

The interactive effects of created salt marsh substrate type, hydrology, and nutrient regime on *Spartina alterniflora* and *Avicennia germinans* productivity and soil development

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Received: 1 November 2017 / Accepted: 15 March 2018 / Published online: 20 March 2018
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Abstract Recent salt marsh and barrier island restoration efforts in the northern Gulf of Mexico have focused on optimizing self-sustaining attributes of restored marshes to provide maximum habitat value and storm protection to vulnerable coastal communities. Salt marshes in this region are dominated by *Spartina alterniflora* and *Avicennia germinans*, two species that are valued for their ability to stabilize soils in intertidal salt marshes. We conducted a controlled greenhouse study to investigate the influences of substrate type, nutrient level, and marsh elevation on the growth and biomass allocation of *S. alterniflora* and *A. germinans*, and the consequent effects on soil development and stability. *S. alterniflora* exhibited optimal growth and survival at the lowest elevation (– 15 cm below the water surface) and was sensitive to high soil salinities at higher elevations (+ 15 cm above the water surface). *A. germinans* performed best at intermediate elevations but was negatively affected by prolonged inundation at lower elevations. We found that although there was not a strong effect of substrate type on plant growth, the development of stressful conditions due to the use of suboptimal materials would likely be exacerbated by placing the

soil at extreme elevations. Soil shear strength was significantly higher in experimental units containing either *S. alterniflora* or *A. germinans* compared to unvegetated soils, suggesting that plants effectively contribute to soil strength in newly placed soils of restored marshes. As marsh vegetation plays a critical role in stabilizing shorelines, salt marsh restoration efforts in the northern Gulf of Mexico and other storm impacted coasts should be designed at optimal elevations to facilitate the establishment and growth of key marsh species.

Keywords Hydrology · Salt marsh restoration · Shear strength · Soil properties

Introduction

In the Northern Gulf of Mexico, barrier islands and salt marshes are recognized as the first lines of defense against storm surge and high winds that threaten coastal communities (Campbell et al. 2005b). However, the valuable storm protection and erosion abatement services provided by these habitats are endangered by the high rates of wetland loss affecting this region, necessitating the restoration of degraded habitat and creation of significant new wetland area (Khalil et al. 2013). In Louisiana, sediments dredged from waterways and offshore sand deposits are often pumped into deteriorating salt marshes at specific

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elevations in a technique known as beneficial use of dredged material (Wagner 2000). Early efforts to reduce marsh loss relied on hard structures, such as revetments or breakwaters to prevent the loss of pumped sediments (Airoldi et al. 2005). Previous studies suggest that the presence of marsh vegetation, either through natural colonization or direct planting, can be effective at stabilizing dredged material as the belowground portions of plants reduce erosion at the marsh–water interface by binding sediments while the aboveground portions slow water velocities and trap new sediments (Woodhouse 1979; van Eerd 1985; Mendelssohn et al. 1991; Gyssels et al. 2005). Further, relying on vegetation for erosion abatement is significantly less costly than building and maintaining hard structures and requires less human intervention over the life-span of the restoration project (Subramanian et al. 2006; Bulleri and Chapman 2010). However, the use of vegetation for soil stabilization and erosion prevention is limited by our understanding of the physiological tolerances of salt marsh plant species to the environmental conditions imposed by newly restored areas.

Salt marshes and back-barrier island marshes in Louisiana's Deltaic Plain are often dominated by mixed stands of *Spartina alterniflora* (smooth cordgrass) and *Avicennia germinans* (black mangrove), which possess multiple physiological and morphological adaptations to tolerate the stressful conditions of the lower intertidal zone (Hester et al. 2005). Because *S. alterniflora* and *A. germinans* are highly adapted to tolerate the extreme environmental conditions of salt marshes, these species are frequently utilized for the vegetative stabilization of dredged material in Louisiana (Knutson et al. 1981; Alleman and Hester 2010). Although *S. alterniflora* and *A. germinans* may be resilient to gradual, chronic stresses such as periodic flooding and moderate soil salinities, the acute stresses imposed by the harsh environmental conditions found in many newly restored areas can pose significant constraints on the growth of these species (Streever 2000; Zedler et al. 2003; Lewis 2005; Alleman and Hester 2010). For instance, past marsh restoration designs have often placed the marsh platform at unnaturally high elevations with the objective of preventing erosion of the fill material for longer periods of time (Fearnley 2008). However, suboptimal, high elevations can have multiple consequences that hinder revegetation following restoration,

including reduced tidal inundation, low soil moisture, elevated soil salinities, and slow accumulation of organic matter (Callaway 2001).

The properties of the substrate used to restore a salt marsh can also have a significant effect on restoration outcomes as soil properties control rates of water infiltration, nutrient retention, and the decomposition of organic matter and can also regulate the effect of plant stressors such as soil salinity and anoxia (Zedler 2005). When substrates with high volumes of clay are used for marsh restoration in sub-tropical areas like Louisiana, solar-heating during low tide exposure can lead to the development of hypersaline, highly compacted soils that restrict water infiltration and severely limit the rooting depth of vegetation (Whisenant 1999; Zedler et al. 2003). In contrast, areas restored with sandy, coarse grained soils have reduced water storage capacity and are prone to rapid leaching of the water and nutrients necessary for plant growth (Hemminga et al. 1988). Problems related to soil texture are often intensified at high elevations where infrequent inundation results in the soil being exposed for long periods of time, leading to elevated soil salinities and low soil moisture that hinders seed germination and plant establishment, thereby limiting revegetation of bare ground (Shumway and Bertness 1992; Callaway and Sabraw 1994; Ewanchuk and Bertness 2004).

Several recent high profile coastal disasters, such as the 2005, 2008, and 2017 hurricane seasons, have highlighted the importance of having robust barrier islands for shoreline protection and hurricane damage reduction along the Gulf coast. The Coastal Wetlands Planning, Protection and Restoration Act task force (CWPPRA) has completed twenty barrier island restoration projects over the past two decades, with several additional projects expected to start construction in the coming years (Raynie and Visser 2002) (Fig. 1). We designed a controlled greenhouse experiment to examine the influence of elevation, nutrient regime and soil properties on the survival and growth of *S. alterniflora* and *A. germinans* and the resultant effects on soil development and shear strength. Soil shear strength is defined as the maximum resistance of a soil to displacement or deformation by shearing stresses (Watts et al. 2003) and can be used as an indicator of a soil's resistance to shear stresses from tidal currents, waves and sheet flow (McKee and McGinnis 2002; Turner et al. 2009; Howes et al. 2010; Turner 2011). The specific objectives of this study

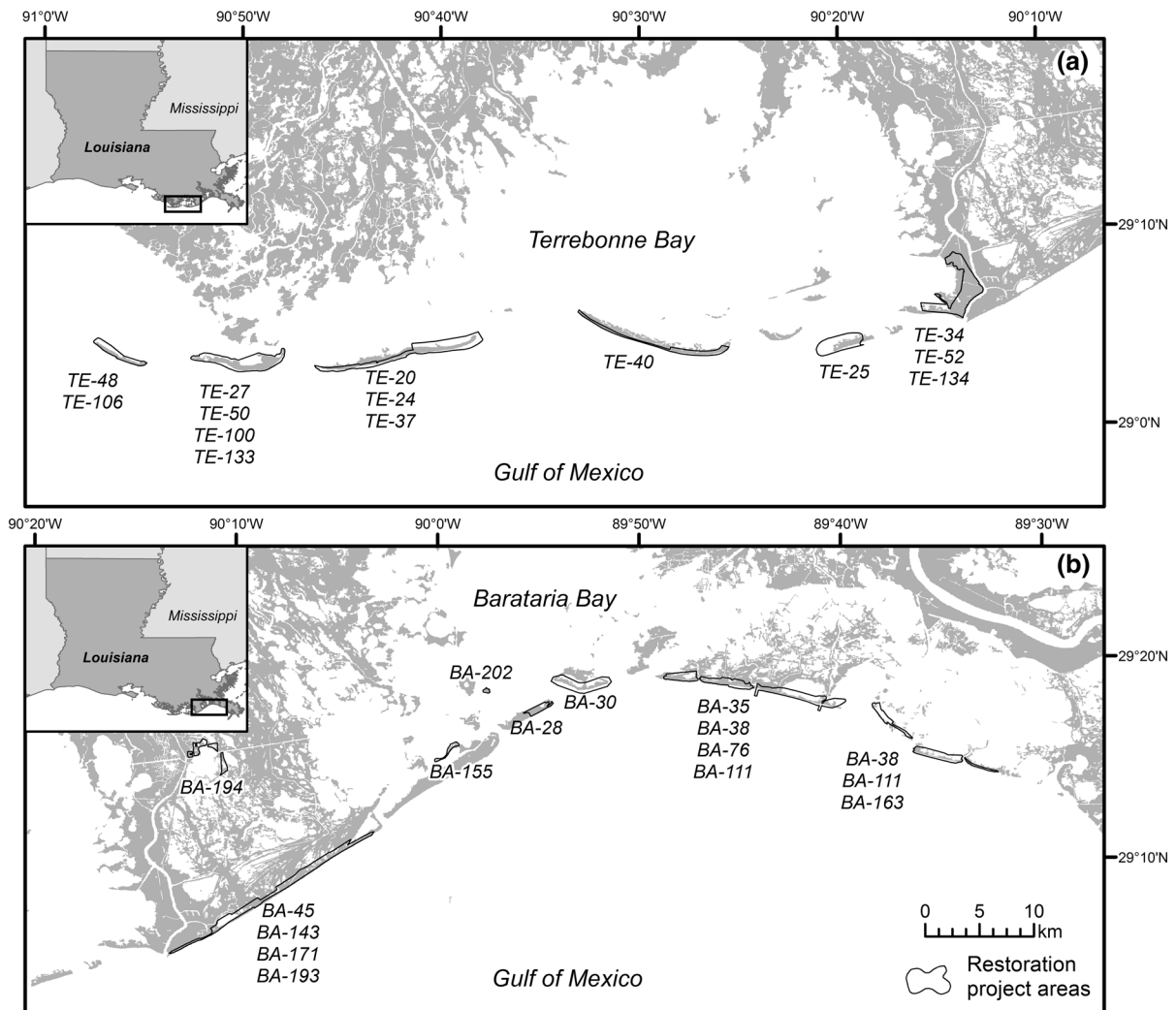


Fig. 1 Completed and planned barrier island and salt marsh restoration projects utilizing dredged material in **a** Terrebonne Bay and **b** Barataria Bay in southeastern Louisiana. Project identifiers are shown below the individual project areas. Additional details about these projects can be found at [https://](https://lacoast.gov)

lacoast.gov. Project area polygons were obtained from Louisiana Coastal Protection and Restoration Authority's Coastal Information Management System (CIMS): <https://cims.coastal.la.gov>

were (1) determine if and how soil properties of the substrate material used to restore a marsh interact with the elevation of the marsh platform to influence the survival and growth of *S. alterniflora* and *A. germinans*, (2) determine the effect of nutrient enrichment on plant biomass allocation patterns and the resultant effects on soil shear strength, and (3) determine the potential influence of the productivity of these species on soil shear strength. The benefits of a broader understanding of the factors structuring plant growth and soil strength in restored wetlands include rapid

establishment and expansion by the desired species, which can reduce the need for costly hard structures, and lead to a greater return on the initial investment.

Methods

Experimental design

We conducted a controlled greenhouse study to determine the effects of marsh soil properties, marsh

platform elevation (i.e., hydrology), and nutrient availability on the growth of the two target plant species: *S. alterniflora* and *A. germinans*, and the resultant changes in soil properties and soil shear strength over a 12-month period. The study utilized a randomized block factorial design consisting of two plant species, three marsh platform elevations relative to the water level, four substrate types, and two nutrient regimes with five blocks yielding a total of 240 experimental units. The four distinct substrate treatments included topsoil, beach sand, soil collected from a natural marsh, and soil from a recently restored marsh. Prior to the initiation of the experiment, we determined the texture of each substrate via the hydrometer method (Table 1) (Bouyoucos 1951). Approximately 4-L of each substrate type was then placed into 60 4-L plastic pots (experimental units). Each experimental unit was then assigned to receive either a high (10 mol/m³ NH₄-N) or low (0.5 mol/m³ NH₄-N) nutrient addition through the application of ammonium nitrate fertilizer (15-9-12 NPK ratio with 8.4% ammoniacal nitrogen by volume, Osmocote® Plus 8–9 month formula, Everris Inc.) at appropriate concentrations in each unit. One individual transplant of either *S. alterniflora* or *A. germinans* was then placed into each of the experimental units.

Each experimental unit was placed on a series of wooden steps within ten large (3785 L), circular plastic reservoirs in a controlled greenhouse environment. The wooden steps were used to achieve the three marsh platform elevation treatments: 15 cm below the water surface (lowest step; – 15 cm elevation treatment), 0 cm (soil surface at water level; 0 cm elevation treatment), and 15 cm above the water surface (highest step; + 15 cm elevation treatment). Reservoirs were blocked on nutrient level so that five reservoirs contained only units with the high nutrient regime while the remaining five reservoirs contained

only units with the low nutrient regime. Each of the five blocks therefore contained one high nutrient reservoir and one low nutrient reservoir. Unvegetated units of each substrate type were added to three of the ten reservoirs to determine if the presence of vegetation confers any additional advantage in soil shear strength. Each reservoir was filled with 30 ppt saltwater (Instant Ocean Sea Salt) up to the substrate surface of the units on the middle step (0 cm). Water was added to the reservoirs as needed and salinities were monitored on a weekly basis. Plants were allowed to grow under the experimental conditions for 1 year prior to harvest.

Data collection

We recorded the wet weight, stem height and number of live and dead leaves on each *S. alterniflora* and *A. germinans* transplant before transplanting into the experimental units. Stem survival and average stem height of each plant was recorded on a quarterly basis to monitor plant growth over time. The experiment was initiated on September 20, 2013 and measurements were conducted on January 17, 2014 (day 120), May 8, 2014 (day 230), and September 22, 2014 (day 368) when the experiment was concluded. At the termination of the experiment, we also measured soil redox potential and soil shear strength of each experimental unit. The soil redox potential (Eh) of each unit was determined at a depth of 7.5 cm using redox probes (Orion Redox/ORP Electrode, Model No. 9179BN, Thermo Scientific) and a handheld millivolt meter. All redox potentials had a value of 200 mV added to the reading to adjust for the potential of the silver-chloride reference electrode. Soil shear strength of each unit was measured with a 33 mm shear vane which was inserted into the soil at depths of 0–5 and 5–15 cm beneath the soil surface and rotated

Table 1 Particle size analysis of each soil type prior to the initiation of the experiment as determined via the hydrometer method. Reproduced with the permission from Bouyoucos (1951)

Sediment type	% sand	% silt	% clay	Classification
Beach sand	99.2	0.7	0.2	Sand
Natural marsh soil	58.8	27.7	13.5	Sandy loam
Restored marsh soil	94.3	3.8	1.9	Sand
Topsoil	88.7	8.8	2.5	Sand

at a constant rate until the soil failed and the vane moved. A soil core was collected from each unit down to a depth of 15 cm (the total depth of the pots) and used for a determination of soil bulk density, organic matter content, soil pH, and soil conductivity. Soil bulk density was calculated as the dry weight of soil per unit volume of the soil sample (Blake and Hartge 1986). Soil organic matter content was determined via the loss-on-ignition procedure in a muffle furnace at 500 °C for 5 h (Wang and Wang 2011). Soil conductivity and pH were determined from a 1:1 soil–water solution created by mixing 20 g of dried soil with 20 mL of deionized water (Kalra 1995). Following collection of soil cores, plants were harvested, partitioned into live and dead aboveground and total belowground portions, rinsed free of soil, placed into paper bags and dried in a convection oven at 60 °C for 2 weeks. The dried biomass was then weighed to determine the total aboveground and belowground biomass in each experimental unit.

Statistical analysis

Differences in aboveground plant growth between the experimental treatments were assessed with repeated measures analysis of variance (ANOVA) where the blocked nutrient level treatment was the random, independent variable and the time of measurement, substrate type and elevation treatments were considered fixed, independent variables. Dependent variables were plant survival, average stem height in the *S. alterniflora* units or total stem height in the *A. germinans* units. A three-way mixed model ANOVA blocked on nutrient regime was used to compare aboveground and belowground biomass and root:shoot ratios in each species at the end of the experiment, as collecting these data required destructive harvest. A similar mixed model analysis was conducted to examine differences in soil physico-chemical properties among the treatment combinations. Finally, an additional mixed model ANOVA was used to compare soil shear strength in vegetated units to that of unvegetated units to determine if the presence of plants provides a soil shear strength advantage. Soil shear strength was also compared between abiotic treatment variables and species to determine the suite of factors that produces the highest shear strength. Tukey post hoc tests were used to compare differences between elevations, substrate

types, nutrient levels and species (where appropriate). All statistical analyses were conducted in JMP (JMP Version 10. SAS Institute Inc., Cary, NC, 1989–2007).

Results

Survival and growth

Spartina alterniflora

Survival of *S. alterniflora* declined rapidly following initial transplantation in fall 2013. Only 47 individuals (39%) had live stem tissue 120 days after transplantation. In several instances, initial die-back of the main stem was followed by the emergence of new shoots, suggesting that significant biomass reserves in roots and rhizomes contributed to re-growth of stems in some of the surviving individuals. Survival of *S. alterniflora* did not differ between time points as most of the mortality occurred in between the initiation of the experiment and the first measurement time (i.e., day 120) (Fig. 2, $F_{2,71,0} = 1.14$, $p = \text{n.s.}$). The highest survival of *S. alterniflora* occurred in units at the – 15 cm elevation treatment ($F_{2,71,0} = 91.46$, $p < 0.0001$). Survival of *S. alterniflora* was lowest at the + 15 cm elevation treatment and intermediate at the 0 cm elevation treatment (contrasts: $p < 0.05$). At the conclusion of the experiment, there were only 2 (3%) surviving plants within the + 15 cm elevation treatment, as opposed to 24 (40%) within the – 15 cm

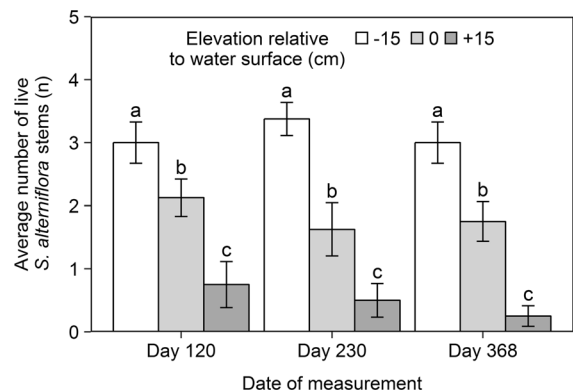


Fig. 2 Average number of surviving *S. alterniflora* stems at each elevation treatment at the three measurement times. Date of measurement represents the number of days since initiation of the experiment. Means with different letters are significantly different at $p < 0.05$

elevation treatment. There was no effect of substrate type or nutrient regime on *S. alterniflora* survival.

As expected, the height of surviving *S. alterniflora* individuals increased dramatically over the course of the experiment (Fig. 3, $F_{2,99.1} = 318.04$, $p < 0.0001$). *S. alterniflora* individuals that received the high nutrient treatment had significantly greater stem heights across time ($F_{1,7.2} = 23.92$, $p < 0.01$). Average stem height in plants grown at the high nutrient level was 25 ± 3 cm in contrast to 17 ± 2 cm in plants grown at the low nutrient level. Stem heights were highest within the -15 cm elevation treatment, followed by the 0 and $+15$ cm elevation treatments ($F_{2,105.2} = 89.29$, $p < 0.0001$). However, there was a significant interaction between soil elevation and time such that average stem heights in the -15 cm elevation treatment increased by a greater amount between each measurement time than plants grown at either the 0 or $+15$ cm elevation treatments ($F_{4,99.5} = 8.30$, $p < 0.0001$).

Final standing above- and belowground biomass of *S. alterniflora* was greater at the -15 cm elevation treatment than in plants grown at either the 0 or $+15$ cm elevation treatments, although the difference between the 0 and -15 cm elevation treatments was not statistically significant (Figs. 4, 5a, b, aboveground: $F_{2,29.2} = 10.17$, $p < 0.001$, belowground: $F_{2,31.5} = 5.09$, $p < 0.05$). The high nutrient treatment stimulated biomass production at a greater rate than the low nutrient treatment in both the aboveground and belowground portions of the plants (aboveground:

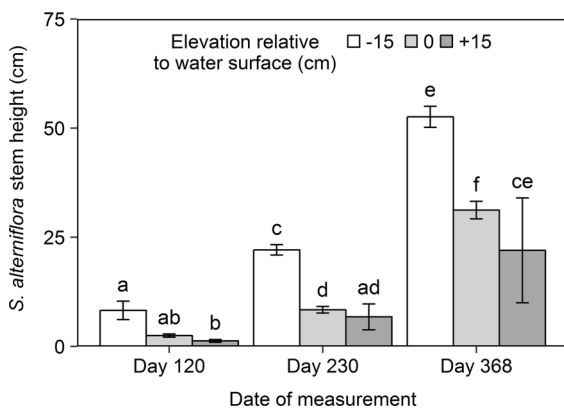


Fig. 3 Average stem height (mean \pm SE) of *S. alterniflora* grown at each elevation treatment at the three measurement times. Date of measurement represents the number of days since initiation of the experiment. Means with different letters are significantly different at $p < 0.05$

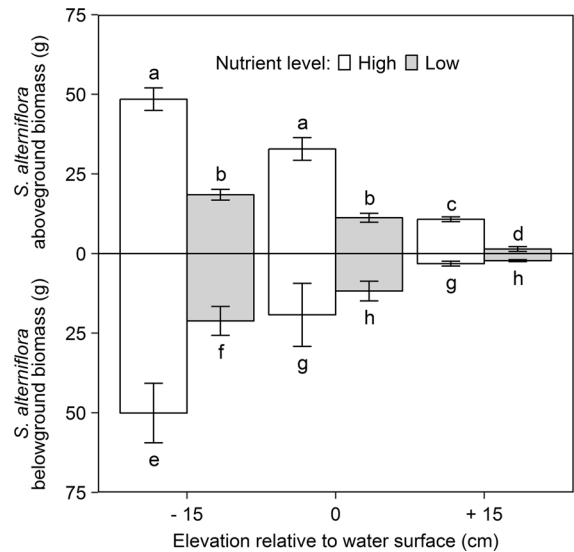


Fig. 4 Above- and belowground biomass (mean \pm SE) of *S. alterniflora* grown at each elevation treatment and nutrient level treatment combination at the conclusion of the experiment. Means with different letters are significantly different at $p < 0.05$

$F_{1,2.3} = 65.69$, $p < 0.01$; belowground: $F_{1,6.6} = 14.78$, $p < 0.01$). Root:shoot ratios were significantly lower in plants grown at the 0 or $+15$ cm elevation treatments compared to those grown at -15 cm elevation treatment (0.65 ± 0.08 , 0.60 ± 0.05 , and 1.06 ± 0.11 , respectively) ($F_{2,91.9} = 8.34$, $p < 0.001$). There was no effect of nutrient regime or substrate type on root:shoot ratios in *S. alterniflora* (Fig. 4).

Avicennia germinans

A. germinans transplants were significantly more resilient to the stress of initial transplantation than *S. alterniflora*. The number of surviving *A. germinans* units declined gradually over the course of the study, from 111 surviving plants (93%) by day 120 to 72 surviving plants (60%) at the conclusion of the study (Fig. 6, $F_{2,71.0} = 23.42$, $p < 0.0001$). In contrast to *S. alterniflora*, which reproduces largely by vegetative spread, *A. germinans* reproduces sexually and as such, plants that experienced mortality of the aboveground portions did not regrow new stems (i.e., coppicing did not occur). *A. germinans* was less flood tolerant than *S. alterniflora* as evidenced by the high mortality rate of plants grown at the -15 cm elevation treatment

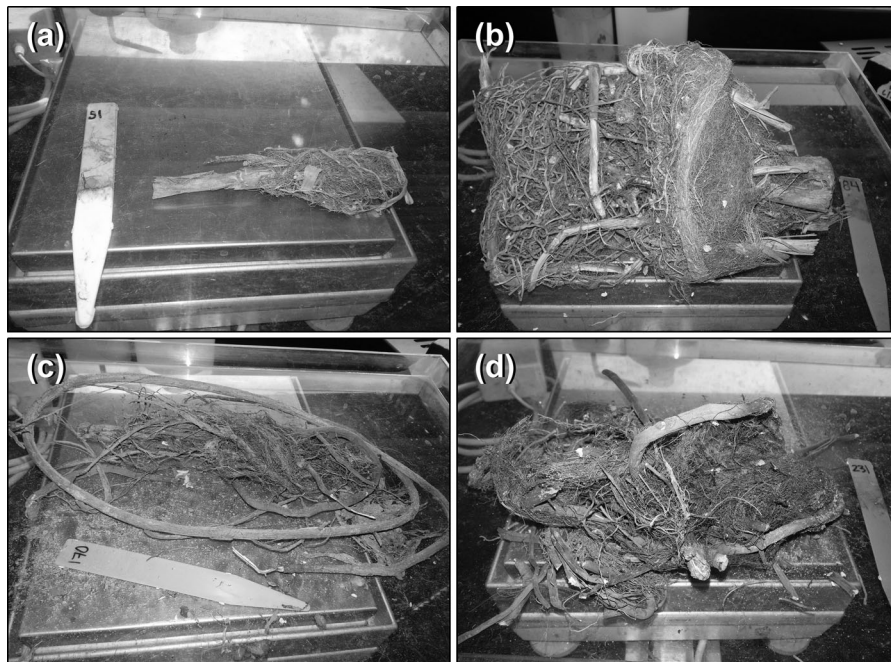


Fig. 5 Dried belowground biomass from experimental units demonstrating the differential effects of the elevation and nutrients treatments on the growth of *S. alterniflora* and *A. germinans*. **a** *S. alterniflora* grown at + 15 cm elevation with the low nutrient treatment; **b** *S. alterniflora* grown at – 15 cm

elevation with the high nutrient treatment; **c** *A. germinans* grown at + 15 cm elevation with the low nutrient treatment; **d** *A. germinans* grown at 0 cm elevation with the high nutrient treatment

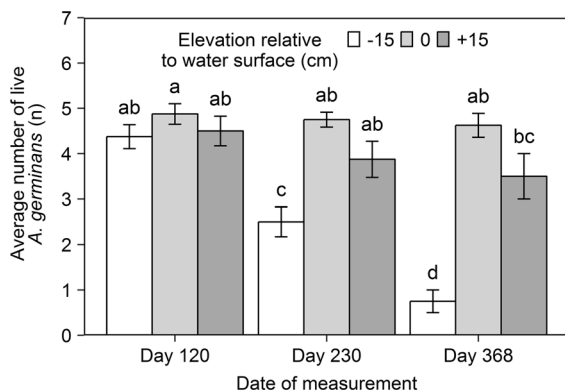


Fig. 6 Average number of surviving *A. germinans* plants at each elevation treatment at the three measurement times. Date of measurement represents the number of days since initiation of the experiment. Means with different letters are significantly different at $p < 0.05$

($F_{2,71.0} = 44.32$, $p < 0.0001$). *A. germinans* survival at the + 15 and – 15 cm elevation treatments declined gradually over the course of the study, whereas plants grown at the 0 cm elevation treatment experienced significantly less mortality over time

($F_{4,71.0} = 9.28$, $p < 0.0001$). The optimum elevation for *A. germinans* survival was the 0 cm elevation treatment where the water level was at the soil surface (contrasts: $p < 0.05$).

Almost all of the increases in *A. germinans* stem height occurred between day 230 and the conclusion of the experiment, as this time interval spanned the months from April to September, which represents the major growing season in southern Louisiana (Fig. 7, $F_{2,261.9} = 153.07$, $p < 0.0001$). Although stem height was tallest in plants grown at the – 15 and 0 cm elevation treatments, possibly due to an etiolation stress response to the flooded conditions ($F_{2,263.8} = 20.76$, $p < 0.0001$, contrasts: $p < 0.05$), the few surviving *A. germinans* grown at the – 15 cm elevation treatment had very thin, weak stems with few branches that contributed little to the total biomass of the plant.

Similar to the fertilizer response exhibited by *S. alterniflora*, *A. germinans* individuals fertilized at the high nutrient level had significantly taller stems ($F_{1,8.2} = 12.21$, $p < 0.01$), although the effects of the nutrient regime treatments were not apparent until the

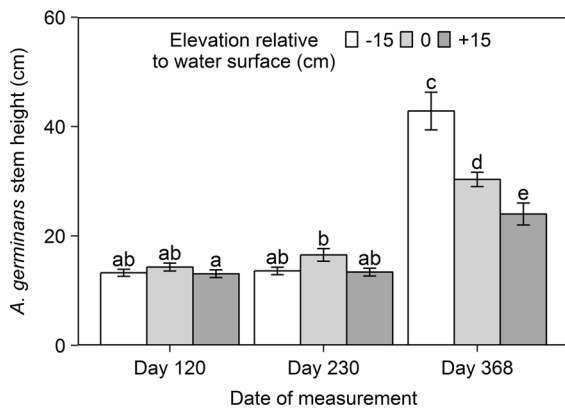


Fig. 7 Average stem height (mean \pm SE) of *A. germinans* grown at each elevation treatment at the three measurement times. Date of measurement represents the number of days since initiation of the experiment. Means with different letters are significantly different at $p < 0.05$

final measurement taken at the end of the study ($F_{2,260.2} = 10.43$, $p < 0.0001$). At the conclusion of the study, average *A. germinans* stem height was 34 ± 2 cm in the high nutrient treatment, compared to 24 ± 1 cm in the low nutrient treatment. Plants grown in different soil types exhibited small yet significant differences in average stem height ($F_{3,262.1} = 5.99$, $p < 0.001$). Plants grown in the topsoil treatment had significantly higher stem heights (20 ± 1 cm) than plants grown in either the restored marsh soil (17 ± 1 cm) or the natural marsh soil (15 ± 1 cm), however stem height in the topsoil treatment was not different than that of plants grown in the beach sand treatment (18 ± 1 cm).

Both above- and belowground biomass production by *A. germinans* was limited by low nutrient levels, as plants receiving the high nutrient treatment displayed significantly greater biomass production (Fig. 8, aboveground: $F_{1,5.9} = 104.83$, $p < 0.0001$; belowground: $F_{1,6.9} = 21.73$, $p < 0.01$). Above- and belowground biomass were both greatest in plants grown at the 0 cm elevation treatment, intermediate in the -15 cm elevation treatment and lowest in plants grown at the +15 cm elevation treatment (Fig. 5c, d, aboveground: $F_{2,58.4} = 12.76$, $p < 0.0001$; belowground: $F_{2,59.8} = 4.99$, $p < 0.01$). Although substrate type did not have a significant effect on belowground biomass production by *A. germinans*, aboveground biomass of *A. germinans* was greatest in the topsoil treatment (9.15 ± 1.20 g), lowest in the natural marsh soil (4.73 ± 0.64 g) and restored marsh soil

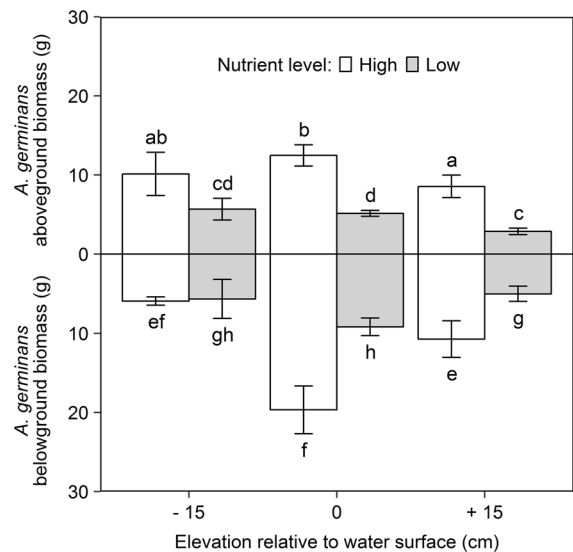


Fig. 8 Above- and belowground biomass production (mean \pm SE) of *A. germinans* grown at each elevation and nutrient treatment combination at the conclusion of the experiment. Means with different letters are significantly different at $p < 0.05$

treatments (5.62 ± 1.02 g) and intermediate in the beach sand treatment (8.35 ± 1.63 g) ($F_{3,58.0} = 6.70$, $p < 0.001$). Root:shoot ratios were significantly lower in plants grown at the 0 or +15 cm elevation treatments compared to those grown at the -15 cm elevation treatment (1.95 ± 0.22 , 2.05 ± 0.31 , and 5.72 ± 0.86 cm, respectively) ($F_{2,92.3} = 16.73$, $p < 0.0001$). There was no effect of nutrient regime or substrate type on root:shoot ratios in *A. germinans*.

Soil physicochemical properties

Soil physicochemical properties were not significantly different between the high and low nutrient treatment ($p = \text{n.s.}$). Soils within the +15 cm elevation treatment were drier and had higher bulk densities than soils at the 0 and -15 cm elevation treatments (Table 2, $F_{2,227.2} = 5.59$, $p < 0.01$). Soil bulk density also differed between the four substrate types ($F_{3,227.8} = 97.83$, $p < 0.0001$). The beach sand and restored marsh soil had the highest bulk density, whereas bulk density was lowest in the topsoil (Table 2). Soil organic matter content displayed the opposite trend and was highest in the topsoil and lowest in the beach sand and restored marsh soil (Table 2, $F_{3,228.7} = 614.46$, $p < 0.0001$). Soil organic

Table 2 Soil physicochemical properties (mean \pm SE) for each soil elevation–soil type treatment combination

Soil elevation (cm)	Substrate type	Bulk density (g/cm ³)	Organic matter (% of dry weight)	Conductivity (mS)	pH	Redox potential (mV)
+ 15	BS	1.45 \pm 0.06 ^a	1.57 \pm 0.25 ^a	11.99 \pm 1.13 ^a	7.62 \pm 0.12 ^a	190.6 \pm 31.9 ^a
	NM	1.32 \pm 0.03 ^b	3.44 \pm 0.24 ^b	19.36 \pm 1.09 ^b	7.42 \pm 0.13 ^a	207.6 \pm 26.8 ^a
	RM	1.40 \pm 0.03 ^a	1.36 \pm 0.08 ^a	13.59 \pm 0.87 ^a	7.85 \pm 0.12 ^b	217.9 \pm 26.2 ^a
	TS	1.01 \pm 0.03 ^c	5.66 \pm 0.32 ^c	19.23 \pm 1.40 ^b	6.82 \pm 0.09 ^c	218.3 \pm 40.7 ^a
0	BS	1.43 \pm 0.04 ^a	1.10 \pm 0.09 ^a	6.19 \pm 0.57 ^c	7.81 \pm 0.15 ^a	– 30.4 \pm 15.9 ^b
	NM	1.33 \pm 0.04 ^b	3.33 \pm 0.36 ^b	7.78 \pm 0.54 ^d	7.61 \pm 0.12 ^a	55.1 \pm 17.5 ^b
	RM	1.43 \pm 0.02 ^a	1.24 \pm 0.08 ^a	6.39 \pm 0.39 ^c	7.93 \pm 0.11 ^b	– 14.6 \pm 25.9 ^b
	TS	1.06 \pm 0.03 ^c	5.22 \pm 0.24 ^c	9.26 \pm 0.48 ^d	6.89 \pm 0.10 ^c	– 13.9 \pm 51.6 ^b
– 15	BS	1.31 \pm 0.05 ^e	0.99 \pm 0.09 ^a	5.97 \pm 0.52 ^c	7.57 \pm 0.12 ^a	– 38.8 \pm 25.0 ^b
	NM	1.28 \pm 0.04 ^f	2.97 \pm 0.24 ^b	7.15 \pm 0.67 ^d	7.57 \pm 0.11 ^a	– 37.6 \pm 25.2 ^b
	RM	1.43 \pm 0.04 ^e	1.12 \pm 0.22 ^a	6.92 \pm 0.52 ^c	7.72 \pm 0.12 ^b	10.3 \pm 18.4 ^b
	TS	0.95 \pm 0.04 ^g	5.23 \pm 0.18 ^c	7.83 \pm 0.50 ^d	7.14 \pm 0.15 ^c	– 85.1 \pm 16.7 ^b

Soil physicochemical chemical properties did not differ between nutrient level treatments. Means with different letters are significantly different at $p < 0.05$

BS beach sand, NM natural marsh soil, RM restored marsh soil, TS topsoil

matter content was not significantly different between the elevation treatments ($p = \text{n.s.}$).

Soil conductivity varied significantly among the substrate types and elevation treatments. The topsoil and natural marsh soils had the highest concentrations of salt on a dry weight basis, as indicated by average soil conductivity values of 12.2 and 11.7 mS, respectively (Table 2, $F_{3,234.8} = 18.20$, $p < 0.0001$, contrasts: $p < 0.05$). Soil conductivity was over twice as high in the + 15 cm elevation treatment as compared to those at the 0 or – 15 cm elevation treatments ($F_{2,233.7} = 171.57$, $p < 0.0001$). Soil pH was not significantly different between the elevation treatments but was significantly different between the four substrate types (Table 2, $F_{3,233.2} = 55.67$, $p < 0.0001$). Only the topsoil had a pH near or below 7, mostly likely a result of the high organic matter content, whereas the restored marsh soil had the highest pH. Soils at the 0 and – 15 cm elevation treatments were significantly more reduced as compared to soil at the + 15 cm treatment (Table 2, $F_{2, 205.8} = 77.83$, $p < 0.0001$, contrasts: $p < 0.05$). However, soil redox potentials were not significantly different between the substrate types ($p = \text{n.s.}$).

Soil shear strength

The presence of vegetation resulted in a significant increase in soil shear strength over unvegetated units at both soil depths (Fig. 9, $F_{2,387.5} = 53.43$, $p < 0.0001$). Soil shear strength was greatest at the deeper, 5–15 cm soil depth compared to the surface horizon (0–5 cm) across all treatment variables ($F_{1,413.6} = 74.96$, $p < 0.0001$). There was also a significant interaction between soil depth and vegetation type ($F_{2,41.6} = 15.29$, $p < 0.0001$). At the surface horizon, soil shear strength was highest in units vegetated by *S. alterniflora*, intermediate in the *A. germinans* units and lowest in the unvegetated units. At the deeper 5–15 cm depth, soil shear strength was again lowest in the unvegetated units and significantly higher in units with either *S. alterniflora* or *A. germinans*. Soil shear strength was not affected by any of the abiotic treatment variables ($p = \text{n.s.}$ for elevation, nutrient regime, and substrate type).

Discussion

Salt marsh and barrier island restoration in the northern Gulf of Mexico has largely focused on maintaining the critical storm protection and erosion

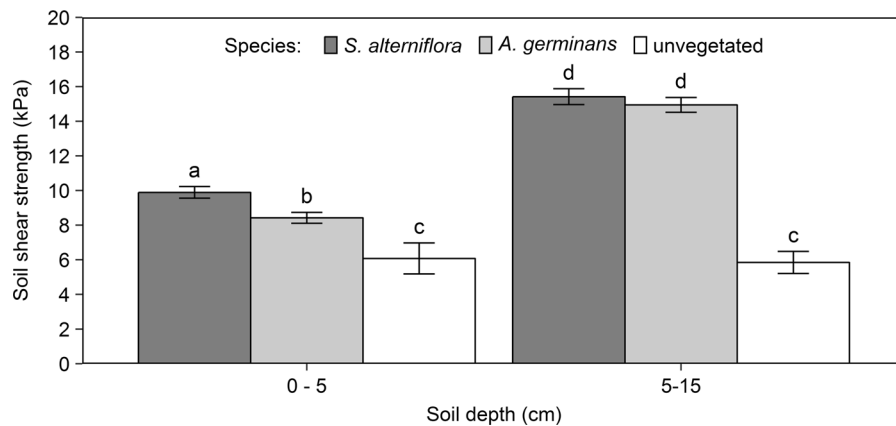


Fig. 9 Soil shear strength (mean \pm SE) within the shallow (0–5 cm) and deep (5–15 cm) soil depths in relation to the species in each unit. Means with different letters are significantly different at $p < 0.05$

abatement services provided by these habitats (Campbell et al. 2005a). Previous restoration efforts have often relied on hard structures to prevent the loss of dredged material (e.g., revetments or breakwaters) that are not only costly to build and maintain, but can also hinder the development of natural coastal habitats. As such, there has been increased interest in understanding the factors that control the stability of these habitats, with the ultimate goal of utilizing low-cost, nature-based solutions, such as vegetation plantings, to construct restored barrier island systems that are largely self-sustaining. Although it is widely accepted that salt marsh vegetation stabilizes barrier island marsh sediments and promotes the trapping and deposition of new sediment (Gedan et al. 2011; Feagin et al. 2015), the effectiveness of vegetation for soil stabilization is dependent upon the ability of the vegetation to establish and grow within the newly restored area.

The presence of salt marsh plants conferred a small yet significant increase in soil shear strength across a range of different soil types. After only one growing season, vegetated units had higher soil shear strengths than unvegetated units, suggesting that even small amounts of plant belowground biomass can contribute to soil shear strength. We found that there was neither a direct effect of substrate properties on shear strength in newly restored salt marsh soils, nor was there an indirect effect on shear strength through the potential influence of soil physicochemical properties on plant growth responses. In contrast, Feagin et al. (2009), suggests that substrate properties, in particular soil

texture, are the key factors controlling soil shear strength in older, natural marshes. Although both *S. alterniflora* and *A. germinans* commonly occur as a mixed assemblage in salt marshes throughout coastal Louisiana, we were unable to test for any combined effects of this vegetation association on soil shear strength due to space limitations within the experimental reservoirs. However, past comparisons of the soil physicochemical properties of *S. alterniflora* dominated areas to adjacent *A. germinans* dominated areas have noted few differences (Perry and Mendessohn 2009; Henry and Twilley 2013) and would suggest that the soil environment is unlikely to be significantly different when these species are grown in combination. Additionally, a field-based comparison of soil physicochemical properties conducted within restored back-barrier island salt marshes of different ages in coastal Louisiana showed that multiple soil physicochemical properties, including soil organic matter content, pH, conductivity, and shear strength, were not significantly different across soil depths ranging from 0–5 to 15–30 cm (Feher et al. 2018).

Although nutrient enrichment had profound effects on patterns of biomass allocation in both species, as illustrated by significantly taller stems and larger above- and belowground biomass stocks in plants that received the high nutrient treatment, nutrient enrichment did not appear to have an effect on soil shear strength in the current study. This outcome contrasts with the field results of a multi-year, site-level fertilization study where stands of *S. alterniflora* receiving high nutrient levels exhibited increased stem

growth and reduced belowground biomass allocation, resulting in soils with significantly lower shear strength compared to unfertilized areas (Turner 2011). However, Feagin et al. (2009) and Turner (2011) were focused on mature salt marshes, whereas our study focused on the soil shear strength of soils from recently restored barrier island salt marshes in a controlled setting. Thus, the potential impacts of soil properties and nutrient enrichment on soil shear strength may not be readily apparent until after multiple growing seasons or years post restoration. Ultimately, the results of this study suggest that intertidal vegetation provides a significant soil shear strength advantage by stabilizing newly placed sediments at young restoration sites where unconsolidated soils have not yet fully compacted and are more vulnerable to erosion.

The elevation of the soil relative to the water level (i.e., hydrology) was the key factor controlling the survival and growth of both *S. alterniflora* and *A. germinans*, although both species exhibited distinct responses to the elevation treatments. *S. alterniflora* was more flood tolerant than *A. germinans* as evidenced by the higher rates of survival and relatively greater above- and belowground biomass of *S. alterniflora* at the lowest elevation treatment, demonstrating the species' unique ability to modulate local soil hypoxia in the rhizosphere through radial oxygen loss (Mendelssohn et al. 1981; Naidoo et al. 1992; Lee et al. 1999). *A. germinans* has been reported to exhibit significantly lower rates of transpirational water loss as compared to *S. alterniflora* (Krauss et al. 2014), which was likely a factor in greater tolerance of a low water table and higher soil salinities recorded in units at the highest elevation treatment. Similar patterns of differences in flood tolerance between the two species has also been observed in established salt marshes throughout coastal Louisiana as *A. germinans* typically occurs at slightly higher elevations along creek-banks, with dominance shifting to *S. alterniflora* as elevation declines slightly toward the more interior portions of the marsh (Perry and Mendessohn 2009). Additionally, *A. germinans* was less sensitive to the initial stress of transplantation into the experimental soils, and the relatively slower growth of *A. germinans* as compared to *S. alterniflora* may represent an energy expenditure tradeoff, whereby *A. germinans* allocates additional resources to coping with stressful conditions at the expense of plant growth, which confers a

greater resilience to acute stress compared to *S. alterniflora*, but may also make *A. germinans* less resilient to chronic stress from prolonged inundation and low oxygen availability (Pezeshki et al. 1990; McKee 1996; Ellison and Farnsworth 1997; Pezeshki 2001).

Although *S. alterniflora* exhibited significantly higher rates of growth over time as compared to *A. germinans*, the combined stressors of water limitation and high soil salinities likely limited survival and growth in the highest elevation treatment, as plants exposed to prolonged drought and high soil salinities often display reduced growth and reproductive capabilities as energy and resources are diverted to the production of compatible solutes needed to lower cytoplasmic water potentials and to combat accumulation of toxic ions in plant tissues (Hester et al. 2001; Brown and Pezeshki 2007). Thus, as long as the elevation of the marsh platform is appropriate for *S. alterniflora* colonization, the suboptimal soil types found at many salt marsh restoration sites may not impose substantial limitations on expansion. Although both *S. alterniflora* and *A. germinans* are well adapted to colonize stressful coastal environments, the efficacy of using salt marsh vegetation for sediment stabilization in recently restored marshes is dependent upon achieving the proper hydrologic regime (Knutson et al. 1981; Alleman and Hester 2010; Gedan et al. 2011).

Other studies examining salt marsh plant growth responses in restored habitats have noted the potentially negative impacts of soil with high bulk density, low soil organic matter, or limited nutrient reserves on colonization and growth (Field 1998; McKee and Faulkner 2000; Osland et al. 2012). Despite the fact that the physicochemical properties of some of the soil treatments utilized in this study were highly dissimilar from the soils found within a typical back-barrier island salt marsh (Fearnley 2008), both species were largely unaffected by the substrate treatments. In fact, as long as other key edaphic conditions are not severely limiting (i.e., elevation and the associated hydrologic regime), colonization by highly productive salt marsh species such as *S. alterniflora* and *A. germinans* can initiate a positive feedback cycle as both species are known to contribute large amounts of organic matter to the soil, which makes the soil environment more hospitable to continued growth and promotes the development of soil aggregates that provide soil stability (Craft 1996; Chen and Twilley

1999; McKee and Faulkner 2000). Therefore, although suboptimal soils alone may not severely restrict the survival and growth of *S. alterniflora* or *A. germinans*, the effect of a suboptimal edaphic environment, when combined with the stress of suboptimal elevation, may limit the successful colonization and growth of these species in restored marshes.

Restoration projects that are initiated with the goal of creating self-sustaining barrier island and salt marsh habitat in the Gulf of Mexico will have the greatest chance of success when full consideration is given to the suite of interacting environmental variables that control the development of these vegetation communities. Although there was no effect of higher nutrient levels on the survival of either *S. alterniflora* or *A. germinans*, multiple studies have noted that fertilization may be necessary when planting in sandy soils or in soils with low nutrient reserves (Broome 1989; Broome and Craft 2000). Similarly, due to the large volumes of dredged material required and the considerable cost associated with transporting this material, it is unlikely that putting additional resources into sourcing better quality soil medium would provide an increased return on investment given the negligible differences observed in plant survival, growth, and soil shear strength between the substrate treatments. Indeed, one of the many issues currently impacting coastal restoration efforts in Louisiana is the limited availability of borrow material for use in dredged material restoration projects (Kulp et al. 2005; Khalil et al. 2010). Since it therefore may not be possible for restoration practitioners in Louisiana to have a choice as to the source or characteristics of the dredged material, a careful consideration of the physicochemical properties of the dredged material and their potential interactions with other aspects of the environmental setting of the restored area (i.e., elevation and hydrologic regime) would none-the-less be informative for both initial restoration planning efforts and also in prescribing effective solutions where adaptive management is needed to improve undesirable restoration outcomes. Although *S. alterniflora* and *A. germinans* are both adapted to thrive in intertidal environments at a narrow range of elevations (– 0.35 to 0.03 m NAVD88: Perry and Mendessohn 2009; see also Alleman and Hester 2011), the subtle physiological dissimilarities between these species impart small but important differences in their ideal elevations for establishment and growth (Figs. 3, 6).

Therefore, restoration plans that seek to facilitate the colonization and growth of the full complement of salt marsh plant species (i.e., mixed stands of both *S. alterniflora* and *A. germinans*) should incorporate a range of low-to-high intertidal elevations that mimic the profile of natural marshes with gradually sloping edges that grade into interior marsh habitat.

Given the critical importance of elevation and the associated hydrologic regime in structuring intertidal plant communities, restoration efforts should pay special attention to building the restored area at the proper elevation for intertidal plant establishment and growth. It has been suggested that achieving optimal marsh elevations may require increased effort in micro-tidal settings such as Louisiana, where the optimal elevational range for intertidal plant growth is extremely small (Alleman and Hester 2011; Rasser et al. 2013). Although there was not a strong effect of soil type alone on vegetation growth in this study, restoration plans that require rapid revegetation to prevent the loss of dredged sediments should consider the potential adverse impacts of soil physicochemical properties, which when combined with water stress due to high elevations, can have a significant impact on both the survival and expansion of salt marsh vegetation. Finally, future restoration success may be enhanced by developing strategies to account for the potential impacts of climate change, where the reduced survival and growth of intertidal vegetation associated with insufficient elevations will likely be exacerbated by future scenarios of higher sea levels (Justić et al. 1996). Thus, although both *S. alterniflora* and *A. germinans* are ideal species for use in salt marsh restoration throughout their ranges due to their high stress tolerance and contributions to soil shear strength, our ability to effectively utilize these plants for sediment stabilization and habitat restoration is dependent upon achieving an adaptive understanding of the suite of environmental conditions that will facilitate their establishment, productivity, and sustainability in dynamic coastal environments.

Acknowledgements Financial support for this study was provided by the Louisiana Barrier Island Comprehensive Monitoring Program (Louisiana CPRA Contract No. 2514-14-03), the Coastal Protection & Restoration Authority/Louisiana SeaGrant Coastal Science Assistantship Program, Coastal Plant Ecology Lab at University of Louisiana at Lafayette, University of Louisiana at Lafayette Graduate Student Association, and the Ecology Center at University of Louisiana at Lafayette.

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