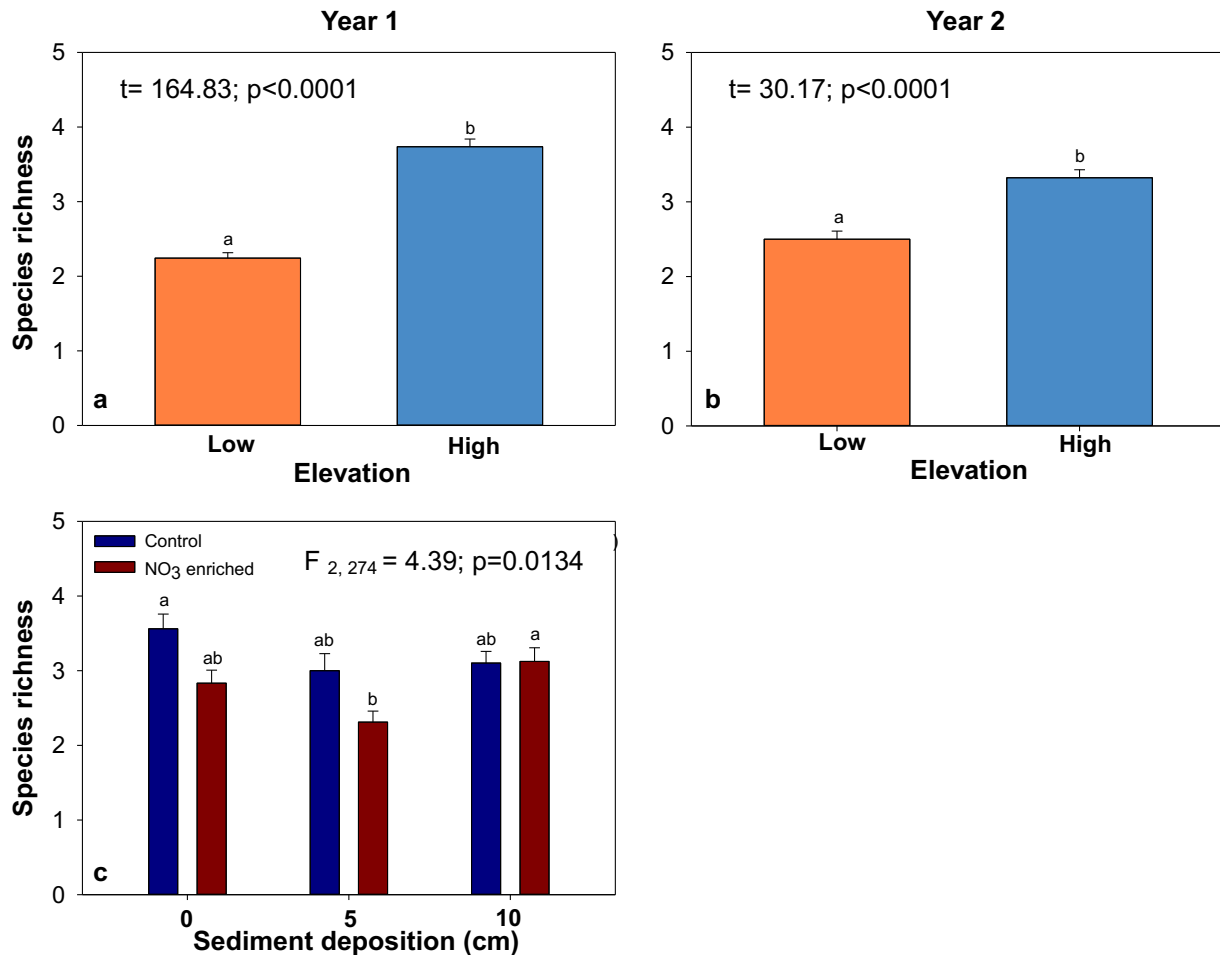
Figure 11. The effect of elevation on species richness in Year 1 (September-October 2018; a) and Year 2 (September-October 2019; b); and the interactive effects of nutrient and sediment deposition treatments on species richness in Year 1 (c). Values are means ± standard error.

Species composition- Plant community structure differed among elevation treatments in both

Year 1 (t = 14.75; P =0.006) and Year 2 (t = 4.39; P = 0.034; Fig. 12 ab). *Sagittaria lancifolia*,

and *Eleocharis macrostachya* was more frequently found at low elevations, whereas *P. repens,*

Vigna luteola, and *Polygonum punctatum* was more frequent at high elevations (Fig. 12 ab).

Sediment deposition had a weak but significant influence on species structure in Year 2 ($F_{2, 3981}$=

2.20; P = 0.049). In general, *S. lancifolia* seemed to prefer less sediment (0 and 5 cm), whereas

E. macrostachya showed preference for greater sediment (5 and 10 cm). *Panicum repens* was

found in all sediment treatments (Fig. 12c). There was no difference in plant community structure as a result of nutrient enrichment.
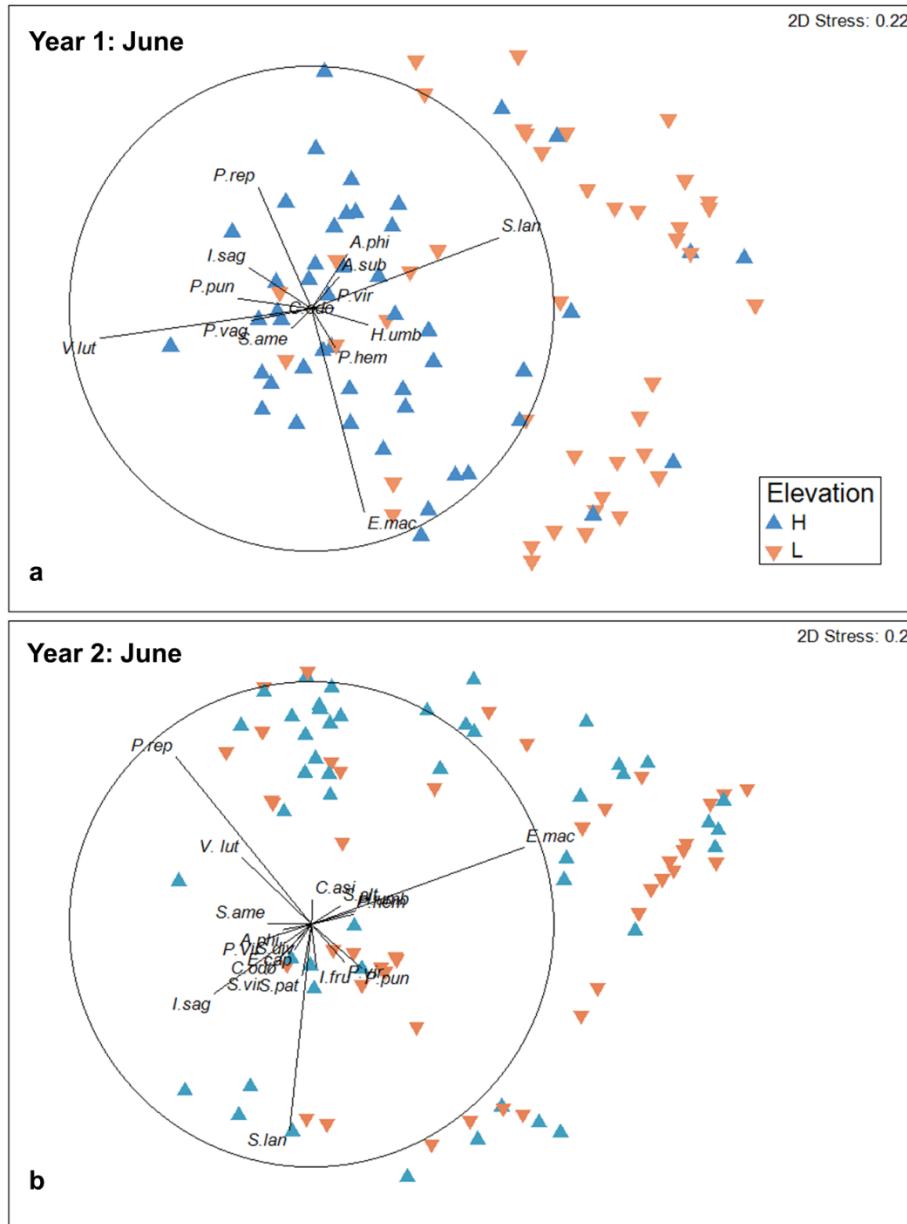
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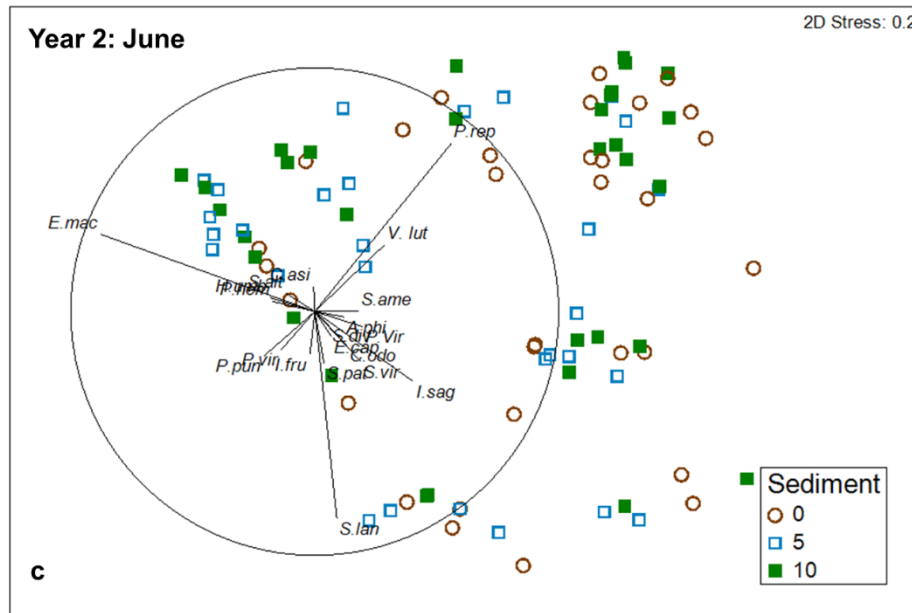
Figure 12. NMDS plot illustrating the influence of a) elevation in Year 1 and b) elevation and c) sediment deposition treatment in Year 2 on plant community structure. Shapes and colors correspond to different elevations and sediment deposition treatment. Vectors represent correlations of individual species distribution in the plot. Abbreviation of plant names can be found in Table 3.

Species-specific treatment effects- The effects and interactions of elevation, sediment addition, and nutrient enrichment treatments were tested on the density of three of the most important (i.e., frequent) species in this study, *S. lancifolia*, *P. repens*, *E. macrostachya*. Stem density of *S. lancifolia* was affected by a three-way interaction between elevation, sediment deposition, and nutrient enrichment in both Years 1 and 2 (Fig. 13). In Year 1, stem density of *S. lancifolia* at low elevation under ambient nutrient conditions was lower with 10 cm of sediment than without sediment (Fig. 13 ab). However, at high elevations and nutrient-enriched conditions, the negative effect of sediment deposition was absent. In Year 2, stem density of *S. lancifolia* was lower at high elevations under ambient nutrients and no sediment than at low elevations, nutrient-enriched and 5 cm of sediment (Fig. 13 cd). Total aboveground biomass of *S. lancifolia*, was

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positively affected by nutrient enrichment (Fig. 14). *Sagittaria lancifolia* was the only species to be affected by height in Year 2 of the study (Fig. 15)

Nutrient enrichment had a negative effect on the density of *P. repens* at low elevations, but not at high elevations in Year 1 ($P = 0.0062$) (Fig. 16a). Stem density increased from Year 1 to Year 2 by 20 ± 8 stems/plug at low elevation and 40 ± 7 stems/ plug at high elevation. In Year 2, elevation was the only factor influencing the density of *P. repens*, where densities were 30 ± 6 stems/pot greater at high compared to low elevations (Fig. 16b).

The density of *E. macrostachya* was higher with both 5 and 10 cm sediment deposition in Year 1 and with 10 cm sediment deposition in Year 2 as compared to pots without sediment (Fig. 17 ab). Aboveground biomass contribution for each species can be observed in Table 5.
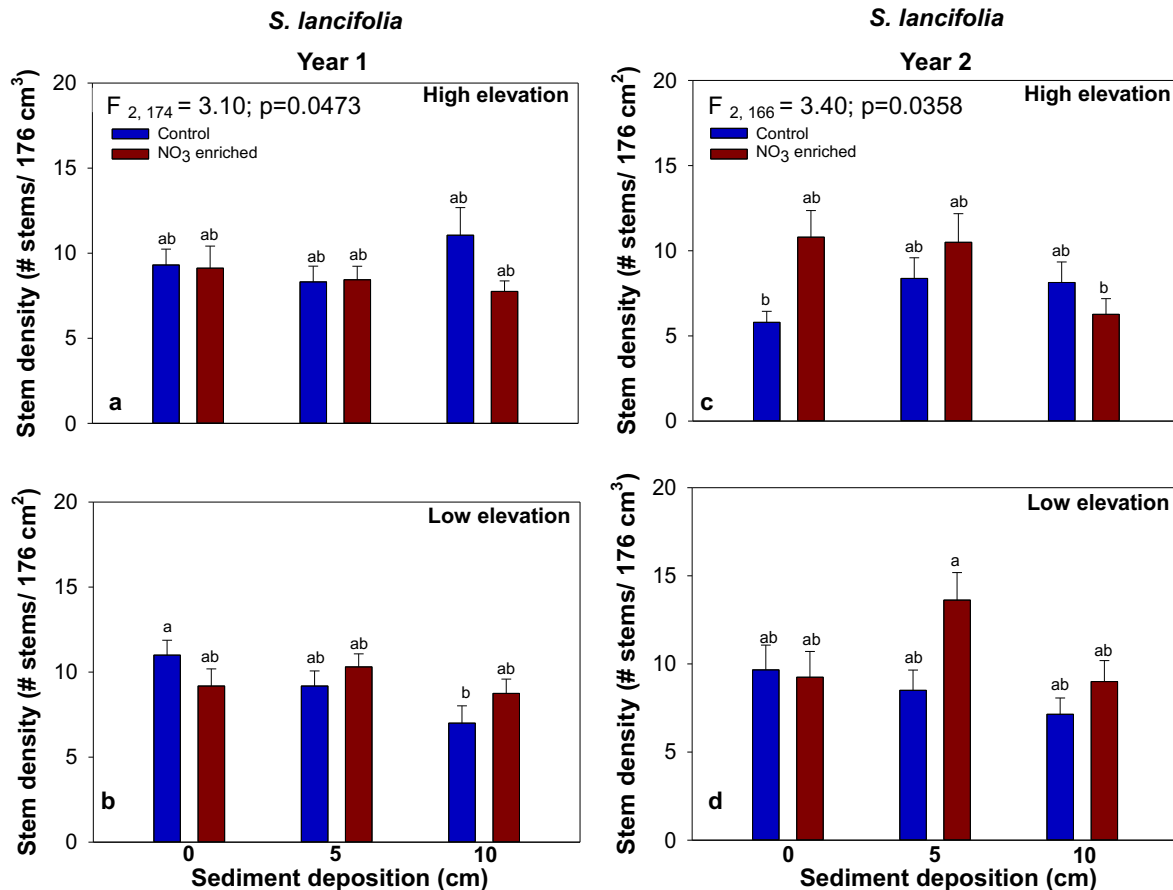
Figure 13. *Sagittaria. lancifolia* stem density in response to elevation, sediment deposition, and nutrient-enrichment in Years 1 (a and b) and 2 (c and d). Values are means ± standard error.
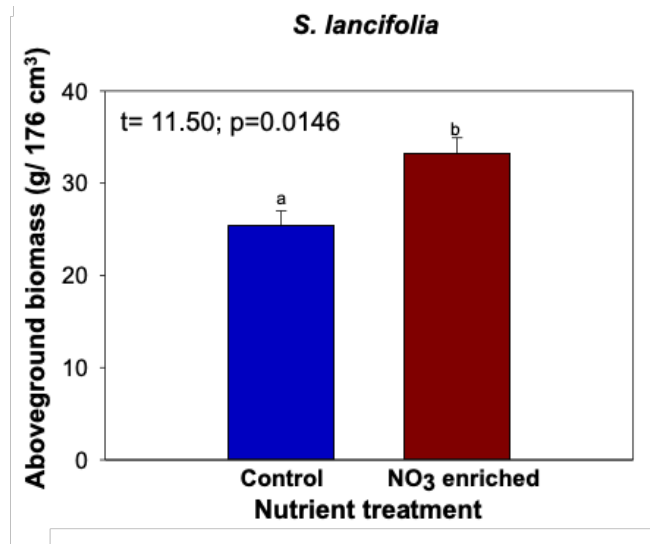
Figure 14. The effect of nutrient-enrichment on the total aboveground biomass results of *S. lancifolia*. Values are means ± standard error.
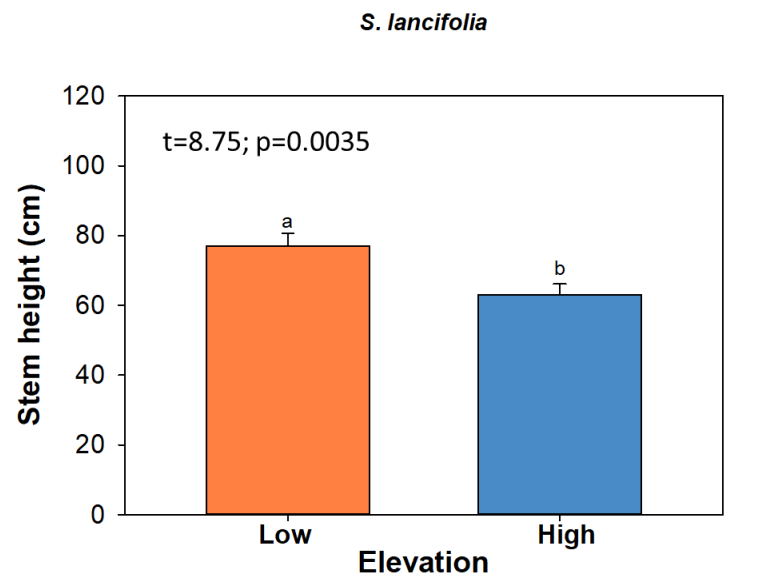
Figure 15. The effect of elevation on height (cm) results of *S. lancifolia*. Values are means ± standard error.
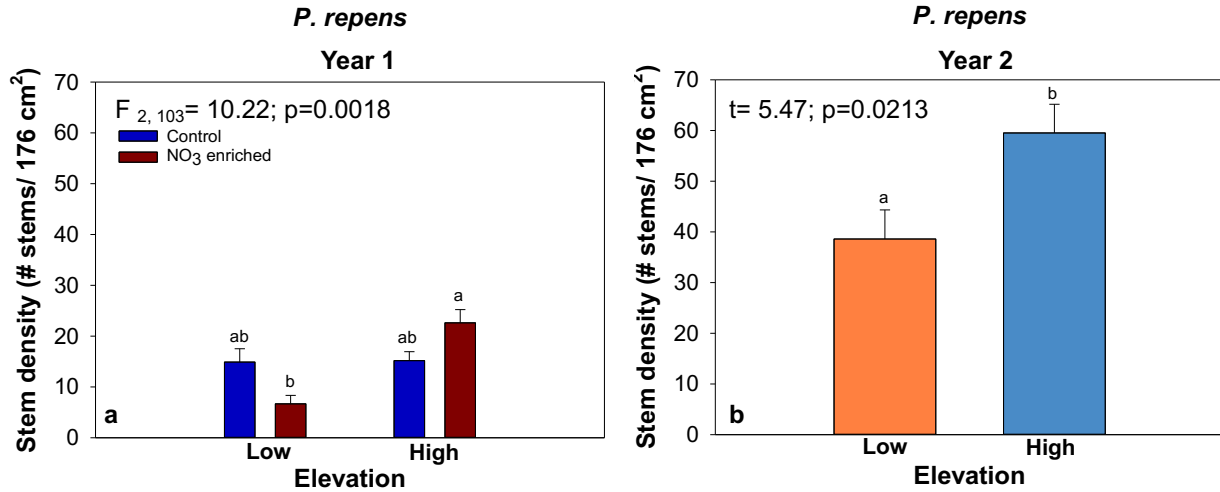
Figure 16. *Panicum repens* stem density in response to elevation and nutrient-enrichment in Year 1 (a) and elevation in Year 2 (b). Values are means ± standard error.
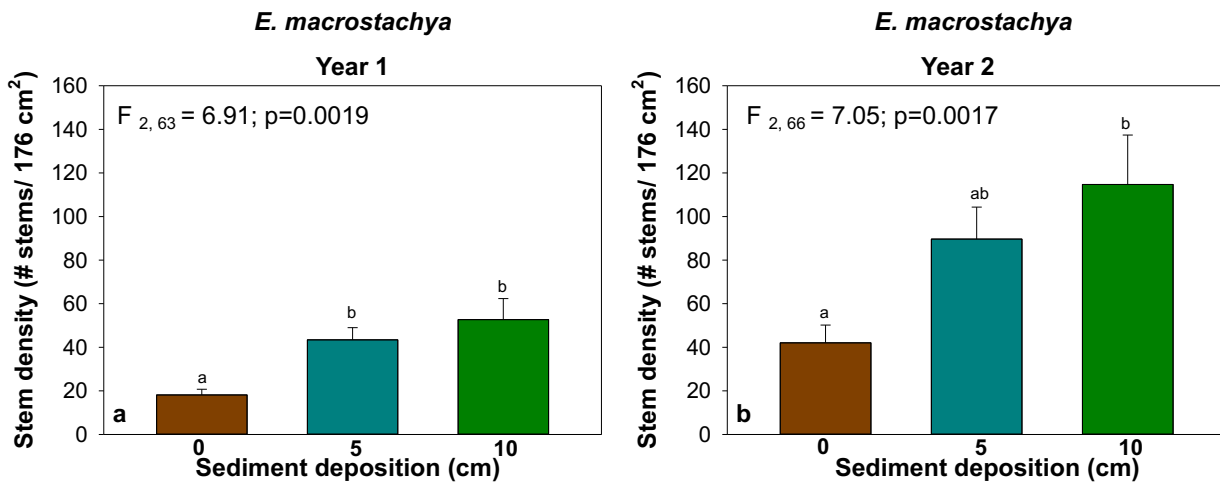
Figure 17. *Eleocharis macrostachya* stem densities in response to sediment deposition in Year 1 (a) and Year 2 (b). Values are means ± standard error.

Table 5. Aboveground biomass (g) for dominant species *S. lancifolia*, *P.repens*, and *E. macrostaycha* by main effects elevation, sediment and nutrient enrichment treatments. Values are means ± standard error (SE) and significant differences between control and enriched mesocosm tanks are shown by * ($p < 0.05$).

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Aboveground biomass (g) by treatment and dominant species

Elevation treatment	Species	Low	(±) SE	High	(±) SE		
	S. lancifolia	30.32	1.66	28.32	1.79		
	P. repens	33.52	7.79	61.78	9.79		
	E. macrostaycha	17.52	4.02	10.13	2.02		
Sediment treatment	**Species**	**0 cm**	**(±) SE**	**5 cm**	**(±) SE**	**10 cm**	**(±) SE**
	S. lancifolia	27.9	2.28	29.83	1.88	30.23	2.17
	P. repens	52.45	9.64	29.88	9.55	62.945	13.12
	E. macrostaycha	10.33	4.87	11.29	1.72	19.08	4.75
Nutrient treatment	**Species**	**Control**	**(±) SE**	**NO$_3$ enriched**	**(±) SE**		
*	*S. lancifolia*	24.41	1.57	35.24	1.69		
	P. repens	50.01	7.83	46.05	10.39		
	E. macrostaycha	12.25	1.51	15.46	4.58		

Root Ingrowth- The effect of treatments on the ingrowth of fine roots was depth -dependent. Fine root ingrowth at 0 – 5 cm depth was significantly greater at high elevations than at lower elevations (t=12.71 p=0.0006; Fig. 18a). At depths between 5 and 15 cm, fine root ingrowth was significantly greater at nutrient enriched high elevations than at both controls and nutrient enriched low elevation (p < 0.05).

The ingrowth of large roots in response to treatments was also depth-dependent. Large root ingrowth at 0-5 cm depth was significantly lower with 10 cm than controls and 5 cm sediment additions ($F_{2, 84}$ =3.13; p=0.0488; Fig. 18c). At depths of 5 to 10 cm, ingrowth of large roots was greater with 5 and 10 cm of sediment than without sediment ($F_{2, 82}$ =4.08; p=0.0204). Moreover, at depths of 5 to 10 cm, large root ingrowth was greater at high elevations than at low elevations (Fig. 18b). Lastly, large root ingrowth at 10-15 cm was significantly greater with 10 cm sediment addition than controls and 5 cm additions ($F_{2, 79}$ =3.17; p=0.0472; Fig. 18c).

Meanwhile at similar depths of 10-15 cm large root ingrowth was significantly greater at nutrient enriched high elevations than at both controls and nutrient enriched low elevation (t=7.32 p=0.0083; Fig. 18b).

Ingrowth of rhizomes was influenced by elevation depending on depth (Fig. 18d). Rhizome ingrowth between both 0 and 5 and 5 and 10 cm depths was significantly greater at high elevation than at low elevation (p < 0.05). At depths of 10-15 cm, rhizome ingrowth was relatively lower and similar at high and low elevations but significantly undistinguishable due to small sample sizes.
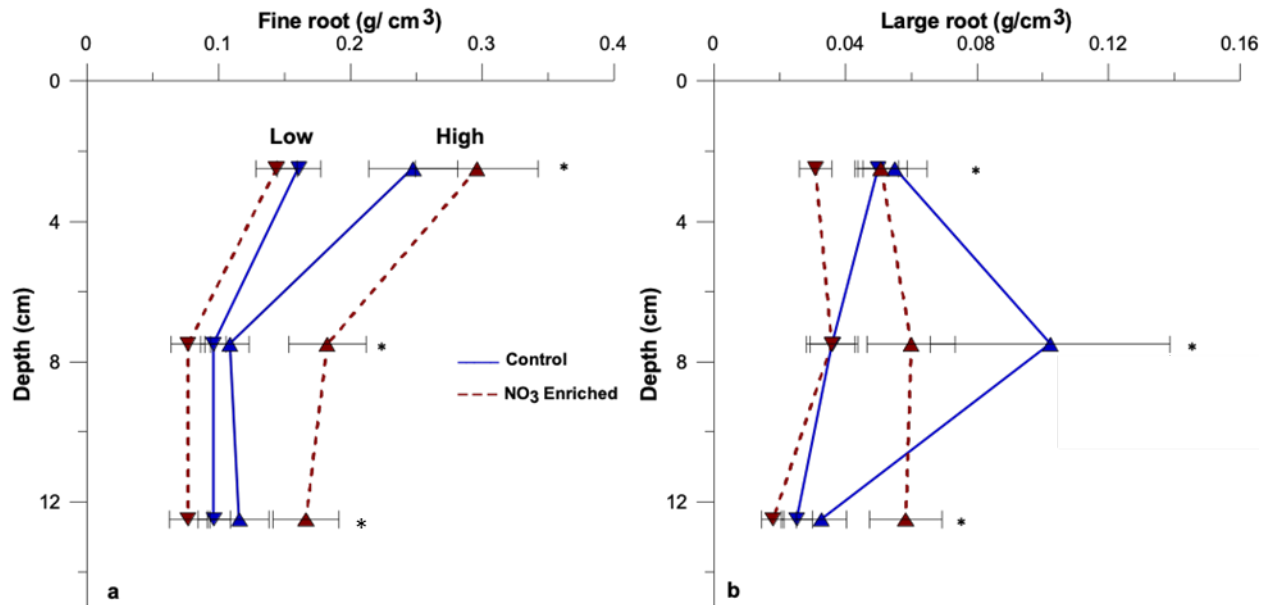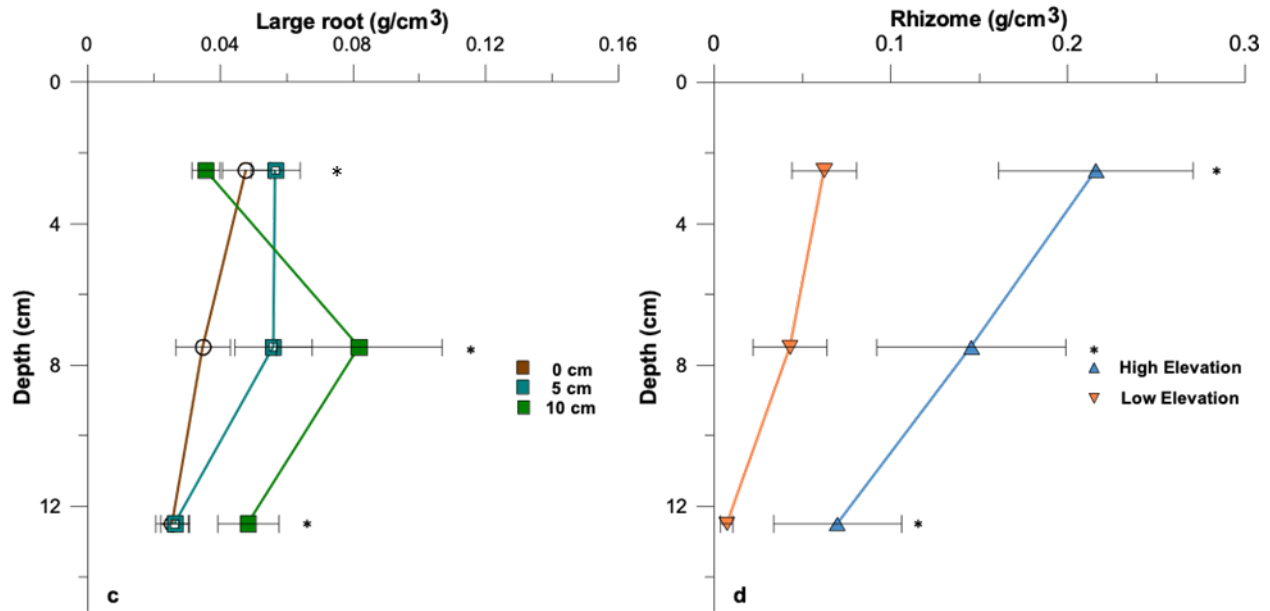
Figure 18. Root ingrowth by deposition in response to an interaction between elevation and nutrient-enrichment (a) fine root, (b) large root, (c) main effects of sediment on large root, (d) main effects of elevation on rhizome. Values are means ± standard error (n = 8).

Totals of belowground biomass accumulated within ingrowth bags were summed by each component (i.e., fine, large, rhizome, fine+large+rhizome, and dead) (Fig. 19). Total fine root ingrowth was affected by elevation and nutrient enrichment (Fig. 19a). Fine root ingrowth at low elevation in both ambient and nutrient-enriched conditions was significantly less than at high elevation under nutrient-enriched conditions (p= 0.0237). Total large root and rhizome ingrowth was primarily affected by elevation (Fig. 19 bc). Large root and rhizome ingrowth at high elevation treatments were 0.08 ± 0.05 g/cm^3 greater (p= 0.0017) and 0.30 ± 0.07 g/cm^3 greater (p= 0.0016) than low elevations, respectively. Total ingrowth was also greater at high versus low elevation (p= 0.0001; Fig. 19d). Accumulation of dead organic material (i.e., particles less than 2.0 mm and greater than 0.75 mm) differed depending on nutrient enrichment and sediment deposition (Fig. 19e). The accumulation of dead fine roots and particles (2.0 mm

<dead<0.75mm) were significantly less with nutrient enriched 10 cm sediment additions than no sediment and 5 cm additions.
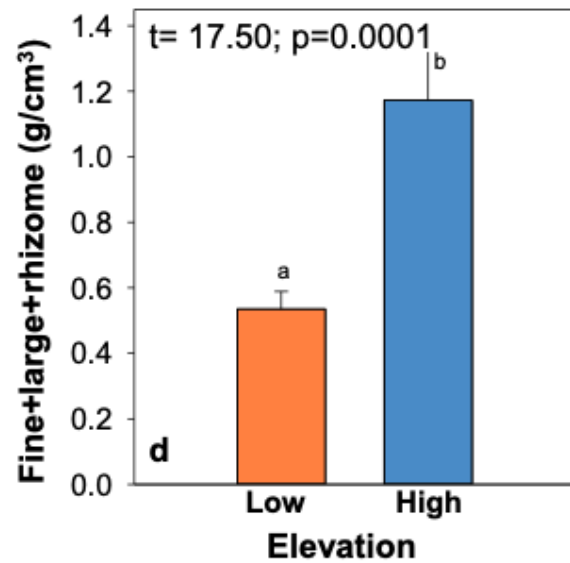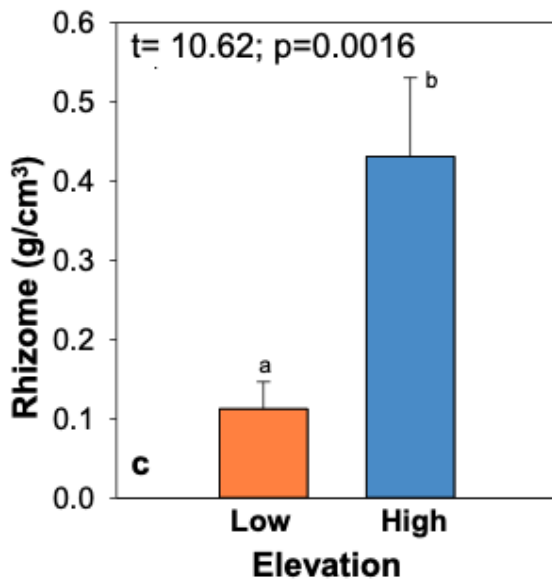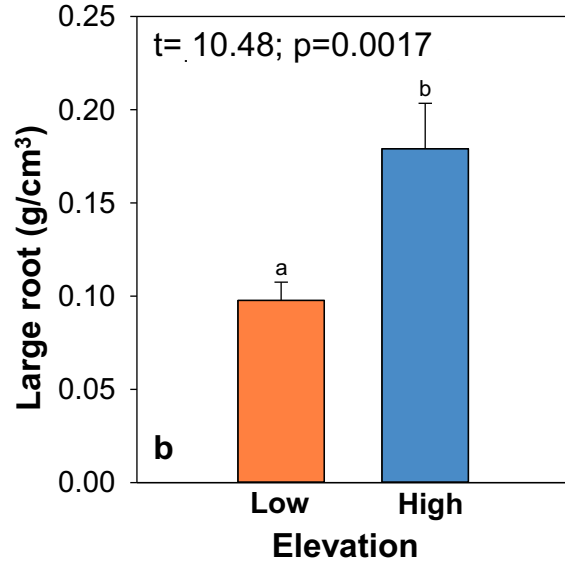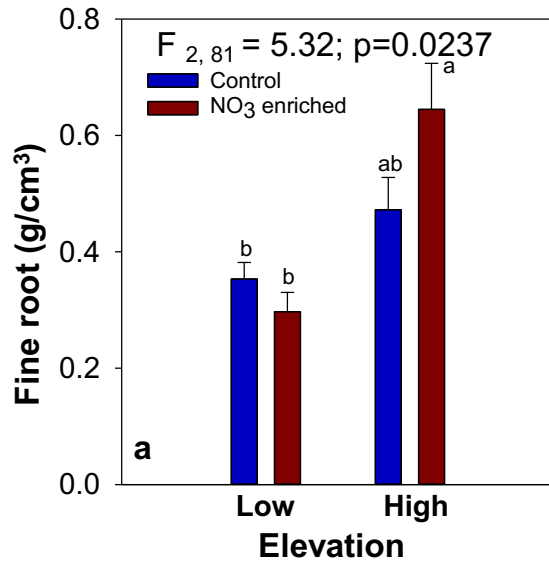
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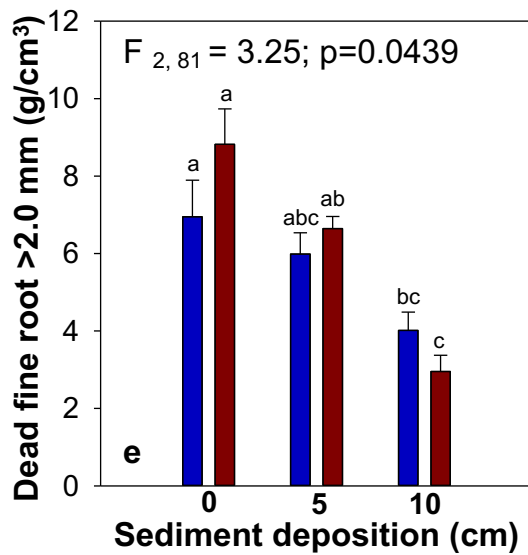
Figure 19. Fine root ingrowth in response to an interaction between elevation and nutrient-enrichment (a) fine root, (b) large root and (c) rhizome response to elevation (d) total live accumulation of fine and large root, and rhizome response to elevation, (e) dead accumulation > 2.0 mm >0.75mm in response to an interaction between sediment deposition and nutrient-enrichment. Values are means ± standard error (n = 8).

Soil properties - As expected, marsh soils that received 5 and 10 cm of sediment additions had lower soil organic matter content as measured by the percentage loss on ignition (LOI) and higher soil bulk density within the top 10 cm of the soil profile (Fig. 20 ab). Subsurface bulk density increased with both sediment treatments indicating elevation loss (Fig. 20b). Low elevation plugs contained 15 ± 7 % greater soil organic matter contents than higher elevation treatments, and sediment enriched soil organic matter nutrient tended to be lower than non-enriched controls (Fig. 21).
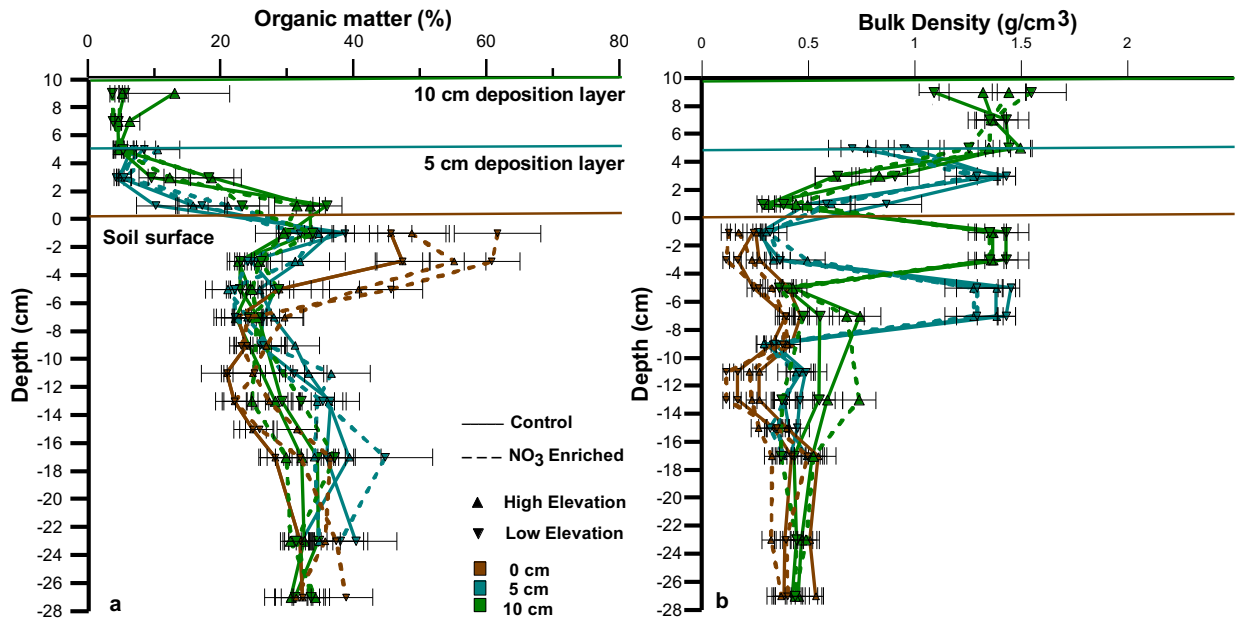
Figure 20. (a) Soil organic matter and (b) bulk density by treatment and deposition. Values are means ± standard errors across two nutrient levels, two elevations, and three sediment depositions.
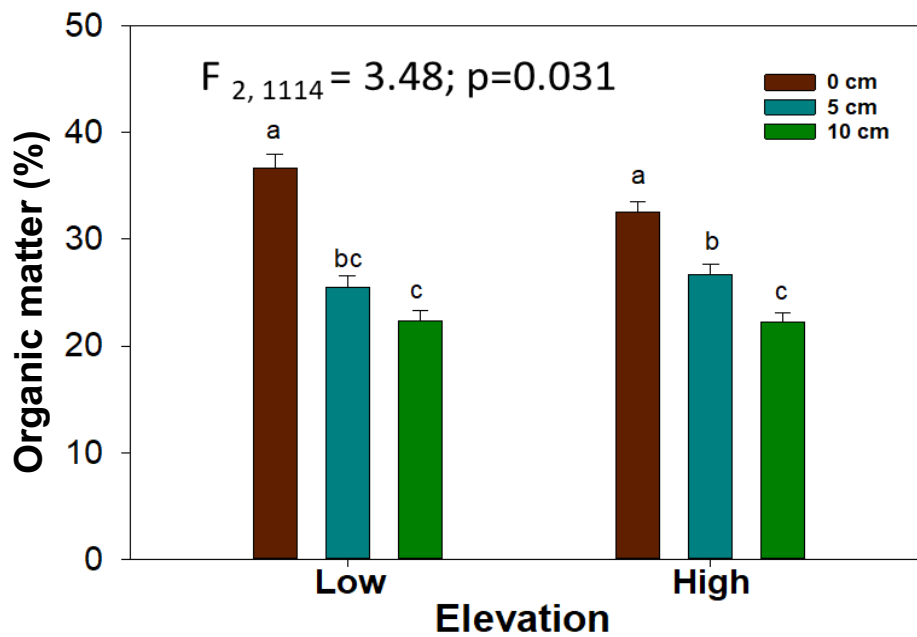
Figure 21. The interactive effects of elevation and sediment deposition (0, 5, and 10 cm) on soil organic matter. Values are means across sediment deposition ± standard errors.

DISSCUSSION

Rapid environmental change is threatening the long-term sustainability and associated ecosystem services provided by coastal wetlands around the globe. It is therefore imperative to understand the factors that regulate complex feedbacks among plant community composition, productivity, and soil properties to better inform coastal wetland restoration and management. In the current study, flooding from lower elevations reduced species richness and composition, density, above-and belowground productivity, and soil organic matter content. Sediment additions of 10 cm had the greatest effect on stem densities, aboveground biomass and large root ingrowth but significant reduced soil organic matter content and soil ammonium-N. Nutrient enrichment increased the biomass of *S. lancifolia* but not total biomass and interacted with elevation and/or sediment deposition to affect other aspects of community structure and productivity. Nutrient-enrichment exacerbated the negative effects of low elevation or increased flooding, while enhancing diversity and productivity at higher elevation or reduced flooding. Similarly, reduced flooding from higher elevation treatments with nutrient-enriched conditions had positive effects on ingrowth fine and large roots at specific soil depths. In combination with mineral sediment, nutrient enrichment increased species richness and stem densities.

To our knowledge, this is one of the first studies to test the interactive effects of elevation, sediment deposition, and nutrient enrichment on wetland plant community dynamics. A total of twenty species emerged from plugs collected from the *Sagittaria lancifolia*-dominated oligohaline marsh. Dominant species included *S. lancifolia*, *P. repens*, *E. machrostycha, V. luteola*, and *P. punctatum*. Species richness was 50% lower at low elevations than high elevation in both years of the experiment which is similar to Baldwin et al., 2001. Species richness in Year 1 was also influenced by an interaction between sediment deposition and nutrient-enrichment.

Under nutrient-enriched conditions, species richness was lower at 5 cm than at 10 cm, whereas under ambient nutrients sediment deposition did not affect species richness as reported in previous studies (Jurik et al. 1994; Wang et al. 1994). Sediment deposition increases the marsh elevation resulting in soils becoming relatively dryer with elevation gains thereby improving soil aeration in the root zone, and plant assimilation of nutrients (Slocum et al., 2005; Stagg and Mendelssohn 2010). In the current study 5 cm of sediment deposition was not enough to overcoming flooding stresses of 5 and 15 cm below MHW to enhance plant assimilation of nutrients. In Year 2, species richness was only affected by elevation. Lower elevations resulted in the absence or decreased frequency of *P. repens, V. luteola*, and *P. punctatum*. As such, in relatively species diverse lower salinity marshes, species-specific productivity responses to inundation may lower the overall species richness if initial sediment elevation gains are not met under nutrient enriched conditions (Smith et al. 1999, Bobbink et al. 2010).

Species composition was primarily influenced by flooding depth in both years of the experiment. *Panicum repens* was a dominant species that was significantly reduced at greater flooding durations. This effect is not unusual as flooding comes at an energetic cost and can result in a decline in stem densities for many wetland plant species including, *P. repens* (current study), *J. roemerianus* (Voss et al., 2013), *S. patens* (Kirwan and Guntenspergen, 2015; Snedden et al., 2015), *S. americanus* (Schile et al., 2017). In contrast, 18 months of increased flooding did not change the density of co-dominant species *S. lancifolia* and *E. macrostaycha*. Numerous studies have demonstrated the ability of common wetland plant species to survive persistently flooded conditions and aforementioned genus *Sagitarria* has been shown to be extremely flood tolerant withstanding 27 months of permanent flooding at water levels above 30 cm (Martin and Shaffer 2006). At low elevations or increased flooding depth and duration, due to changes in

density, *P.repens* was outcompeted by more flood tolerant species, like *S. lancifolia* and *E. macrostaycha,* thus indicating potential species changes with large scale sediment diversions .

Sediment addition also contributed to species composition changes in Year 2, however not all species behaved similarly. Stem density of *E. macrostacha* doubled and tripled with 5 and 10 cm sediment additions, respectively. Stem densities of *S. lancifolia* only increased with 5 cm sediment addition and *P.repens* only increased with 10 cm additions. Interestingly, there was more overlap in species abundance from Year 1 to Year 2 as a result of sediment treatments, thus indicating conditions becoming more similar. Species composition was not influenced by nutrient enrichment and instead hydroperiod and sedimentation more strongly influence wetland plant species abundance and frequency in *S. lancifolia* dominant tidal freshwater marshes.

Overall, total stem density was lower at low elevation than at high elevation. In addition, our findings indicate sediment depositions of 10 cm had a greater positive effect on stem densities than no sediment and 5 cm additions thus indicating the potential for increased sediment trapping efficiency and surface accretion rates (DeLaune et al. 1990; VanZomeren et al., 2018). Other studies have shown a minimum sediment deposition is necessary to just overcome the negative effect of flooding (Graham and Mendelssohn 2013; Baustian and Mendelssohn 2015) and here it took two years for 5 cm additions applied during the first year to have a positive effect on stem densities, whereas 10 cm additions had positive effects during the first and second years. If sediment additions are not met with enough elevation gains, the negative effects associated with relative sea level rise and excessive flooding, will continue to result in a decline in stem densities. While in the current study increasing sediment additions increased stem densities, additional sediments requirements and time may be necessary to achieve similar results in areas with greater inundation depths.

Stem height decreased with sediment placement over the course of year one however this was negligible as it appeared height difference were similar to sediment depositions. More importantly, greater flood depths increased stem height by the end of the experiment. The elongation of stems is consistent with other observations in wetland systems as soil waterlogging has been shown to severely limit root respiration altering plant metabolism and morphological growth allocations (Kozowski 1984, Mendelssohn and Burdick 1988; Lou et al., 2016). There are costs related to increased height and total aboveground mass is generally found to decrease with increasing plant height (Menges, 1987). In the present study increased flooding depth resulted in fewer stems and less aboveground biomass of *S. lancifolia* but were on average 15 cm larger than those at high elevation.

Net aboveground biomass was 30 g lower at low elevation than at high elevation. In addition, our findings indicate that 10 cm of sediment had a greater effect on aboveground productivity compared to than no sediment and 5 cm of sediment depositions (Reimold et al. 1978; Owen et al. 2004). While previous studies have shown a positive relationship between nutrient enrichment and aboveground plant biomass, this trend was not generally observed in the current study (Valiela and Teal 1974; Graham and Mendelssohn, 2010; Shaffer et al., 2015). However, this effect was observed in a single dominant species, *S. lancifolia*. Flood tolerant species, like *S. lancifolia,* have be shown to allocate additional resources to flood tolerant mechanisms, such as height at the cost of reduced nutrient uptake efficiency, growth, and reproduction, which is supported by our results (Mendelssohn et al., 1981; Bradley and Morris, 1990; Baldwin et al., 2001). *Sagitarria lancifolia* was the only species to increase in height as a result of greater inundation depths by the end of the experiment. This suggests that low marsh

species such as *S. lancifolia* may allocate nutrients towards existing structures rather than new production under increased flooding and nutrient enriched conditions.

Higher elevations or reduced flooding treatments resulted in greater ingrowth accumulation of large root, rhizome, and total belowground biomass. Under flooded conditions, both the amount and balances of various plant growth hormones lead to internode elongation and aerenchyma tissue development, thereby influencing above and belowground production (Kozlowski 1984). Accumulated fine root ingrowth was the only root structure influenced by the interaction of nutrient enrichment and elevation. However, our ingrowth root study indicates elevation, not nutrient loading, controls total belowground biomass productivity, unlike similar studies. While a similar greenhouse nitrogen enrichment study (0, 50, 200 and 1200 kg N ha $^{-1}$ year $^{-1}$) evaluated belowground biomass response through ingrowth measurement methods and determined live root biomass increases with nitrogen enrichment (Graham and Mendelssohn 2015). The current study used significantly less nitrogen concentrations and nutrients were applied directly to the water column. Keller et al. (2005), observed small to moderate additions of nitrogen had a limited impact on soil respiration and a large amount of nitrogen increased this response. Moreover, water column nitrate-N rapidly decreased by 26 uM (80%) fourteen days post enrichment that were similar to controls concentrations by the end of the first growing season. In addition, porewater nitrate-N concentrations were similar regardless of nutrient enrichment at 240 days of the experiment. Under similar nitrogen enrichments, Van Zomeren et al., 2012 determined that 36% of the added soluble N^{15}-labeled nitrate-N was present in the soil and plant compartments, while the majority (64%) was removed through gaseous loss via denitrification. Similar to Poormahdi et al., 2018, these findings suggest nitrogen-loading rates equivalent to that of 2.0 mg/L N might not surpass the short-term assimilation capacity of the

soil and vegetation in a *S. lancifolia* dominated wetlands as nitrate is quickly denitrified, transformed, or assimilated; however greater amounts of nitrogen may prove different.

Previous studies indicate nutrient enrichment alone causes both positive and negative effects on belowground productivity (Valiela et al., 1976; Darby and Turner, 2008a, b; Deegan et al., 2012; Nelson and Zavaleta, 2012). This study indicates the effects of nutrient enrichment on belowground biomass may be dependent on root type, hydrologic regimes and deposition. For instance, fine root ingrowth at depths of 0-5 cm was greater at high elevation than at low elevation and nutrient enrichment contributed to greater fine root ingrowth at depths between 5-15 cm. Moreover, large root ingrowth was greater with nutrient enrichment at high elevations and depths between 10-15 cm. Sediment additions of 10 cm reduced large root ingrowth at 0-5 cm but were greater than, 5 cm depositions and controls at depths of 5 -15 cm. The reduction in large root ingrowth at depths between 0-5 cm may be a result of greater bulk densities at the surface. When comparing our 5 and 10 cm sediment treatments to native soils, bulk density was greatest with 10 cm additions. Bulk density values in the present study fall within the range of those measured in un-buried oligohaline marsh soils (Kiehn et al., 2013) and sediment amended soil with 5 to 9 cm of burial (Berkowitz et al., 2019 and Schrifet et al., 2008). Elevation gains made through sediment additions alter flooding and drying dynamics and shift conditions from anoxic to aerobic conditions, resulting in the rapid nitrification of ammonium. Increasing nitrate availability has been shown to increase nitrification and denitrification rates in anerobic bulk soils of the rhizosphere and here porewater ammonium-N concentrations were also lowest with 10 cm sediment enrichment (Reddy et al., 1989; Arth et al., 1998). While the reduction in ammonium-N may be a result of nitrification alone, the increase of ingrowth fine and larges roots may have also contributed to this loss through uptake. Similar to findings by Graham and

Mendelssohn 2015, nutrient enrichment may, in the short-term, contribute to soil organic matter accumulation by increasing belowground growth as plants exploit new resource space.

CONCLUSIONS

The Louisiana coastal zone is experiencing high rates of wetland loss brought about by the combined effects of relative sea-level rise and hydrological isolation (i.e., Mississippi River Levee Complex). One proposed method for reducing coastal land loss is to reconnect the Mississippi River to the isolated coastal basins through river sediment diversions (Mitsch et al. 2001). Large scale sediment diversions are being planned to transport river water and sediment from the Mississippi River to deteriorating wetland basins through managed openings in the levee with the goal of reducing wetland loss by increasing sediment deposition and stimulating plant growth and accretion (DeLaune et al. 1990; Day et al. 2007; VanZomeren et al., 2018). In contrast, diversions will also increase flooding durations and nutrient loads to existing marshes, which may alter plant communities (Boorman 1999; Reddy et al., 2010 ;Voss et al., 2013) and stimulate N cycling-via microbial uptake, resulting in lower rates of root productivity, soil organic matter accumulation and accretion (Melillo et al., 1984; Deegan et al., 2012; Wigand et al., 2015).

Predicting the effects of sediment diversions on wetland plant productivity is complicated due to uncertainties in the effects of sediment inputs with distance from the outfall or discharge of the diversion but here we provide a conceptual model of the possible ecosystem response to three major factors associated with large scale sediment diversions with distance from the outfall (i.e., water discharge, nutrient loading, and sediment deposition) (Fig. 22). Deposition is anticipated to be highest near the outfall (CPRA 2017). Therefore, in the present study we acknowledge a sediment deposition threshold of 10 cm is necessary for any positive effects to be observed. Moreover, increased nutrient concentrations are expected to accompany areas of greater sediment deposition. As a result of the sediment*nutrient interactions, we expect

increases in total stem densities, aboveground biomass, large roots and bulk densities closest to the outfall. Water discharge from sediment diversions is predicted to increase accretion primarily due to elevated sediment supply however as the sediment threshold diminishes so will the positive effects. When the sediment threshold of 10 cm is not met, nutrient loading will persist but be limited to the subfactors of nutrient assimilation, denitrification, and adsorption when interacting with water discharge and/or submergence depth. We anticipate positive effects in areas with flooding depths less than 5 cm below MHW experiencing excess nutrient concentrations of 2.0 mg/L N. Based on the current study and our elevation*nutrient interactions, these areas are anticipated to have greater belowground biomass contributions of fine and large roots; however, in areas were submergence depth is 10 cm below MHW these effects will not be observed. Wetland plant productivity in Louisiana is relatively high (Hopkinson et al. 1980) but as nutrient concentrations are reduced to ambient conditions water discharge associated with sediment diversions is predicted to have negative effects on stem densities, above and belowground biomass but only when submergence depth is 10 cm or greater below MHW. Lastly, changes in plant community structure will be more prominent in areas of greater submergence depth and duration.
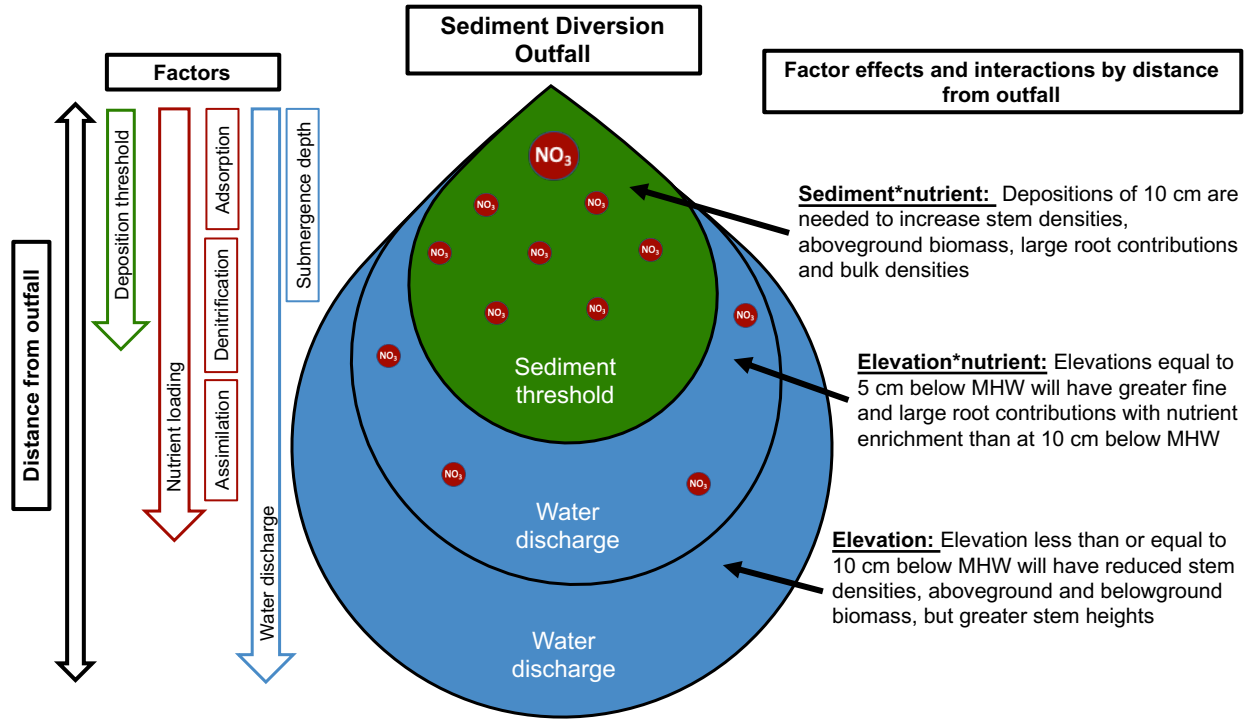
Figure 22. A conceptual model of a large-scale sediment diversion impact area and the effects and interactions on plant productivity based on limiting factors by distance from the outfall. Nearest the outfall the deposition threshold (green) and nutrient loading (red) will be greatest and this interaction will dominate. When the sediment threshold of 10 cm is not met, nutrient loading will persist but be limited to the subfactors of nutrient assimilation, denitrification, and adsorption when interacting with water discharge (blue). Furthest from the outfall water discharge and the subsequent submergence depth will primarily influence plant productivity.

Our goal was to evaluate the potential impacts of Mississippi River sediment diversions on oligohaline *S. lancifolia* dominated wetlands, which we tested with two hydrological regimes and applications of sediment and nutrients. While elevation was the most important determinant of plant community composition and productivity, there were tradeoffs between sediment and nutrient enrichment. In general, sediment deposition increased plant productivity, and nutrient enrichment had positive effects under conditions of less flooding. Generally, greater sediment deposition increased plant productivity, but species-specific responses were observed. Moreover, the combination of 10 cm of sediment deposition and nutrient enrichment had a positive effect

on stem density which has the potential to increase sediment trapping efficiency and surface

accretion rates. Nutrient loading and therefore eutrophication will be a consequence associated

with river diversions, however concentrations of 2.0 mg/L (32.25 uM/L) N did not affect species

richness and composition, density, and above-and belowground biomass alone. It is still

unknown whether longer periods of nutrient enrichment will increase nutrient concentrations in

plant tissues overtime, such that organic litter quality (e.g., lignin-N) is altered as increased

nitrogen content have been directly quantified with leaf litter (Valiela et al. 1985; Rybczyk 1996;

Melillo et al. 1982). Lastly, our study indicates the effects of nutrient enrichment on

belowground biomass may be dependent on root type, hydrologic regimes and deposition.

APPENDIX A. CHAPTER 2

USING STABLE ISOTOPES TO IDENTIFY RATES OF NITROGEN ASSIMILATION AS A RESULT OF NUTRIENT AND SEDIMENT ENRICHMENT IN OLIGOHALINE, DETERIORATING, AND SEMI-CONSTRUCTED WETLANDS

ATTENTION: Due to COVID-19 we were still awaiting laboratory analyses on this study and thus no results or discussion is included in this chapter.

APPENDIX B. INTRODUCTION FOR CHAPTER 2

The application of isotopic tracers is a common method used to track the spatial and temporal fate of nitrogen isotope ratios in aquatic systems. Much of this work has focused to determine the nitrogen (N) removal capacity of storm water treatment wetlands as a result of agriculture and wastewater run-off. However, the nitrogen removal capacity does vary, and it is still not completely understood or predictable amongst different marsh ecosystems (Messer et al., 2017). In the short-term, understanding the distribution and transformations of nitrogen products can predict the maximum removal potential, optimum N loading capacity, future bioavailability, and potential N remobilization with increased sedimentation across vegetated coastal communities.

Increased nutrient availability to macrophytes can result in litter with increase nutrient ratios (i.e., C:N), leading to litter that decomposes much quicker and immobilize less nutrients (Marinucci et al. 1983, Neely and Davis 1985, Valiela et al. 1985, Webster and Benfield 1986). Decomposition of plant litter is an important component of nutrient cycling in wetlands and macrophyte litter alternately takes up and releases nutrients as it decomposes (Melillo et al. 1984). Decomposition begins as litter releases soluble nutrients by leaching and if the litter is relatively rich in carbon and poor in nutrients, it is assimilated by soil microorganisms as immobilized exogenous nutrients. As decomposition continues mineralization predominates over immobilization and the litter gradually releases nutrients to the surrounding plant communities. However, if the litter is relatively rich in carbon and rich in nutrients, litter derived nutrient may be immobilized for greater durations, increasing the N availability in the sediment and cascading effects on plant productivity (Davis and van der Valk 1978, Rice and Tenore 1981; Correll et al. 1975, Barko and Smart 1983). Rates of leaf litter decay have been directly correlated to initial

tissue N content of the litter and a review of 24 wetland decomposition studies indicated this positive decay rate response (Rybczyk et al. 1996). Most importantly, early stages of decay tended to be affected by nutrients (i.e, N), whereas later stages of decay were not. Therefore, excess of NO_3^- could stimulate the decay of organic matter and shift above and belowground productivity contributions initially, but long-term decomposition may be reliant on the availability of labile organic carbon in the soil (Melillo et al., 1984; Wigand et al., 2015).

Mineral sediment plays a significant role in organic matter and nutrient preservation, as organic aggregates adsorb onto minerals surfaces (e.g., N, P, K, Fe, Mn, and others), thereby immobilizing resources and contributes to marsh maintenance (Boto and Patrick 1978; Rovira and Vallejo, 2003; Slocum et al., 2005; Turner et al.,2006; Graham and Mendelssohn, 2013). Moreover, positive effects of sediment inputs can be particularly seen in degrading wetlands, primarily through elevation gains that reduce flooding and improve soil aeration. Long term effects can be seen as inorganic sediment reduce phytotoxin hydrogen sulfides and increase soil bulk densities that promote seed and rhizome development (Craft et al., 1999; Slocum and Mendelssohn, 2008; Stagg and Mendelssohn, 2010; Baustian and Mendelssohn, 2015). Conversely, sediment application alone, may increase organic matter decomposition at the surface through enhanced aeration of the rhizosphere (Mudd et al., 2010; Graham and Mendelssohn, 2013). Previous studies have found lower soil organic matter percentages and total nutrient in constructed wetlands with dredged sediments when compared to references sites (Craft et al., 1999). This response is expected, as physiochemical properties such as organic matter, TC, and TN require periods of time to accumulate in reference sites (Ballantine and Schneider, 2009; Craft et al., 1999). Nutrient input via sedimentation is the single most important new nutrient source in salt marshes of the Barataria Basin in Louisiana (DeLaune and

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Patrick 1980). While there is general agreement wetlands act as essential transformers of N, there is limited information on how increased mineral sediments will affect these process that control N retentions and export for varying systems (i.e., fresh, intermediate, brackish, salt, and create marshes.

Nitrogen pools and transformation rates have been determined in many studies by summing the various processes to create a mass balance that estimates net N retention and loss (Valiela and Teal 1979; Abd. Aziz and Ned- well 1986; De Laune et al. 1989). However, the import of N is generally insufficient to meet both the need for annual plant uptake and active N cycling via translocation and remineralization in the sediment, which is considered to make up about 54-95% of the transformations (Hopkinson and Schubauer 1984; De Laune et al. 1989; Dame et al. 1991). To evaluate relationships between nutrients and plant responses, biogeochemical processes, and nutrient retention and export across varying ecotones, a full factorial nutrient and sediment field study was implemented in early May 2019, consisting of three different marshes either dominated by *Sagittaria lancifolia*, *Spartina patens*, or *Schoenoplectus americanus*. Each system was labeled with the stable isotope Nitrogen-15 (N^{15}) early in the growing season (June 15 2019) by injecting calcium nitrate (10 atom % N^{15}) in three installments once per day at mid-tide so as to limit loss of the tracer downward through percolation. A total of 250 mL of label was injected at 10 cm depth for a total of 1.2 g N^{15} per plot. Data collection occurred on day 5, 15, 30, and 200 following last injection, consisting of species richness and abundance, aboveground biomass, belowground biomass, and soil. Plant tissues and soil were examined to determine the processing and fate of dissolved NO_3^- in these plant communities. By examining the effects of multiple integrated environmental conditions,

including nutrient and sediment availability on marsh dominance, we can better predict

responses and recovery in complex natural systems.

APPENDIX C. METHODS FOR CHAPTER 2

Study description and experimental design

Experiments were conducted in the upper Barataria Basin, Louisiana. The area is part of the larger Barataria Basin Watershed covering approximately 760 square miles and characterized by low, flat terrain with numerous navigation channels, drainage canals and natural bayous that drain into Lake Des Allemands. The basin is host to a variety of coastal habitats, including bottomland hardwood forest, swamps, marshes ranging from fresh to saltwater, bays and barrier islands. The area is severely sediment depraved and the mid-basin marshes have all but disintegrated meanwhile the upper basin marshes are showing signs of deterioration.

The ^{15}N tracer experiments were conducted in three marshes consisting of a *Sagittaria lancifolia-* dominated oligohaline marsh, a *Spartina patens-* dominated deteriorating brackish marsh (The deteriorating marsh), and a *Schoenoplectus americanus-* dominated created marsh near Barataria Bay, Louisiana. The oligohaline marsh (CRMS site 4245; Lat, Long: 29.67202, -90.13549), is the furthest north site and receives greater freshwater inputs and has a diverse suite of species (e.g., *Sagittaria lancifolia*, *Panicum repens*, *Vigna luteola, Polygonium punctatum, Spartina patens, Eleocharis macrostachya*). Marsh elevation is approximately 0.60 ft (NAVD88 Geoid12A) and mean water salinity ranges from 0.11-18.75 ppt. The deteriorating marsh is the furthest south and shows signs of deterioration (CRMS station 0248; Lat, Long: 29.59944, -90.07299) classified as low diversity, (i.e., *Spartina patens* and *Schoenoplectus americanus* dominant) and has mean water salinities ranging from 0.17-25.30 ppt. The created marsh (Lat, Long: 29.363767, -90.31904), is dominated by *Schoenoplectus americanus*, *Bacopa monnieri, and Lythrum lineare.* The created marsh located directly east of the Mississippi River (ID: BA-0043-EB), is 415 acres and was constructed using 3.8 million cubic yards of sediment dredged

from the Mississippi River. Unlike the oligohaline and deteriorating marshes, where the soils are highly organic and mixed with fine silts and clays, the created marsh soil is comprised of a ±10 cm fine organic layer above a ± 1 m sand layer.

In May 2019, 24 cores barrels were haphazardly installed ~10 m apart at each site using (Polyvinyl chloride, (PVC)) core barrels 15.24 cm diameter by 40 cm height) and were selected to prevent lateral flow of tracer and nutrient treatment. Core barrels were inserted approximately 35 cm into the soil. Cores received one of two nutrient treatments (ambient (control) or nutrient enriched), and one of two sediment treatments (0 (control) or 5 cm). Cores were allowed to acclimatize for two months prior to stable isotope injection and subsequent temporal removal.

Treatments

Nutrient-enrichment - The nutrient-enriched treatment was 2.0 mg/L N as $(CaNO_3)_2$ and 0.3 mg/L P as H_2PO_4 replicated in eight plots for a total three replicates per time point per treatment (n=3). Nutrients in granular form were added directly to the surface of the plots. These nutrient concentrations were slightly above the nutrient concentrations measured through a freshwater diversion of the Mississippi River in 1997 (1.28 mg/L mg N, and 0.05 mg/L P) (Roy et al. 2013). Ambient plots received no nutrient enrichment and were replicated similarly, for a total of three replicate per time point per treatment.

Sediment deposition - Plots were assigned to one of two sediment applications; 0 (control) or 5 cm of sediment additions. Each sediment treatment was replicated for a total of three replicates per time point per treatment. Sediment was sourced through a local dredging company and was removed from the Mississippi River prior to the experiment. To prevent contamination and ensure mineral sediments were homogenized, the Mississippi Dredge fill material was pasteurized using an autoclave (model# 2540M Tuttmoner Brinkman) at 121 °C for 25 minutes.

The material was then sieved through a 2 mm mesh screen and stored prior to transportation to field sites.

$^{15}NO_3$ addition -The sediment nitrate pool was labeled in each system with stable isotope Nitrogen-15 (N^{15}) early in the growing season (June 30-July 3, 2019) by injecting calcium nitrate (10 atom % N^{15}) into each plot. Four evenly spaced installments were achieved every other day (n=3), at mid-tide so as to limit loss of the tracer downward through percolation. A total of 250 mL of label was injected at 10 cm deposition for a total of 1.2 g N^{15} per plot using di-ionized water, which was sufficient to enrich the sediment from ±0.367 to ±10.00 atom %. Deposition s per injection were adjusted for sediment placement.

Measurements

Data collection occurred on day 5, 15, and 30 following last injection and consisted of species richness, composition, aboveground biomass, belowground biomass, and soil analysis. All aboveground plant material was clipped before plug extraction. Plugs were extracted and sealed at the bottom using a flexible (PVC) cap and transported to the Louisiana State University Laboratory in Baton Rouge, LA for processing. Furthermore, all samples were stored at 4°C until processed.

Plant species richness, composition and relative dominance- Species richness was recorded in each core on day 5, 15, and 30 post injection for each location. Species-specific stem densities were determined by counting the number of stems present in each core per species. Average heights were measured to the nearest centimeter by measuring each stem by species.

Aboveground biomass- To measure total productivity aboveground, dead and live biomass was manually sorted for each plug to form a cumulative account of total aboveground biomass per

treatment. Aboveground biomass was clipped at the soil surface and sorted by species and sub-sorted into leaves and stems. Plant material was then dried to a constant mass at 60°C and weighed. Total aboveground biomass for each species was calculated by summing the dead biomass and live biomass. Vegetation was undisturbed pre-treatment at the beginning of the study, aboveground productivity was calculated as grams dry weight per year based on the 150 day study period.

Belowground biomass- All soil cores were sectioned into 15 cm sections, weighed, cut in half, and half was used to determine belowground biomass productivity. In the lab, sections were rinsed, and material was then gently washed over a 2 mm mesh sieve, separated as either live (fine root, large root, rhizome) or dead (fine and course), and dried to a constant mass at 60° C and weighed. Coarse dead and fine organic matter was distinguished by size fractionation; all material not retained on a 2.0 mm sieve was coarse and material that washed through 2.0 mm and retained on 0.71 mm mesh was considered fine.

Soil bulk density and organic matter content- The other half of the biomass core sections were used to measure soil blk density and organic matter content. Half samples were initial weighed wet and weighed again after determining constant mass at 60°C. In addition, after constant mass was determined moisture content (%) was determined along with dry bulk density (g/cm^{-3}). Bulk density was calculated as the dry weight divided by the volume of the cylinder ($g\ cm^3$). A portion of the dry sediment samples were sectioned, re-weighed, then placed in a muffle furnace at 550° C for four hours to determine the proportion of sample lost on ignition (LOI).

APPENDIX D. RESULTS AND DISSCUSSION FOR CHAPTER 2

Due to COVID-19 the analysis of samples and the subsequent results and discussion are not available at this time.

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VITA

Donnie Joe Day III received his bachelor's degree from Ohio University in Plant Biology. He furthered his education at Louisiana State University through the Department of Oceanography and Coastal Science and plans to graduate with a Master's of Science in May 2021. While at Louisiana State University, Donnie worked on many collaborative projects with the Department of Civil and Environmental Engineering, United States Army Corp of Engineers-Coastal Hydrology Lab (USACE-CHL), and Chenier Environmental Consulting. Upon completion of his master's degree, he will begin work on his doctorate at The University of Toledo.