RESEARCH ARTICLE

Jump-starting coastal wetland restoration: a comparison of marsh and mangrove foundation species

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During coastal wetland restoration, foundation plant species are critical in creating habitat, modulating ecosystem functions, and supporting ecological communities. Following initial hydrologic restoration, foundation plant species can help stabilize sediments and jump-start ecosystem development. Different foundation species, however, have different traits and environmental tolerances. To understand how these traits and tolerances impact restoration trajectories, there is a need for comparative studies among foundation species. In subtropical and tropical climates, coastal wetland restoration practitioners can sometimes choose between salt marsh and/or mangrove foundation species. Here, we compared the early life history traits and environmental tolerances of two foundation species: (1) a salt marsh grass (*Spartina alterniflora*) and (2) a mangrove tree (*Avicennia germinans*). In an 18-month study of a recently restored coastal wetland in southeastern Louisiana (USA), we examined growth and survival along an elevation gradient and compared expansion and recruitment rates. We found that the rapid growth, expansion, and recruitment rates of the salt marsh grass make it a better species for quickly establishing ecological structure at suitable elevations. The slower growth, limited expansion, and lower recruitment of the mangrove species show its restricted capacity for immediate structural restoration, especially in areas where it co-occurs with perennial salt marsh species. Our findings suggest that the structural attributes needed in recently restored areas can be achieved sooner using fast-growing foundation species. Following salt marsh grass establishment, mangroves can then be used to further assist ecosystem development. This work highlights how appropriate foundation species can help jump-start ecosystem development to meet restoration objectives.

Key words: coastal wetland, foundation species, life history strategy, mangrove, restoration, salt marsh

Implications for Practice

- Fast-growing, perennial foundation species can jump-start structural restoration to regain wetland area.
- Identifying species tolerances and understanding their early growth traits can direct selection and planting practices for foundation species.
- Balancing short-term (e.g. erosion control, vegetation structure) and long-term (e.g. plant community development and restoration of ecosystem processes and functions) restoration objectives is possible if species-specific life history traits and tolerances are understood.

Introduction

Foundation species have a disproportionate influence on the structure, function, and maintenance of ecosystems (Dayton 1972) and are often indistinguishable from the system itself (Ellison 2019). Loss of these species can have a significant impact on ecosystem stability, function, and the supply of ecosystem services (Ellison et al. 2005). Structural characteristics are one of the most well-studied attributes that foundation species provide, with numerous examples from terrestrial forests, salt marshes, kelp forests, seagrass beds, and mangrove forests (Ellison et al. 2005; Gedan & Bertness 2010; Angelini et al. 2011; Osland et al. 2013; Gedan et al. 2014). The

ecological structure provided by foundation species, often by primary producers, is valued by humans for the many ecosystem services that are supported (e.g. climate regulation via carbon storage and sequestration, water purification via nutrient cycling, nursery habitat for important species, and coastal protection via wave attenuation and erosion control) (Barbier et al. 2011; Kelleway et al. 2017). During restoration of degraded ecosystems, foundation species often play a pivotal role in creating structure and habitat and enabling ecosystem development.

The identification and selection of foundation species is a critical step during ecological restoration (Ellison 2019), and there is a pressing need to advance the understanding of ecosystem

development following foundation species planting and establishment (Altieri et al. 2007; Angelini et al. 2011; Osland et al. 2013; Gedan et al. 2014; Osland et al. 2014b). In species-poor ecosystems, where few species are capable of surviving stressful conditions, there is typically only a single dominant foundation species (Angelini et al. 2011). Other foundation species are likely to be found in adjacent patches due to different abiotic conditions, stress tolerances, and/or competition (Levine et al. 1998; Angelini et al. 2011; Altieri et al. 2012). Adjacent foundation species patches are most commonly found where environmental gradients are steep (e.g. intertidal and alpine ecosystems) or tolerance thresholds are met. In some ecosystems, different foundation species can play similar functional roles in the same or overlapping patches (Osland et al. 2013; Gedan et al. 2014); however, this overlap in functionality is likely only to occur at species range limits, near species-specific thresholds along environmental gradients, or in areas that are currently recovering from disturbance.

In subtropical coastal wetlands, an ecotone between salt marshes and mangroves exists (Bertness & Ellison 1987; Alongi 2009: Osland et al. 2013). Both salt marsh and mangrove plants are commonly described as foundation species because of the substantial role they have in shaping the tidal wetland communities they occupy (Ellison et al. 2005; Osland et al. 2012, 2013). Salt marshes are dominated by herbaceous vegetation and are most abundant in temperate and subpolar regions (Mitsch & Gosselink 2000), whereas mangroves are dominated by freeze-intolerant, woody trees and shrubs on tropical and subtropical coasts (Duke 1993). Interactions between these foundation species have been studied at a variety of life history stages (Clarke & Myerscough 1993; Patterson et al. 1993; Stevens et al. 2006; Pickens & Hester 2011; Yando et al. 2018) and through the lens of global climate change. Little work, however, has been done to understand trade offs in growth strategies and possible interactions between foundation plant species along environmental gradients from a restoration and management perspective.

Ecosystem restoration is becoming an increasingly valuable tool in systems that are destroyed, degraded, or perturbed by both natural and human disturbances. Salt marsh and mangrove ecosystems have experienced some of the highest relative levels of disturbance and loss worldwide (Kennish 2001; Airoldi & Beck 2007; Leadley et al. 2013; Richards & Friess 2016). Despite extensive loss and degradation, both salt marshes and mangroves are highly valued for their ecosystem services (e.g. coastal protection via wave attenuation and erosion control, climate regulation via carbon storage and sequestration, support of fisheries via nursery habitat) (Barbier et al. 2011; Kelleway et al. 2017), but systematic comparisons of the foundation species that dominate these ecosystems remain rare. In the northern Gulf of Mexico, and particularly in coastal Louisiana, where a dynamic salt marsh-mangrove ecotone exists, the rate of coastal wetland loss, due to anthropogenic degradation and relative sea-level rise, is among the highest in the world (Penland et al. 1990; Turner 1997; Couvillion et al. 2017). To compensate for this loss, large-scale coastal restoration efforts have been implemented and coastal wetland restoration is a key

component (e.g. 2017 Coastal Master Plan) (Coastal Protection and Restoration Authority 2017). During ecological restoration, practitioners must balance the constraints of critical short-term objectives, such as site creation or manipulation (e.g. erosion control, soil compaction, elevation loss, and sediment type), with long-term goals, such as the provision of habitat, targeted species assemblages and communities, the development of healthy soil conditions, and the delivery of key ecosystem services and functions (Hilderbrand et al. 2005). The planting of key salt marsh and mangrove foundation species in restoration projects is common, but direct comparisons of survival, growth, expansion, and natural recruitment along elevation gradients are lacking, particularly during critical early stages after physical/hydrologic restoration (Lewis & Dunstan 1975; Crewz & Lewis 1991).

In this study, we utilized a recently restored coastal saline wetland to understand 1) how the growth strategy and survival of two foundation species differs along an elevation gradient, 2) how rates of expansion and recruitment differ between two foundation species, and 3) which foundation species is best suited for the rapid formation of necessary structural attributes? We compared a common salt marsh grass foundation species (*Spartina alterniflora*) to a mangrove tree foundation species (*Avicennia germinans*) (Fig. 1). Our overarching aim was to advance the understanding of the importance of the early life history strategies and potential interspecific interactions that might exist between these foundation plant species in the critical period soon after physical restoration, while providing valuable information to coastal scientists and restoration practitioners.

Methods

Study Site

We completed this study in a previously operational canal in Port Fourchon, Louisiana, USA (Fig. 2A) (29.132°N, 90.224°W). This canal has been the site of ongoing wetland restoration with adjacent sections completed in 2012, 2013, and 2014 utilizing dredge spoil sediments from the nearby Bayou Lafourche. This experiment was started in March of 2015 in the most recently filled sections (2013 and 2014) and planted with both *Avicennia germinans* (hereafter *Avicennia*) and *Spartina alterniflora* (hereafter *Spartina*). Planting was completed in coordination with the Coalition to Restore Coastal Louisiana, with over 50 volunteers directed and overseen by E.S.Y. to plant individuals according to the study design described herein. The site was monitored at 3 months, 7 months, 12 months, and 18 months after initial planting (March 2015 to September 2016). Two experimental areas were established (Fig. 2B & 2C).

Elevation Gradient — Experimental Area I

Utilizing the elevation gradient formed from the placement of dredge spoil material, three distinct planting elevations were identified at 0.25, 0.35, and 0.45 m (±0.025 m) NAVD88 (Geoid12A). Elevation for all plots was determined by first
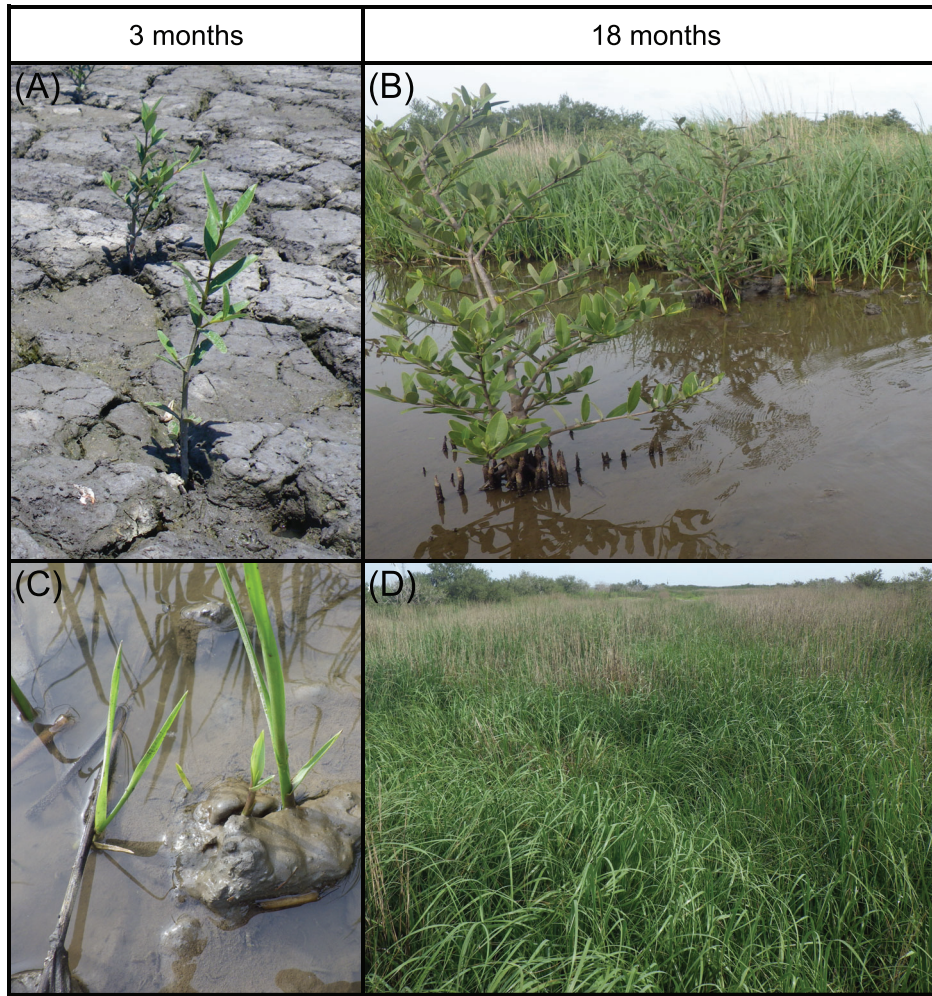
Figure 1. Representative images of mangrove (*Avicennia germinans*) and salt marsh grass (*Spartina alterniflora*) at 3 months (A, C) and 18 months (B, D) after planting, respectively.

establishing stable benchmarks, which had previously been measured using a high-precision Global Navigation Satellite System (Trimble R8 and TSC3), in combination with a real-time Continuously Operating Reference Station network (Louisiana State University's GULFNet network). A laser level (Spectra Precision Laser, LL300; Trimble Navigation Ltd., Sunnyvale, CA, USA) was then used to identify suitable areas for each planting elevation. Elevations were related to local tidal gauges (Coastal Reference Monitoring System- Coastal Protection and Restoration Authority; ID#: CRMS0292; https://lacoast .gov/crms/#) to determine the percentage of time the soil surface was flooded (hereafter referred to as percent time flooded). Additionally, elevations were remeasured after 18 months to determine if subsidence had occurred within the study site. At each elevation, eight 16-m^2 plots (4 × 4 m^2) were established (Fig. 2B). All plots were planted with *Avicennia* at 1.52-m spacing, with the exception of a grouping of five individuals in the center 1-m^2 subplot, for a total of 13 mangrove transplants per plot with initial heights that ranged from 30 to 45 cm (Fig. 2B).

A 1.52-m (5-ft) spacing is commonly used in Louisiana mangrove restoration plantings. Plots were also randomly assigned to be planted with *Spartina* at high (0.3-m spacing) or low (1.52-m spacing) densities at each elevation to determine if *Spartina* density may facilitate *Avicennia* growth, with all individuals offset by at least 0.15 m when plantings overlapped (Fig. 2B). These density treatment levels were combined in subsequent analyses, however, as there was no significant difference between the two density levels at any sampling period nor for any measurement after planting.

Avicennia cover, tree height, total biomass, and percent survival from initial planting were measured at each sampling period. Percent live and dead cover were visually estimated at the plot level. Tree height was measured, and total aboveground biomass was calculated for each sampling period using an allometric equation (Osland et al. 2014*a*, 2014*b*). Specific leaf area (SLA) was measured at the 18-month sampling period from five representative *Avicennia* leaves from five different trees in each plot. If fewer than five trees were present, then the five leaves were equally taken from
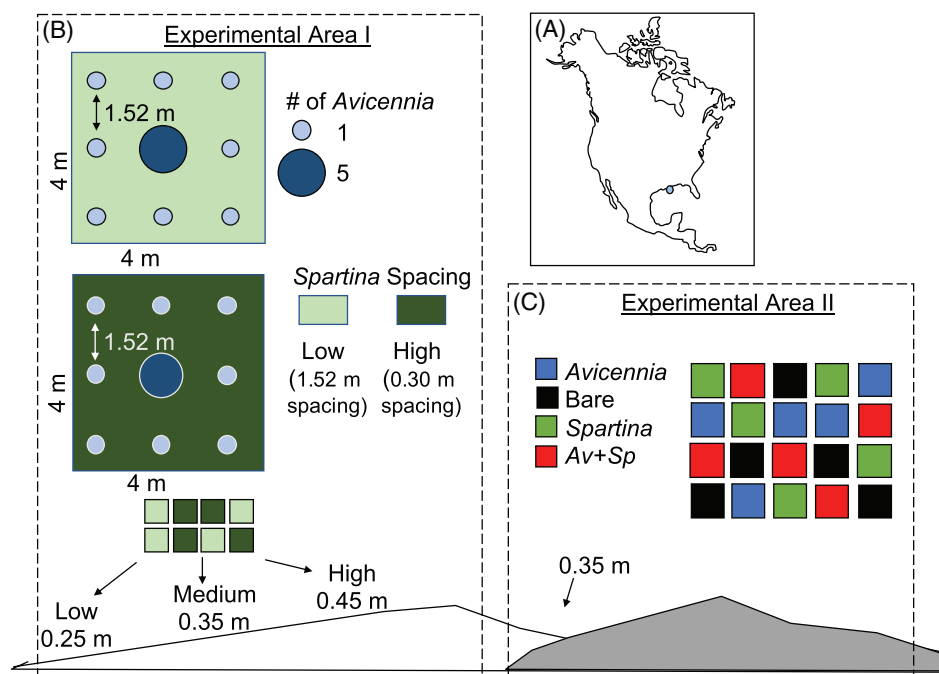
Figure 2. (A) Map of location of study site in Port Fourchon, Louisiana (USA), (B) layout of Experimental Area I at low, medium, and high elevations in the 2013 fill site (white polygon) with plot layout and planting spacing for *Avicennia* (dark and light blue) and *Spartina* (dark and light green), and (C) layout of Experimental Area II in the overlap between the 2013 and 2014 fill site foundation species that were planted in both experimental areas. Treatments: *Avicennia* (blue), Bare (black), *Spartina* (green), and *Avicennia/Spartina* (Av + Sp; red).

the available individuals. SLA was determined by dividing leaf area by dry leaf mass. The area of each leaf was calculated using ImageJ software (Rasband 1997–2018), and dry mass of leaves was measured after drying at 65°C for 2 weeks.

Spartina percent live and dead cover were measured at the plot level, and mean *Spartina* canopy heights were determined at each sampling period. Additionally, during the 18-month sampling period, a 0.11-m^2 plot (0.33 × 0.33 m^2) was randomly selected, and all salt marsh aboveground biomass was clipped at the soil surface and stored at 4°C until processed. Collected stems were counted, and all stems were dried at 65°C for 2 weeks to determine total dry aboveground biomass (g). Adjusted biomass for each plot was calculated at the meter-squared level using the plot cover estimates (g/m^2), as not to overestimate *Spartina* biomass.

Expansion and Recruitment — Experimental Area II

To examine expansion and recruitment, a second experimental area was established in an adjacent portion of the same restoration site (Fig. 2C). This secondary experimental area was located at 0.32 m (±0.01) (NAVD88-Geoid12A) elevation using the same methods as described in Experimental Area I. This elevation was selected as it is suitable for both *Avicennia* and *Spartina* foundation species. Elevations were measured prior to the experiment and after 18 months to account for any elevation loss due to sediment compaction or erosion within the study area. Both measurements were related to local tidal gauges

(Coastal Reference Monitoring System-Coastal Protection and Restoration Authority; ID#: CRMS0292; https://lacoast.gov/crms/#) to determine percent time flooded. We established twenty 16-m^2 plots (4 × 4 m^2) in this area and planted them with one of four treatments: (1) *Avicennia*, (2) *Spartina*, (3) *Avicennia/Spartina*, or (4) bare (not planted) in a randomized design (Fig. 2C). All plantings were at 1.52-m spacing for a total of nine plants per species per plot. We measured *Avicennia* and *Spartina* live and dead percent cover and calculated percent survival of *Avicennia* within each plot. At the 12-month sampling period, the number of *Spartina* progenitor clumps (original transplants or natural recruits), and rates of lateral expansion were measured from the previous year's dead stems to the external expanding edge.

Soil

For all plots in both experimental areas, we collected a 15-cm deep, 5.08-cm diameter soil core prior to the start of the experiment (0 months) and at each sampling period (3, 7, 12, and 18 months) to quantify soil development. Cores were only collected in the top 15 cm of the soil column to capture changes after restoration in the root zone area and where any newly accreted soil might be. Cores were collected and stored at 4°C until analyses were completed. All soils were dried at 65°C until constant mass was achieved, and bulk density was determined by simple dry weight to volume ratio (Blake & Hartge 1986). Soil organic matter (SOM) was quantified via loss on ignition in a muffle furnace at 500°C for 5 hours (similar to Wang et al. 2011).

Data Analyses

Data analyses for "Elevation Gradient–Experimental Area I" included linear and quadratic regressions and for "Expansion and Recruitment–Experimental Area II" included linear regressions. All regression analyses were completed in a mixed model framework using the package "nlme" (Pinheiro et al. 2019) in R (Version 3.4.2) (R Core Team 2014) and RStudio (Team RStudio 2015) to analyze our repeated measures design. Dependent variables included *Avicennia* survival, tree height, biomass, and cover along with *Spartina* cover and canopy height. Independent variables included three fixed effects (month and sampling elevation or month and planting treatment) and one random effect (plot identification, which was used to account for the non-independence in repeated measurements). Model selection was completed by using corrected Akaike information criterion values and eliminating non-significant model terms.

Analysis of variance and Tukey's post-hoc tests were used to compare differences within the 12- and 18-month sampling period measurements. Dependent variables for analyses included elevation, *Avicennia* SLA, *Spartina* biomass, *Spartina* stem density, and *Spartina* expansion rate, whereas independent variables included sampling elevation or treatment type. All means are presented with standard errors.

Results

Elevation Gradient — Experimental Area I

Avicennia percent survival declined over time, with greater survival at low elevations compared to high elevations ($p < 0.01$; Fig. 3A; Tables 1 & S1). Tree height and total mangrove biomass increased over time, but did not differ by elevation (Fig. 3C & 3E; Tables 1 & S1). At the 18-month sampling period, *Avicennia* SLA was significantly greater at low elevations (78.1 ± 3.0 cm^2/g) compared to both medium (47.5 ± 8.0 cm^2/g; $p < 0.01$) and high elevations (42.4 ± 6.6 cm^2/g; $p < 0.01$) (Table 1). *Avicennia* cover in this experimental area ranged from 0–15% over the monitoring period, but was highly variable and patchy.

Spartina live cover increased over time at all elevations, with the lowest elevation reaching approximately 95% cover after 18 months—a rate far faster than both medium and high elevation plots ($p < 0.001$; Fig. 3B; Tables 1 & S1). *Spartina* canopy heights also increased over time, and significantly greater canopy heights were present at the lowest elevations ($p < 0.05$; Fig. 3D; Tables 1 & S1). *Spartina* stem density at 18 months did not differ statistically by elevation, but had high variability at all elevations (Low: 139 ± 21.9 stems/m^2; Medium: 114 ± 25.16 stems/m^2; High: 56 ± 23.2 stems/m^2). Adjusted biomass differed at the 18-month sampling in *Spartina*, with significantly greater biomass in low elevation plots compared to medium ($p < 0.005$) and high elevation plots ($p < 0.001$) (Fig. 3F; Tables 1 & S1).

Soil metrics in this experimental area had increasing bulk densities over time for all elevations, but were lower in low elevation plots at all time points compared to high elevations
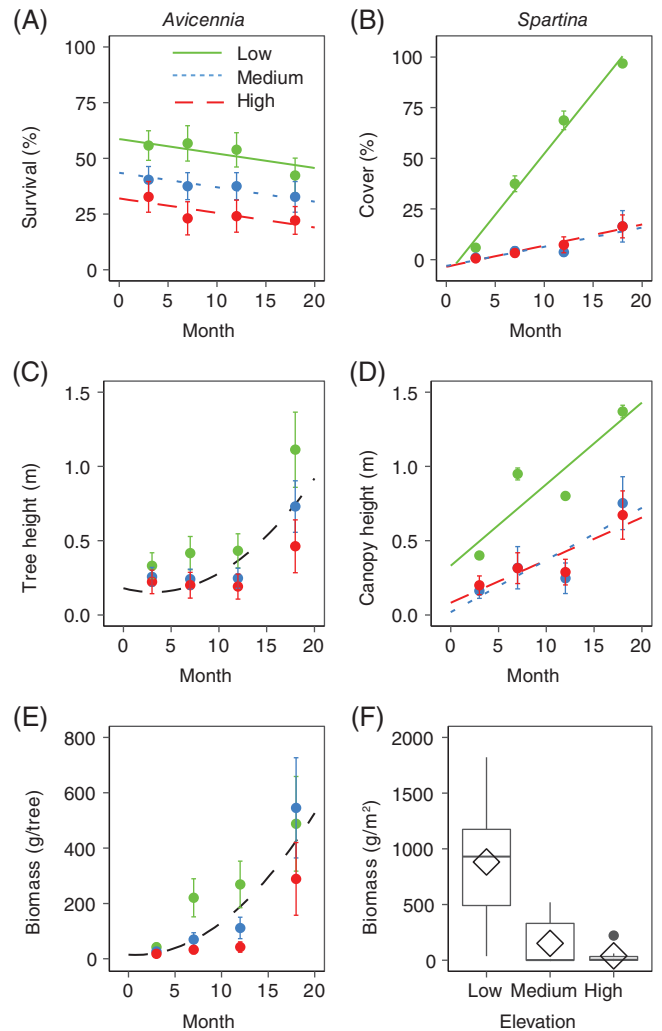

Figure 3. Experimental Area I—relationship between time and (A) *Avicennia* survival, (B) *Spartina* cover, (C) *Avicennia* tree height, (D) *Spartina* canopy height, (E) *Avicennia* tree biomass, and (F) boxplot of *Spartina* biomass between elevations at 18 months. All linear regressions (A, B, D) have low (green-solid), medium (blue-dotted), and high (red dashed) elevations with means (±SE). All quadratic regressions (C, E) have mean (±SE) values for low (green), medium (blue), and high (red). Interior diamonds in boxplot (F) represent mean values.

($p < 0.001$) (Tables 1 & S1). SOM did not differ over time, but was diminished in high (3.4 ± 0.3%) and medium elevation plots (2.9 ± 0.3%) compared to low elevation plots (4.7 ± 0.3%; $p < 0.001$) (Tables 1 & S1).

After 18 months, elevations were remeasured, and although significant elevation increases were detected (4–6 cm) (Table 1), these differences are within the margin of error of the survey equipment and fluctuations in soil surface elevation due to subsurface hydrological variation (Nuttle et al. 1990). Nonetheless, relative differences were maintained, and over the course of the 18-month study, the low, medium, and high elevations were flooded 27, 11, and 3% of the time, respectively.

Table 1. Model type, degrees of freedom, F-statistic, and p-value for time, elevation, treatment, and time x treatment for all metrics in both Experimental Area I and II. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. ANOVA, analysis of variance; NS, non-significant.

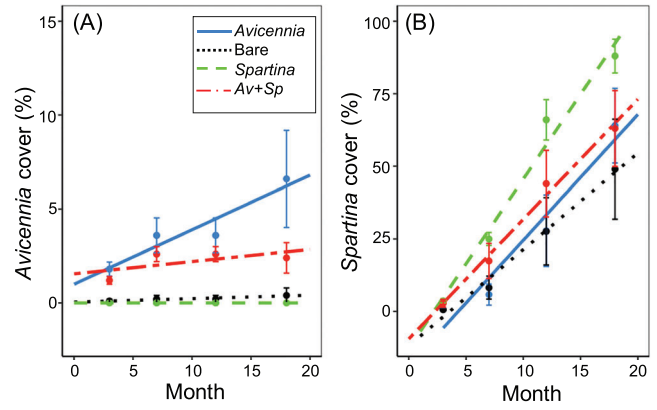|		Model Type	Time	Elevation	Time× Elevation	Treatment	Time × Treatment
Experimental Area I							
Avicennia	Survival	Linear	$F_{1,71}=10.8$**	$F_{2,21}=4.9$*	NS		
	Tree height	Quadratic	$F_{1,70}=28.6$***	NS	NS		
	Biomass	Quadratic	$F_{2,69}=37.0$***	NS	NS		
	SLA	ANOVA		$F_{2,21}=9.62$***			
Spartina	Cover	Linear	$F_{1,69}=283.1$***	$F_{2,21}=104.0$***	$F_{2,69}=111.5$***		
	Canopy height	Linear	$F_{1,69}=108.0$***	$F_{2,21}=11.6$***	$F_{2,69}=4.3$*		
	Stem density	ANOVA		NS			
	Adjusted biomass	ANOVA		$F_{2,21}=13.21$***			
Soil & Hydrology	Bulk density	Linear	$F_{1,94}=10.7$ *	$F_{2,21}=5.7$**			
	SOM	Linear	NS	$F_{2,21}=9.3$**			
	Elevation	Linear	$F_{1,23}=72.6$***	$F_{2,21}=211.1$***			
Experimental Area II							
Avicennia	Cover	Linear	$F_{1,56}=13.9$***	NS	NS	$F_{3,16}=9.1$***	$F_{3,56}=7.2$***
Spartina	Cover	Linear	$F_{1,56}=231.5$***	NS	NS	NS	$F_{3,56}=7.2$***
	Number of progenitor clumps	ANOVA		NS		$F_{3,16}=7.96$***	$F_{3,56}=3.3$*
Soil & Hydrology	Bulk density	Quadratic	$F_{2,76}=10.9$**	NS		NS	NS
	SOM	Linear	NS	NS		NS	NS
	Elevation	Linear	NS	NS		NS	NS

Figure 4. Experimental Area II—*Avicennia* (A) and *Spartina* (B) cover over time by planting treatment with means (±SE) and linear regressions. Treatments: *Avicennia* (blue-solid), Bare (black-dotted), *Spartina* (green-dashed), and *Avicennia/Spartina* (Av + Sp; red-dashed-dot). Note differences in *y*-axes.

Expansion and Recruitment — Experimental Area II

Avicennia live cover increased faster in the *Avicennia* monoculture treatment ($p < 0.005$) than the *Spartina/Avicennia*, *Spartina*, and bare treatments (Fig. 4A; Tables 1 & S2). *Spartina/Avicennia*, *Spartina*, and bare treatments did not increase in *Avicennia* live cover nor did they differ in cover amounts (Fig. 4A; Tables 1 & S2). Natural recruitment of *Avicennia* was only observed once in one bare treatment plot.

Spartina live cover increased in all treatments and increased faster in plots planted with only *Spartina* compared to bare treatments ($p < 0.005$; Fig. 4B, Tables 1 & S2). After 1 year, the mean rate of *Spartina* lateral expansion was 0.94 ± 0.05 m/year regardless of treatment. The number of progenitor clumps (N), however, did differ after 1 year ($p < 0.002$; Table 1) with a greater number of progenitor clumps present in the *Spartina* treatment (5.2 ± 0.5 N/plot), compared to the bare (1.8 ± 0.4 N/plot; $p < 0.005$) and *Avicennia* treatments (2.0 ± 0.6 N/plot; $p < 0.005$). The *Spartina/Avicennia* treatment had an intermediate number of progenitor clumps (3.4 ± 0.8 N/plot) that did not differ from any of the other treatments.

Soil bulk density in this experimental area displayed a quadratic relationship over time with a peak bulk density at approximately 5 months after planting (Tables 1 & S2), but did not differ between treatment (Tables 1 & S2). SOM did not differ by time or treatment and ranged between 4 and 7% SOM (Tables 1 & S2). In this secondary experimental area, elevation did not change significantly from its original elevation of 0.32 m (± 0.01) (NAVD88-Geoid12A) and was flooded an average of 15% of the time (Table 1).

Discussion

The direct comparison of foundation species survival, growth, expansion, and recruitment along elevation gradients is needed to advance our understanding of ecosystem development during the critical early stages after physical restoration of coastal

wetlands. Our study highlights key differences between these salt marsh and mangrove foundation species and can thus inform scientists and restoration practitioners of how selection of appropriate foundation species can lead to rapid structural and functional attributes needed to jump-start long-term ecosystem restoration goals and natural ecosystem function.

Elevation Gradient — Experimental Area I

Our study's comparison of these two foundation species along an elevation gradient highlights where the species overlap and do not overlap in the landscape, while providing metrics of growth and survival success in the critical period after physical restoration. Furthermore, our findings show limited competition and interaction dynamics between the two species in the first 18 months after restoration. After 18 months *Spartina* cover increased to approximately 95% and biomass averaged >900 g/m² at the lowest elevation, whereas a progressively muted response was seen with increasing elevation. Eighteen months after planting, we observed similar aboveground biomass at the lowest elevation as reported in other natural *Spartina* dominated marshes, but the values in this study were on the lower end of values previously observed in Louisiana (reviewed by Stagg et al. 2017). Medium and high elevations, however, had lower biomass compared to reference locations. *Spartina* growth at medium and high elevation sites was lower, but continued to increase over time, likely due to asexual reproduction (clonal growth) and subsequent resource sharing that can occur between ramets in stressful conditions (Pennings & Callaway 2000). *Avicennia*'s lack of response to the elevation gradient is likely due to its slower growth rates (Alleman & Hester 2011*b*), lack of asexual expansion (Baldwin et al. 2001), stressful abiotic conditions in the first 9–12 months, and possible competition, via growth inhibition, by surrounding *Spartina* (Patterson et al. 1993; McKee & Rooth 2008; Pickens 2012). *Avicennia* was able to grow at all elevations with varying survival, but differences between individuals only manifested themselves in SLA. At the lowest elevation, SLA was significantly greater, indicating a lack of water stress (Knight & Ackerly 2003), but also may be indicative of competitive shading from the surrounding *Spartina* canopy (Liu et al. 2016). Tree height and biomass increased over time and did not differ by elevation but did show some differences in growth morphology by 18 months. Low elevation individuals maintained tall, narrow growth forms, while medium and high elevation trees were shorter and stouter (Yando, pers. obs.). This is likely a function of light availability and possible competition, with trees forced to grow vertically when surrounded by the more dominant *Spartina* at low elevations (Iwasa et al. 1985), a trend that we expect to become more pronounced over time. Despite an area of overlap at low and medium elevations and likely changes to interactions over time, our study clearly shows that as a foundation species, *Spartina* provides significantly faster structural development compared to *Avicennia* after 18 months. Furthermore, regardless of elevation or cover metrics, SOM did not differ overtime, which is not surprising given that other studies have shown that soil development can take decades (Craft et al.

2002; Edwards & Proffitt 2003; Osland et al. 2012; Walcker et al. 2018). The initial 18-month period, however, is critical to prevent erosion, maintain desired elevations and hydrology, establish a plant community, and begin to ameliorate abiotic parameters that other species require before they are capable of colonizing a given location.

Expansion and Recruitment — Experimental Area II

Expansion and recruitment are critical to the structural provisioning that foundation species provide in all restoration sites and are key to integration within the greater landscape complex, as foundation species are central players in the broader system (Ellison 2019). Species interactions are also important to consider as species disperse, expand, and establish, and as suitable spaces in the environment are filled. Our findings show that in 18 months, *Avicennia* expanded relatively little and had very few new recruits, while *Spartina* had rapid expansion as well as some recruitment. *Avicennia*'s slow expansion and lack of natural recruitment rate in this site may be attributed to slower growth capacity (Alleman & Hester 2011*b*), difficulty competing with surrounding marsh at early life stages (Patterson et al. 1993; McKee & Rooth 2008; Pickens 2012; Howard et al. 2015), a lack of asexual reproduction (Baldwin et al. 2001), and only one reproductive period prior to the end of the experiment. Mangrove propagules during this single reproductive period were often found desiccated or rotten as much of the site remained bare after the first 6–8 months (Yando, pers. obs.), despite having adult trees that were producing propagules in close proximity to this restoration area. Additionally, we observed that planted individuals reach reproductive maturity at the 18-month sampling period, a common occurrence for 3- to 4-year-old *Avicennia* individuals in the northern Gulf of Mexico (Yando, per. obs.; also see Dangremond & Feller 2016). *Spartina*, on the other hand, displayed expansion rates of approximately 1 m per year for progenitor clumps, similar to other documented expansion rates in the literature (Hartman 1988; Proffitt et al. 2003). This rapid expansion can be largely attributed to asexual reproduction, as *Spartina* does not have a persistent inter-annual seedbank (Xiao et al. 2009). Seedlings from the previous year made up only a small number of overall stems (Yando, pers. obs.), and most areas had clearly expanded asexually from existing progenitor clumps. *Spartina* regularly tillers via ramets from its rhizomatous base, quickly filling in gaps once established in an area (Jones et al. 2016). Other studies have highlighted the importance of clonal growth in expanding into highly stressful conditions, particularly in saline and hypersaline environments (Pennings & Callaway 2000). Moreover, in terms of natural recruitment, we observed large numbers of broken fragments of *Spartina* stems and rhizomes strewn throughout the site at the 12-month and 18-month sampling periods. We attribute this high number of vegetative fragments to feral hogs (*Sus scrofa*), which were regularly present at the site and were observed via camera traps rooting into soil at the base of *Spartina* patches and pulling up plants with their rhizomes intact (Yando, pers. obs.). This behavior resulted in vegetative fragments gaining the opportunity to

disperse to favorable areas for establishment and forming new progenitor clumps (Yando, pers. obs.), a phenomenon that would not occur without significant, reoccurring, systematic disturbances. Conservatively, we estimate that progenitor clumps resulting from hog activity accounted for approximately two progenitor clumps per 16-m^2 plot based on those plots that did not have any *Spartina* planted in them and personal observations of the surrounding unplanted areas. Additionally, we believe this hog activity may also lead to increased asexual expansion rates through the exposure of tillers and the breaking up of dense soils (Sloey & Hester 2015), which can be an issue in recently restored wetland environments. Long-term marsh sustainability and soil development, however, are likely to be negatively influenced by a continuous disturbance of this kind (Persico et al. 2017). Finally, as noted for Experimental Area I, SOM in Experimental Area II did not change during this short time, and elevations and subsequent flooding periods were maintained.

Implications for Restoration Practice

Ultimately, a critical question at the latitudinal salt marsh-mangrove ecotone is which foundation species is better to plant in recently restored coastal wetland locations to maximize rapid structural provisioning after physical restoration? Our findings clearly demonstrate that the salt marsh grass foundation species, *Spartina*, is far more suited for rapid structural provisioning after physical restoration due to its growth, survival, expansion, and recruitment strategy, and its overall performance compared to the mangrove tree foundation species, *Avicennia*. If planting mangrove tree foundation seedlings at a restoration site is desired, our findings demonstrate that *Avicennia* would need to be planted at prohibitively high densities in order to produce similar structural attributes attained by *Spartina* at low and intermediate elevations, one of the key metrics of foundation species. These findings agree with studies from Florida that highlight the role of *Spartina* in mangrove restoration projects, where the rapid expansion of this species has been used to prevent erosion and capture sediment in recently restored sites (Lewis & Dunstan 1975; Lewis 1982). Additionally, other studies have highlighted the preferences of some commercially important species (e.g. blue crabs) to *Spartina* dominated areas when compared to *Avicennia* (Johnston & Caretti 2017) and shifts in community composition of fauna with *Avicennia* expansion and recruitment (Scheffel et al. 2018), but more research is needed to examine habitat preference and differences in nursery habitat productivity between these two foundation species.

At high elevations, *Avicennia* may be suitable to plant as *Spartina* does not survive well, if at all, at these higher elevations. The partial overlap in the tidal frame has been previously documented between these two species (Patterson & Mendelssohn 1991; Alleman & Hester 2011a), but is often ignored by restoration practitioners (although see Lewis & Dunstan 1975). The highest elevations in the present study are only suitable for *Avicennia*, but are also at the upper elevation range for naturally established, mature *Avicennia* adults in Louisiana as reported by Alleman and Hester (2011b). *Spartina*

clonal growth may eventually expand into these high elevation areas (Crewz & Lewis 1991; Pennings & Callaway 2000) or succulent dominated communities may naturally establish via seed. Alternatively, project engineers could design sites with lower maximum soil elevations (<0.35 m NAVD-Geoid12A), as has successfully been completed in newer adjacent portions of this same restoration site (e.g. Experimental Area II). Eventually most of this site is likely to be covered by *Avicennia* regardless of the initial planting scheme (Lewis & Dunstan 1975; Osland et al. 2012), as nearby mangrove source populations are readily found, copious numbers of mangrove propagules have been observed at the site after the 18-month sampling period (Yando, pers. obs.), and mangroves are increasing in coverage in the overall area (Osland et al. 2017). *Avicennia* and *Spartina* do not have a complete overlap as previously discussed, and even in future scenarios with mangrove expansion due to warmer winter temperatures, *Spartina* is still likely to exist at low elevations (Patterson & Mendelssohn 1991; Alleman & Hester 2011a). While it has been argued that habitat complexity/mosaics may be more desirable for overall resiliency and diverse function of landscapes (Bell et al. 1997; Corbin & Holl 2012), this area is within the salt marsh-mangrove ecotone and large patches of both salt marsh and mangrove can be found nearby. *Avicennia*'s susceptibility to freeze impacts may also make areas planted with mangrove vulnerable to diebacks if and when future freeze events of sufficient intensity occur, as has been observed in southeastern Louisiana (Stevens et al. 2006; Osland et al. 2017; Yando, pers. obs., 2018). Other disturbances may have additional, and possibly non-symmetrical, impacts on mangrove and salt marsh foundation species depending on their severity and frequency (e.g. wrack deposition, storm events, herbivory, fire) (Nyman & Chabreck 1995; Guo et al. 2017; Castorani et al. 2018; Smith et al. 2018). By planting *Spartina*, rapid vegetative restoration can be attained, limiting the risk of die-off from freeze events, and providing the needed structure for long-term restoration of key ecosystem functions such as basal carbon food web support, habitat provisioning, soil stabilization, and nutrient cycling.

These findings have critical implications for understanding foundation species interactions within the context of restoration. By identifying and utilizing foundation species that are capable of quickly providing structure in a recently restored location, it may be possible to jump-start long-term restoration and ecosystem development. This study helps improve our understanding of the attributes and potential interactions of foundation species and provides solutions to meet both short-term and long-term restoration objectives.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Means (±SE) for soil, *Avicennia*, and *Spartina* metrics for Experimental Area I at low, medium, and high elevations at all sampling periods.

Table S2. Means (±SE) for soil, *Avicennia*, and *Spartina* metrics for Experimental Area II in all treatments at all sampling periods.