THE ECOLOGICAL RESPONSES OF WETLAND PLANT SPECIES TO HYDROPERIOD DETERMINED BY MANIPULATED SOIL SURFACE ELEVATION

A Thesis

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Abstract

As sea level rise, subsidence, and abandonment of natural deltaic processes due to a highly engineered Mississippi River continue to threaten Louisiana's coastal wetlands, the need for a system-wide understanding of natural wetland land-building and preservation processes has never been greater. A key component of any wetland is the ever-changing water environment that periodically floods and dries the marsh platforms. The flooding depth, duration, and frequency, known as the hydroperiod, along with salinity and soil fertility are key determining factors of vegetation and marsh types at a particular location. Different types of vegetation will have different growth characteristics such as root production, which contributes to soil formation. We hypothesize that plant growth response to flooding inundation varies with species in brackish and saline marshes, and that maximum growth response occurs at neither extreme but some mid-inundation range. We further predict that varying hydroperiod and salinity from the brackish to saline zone determines the soil microbial community composition, controlling the cycling of wetland nutrients. This study found that while both dominant brackish and saline species favor high inundation over low inundation, they both also produce the most biomass under a combination of inundated and dry conditions. We also found evidence that the key turning point in soil-surface elevation where inundation becomes too great to support growth can occur on a very small scale, and that identifying salinity transition zones and the response of microorganisms to environmental conditions can be very powerful tools for assessing soil formation properties or predictions. By artificially manipulating soil surface elevation in "marsh organ" mesocosms across a salinity gradient in coastal Louisiana, the relationship between plant growth and inundation can be explored to understand how marsh productivity responds to sea level rise scenarios.

1. Introduction

Louisiana's coastal zone includes extensive wetlands that provide many ecosystem services such as storm surge protection, fish habitat, and improved water quality. Global climate change impacts such as sea-level rise threaten coastal wetlands, and accelerating sea-level rise compounded with natural subsidence in abandoned river deltas presents a real threat to the longevity of Louisiana's wetlands. Furthermore, Mississippi River engineering has reduced sediment supply to coastal deltaic floodplain wetlands affecting soil vertical accretion rates, a key component of the wetland land building process. As sea level rises and coastal lands sink at rates greater than vertical accretion rates, wetlands are converted to water area with saltwater reaching further inland altering water chemistry in traditionally brackish or freshwater ecosystems. Salinity, along with hydroperiod, are two of the most important factors determining dominant vegetation of wetland typologies and therefore has a great affect on the wetland shape and function (Wigand et al., 2017). All of these compounding processes are exacerbating wetland habitat change and land loss in coastal Louisiana. Understanding wetland growth relationships with elevation and salinity is critical to estimates of what will be impact of future sea level rise (Rovai et al., 2022).

Wetland inundation, defined as the percent-time that the marsh surface is flooded throughout the year, is determined by the surface elevation of that wetland relative to changes in water levels. Water levels on wetland soil surface is constantly changing, controlled by tides, rainfall, river discharge, seasonal coastal frontal passages, and human engineering. Wetlands with higher surface elevations are inundated less frequently and as a result are populated with specific types of vegetation, whereas lower wetland surface elevations are inundated more frequently and support different types of vegetation. Wetland plant species not only have a range of inundation that controls community composition, but also respond to ranges in soil salinity that determine community types (Holm and Sasser, 2001). While wetland plants are specially adapted to survive the ever-changing intertidal environment (Janousek et al., 2016), there is a higher and lower wetland surface elevation where the inundation is either so infrequent or of long duration, respectively, that no wetland plants occur. Between those maximum and minimum growth elevations is a range of inundations that represents maximum biomass that is species-specific. “Marsh Organs” are an experimental design to explore how inundation ranges control maximum biomass production of wetland plant species (Morris, 2007). Mesocosms represented by cores with plugs of monospecific species are arranged at increasing elevations spanning the anticipated inundation range from 0-100% of the time during field incubation to artificially manipulate hydroperiod and assess plant growth. Aboveground biomass is measured at the beginning and end of the field incubation period (2-3 months) to estimate wetland productivity relative to wetland surface elevation. In addition, belowground biomass is measured to quantify and predict total marsh production in response to inundation treatments.

Understanding plant growth dynamics in response to varying hydroperiods is crucial for assessing and enhancing the contribution of plant production to wetland soil formation and increase in surface elevation, particularly in the context of coastal regions like Louisiana. These marsh ecosystems historically demonstrate an equilibrium governed by mean sea level, land elevation, plant production and surface accretion (Morris et al., 2002). Production of aboveground biomass contributes to surface litter which is decomposed into organic matter by soil microbes. Belowground biomass production creates networks of productive roots and rhizomes contributing directly to soil structure and formation (Morris et al., 2016). All of these plant structures add organic matter to soil which helps build soil surface elevation and maintain growth conditions in coastal wetlands (Cahoon et al., 2004). Marsh macrophytes In rapidly subsiding and eroding marshes experiencing the added challenge of sea-level rise, the elevation-building property of soil formation is the primary defense against flooding. Observing changes in plant production as a result of elevation changes in a tidal wetland is a powerful tool for assessing and predicting organic sedimentation and soil formation under varying inundation conditions.

Soil microbes play a crucial role in supporting plant growth as they break down organic matter into nutrient forms usable by plants. As sea level rise increases, more coastal freshwater marsh is converted to brackish or saline marsh leading to key changes in soil chemistry (Weingarten & Jackson, 2022). Inundation, flooding, and salinity can all significantly impact microbial communities in soil, leading to changes in their composition and functions. More productive, freshwater wetlands are able to store more carbon as biomass, but this benefit comes at the cost of higher greenhouse gas emissions due to increased soil respiration and methanogens (Weingarten & Jackson, 2022). In intertidal and high salinity wetlands, certain plant-soil-microbe interactions are blocked which can lead to an excess of nitrate and phosphate and cause eutrophic conditions. Highly inundated soils have reduced oxygen availability which favors anaerobic microbes and promotes methane production, whereas high salinity soils introduce osmotic stress and reduced nutrient availability. These findings suggest that a higher percentage of brackish and saline marshes will lead to decreased nutrient cycling rates and that the relationship between C/N/P cycling microbes and inundation or salinity changes must be explored (Weingarten & Jackson, 2022).

Other marsh-organ studies have utilized the elevation treatment design and found that plant survival is highest at mid-range percent-time inundations and low at extreme elevations which receive either 0 or 100% inundation (Peng et al., 2018). This finding suggests a biomass curve across the 0-100% inundation range which peaks somewhere at the intermediate inundations (Morris et al., 2002). This expected curve of maximum biomass with changes in salinity and inundation has somewhat different patterns in coastal Louisiana (Snedden et al., 2014). In brackish and saline marshes, locally-dominant species such as *Schoenoplectus americanus* and *Spartina patens* tend to have greatest above-and-below-ground biomass at higher elevations, where inundation is lowest; and subtle changes in hydroperiod can have detrimental effects on productivity (Snedden et al., 2014). These findings are similar to marsh organ experiments in a New England salt marsh (Wigand et al., 2017). Contrary to the negative growth-inundation relationship in the brackish and saline marsh species, freshwater species such as *Colocasia esculenta* have been shown to increase productivity with inundation (Rovai et al., 2022). Evidence of such species-specific salinity and inundation preferences emphasizes the benefit of exploring growth-inundation relationships across different species and salinities.

The primary objective of this thesis is to test the plant growth-inundation relationship for species along salinity gradient using marsh-organ mesocosms across the full range of elevations that experience flooding throughout the growing season. By simulating the hydroperiods of higher and lower marsh elevations relative to the local average during plant growth, I tested how biomass productivity is affected by inundation frequency of marsh soil surface. This objective is accomplished by installing marsh organ structures at carefully selected sites along a salinity gradient in Louisiana's coastal marshes near Coastwide Reference Monitoring Systems (CRMS) stations with pre-existing water level and salinity data. I tested the hypothesis that

(1) maximum plant biomass response to flooding inundation varies with species in brackish vs saline environments;

(2) maximum plant biomass response occurs at the mid-inundation range in both the brackish and saline environments;

(3) soil microbial community composition varies with flooding inundation and salinity.

2. Methods

2.1. Study Sites

Two sites were chosen in Fourleague Bay in southeast Louisiana to test the effects of hydroperiod on plant growth in two different salinity zones. Fourleague Bay and its surrounding wetlands are part of the Atchafalaya River Basin which is actively building land mass in coastal Louisiana due to large sediment inputs from the Mississippi River. The Atchafalaya Basin receives roughly 30% of the discharge from the Mississippi River (Allison et al., 2012), which distributes sediment and eventually builds elevation in nearby wetlands. While river discharge plays an important part in the water level, salinity, and sedimentation rates of these Fourleague Bay wetlands, tidal influences from the nearby Gulf of Mexico cause variable mixing of fresh and saltwater resulting in a salinity gradient. The salinity of the water environment in which a plant grows affects soil chemistry which will ultimately determine the species that can grow in the area; therefore, study sites were established in both saline and brackish marsh types.

Figure 1. Map of coastal Louisiana showing location of brackish (blue) and saline (red) marsh sites near Fourleague Bay (white) where marsh-organ experiments were performed

Marsh organ sites were selected near coastal reference monitoring stations, hereafter referred to as CRMS, managed by Louisiana's Coastal Protection and Restoration agency (CPRA) (www.lacoast.gov/crms). The brackish site was chosen near CRMS 0399 which is established in wetlands between Fourleague Bay and Lost Lake (Figure 1). The site is highly vegetated with marsh grasses dominated by *Spartina patens* and *Shoenoplectus americanus.* The average marsh elevation is 0.13m (Geoid 18, NAVD88) and soil salinity at the brackish site varies from 7.75 to 12.25 ppt (www.lacoast.gov/crms). The saline site was chosen near CRMS station 0322 which is south of Fourleague Bay along Old Oyster Bayou. The site is dominated by *Spartina alterniflora* and *Spartina patens*. The saline site has an average marsh elevation of 0.05m (Geoid 18, NAVD88) and soil salinity at the saline site ranges from 0.75 to 2.90 ppt (www.lacoast.gov/crms). Both sites experience yearly changes in plant production which is largely due to the water level variability from year to year as the result of changes in river discharge and tidal influence, making them ideal locations for an experiment focused on a plant's growth response to hydroperiod.

2.2. Species Selection

Production of local marsh macrophytes increases the elevation equilibrium while increasing relative sea-level lowers equilibrium conditions (Morris et al., 2002). In the interest of investigating optimum elevation and flooding conditions for plant production across varying salinity, species were chosen from the dominant taxas present at the sites as shown by the CRMS data for the brackish site (Fig. 2) and saline site (Fig. 3). *Shoenoplectus americanus* was the species chosen to populate the mesocosms at the brackish site, and *Spartina patens* was the species chosen to populate the mesocosms at the saline site. Both wetland plant species have unique tolerances for salinity and inundation that allow for their success in these highly variable wetland regions that determine the geographic distribution of their area coverage. Selecting species that make up such a significant portion of the site's respective marsh area coverage is important for gaining the most relevant information about how future changes in hydroperiod will alter that site's soil formation capacity.

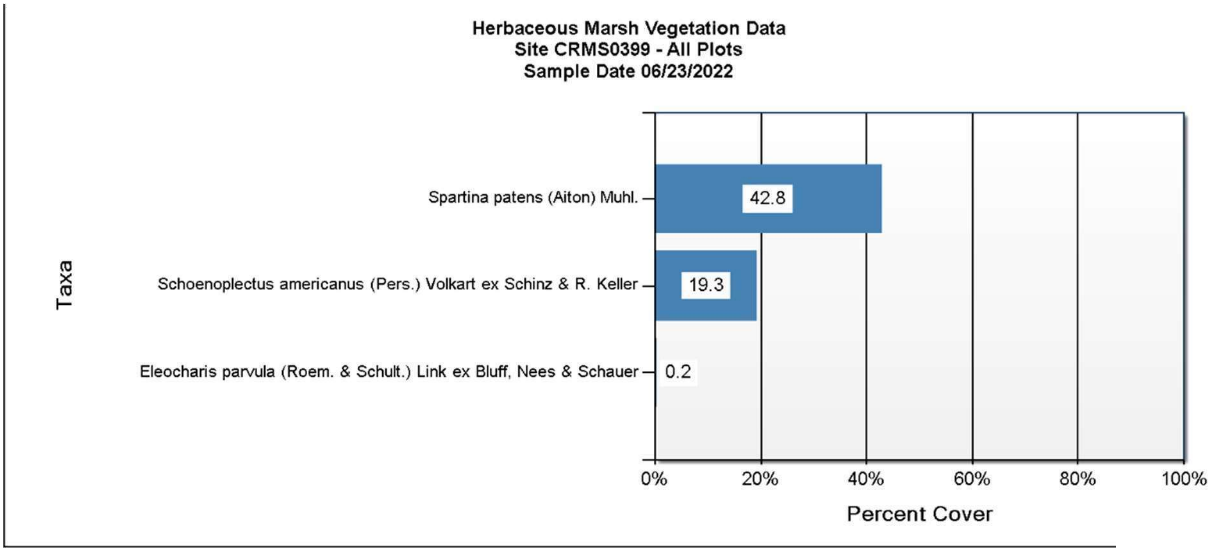

Figure 2. Dominant taxa and percent land cover at brackish site (CRMS 0399). (www.lacoast.gov/crms)

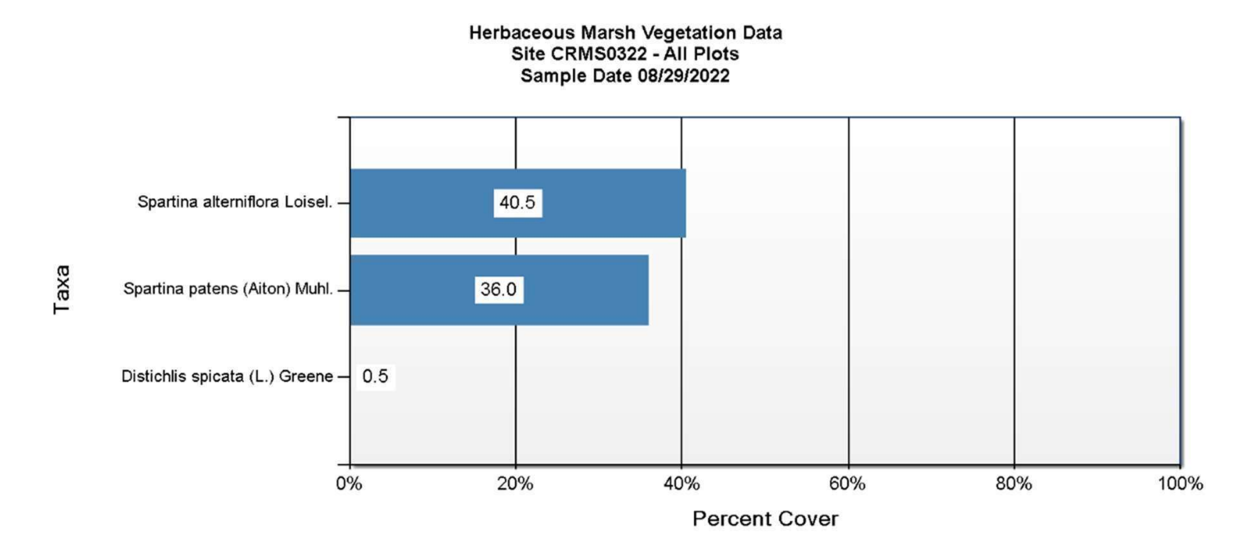

Figure 3. Dominant taxa and percent land cover at the saline site. (www.lacoast.gov/crms)

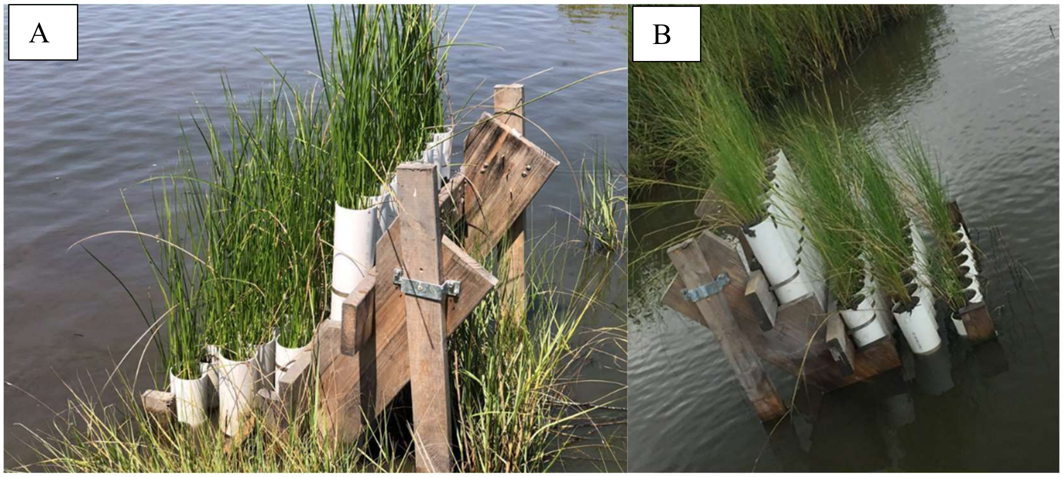

Figure 4. (A) *Schoenoplectus americanus* marsh organ at the brackish site (CRMS 0399). (B) *Spartina patens* marsh organ at the saline site

2.3. Marsh Organ Growth Experiment

"Marsh organs" are plant mesocosms made up of cores positioned at different elevations to simulate different flooding regimes (Fig. 4). Just like any natural patch of wetland soil, a mesocosm at a lower elevation will experience more flooding and higher inundation time while a mesocosm at a higher elevation will experience less flooding and lower inundation time. By positioning plant mesocosms across a range of elevations to capture the full water inundation range at a given site, patterns can be seen reflecting a plant's response to a manipulated hydroperiod and insights can be gained about the future plant coverage of a marsh at a certain elevation.

Marsh organ structures were built and installed at each site for three consecutive growing seasons, roughly April-September of 2021, 2022, and 2023. The bases for the structures were made with two stair-stepped 2x12 inch lumber planks connected by 2x6 inch lumber planks that act as shelves to house mesocosms in various experimental elevation-treatment rows. All lumber was untreated, and all fastening hardware was stainless steel in order to avoid chemical interactions over long periods of submergence in salty water. Four-inch diameter PVC pipes, which act as the actual mesocosm, were then measured and cut to predetermined sizes based on site-specific water level analysis and secured to the 2x6 inch lumber shelves with adjustable hose clamps for final elevation adjustments. Once the structures are built, they are installed at the site by sinking the structure to a predetermined elevation that will give the best chance for the experimental rows to capture the full range of hydroperiod. Elevations are checked with confidence in the field using an RTK GPS. After confirming the correct elevation with the RTK, four long 2x4 inch lumber planks are pushed three meters into the earth and drilled to the base of the structure to prevent movement or shifting throughout the growing season. The structures were oriented so that the tallest mesocosms were to the north so that any shading effect would be minimized (Snedden et al., 2014).

Figure 5. Marsh organ design with 5 elevation treatments and 8 mesocosms per row used during the 2021 growing season. Similar designs were used for all the other growing season experiments

With structures in place and mesocosms fixed in position, local soil was then harvested with shovels and packed into the pipes until they were filled and ready to be planted. Significant soil compaction can occur when soil is relocated in this fashion due to the incorporation of small air bubbles during the transfer process. Compaction must be addressed in a marsh organ experiment that relies upon specific soil surface elevations, so a two-week soil-settlement period was allowed between initial construction and filling; and mesocosm planting at the beginning of the growing season. Planting of marsh organ mesocosms consisted of carefully harvesting young specimens of the target species from the surrounding marsh and transplanting one plant into each mesocosm on the marsh organ structures. Plants were then clipped to a consistent biomass, and replicate specimens were taken back to the lab to measure initial biomass and necromass values. Subsequent visits to the sites occurred regularly throughout the growing season, every two weeks on average, for routine maintenance and data collection, including topping up mesocosms with more locally-harvested soil to maintain target soil surface elevations and clearing structures of floating debris.

Marsh organ structures were installed near CRMS at the respective brackish and saline sites so that previous years of water level data during the growing season months could be analyzed at each site and used to find the experimental treatment elevations that would best capture the full inundation range. Eight years of water level records from the CRMS database were used to generate exceedance curves which show percent-time inundations of different elevations across each site's water level range during the growing season (Fig. 6, 7). With the goal covering both hydroperiod extremes and a range of inundations in between, one elevation row was designed to be just below the lowest average growing-season water level, one just above the highest average growing-season water level, and the remaining rows distributed between the extreme elevations in even increments of percent-time inundated.

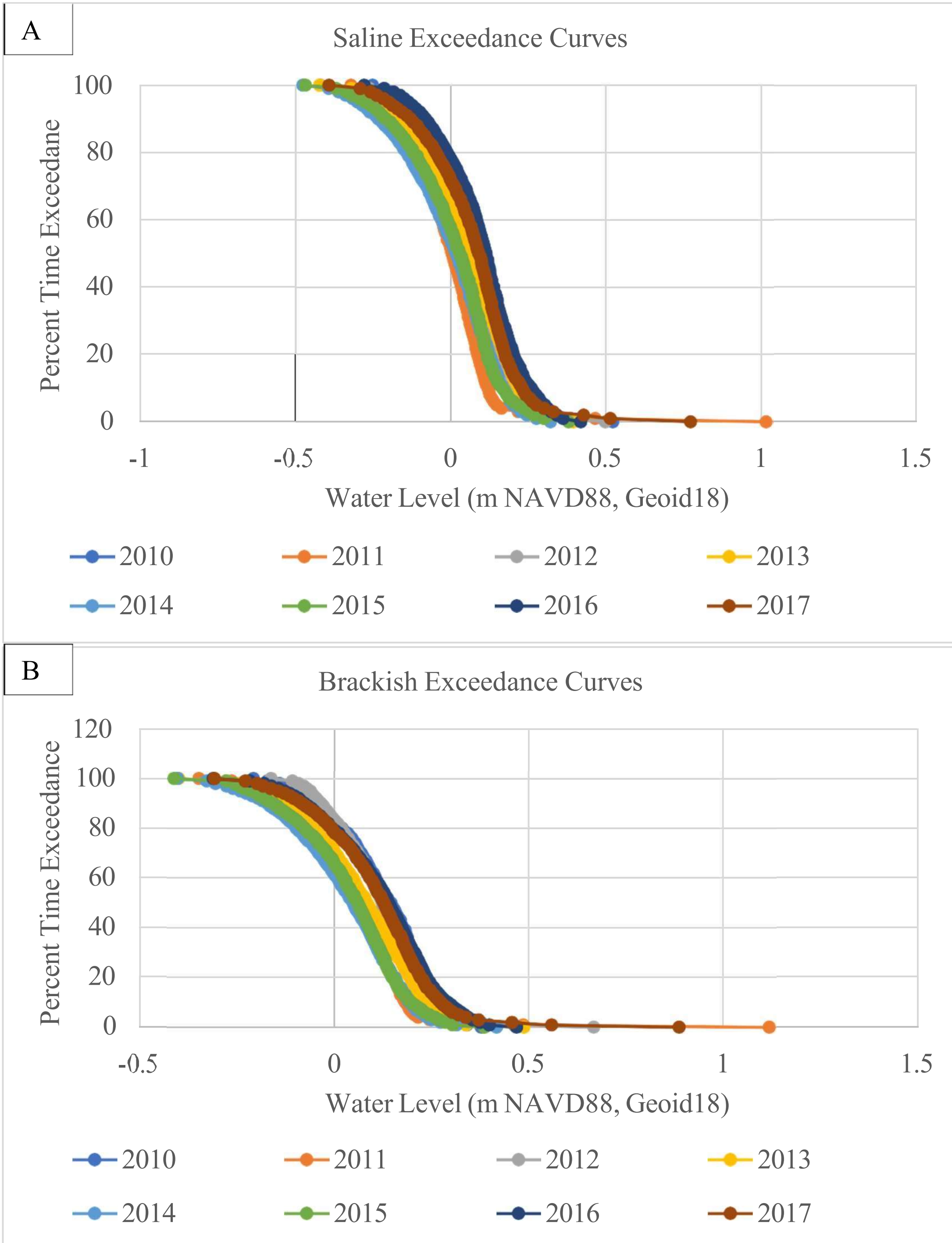

Figure 6. Exceedance curves based on CRMS water level data from March-October of 2010-2017 and 2021 for the (A) brackish site (CRMS 0399) and (B) saline site (CRMS 0322)

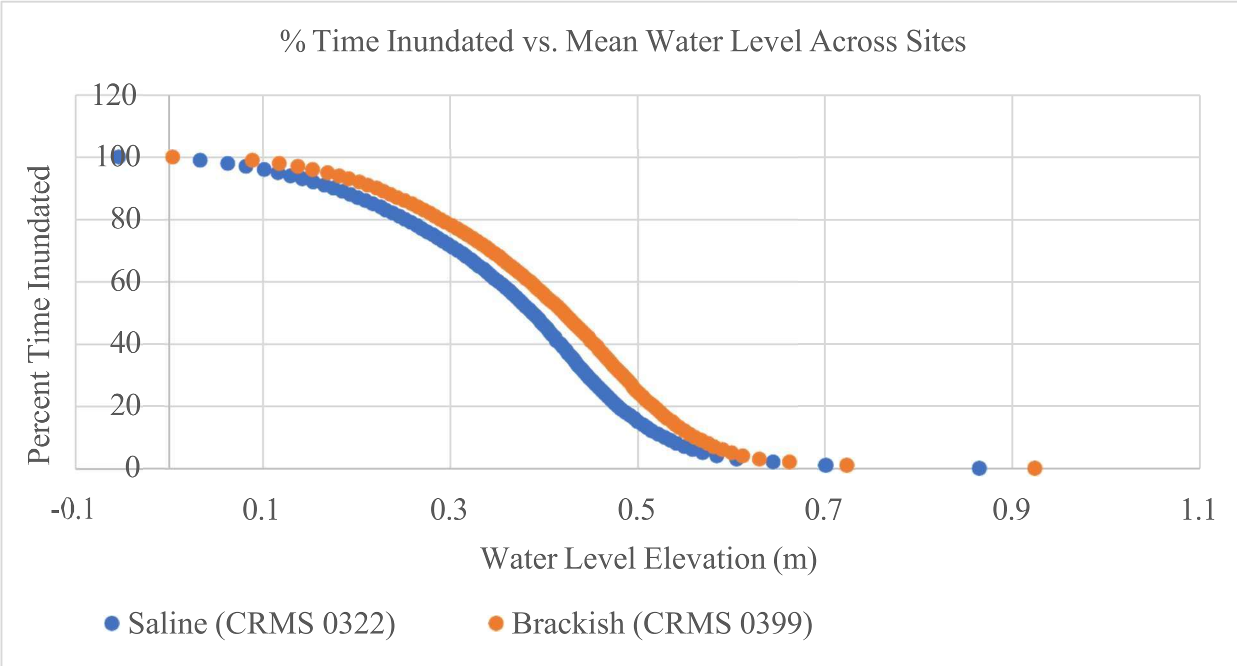

Figure 7. Eight-year average exceedance curves for sites along the salinity gradient

While a multi-year and site-specific water level analysis was employed to determine experimental elevations, unusually high or low-water years, as well as frequent, intense summer storms experienced in southeast Louisiana, can negatively affect expected treatments by changing anticipated inundation levels. Since exact water level behavior cannot be predicted with certainty, this study has been repeated and tweaked across three growing seasons, 2021-2023, to provide the best chance of gathering productivity data across the full inundation range. The latter two growing seasons also added identical replicate marsh organ structures (about 10m away from original) at each of the two sites to lower the chance of some extremely localized phenomenon that could alter results. Experimental design elevations and percent-time inundations, defined as the percentage of time that a given elevation is inundated during the growing season, are given in the table below for each year that the experiment was performed (Table 1). Again, these experimental row and replicate numbers, as well as specific row elevations, were tweaked each year to reflect the best logistically-feasible chance to capture the plant biomass-inundation relationship.

Table 1. Marsh organ design elevation treatments with expected percent-time inundations for each growing season

Brackish Site			Saline Site		
2021 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
5	0.57	0	5	0.49	0
4	0.17	25	4	0.14	25
3	0.10	50	3	0.06	50
2	0	75	2	-0.05	75
1	-0.34	100	1	-0.37	100
2022 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
7	0.58	0	7	0.53	0
6	0.22	16	6	0.18	16
5	0.17	33	5	0.12	33
4	0.11	50	4	0.07	50
3	0.05	66	3	0.01	66
2	-0.04	83	2	-0.09	83
1	-0.34	100	1	-0.38	100
2023 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
6	0.50	0	6	0.45	0
5	0.26	20	5	0.20	20

(table cont'd.)

Brackish Site			Saline Site		
2023 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
4	0.18	40	4	0.12	40
3	0.10	60	3	0.03	60
2	0.02	80	2	-0.10	80
1	-0.34	100	1	-0.40	100

Figure 8. Seven-row marsh organ design with four mesocosms per row from 2022 growing season

Slight alterations in the marsh organ experimental design occurred each growing season in an attempt to increase the quality of the results and satisfy logistical needs. The 2021 growing season design featured one marsh organ structure per site, each with five elevation treatment rows of eight replicate mesocosms. Target row elevations were chosen from the eight-year exceedance curves to produce plants that experienced roughly 100, 75, 50 ,25, and 0 percent-time inundated during the growing season from the bottom row of the structure to the top row, respectively (Table 1). The 2022 growing season design sought to gain a finer resolution of the changes in hydroperiod by installing entire replicate marsh organs at both sites consisting of seven elevation treatment rows of four replicate mesocosms. These seven elevation treatment rows were designed to experience 100, 83.3, 66.7, 50, 33.4, and 0 percent-time inundated during the growing season from the bottom row to the top row. The final design for the 2023 growing season was a middle ground between the first two iterations of the experiment, featuring replicate marsh organ structures at both sites each with six elevation rows of five replicate mesocosms (Table 1). This design provided the best replication of experimental treatments while still capturing a broad range of inundations, designed to be 100, 80, 60, 40, 20, and 0 percent-inundated over the growing season from the bottom row to the top row.

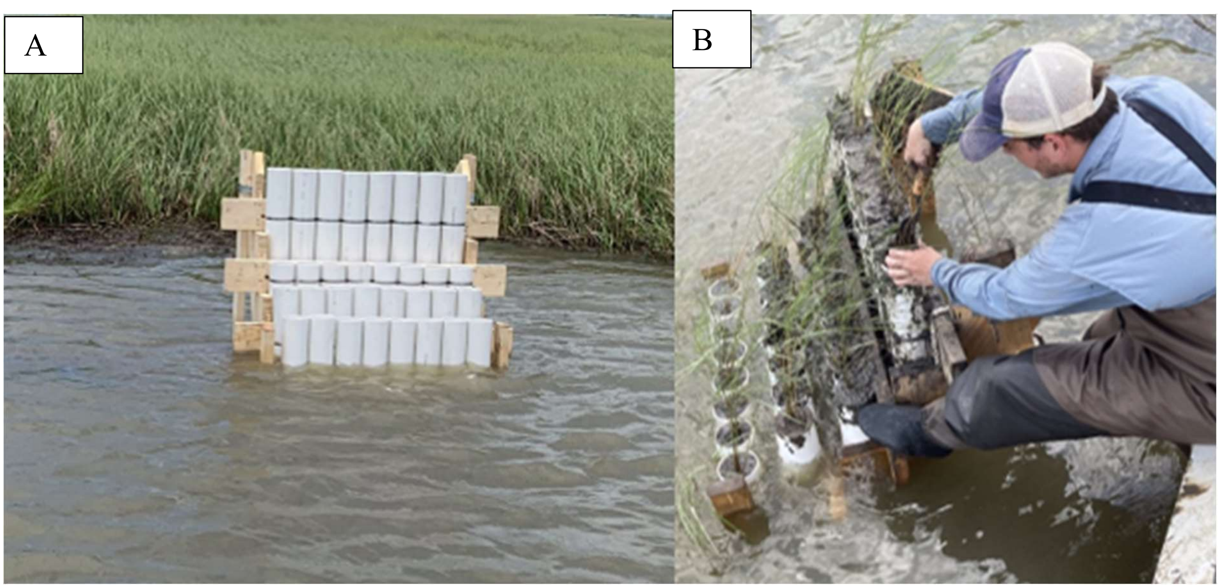

Figure 9. Marsh organ installation from(A) and planting of *Spartina patens* (B) at saline site for 2021 growing season

Figure 10. Clipped *Spartina patens* plugs ready to be planted in mesocosms for 2021 growing season

Figure 11. *Schoenoplectus americanus* mesocosms right after planting at the brackish site

Figure 12. Marsh organ installation (A) and filling (B) at the saline site for 2022 growing season

Figure 13. Locally-harvested *Spartina* patens specimen for 2022 growing season

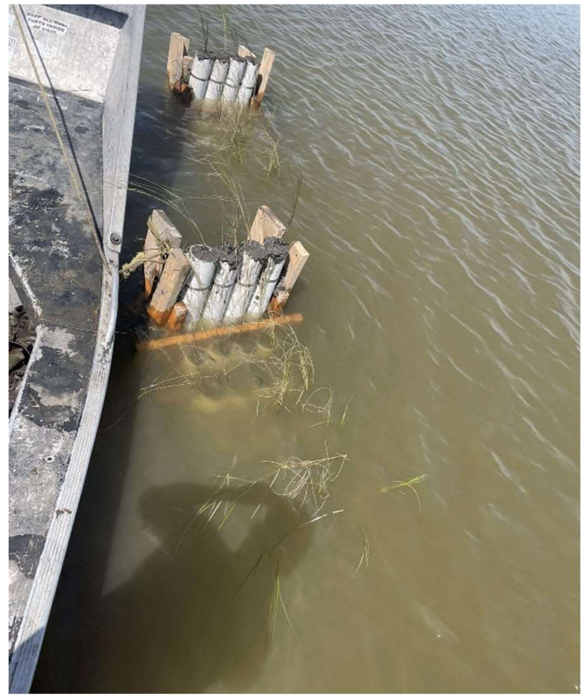

Figure 14. Newly replanted *Spartina patens* in mesocosms at the saline site for 2022 growing season

Figure 15. *Schoenoplectus americanus* at the brackish site for 2022 growing season

2.4. Data Collection

Solinst leveloggers and barologgers were installed at both sites to measure water level, water temperature, salinity, and barometric pressure throughout the growing season. The loggers were housed in vertically stationed PVC pipes nearby the marsh organ structures. The water levelogger was hung with a rope to be suspended 2 inches above the channel bed, and the pipe has a slit cut in it so that the water level within the pipe reflects that of the channel. The barologger was fixed to the top of the PVC pipe to measure atmospheric pressure, and both loggers recorded measurements in 15-minute intervals. Solinst leveloggers measure water level by recording the total pressure above the sensor, but levelogger data must be paired with barologger data in order to separate the water pressure above the sensor from the atmospheric pressure above the sensor. “Barometric compensation” within the Solinst levelogger software automatically pairs coinciding levelogger and barologger data to convert the water pressure above the sensor into water level above the sensor. The RTK GPS was used to get accurate elevation data for the channel beds at the levelogger locations, allowing for accurate conversions of raw levelogger data to site specific water level measurements.

A porewater sampling design was employed for the 2021 season in order to parameterize soil nutrients, conductivity as a teller of salinity, and sulfide concentration. A stainless steel porewater sipper with a fine mesh filter was used in conjunction with Tygon tubing and a syringe to penetrate the soil surface and collect porewater from the root zone. Planning to sample every month of the growing season, the design included two replicate 15 mL nutrient samples, two replicate 15 mL sulfide samples, and one 25 mL conductivity sample. Samples were kept on ice until immediate analysis after collection in the lab. Nutrient samples were analyzed on an

AutoAnalyzer for NO2, PO4, NH4, and N+N concentrations, sulfide sample measurements were fit to a calibration curve and converted to sulfide concentration, and samples were measured for conductivity with a YSI probe.

At the end of the growing season, all mesocosms were harvested and separated into aboveground and belowground biomass. Aboveground biomass was clipped, and the soil core was excavated and collected to around 30 cm depth to ensure no plant material was missed. All mesocosm plant samples were thoroughly washed and sorted using 1-mm mesh sieves into biomass or necromass distinctions. Strategies for identification of biomass include looking for qualities such as light green or brown color, turgidity, or passing a float test; where necromass is generally characterized as black in color and highly malleable. Once samples were washed and sorted, they were dried in an oven at 60º C until their weight changed by less than 4% over a 24-hr period. After samples were sufficiently dried, the final biomass and necromass values were recorded. Mesocosm samples were harvested in August of 2021 (in order to avoid damage from Hurricane Ida) and in September of 2022 and 2023.

2.5. Microbiome Experimental Design

It is worthwhile to know which microbiome communities are dominating which salinity and inundation ranges and how the presence or absence of these communities might be affecting plant growth, so the 2022 and 2023 growing season designs included microbiome sample collection at the end of growth just before harvesting. Plant growth differences across treatment rows indicate variability of microbial community composition, and DNA sequencing of surface and root-zone soils can identify the microbes that dominate the given tidal and salinity range.

Microbiome samples were collected from each mesocosm using a sterile, plastic 50 mL syringe with the top cut off to function as a small vacuum-corer. Ten cm-depth cores were sampled, and 2 cm-depth samples were collected from each side of the core to differentiate the soil-surface microbes from deeper soil microbes, at depths 0-2 cm and 8-10 cm respectively. For the 2022 season's four mesocosm-per-row design, two composite soil-surface and root-zone samples were created from randomly-paired, equal-elevation mesocosms for each row one through six. This design, sampling 96 mesocosms, best represented the variability of the replicate marsh organ experimental structure considering the high cost of sequencing. DNA extraction and sequencing was performed on the Illumina MiSeq platform at the Molecular and Genomics Core Facility of the University of Mississippi Medical Center (Jackson, MS, USA) using 2 × 250 PE reads (sequences archived in NCBI Sequence Read Archive under Accession PRJNA763531) (Weingarten & Jackson, 2022).

3. Results and Discussion

3.1. Growing Season Hydrographs

Results from each growing season were used to design and improve the subsequent season's manipulation; however, each growing season had unique challenges from unpredictable water levels to frequent tropical storms and hurricanes. Water level variability during the growing season, high rates of compaction and sinking within cores at each site, and harsh weather conditions characteristic of coastal Louisiana marshes during the hot summer months contributed to the difficulty of perfectly simulating the intended design hydroperiods. This resulted in increasing the number of experimental elevation treatments from the first design in 2021 as an effective strategy for lowering the chance of missing a significant inundation range. Hydrographs at each marsh organ for each year are shown for the experiment duration, from mesocosm planting to harvesting (Fig. 16-23). Water level data gained from Solinst leveloggers via barometric compensation is overlain horizontal elevation treatment lines representing marsh organ rows. A certain elevation is inundated when the water level measurement rises above it and dry when the water level is below it, thus inundation time throughout the growing season can be found for each experimental elevation. The percent-time inundation for each mesocosm elevation represents the percentage of time that the mesocosm was inundated for the experimental duration and is shown below (Table 2).

While row elevations for the 2021 season were designed to evenly cover the inundation range at 0, 25, 50, 75, and 100% time-inundations; the high surface area of the 40-mesocosm marsh organs made it impossible to sink the structure far enough to reach the exact design elevations. As a result, some row elevations were higher and inundations were lower than expected (Table 2, Fig. 17). Measured percent-time inundations from marsh organ planting on

June 8th, 2021, to marsh organ harvesting on August 27th, 2021, at saline site were 0, 3, 9, 25, and 79% from the top to the bottom row (Table 2, Fig. 17). While valuable insights are gained from the comparison between growth effects of highly inundated soils (79%) and dry soils (0%), the 2021 hydrographs for saline site show that the potentially crucial intermediate range of inundations (25-75%) is easily missed by just about 10-15cm. Similarly higher than expected in elevation, measured percent-time inundations for the 2021 growing season at brackish site were 0, 10, 15, 53, and 97% from top row to bottom row (Table 2, Fig. 16). While water level trends were similar at both sites due to relatively close proximity, brackish site experienced slightly higher water levels which resulted in better inundations results for rows 1 and 2 (97% and 53%, respectively).

Table 2. A table showing all elevation treatments associated and percent-time inundations for each growing season, 2021-2023

Brackish Site			Saline Site		
2021 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
5	0.72	0	5	0.76	0
4	0.33	3	4	0.38	10
3	0.30	9	3	0.31	15
2	0.17	25	2	0.21	53
1	-0.07	79	1	-0.06	97
2022 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
7	0.58	0	7	0.53	0
6	0.22	30	6	0.18	27
5	0.17	67	5	0.12	38
4	0.11	83	4	0.07	48
3	0.05	90	3	0.01	57
2	-0.04	100	2	-0.09	72
1	-0.34	100	1	-0.38	100
2023 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
6A	0.50	0	6A	0.33	3
5A	0.26	34	5A	0.11	31
4A	0.18	55	4A	0.07	37
3A	0.10	75	3A	-0.04	54
2A	0.02	89	2A	-0.26	94

(table cont’d.)

Brackish Site			Saline Site		
2023 Growing Season					
Row	Elevation (m, NAVD88)	% Inundation	Row	Elevation (m, NAVD88)	% Inundation
1A	-0.34	100	1A	-0.41	100
6B	0.50	0	6B	0.28	6
5B	0.26	34	5B	0	47
4B	0.18	55	4B	-0.07	59
3B	0.10	75	3B	-0.14	69
2B	0.02	89	2B	-0.28	100
1B	-0.34	100	1B	-0.36	100

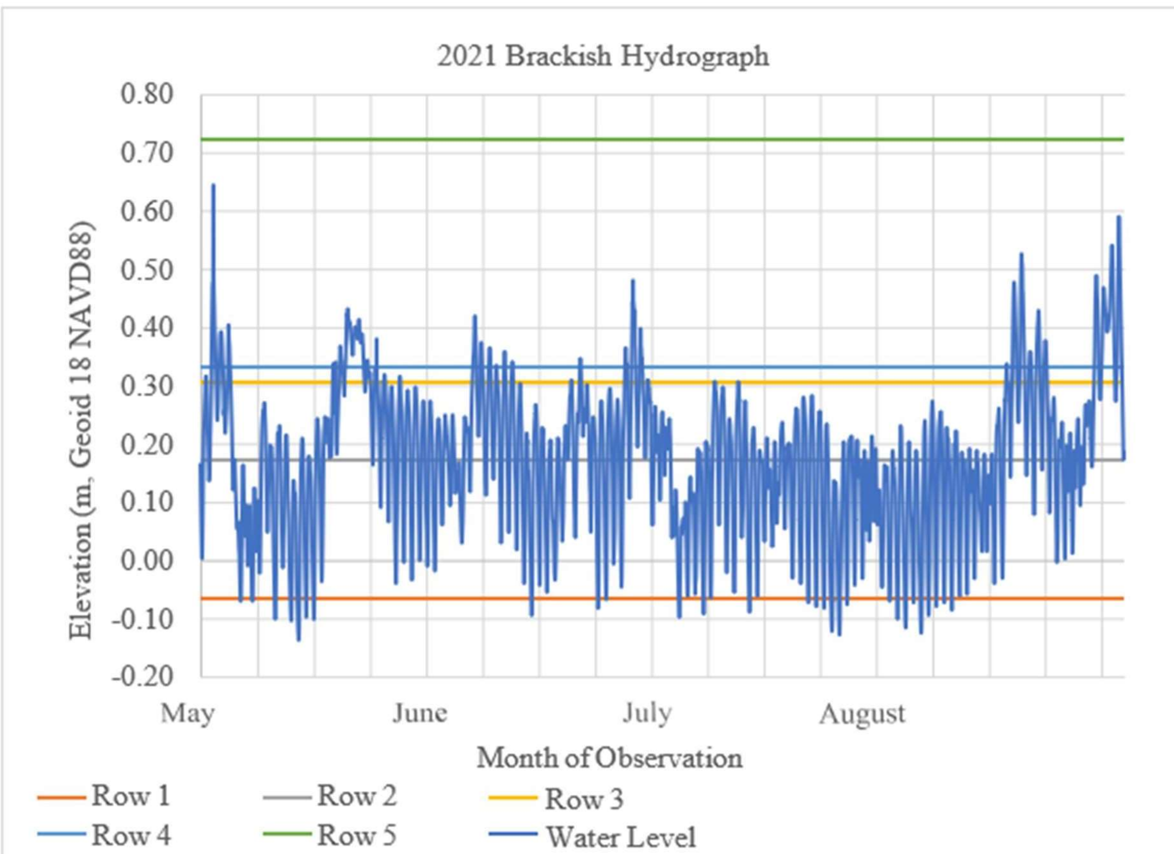

Figure 16. Hydrograph at brackish site marsh organ from May 1st-August 27th, 2021

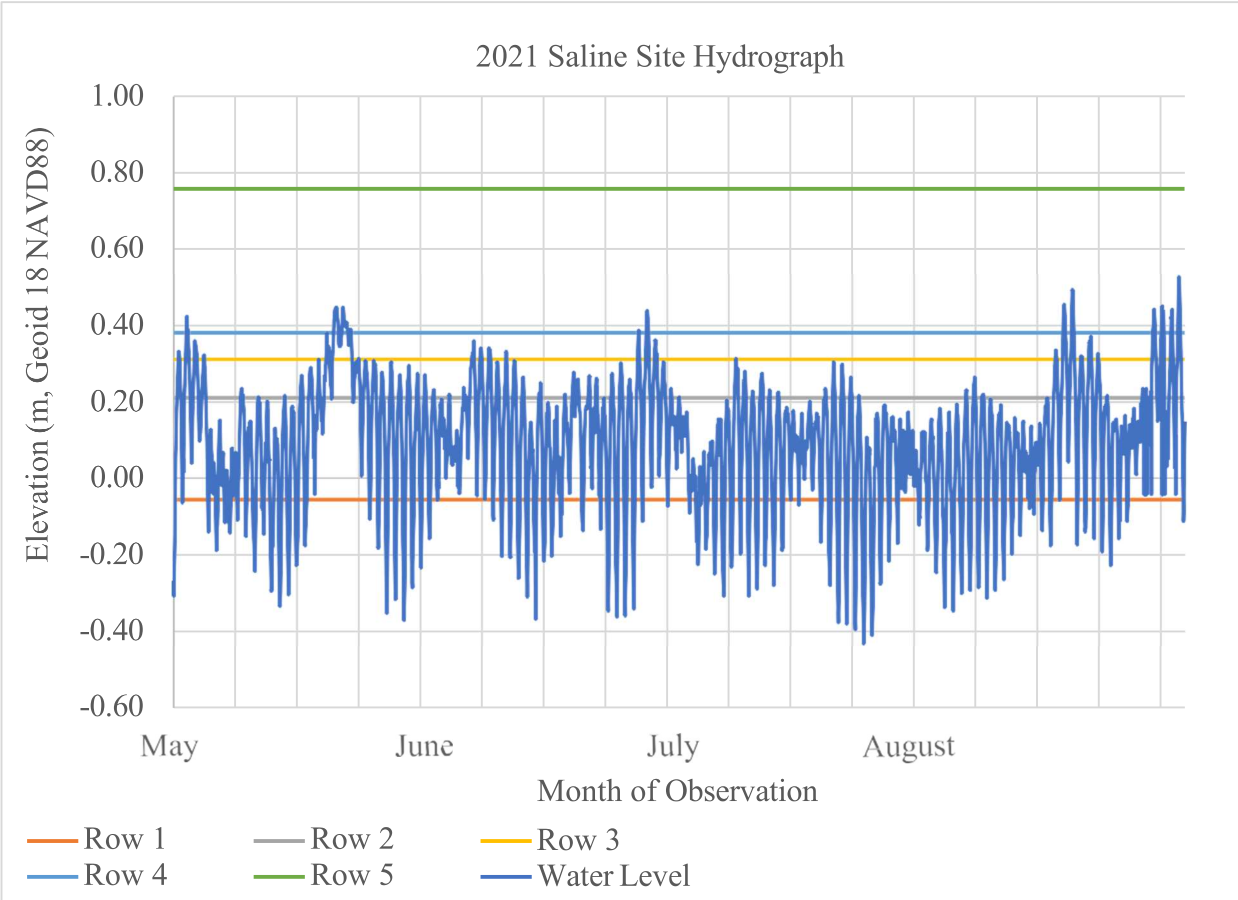

Figure 17. Hydrograph at Saline site marsh organ from May 1st-August 27th, 2021

New marsh organs for 2022 decreased surface area by minimizing replicates within treatment rows to four and were installed in slightly deeper parts of the channel at each site to achieve lower elevations and better capture the full range of inundation. This strategy provided its own challenges, as the more-narrow structure base combined with the steeper elevation of the channel beds at lower elevations caused unevenness and sinking of marsh organ structures. A combination of transplant stress, sinking elevation, and slightly higher water levels directly after planting resulted in mortality of most 2022 specimens. While the taller rows of each structure remained mostly un-inundated, the lower five rows all experienced similarly high inundations (Fig. 18-19) which were inhospitable for *Schoenoplectus americanus* and *Spartina patens*.

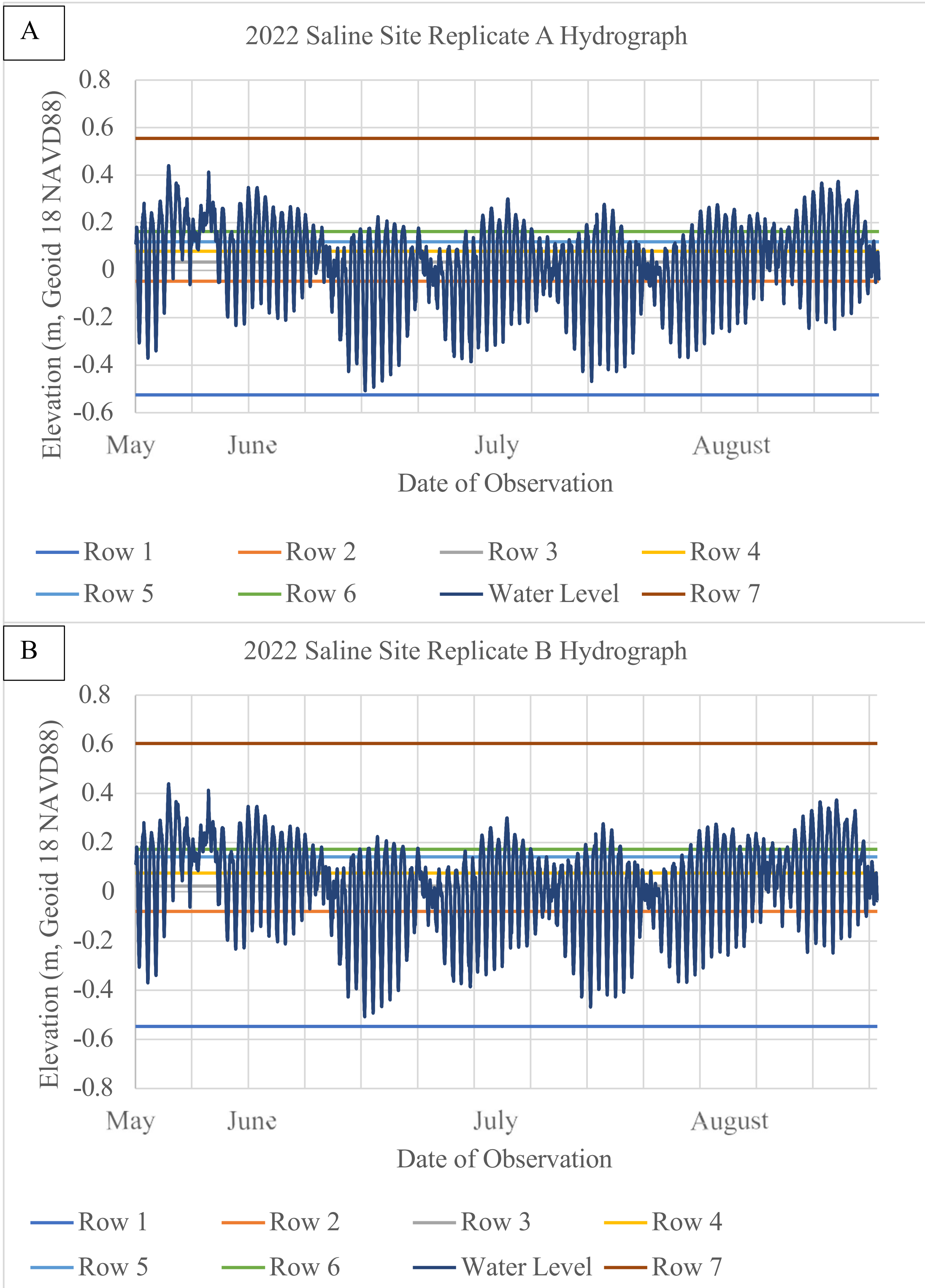

Figure 18. Hydrographs for marsh organ replicates (A) and (B) at the saline site for May 16th-August 16th, 2022

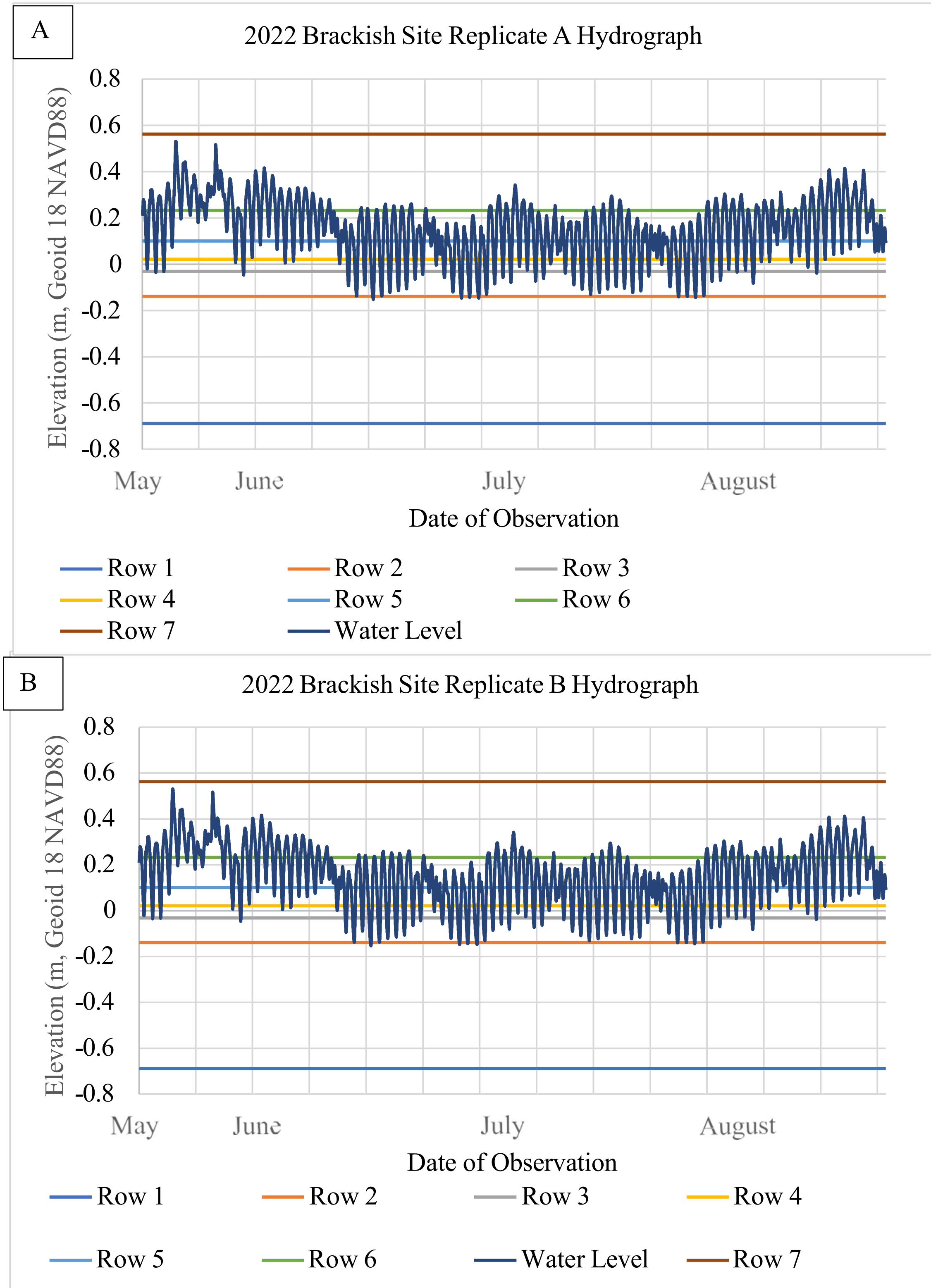

Figure 19. Hydrographs for marsh organ replicates A (A) and B (B) at the brackish site for May 16th-August 16th, 2022

Hydrographs for the final growing season in 2023 are shown below and demonstrate a much better capture of full inundation range (Fig. 20, 21). The hydrographs cover the entire experimental duration from marsh organ planting on May 26th to marsh organ harvesting on September 6th, 2023. At the brackish site, both marsh organ structure replicates settled at near-identical elevations, resulting in identical hydrographs. Percent-time inundations at the brackish site were 0, 34, 55, 75, 89, and 100% from top row to bottom row (Table 2). At the saline site, marsh organ structure replicate B settled around 10-15 cm lower than replicate A due to a suspected soft spot in the channel bed, resulting in lower elevation and higher inundations. Percent-time inundations at the saline site were 3, 31, 37, 54, and 94% from top row to bottom row for replicate A; and 6, 47, 59, 69, 100, and 100% for that of replicate B (Table 2). A "bottoming out' effect can be observed in the hydrographs for 2023's saline site (Fig. 21), in which water level is likely dropping below the levelogger elevation. While this effect prevents insights related to depth of flooding during inundation, percent-time inundated should still be accurate for each row barring a water level drop below -0.41 m (Geoid 18, NAVD88), which would be extremely uncharacteristic for the saline site according to recent growing season water level data.

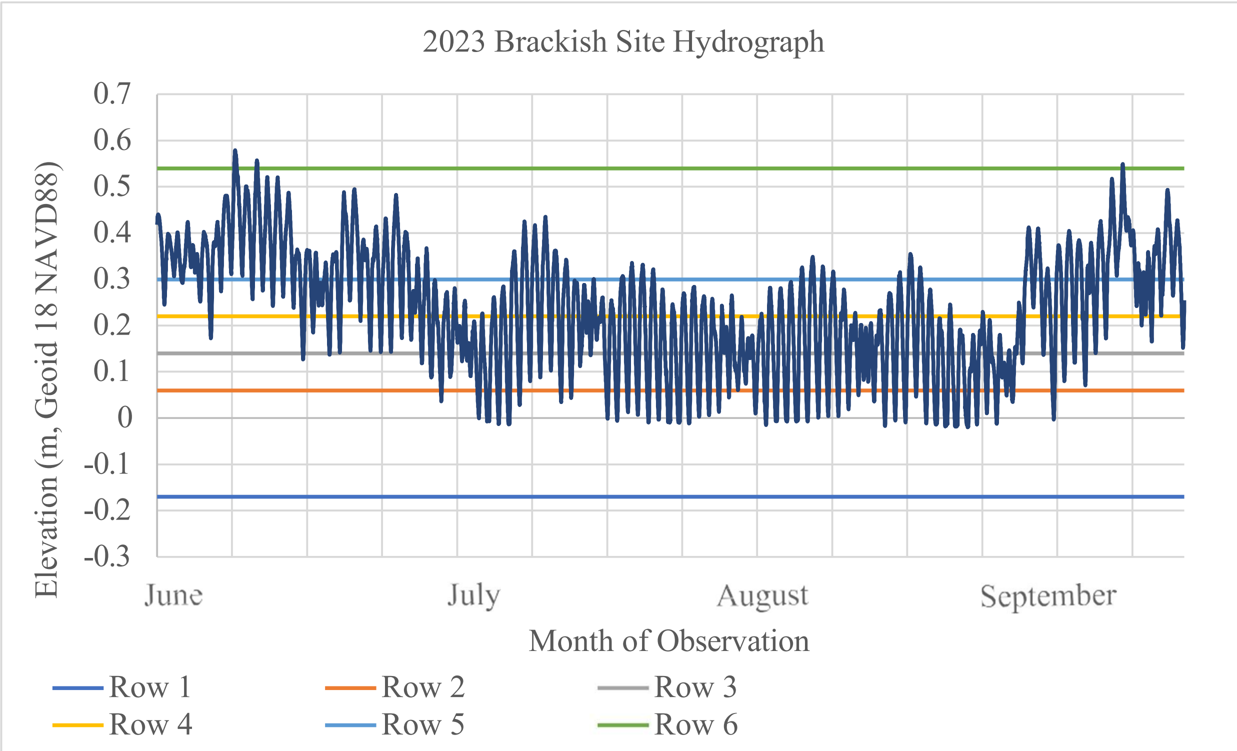

Figure 20. Hydrograph at brackish marsh organ from May 26th-September 6th, 2023

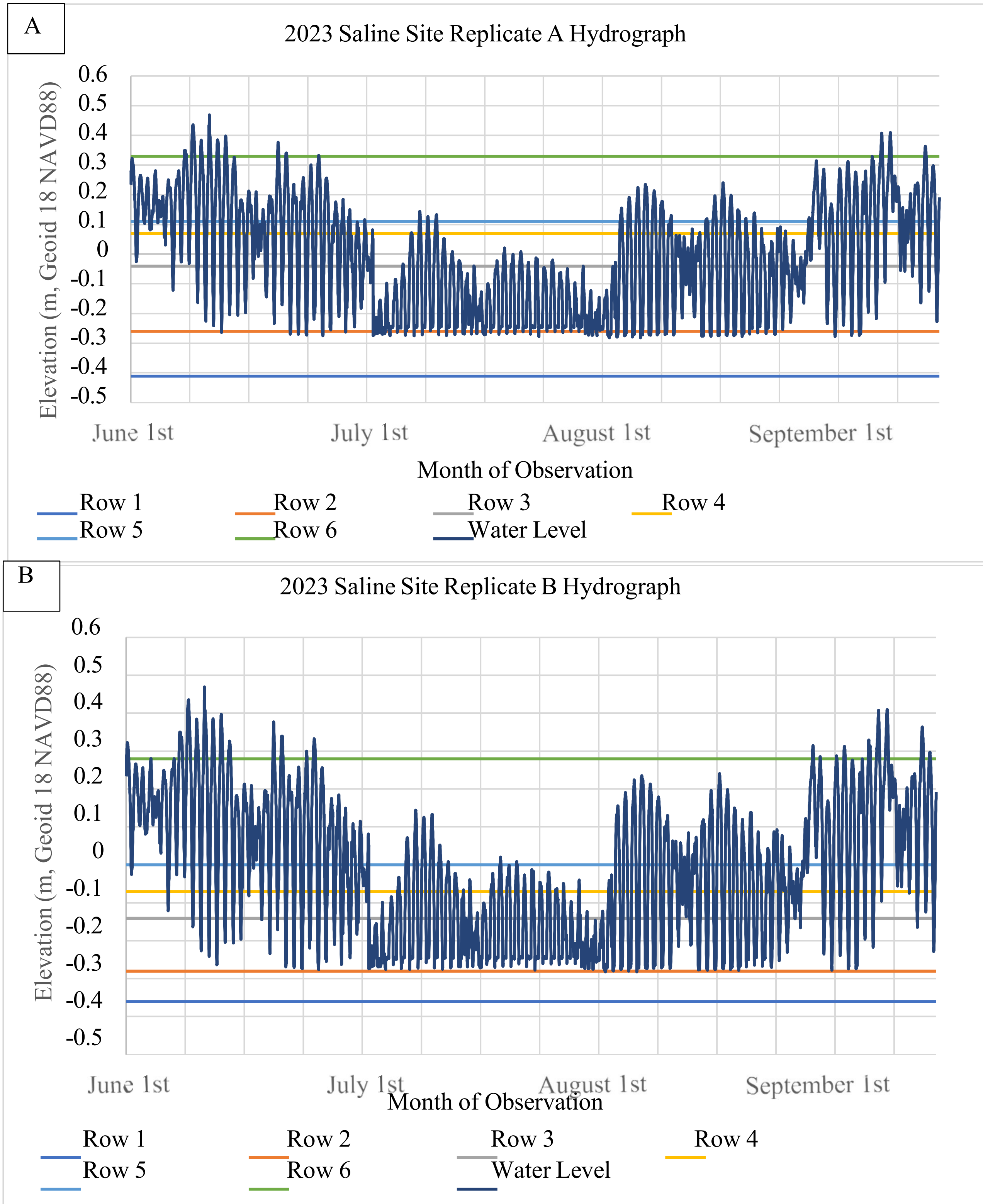

Figure 21. Hydrographs at saline marsh organ replicate A (A) and B (B) from May 26th-September 6th, 2023

3.2. Biomass and Necromass Distributions

Porewater was collected from the plant mesocosms during the 2021 growing season with varying degrees of success due to high compaction and little-to-no pore space within the mesocosms. The action of digging up nearby marsh soil introduces air bubbles and pore spaces to the soil that is used to fill the mesocosms, which recompacts over the span of subsequent site visits due to natural process such as gravity and the added constraint of limited mesocosm volume with expanding root area. For most porewater sampling attempts during the 2021 season, the porewater sipper was unable to collect any porewater for even mesocosms that were inundated at the time, indicating that the soils were so compact that there was little pore space for porewater. While the sampling strategy was ultimately abandoned for subsequent growing season, the limited results from one successful sampling at the brackish site and two successful samplings at the saline site are shown in the figures below (Fig. 22-27).

As would be expected, conductivity was higher in the saline marsh soil, even in the three highest elevation treatments which were inundated less than 15% of the growing season. Conductivity in the saline marsh organ soils was measured once on August 6th and again on September 9th and recorded between 17000-18000 µS and around 1350 µS in the higher inundated, naturally occurring marsh (Fig. 22). It is counterintuitive to think that soils inundated with saline water more frequently would have lower conductivity than less inundated soils, but it is important to consider how wetland plants react to growth and osmotic stress. *Spartina patens* specimens growing at low-inundated elevations, especially when restricted to a 4 in diameter mesocosm, must develop deep roots to establish connection to a water source. When these specially adapted wetland plants encounter high salinities, they are able to exclude salt from their tissues which can increase soil salinity independently of direct inundation (Sloey, 2021). It is also true that compaction was addressed bi-monthly by filling mesocosm headspace with inundated soils, which could have affected porewater data but was necessary to maintain elevation, the crucial variable in this experiment. Conductivity in the brackish site was measured only on August 18th and ranged from 6000-9000 µS in four lowest-inundation mesocosms, while the higher-inundated marsh sample only measured 4000 µS (Fig. 22).

Soil sulfide concentration was highest in the naturally occurring marsh for both salinity treatments and higher overall in the saline marsh, measuring 1 mM at the brackish site and 1-4 mM at the saline site (Fig. 23). Sulfide concentration was much lower in the primarily un-inundated elevation treatments but still increased with inundation. This stands to reason as soil microbes are known to reduce sulfide from sulfate at higher rates under anoxic conditions brought about by flooding and inundation (He et al., 2021).

It is hard to be confident about conclusions from such a limited sampling result, and it was difficult to identify porewater nutrient trends. NO2 concentrations were highest in non-inundated mesocosms in the brackish site at 5 µmol/L, but highest in the more-inundated mesocosms at the saline site at 2.8 µmol/L (Fig. 24). PO4 concentrations were minimal across measured elevation and salinity treatments (<5 µmol/L) but much higher in samples from the naturally occurring marsh, 30 µmol/L at the brackish site and 25 µmol/L at the saline site (Fig. 25). NH4 differed across salinity treatments, peaking at 35 µmol/L in the brackish marsh but at over 150 µmol/L in the 15% inundated saline mesocosm (Fig. 26). N+N concentrations were consistently between 1.5-2 µmol/L in the brackish treatments and marsh and between 1.5-4.5 µmol/L at the saline site (Fig. 27).

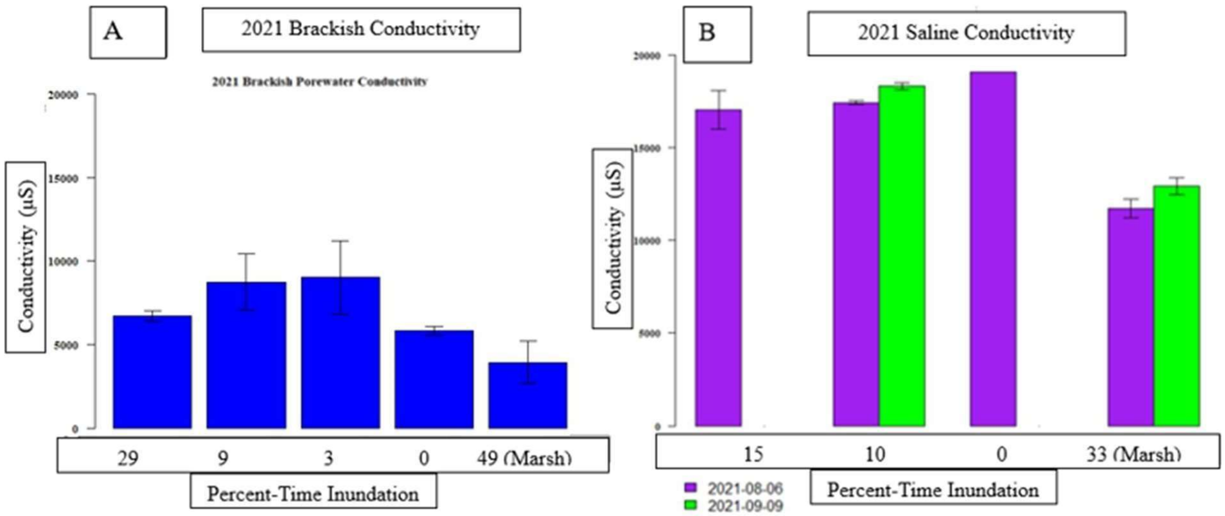

Figure 22. 2021 Porewater Conductivity at the brackish site (A) and the saline site (B)

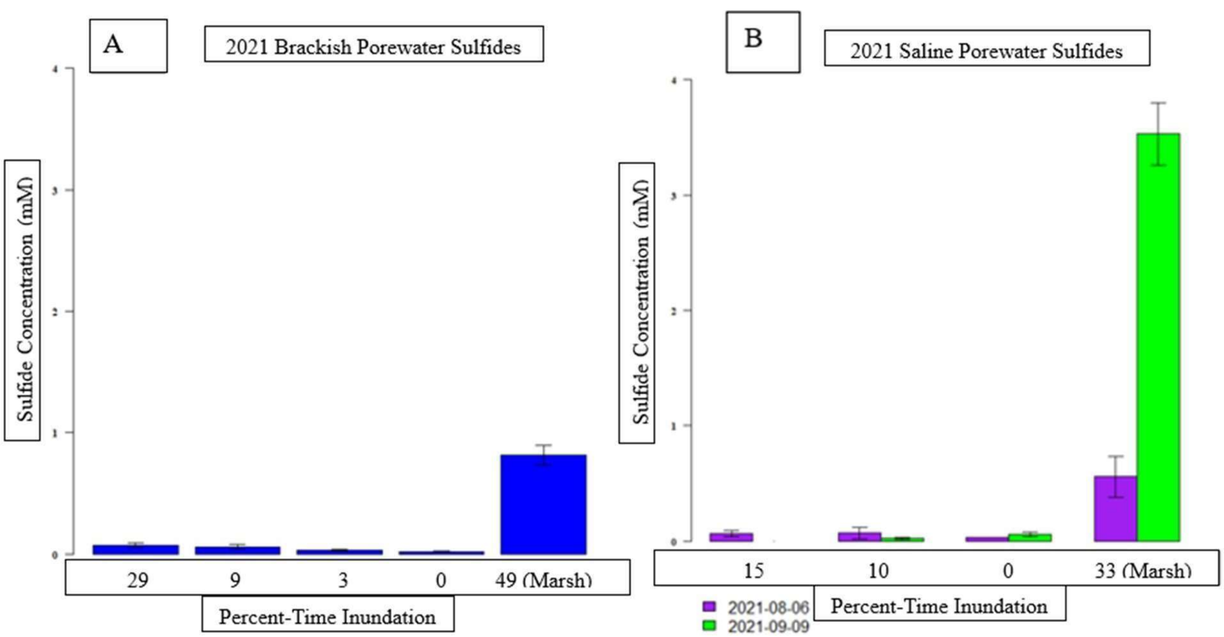

Figure 23. 2021 Porewater Sulfide Concentrations at the brackish site (A) and the saline site (B)

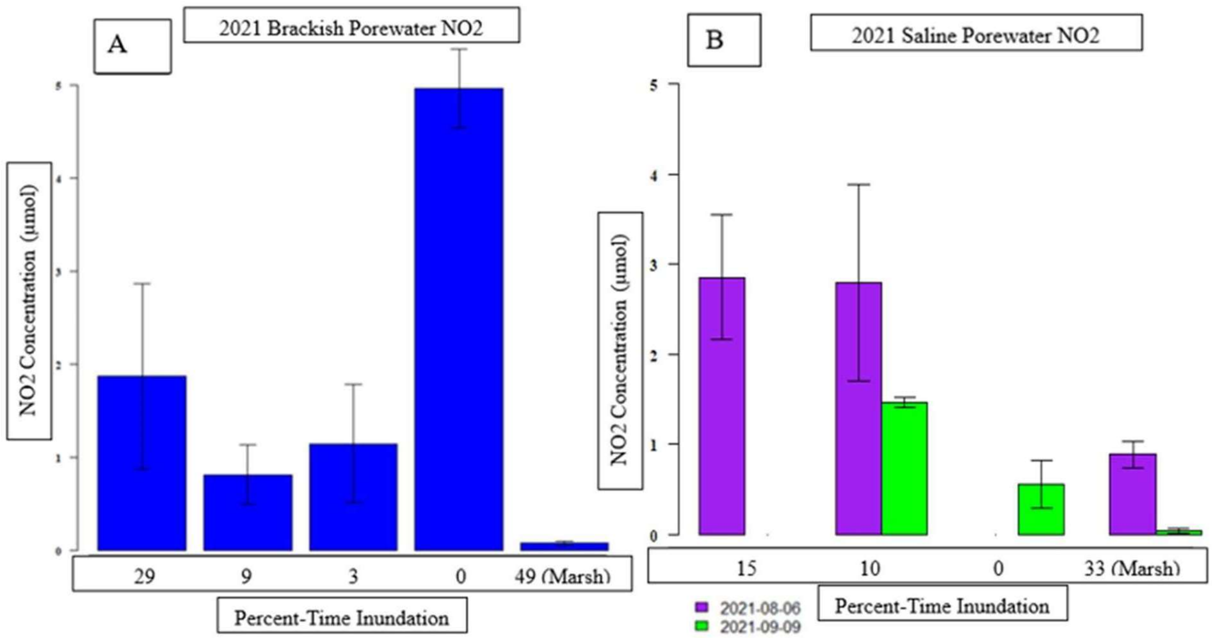

Figure 24. 2021 Porewater NO2 Concentrations at the brackish site (A) and the saline site (B)

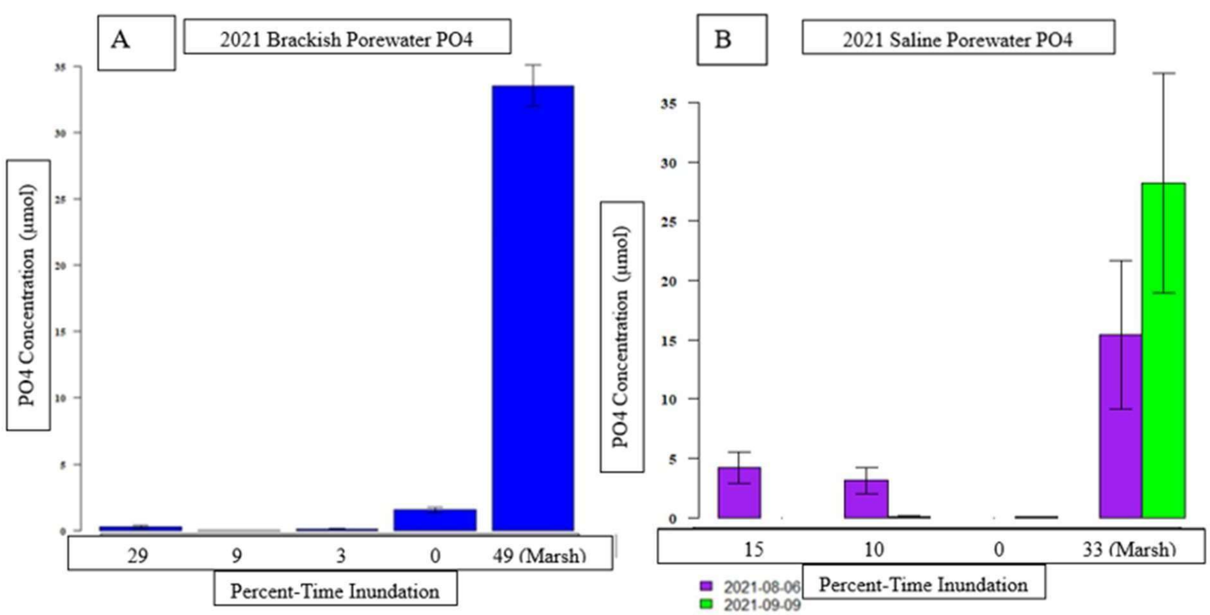

Figure 25. 2021 Porewater PO4 Concentrations at the brackish site (A) and the saline site (B)

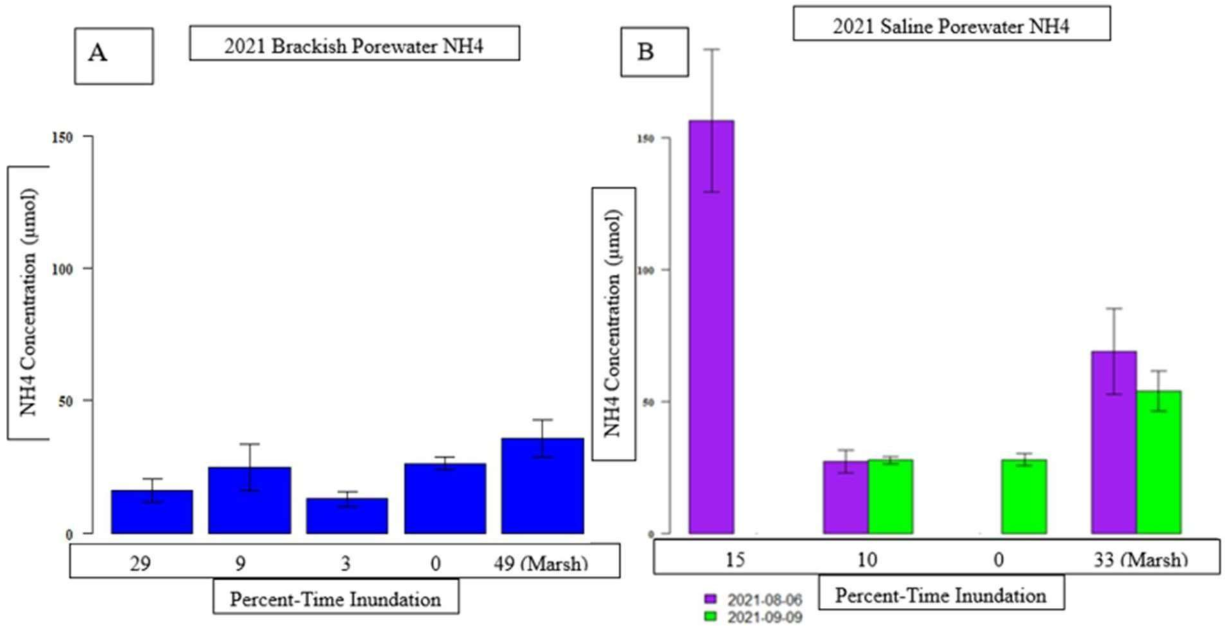

Figure 26. 2021 Porewater NH4 Concentrations at the brackish site (A) and the saline site (B)

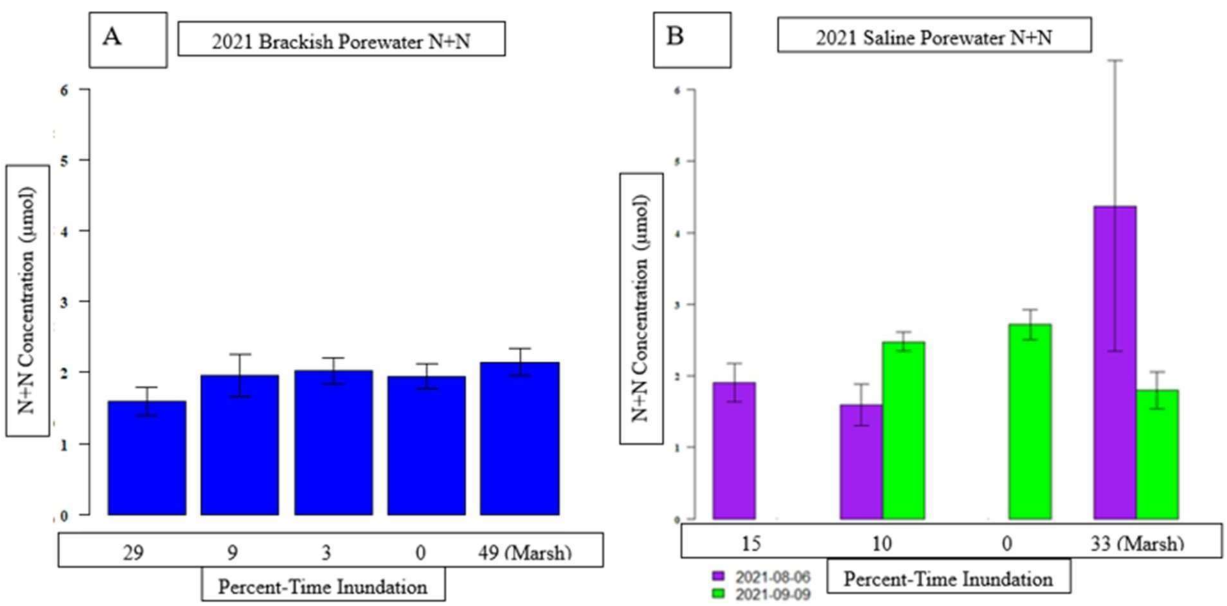

Figure 27. 2021 Porewater N+N Concentrations at the brackish site (A) and the saline site (B)

While both species *Spartina patens* and *Schoenoplectus americanus* were able to survive across all elevation and inundation treatments for the 2021 growing season, there is a clear trend of the hydroperiod treatment effects on each species in the other growing seasons. At the brackish site, *Schoenoplectus americanus* preferred lower inundations for aboveground biomass production, peaking at 17 grams at 25% inundation (Fig. 28). Aboveground biomass production dropped off significantly approaching the 100% inundation range, averaging only 5 grams of biomass at 79% inundation, showing the stresses introduced to plant growth under high inundation and anaerobic conditions. At the saline site, *Spartina patens* similarly preferred lower inundations with aboveground biomass dropping off even more drastically in the high inundation range, averaging less than 2 grams of biomass at 97% inundation ((Fig. 28). This biomass production peaked around 14 grams at 10% inundation, illustrating a lower tolerance for high inundation and anaerobic soil conditions (Fig. 28). Aboveground necromass allocation was higher at the brackish site but also differed from trends in the aboveground biomass. For healthy plants with relatively low inundation stress, aboveground necromass allocation was relatively minimal (Fig. 28).

Belowground biomass production was highest at the lower inundations for both salinity treatments, peaking at 42 grams and zero inundation at the saline site, supporting the trend of the preference of *Spartina patens* to high elevation. In the brackish marsh, *Schoenoplectus americanus* produced a high of 25 grams of belowground biomass also at 25% inundation, although growth effect decreased under less than 25% inundation. Contrasting to relatively small quantities of aboveground necromass peaking at the brackish site, belowground necromass outweighed belowground biomass for all treatments and was highest at the saline site (Fig. 29). It stands to reason that higher salinities and inundations could produce higher necromass production in a more-stressful growth environment for *Spartina patens*, but allochthonous inputs of sediment to remediate compaction could have introduced foreign necromass to the mesocosm. The main takeaway from this 2021 biomass allocation data is that wetland plants near the saline and brackish marshes of Fourleague Bay grow very well under low to intermediate levels of osmotic and inundation stress, while there seems to be a tipping point somewhere beyond 25% time-inundation where plant production drops off dramatically.

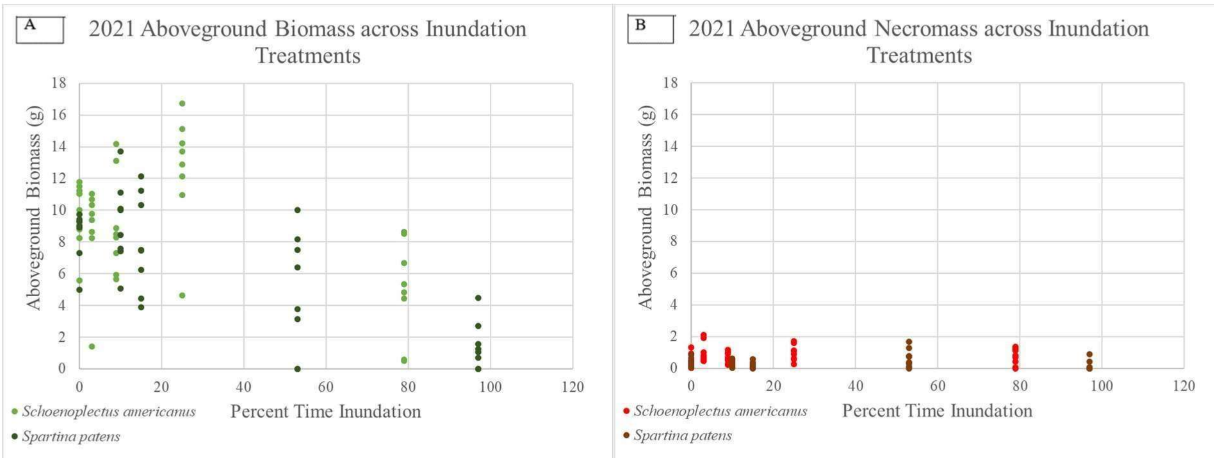

Figure 28. Aboveground biomass (A) and necromass (B) data from 2021 organs across percent-time inundation during growth

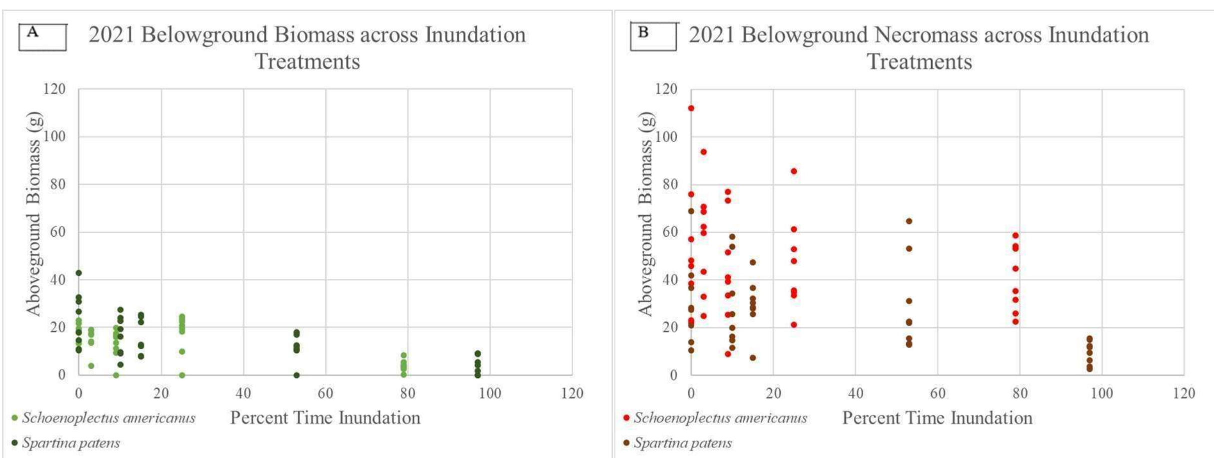

Figure 29. Belowground biomass (A) and necromass (B) data from 2021 organs across percent - time inundation during growth

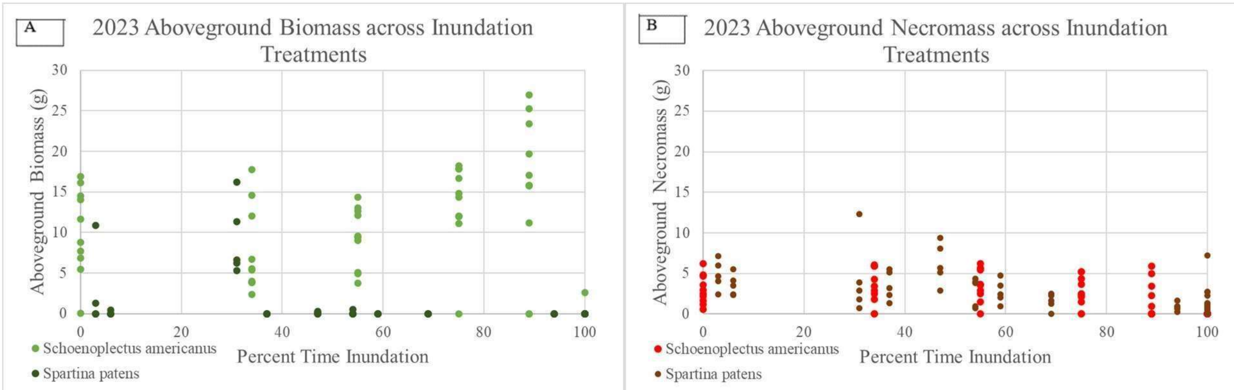

Figure 30. Aboveground biomass (A) and necromass (B) data from 2023 organs across percent-time inundation during growth

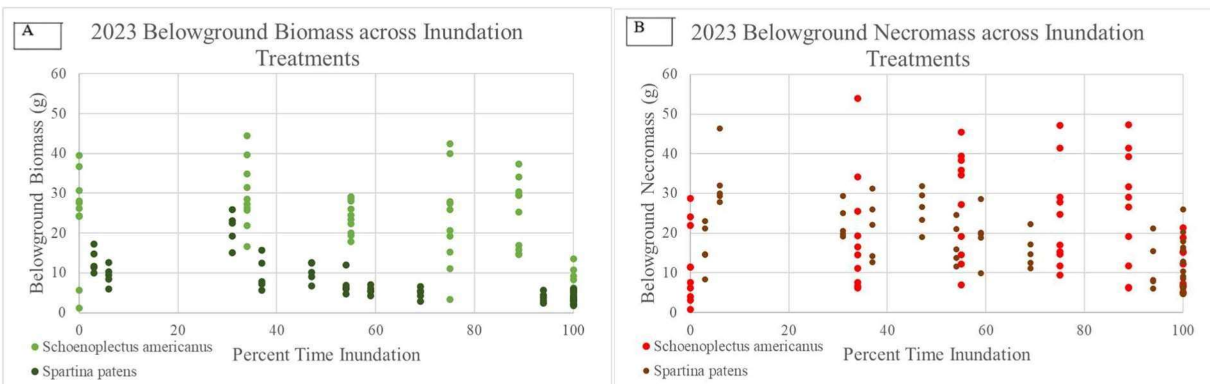

Figure 31. Belowground biomass (A) and necromass (B) data from 2023 organs across percent-time inundation during growth

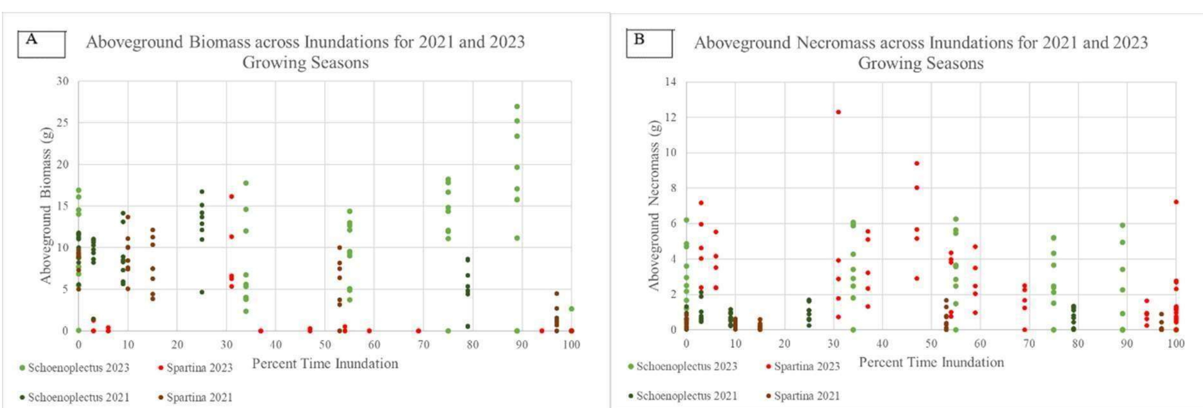

Figure 32. Aboveground biomass (A) and necromass (B) data from both growing seasons across percent-time inundation during growth

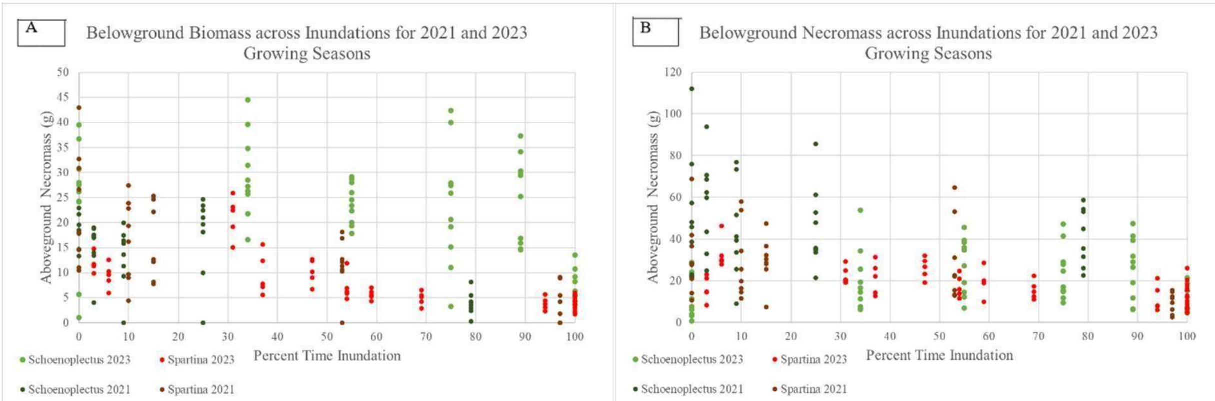

Figure 33. Belowground biomass (A) and necromass (B) data from both growing seasons across percent-time inundation during growth

The aboveground biomass and necromass data from the 2023 growing season further adds to the story of the inhospitable growth conditions in a fully inundated salt marsh. Similar to the 2021 growth data, not only was plant production stopped at 100% inundation, but also aboveground biomass production peaked at a non-zero inundation (Fig. 30). Marsh organ replicates at the brackish site produced the highest aboveground biomass on average around 14 grams at 75% inundation, with specimens as large as 27 grams at 89% inundation (Fig. 30); whereas 79% inundation in 2021 resulted in a decrease in aboveground biomass production by half (Fig. 28). Aboveground necromass was higher for both salinity treatments at the lower inundations and three-to-six times larger than that of the 2021 growing season. While this phenomenon could be the result of harvesting plant samples slighter later in the growing season for the 2023 campaign, it could also be explained by a stress-inducing period of dry weather in which higher elevation plants needed to convert portions of biomass to necromass in order to lessen water and nutrient requirements, while highly inundated plants would not have undergone this stress.

Belowground biomass for the 2023 growing season similarly peaked under low inundation conditions and struggled under higher inundation conditions but was more sustainable under higher flooding in the brackish site. *Shoenoplectus americanus* root production peaked around 45 grams at 34% inundation and maintained at least 15 grams of biomass until inundation exceeded 89% of time, where flooding-related stress caused biomass production to decrease (Fig. 31). *Spartina patens* produced a maximum belowground biomass of 26 grams at 31% inundation time which continued decreasing under increased inundation, showing little root production at lower elevations associated with dead plants at total inundation (Fig. 31). While belowground biomass production in the saline site was similarly low at both inundation extremes, belowground production at the brackish site was less affected by dry conditions (Fig. 31). Necromass results for the 2023 season were higher on average in excess of 50% inundation at the brackish site supporting that high inundation stress can cause an increase in necromass production. At the saline site belowground necromass production peaked at only 6% inundation time (Fig. 31), but a lack of healthy plants across varying inundation treatments at the end of the 2023 growing season complicates conclusions drawn from the maximum recorded necromass growing under rarely-flooded conditions.

Experiments carried out over individual growing seasons spanning the growing season from April to September do well in exemplifying growth effects on an immediate time scale but are limited by the constant variability of wetland water level from year to year. This fact illustrates the importance of evaluating biomass production on a multi-year time scale for making predictions on the elevation equilibrium needed under various sea level rise scenarios. In coastal Louisiana especially, where subtle elevation changes correspond to significant inundation and growth differences, flooding conditions can have various growth effects from one growing season to the next. Brackish organs from 2021 produced lower biomass compared to the 2023 growing season organs at comparable inundations, while saline 2021 organs demonstrated better vitality under higher inundation conditions than the 2023 organs while still supporting the general growth preference of lower inundation time (Fig 32-33). Inconsistency in growth response data points to difficulties in establishing permanent soil surface elevation in regions of active erosion and subsidence, constrictive growth effect within a 4-inch diameter mesocosm, and other potential localized effects or allochthonous nutrient inputs.

While peak biomass and necromass values varied across intermediate inundations from the 2021 to the 2023 growing season, one clear trend in the data was the plant-growth stress that results from prolonged, frequent flooding. Biomass allocation, salt excretion, and soil microbes help wetland plants like *Schoenoplectus americanus* and *Spartina patens* survive a degree of osmotic and inundation stresses, there exists an elevation for every wetland plant where inundation is too high to support growth, which is a particular concern in wetlands where subsidence and erosion combine with sea level rise. If the ideal percent-time inundations of wetland plants can continue to be investigated and validated, a landscape-scale understanding of wetland soil formation and land building processes might become clearer.

3.3. Microbiome Analyses

The following microbiome ordination plots describe microbiome community species composition by sequencing DNA of soils having experienced varying percentages of inundated growth conditions throughout the 2022 growing season (Fig. 31, 32). Microbial species were identified and grouped based on biological similarity to analyze their distribution across salinity and inundation gradients for patterns. Since the 2022 season was characterized by high inundations early in the growing season leading to vast plant mortality, the differences in soil chemistry associated with a living and dead root zone were expected to result in a varying distribution of microorganisms. The separation of the high-elevation row six grid points from the rest of the data supports that dry soils favor a particular microbiome of aerobic organisms while flooded soils provide anaerobic conditions that result in a distinctly different microbiome (Fig. 31). Further microbiome relationships were investigated by repeating the ordination plot without the un-inundated soil samples, revealing if varying salinity and marsh classification adds further variability to similarly inundated soils (Fig. 32). The distinct grouping of samples from the brackish marsh on the left of the plot and the samples from the saline marsh in the middle of the plot supports that marsh classification is also a determining factor for microbiome community composition.

The 2023 growing season provided better growth results across the inundation range which resulted in more robust microbiome data and conclusions. Non-metric multidimensional scaling (Fig. 34-36.C) groups similar microbiome species across samples to analyze correlations between microbiome community composition and inundation conditions. There is a clear distinction between brackish and saline microbiomes from 2023 (Fig. 36.A), as well as a clear grouping of varying flooding conditions at both sites (Fig. 36.B-C). Amplicon sequence variants (Fig. 36.D) represent a DNA sequencing analysis that identifies species richness, which from the 2023 data changes as soils become more inundated. Simpson diversity (Fig. 36.E) provides an index to measure distinct microbiome communities across samples and corroborated further that microbiome community changed as flooding increased in 2023.

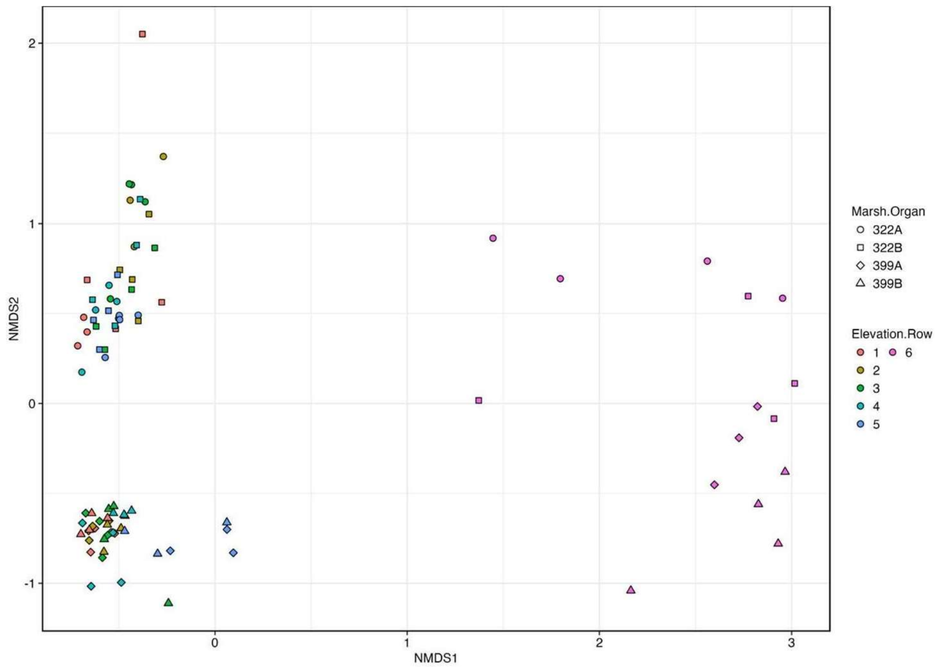

Figure 34. Ordination plot of microbiome DNA sequencing performed on both saline and brackish soil samples from 2022 experiencing percent-time inundations from 0-100%

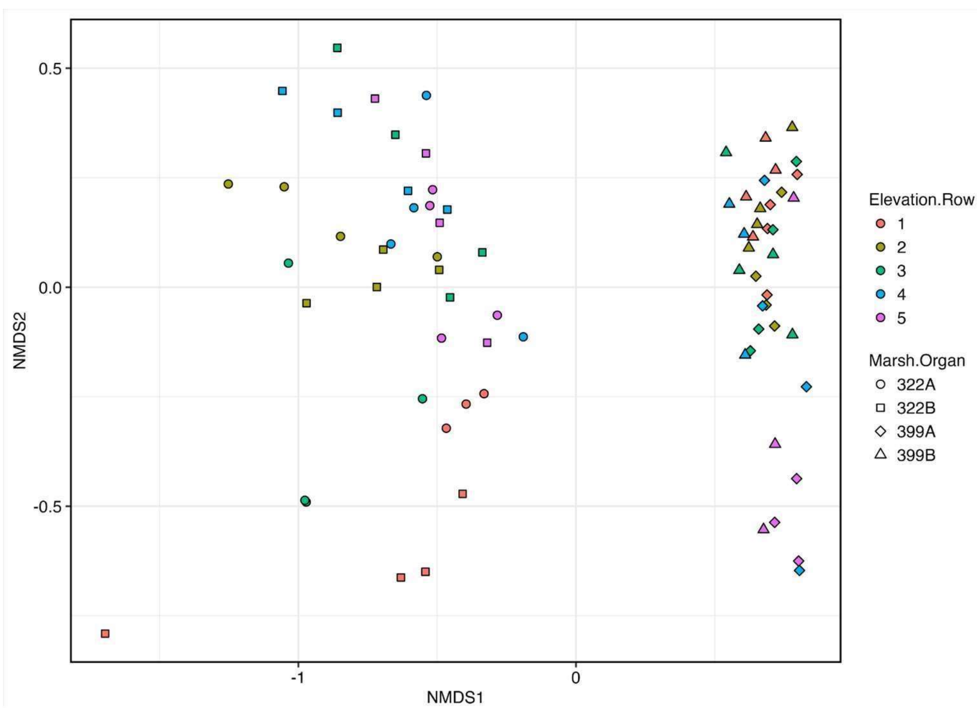

Figure 35. Ordination plot of microbiome DNA sequencing of inundated saline and brackish samples from 2022

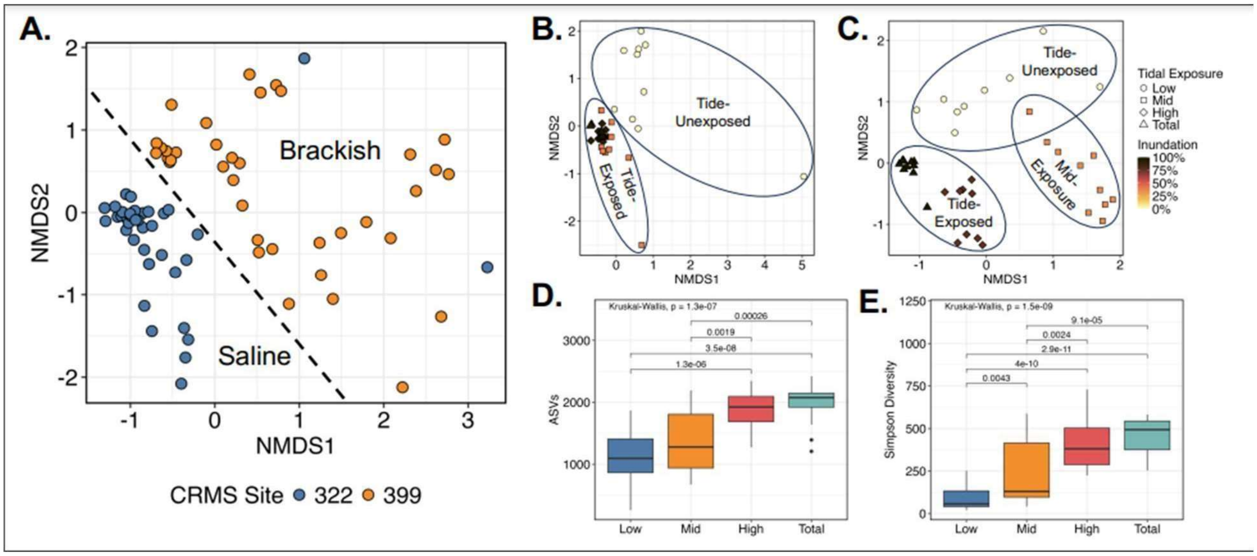

Figure 36. Microbiome sequencing data from 2023 sampling campaign showing separation by site (A), separation by tidal exposure at saline (B) and brackish (C) sites, species richness (D), and species diversity (E)

4. Conclusion

In conclusion, the issue of plant growth in coastal Louisiana wetlands is a complex interplay of factors, including salinity, inundation, and elevation. As this study has shown, the relationship between these variables can have a significant impact on the growth and survival of wetland plant species. The experiments conducted over three growing seasons revealed the challenges of accurately simulating desired hydroperiods and capturing the full range of inundation conditions. While the 2021 season faced difficulties in achieving the desired inundation levels, subsequent seasons adjusted design and site selection to better capture the intended range. The 2023 growing season provided further validation for the idea that biomass and necromass production in *Schoenoplectus americanus* and *Spartina patens* peak under semi-flooded conditions, while too great of inundation will inhibit growth and threaten land building processes, and the 2022 growing season provided a glimpse into the soil microbiology in an attempt to link measured growth responses with environmental chemical interactions.

In general, plants exhibit lower survival rates under high inundation conditions due to several physiological and ecological challenges they face in waterlogged environments. Excess water in the soil limits the exchange of gases between plant roots and the atmosphere. Underwater, the availability of oxygen decreases, and plant roots require oxygen for essential metabolic processes. Prolonged oxygen deprivation can lead to root rot, reduced nutrient uptake, and overall stress, making it difficult for plants to thrive. Sustained flooding can suffocate plant roots. As water levels rise, air pockets in the soil disappear, and roots may be deprived of the oxygen needed for respiration. Without oxygen, root cells can die, weakening the plant's ability to absorb water and nutrients. High inundation can shift the composition of soil microbial communities. Changes in microorganisms that assist in nutrient cycling, such as mycorrhizal fungi, can affect a plant's ability to obtain nutrients. These shifts can create a challenging environment for plants under high inundation. High inundation is a significant source of stress for most plants. Elevated stress levels can activate stress-response mechanisms in plants, diverting energy and resources away from growth and reproduction and instead toward coping with the adverse conditions.

Biomass production in coastal wetlands is essential for ecosystem health in that it increases nutrient cycling, carbon sequestration, and soil formation. Greater plant biomass, corresponding to larger plant root and shoot area, provides the substrate for elevation building which is the main defense against rising sea level, subsidence, and erosion in degrading marshes. Increased plant matter also increases the stability of coastal land and soil shear strength, providing the protective quality of wetlands against storm surges and extreme weather events. In light of this relationship between structural soil properties and plant production, the importance of wetland plant growth response to varying inundation and salinity for coastal engineering applications becomes clear. This experiment illustrates the distinct changes in biomass production as a direct result of hydroperiod and salinity, which should be a consideration in any engineering effort associated with the coastal zone and beyond, from marsh restoration projects to river diversions. As more wetland land area is affected by increasing hydroperiod and salt water intrusion, this growth response becomes increasingly applicable for coastal engineering and the larger engineering realm as a whole.

These findings underline the importance of understanding the nuances of plant growth in response to environmental variables, as it has implications for the resilience and stability of coastal wetland ecosystems. Notably, the study's exploration of the microbiome and its response to salinity and inundation adds an additional layer of complexity to the understanding of wetland ecosystems.

In the context of Louisiana's ongoing coastal land loss, this research contributes valuable insights into the dynamics of plant communities in these vulnerable areas. The data generated by this study can inform wetland restoration efforts, aid in assessing the potential impact of future changes in inundation regimes, and ultimately contribute to the long-term preservation of Louisiana's vital wetlands.

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Vita

Brandon Wolff is a Louisiana native who has always been passionate about plants, animals, and the environment. Growing up in New Orleans, some of his fondest memories include swamp tours, swimming in the bayou, and playing at his grandfather's camp near Louisiana's coast. Born in 1998, Brandon has seen the impacts of many hurricanes on his beloved Louisiana home, including Hurricanes Katrina, Rita, Gustav, Isaac, and Ida. In light of modern environmental issues and through witnessing first-handedly the consequences of natural disasters in his home state, Brandon formed a strong desire to protect the ecosystems that his community depends on and get involved with the global effort to minimize climate change consequences through coastal and environmental engineering. Brandon graduated from Jesuit High School in New Orleans in 2016 and immediately began his B.S. in Applied Coastal Environmental Science at LSU, which he received in 2020. He began LSU's M.S. in Coastal and Ecological Engineering program in January 2021 and worked under Dr. Clint Willson and Dr. Robert Twilley in his Coastal Systems Ecology lab. He has received unlimited guidance and support from his advisors, coworkers, and professors, and expects to graduate in May 2024. After the completion of his master's degree requirements, Brandon plans to work as a coastal engineer in New Orleans and be on the forefront of ecosystem restoration and protection efforts in the state and beyond. Brandon loved his time as both an undergraduate and graduate student at LSU, but he looks forward to rejoining his family and fiancé, Caroline, in New Orleans.