



Responses of two fringing salt marsh plant species along a wave climate gradient

Nigel A. Temple^{1,2,*}, Eric L. Sparks^{1,2,3}, Bret M. Webb⁴, Just Cebrian⁵,
Matthew F. Virden^{1,2}, Andrew E. Lucore^{1,2}, Haley B. Moss¹

¹Coastal Research and Extension Center, Mississippi State University, Biloxi, MS 39532, USA

²Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA

³Mississippi-Alabama Sea Grant Consortium, Ocean Springs, MS 39564, USA

⁴Department of Civil, Coastal, and Environmental Engineering, University of South Alabama, Mobile, AL 36688, USA

⁵Northern Gulf Institute, Stennis Space Center, MS 39529, USA

ABSTRACT: Salt marshes are increasingly valued for their role in coastal defense. In particular, marsh plants slow the progression of waves, thereby decreasing wave heights, orbital velocities and associated energy. Practical application of these effects has driven substantial research estimating the effects of plants on waves. However, the effects of waves on plants remain understudied, especially regarding plant responses along a wave climate gradient. To begin to understand these responses, we collected above- and belowground plant data and wave data from 60 sites across Mobile Bay, USA, and tributaries and evaluated plant responses along the range of assessed wave climate conditions. Plant responses among the dominant species, *Juncus roemerianus* and *Spartina alterniflora*, varied along the wave climate gradient. However, the basal diameter of shoots in both species declined linearly with increasing wave climate. While wave climate had no observable effect on other *S. alterniflora* parameters, the declining diameter of *J. roemerianus* shoots along the same gradient was commensurate with a decline in the percentage of live canopy shoots aboveground and an increase in root and rhizome biomass in the active rooting zone belowground. In contrast to previous studies, other responses including the height, biomass and density of aboveground shoots in both species were not related to wave climate. More broadly, these results demonstrate that plant features important for wave attenuation such as shoot diameter can change in response to varying wave conditions. These feedbacks should be incorporated to improve coastal modeling and successes of coastal conservation, restoration and enhancement projects.

KEY WORDS: Wave climate · Basal diameter · Salt marsh

1. INTRODUCTION

Coastal wetland plants face many challenges including natural stressors such as salinity (Howard & Mendelssohn 1999), erosion from waves and currents (Green & Coco 2014) and interspecific competition for suitable habitat (Pennings et al. 2005), and human-induced threats such as development (e.g. 'coastal squeeze', Constantin et al. 2019), sediment deprivation (Tweel & Turner 2012) and sea-level rise

(Osland et al. 2017). While the convergence of these threats can lead to marsh collapse in certain situations (Weston 2014), wetland plants, like other pioneering plant species, have exhibited exceptional adaptive capacity to modify above- and belowground growth behaviors in response to a dynamic environment. Examples of shifting plant responses in coastal environments include shoot tissue osmotic adjustment in response to increasing salinity (Vasquez et al. 2006), enhanced shoot production in

*Corresponding author: 757nigel@gmail.com

response to increasing sediment burial (Temple et al. 2019), adventitious rooting in response to increasing inundation (Nyman et al. 2006) and biological elevation maintenance (Kirwan & Megonigal 2013). These studies have identified plant mechanistic responses to common coastal stressors, such as salinity, inundation and competition, but plant growth responses to waves remain understudied even as waves have become an increasingly common feature in most aquatic environments as a result of boating activity (McConchie & Toleman 2003, Bilkovic et al. 2019).

From the plant perspective, the expression of different traits in response to waves is often described as a tradeoff between traits that allow them to avoid wave mechanical stress and those that enhance their ability to slow the progress of waves (i.e. avoidance and tolerance traits; Puijalon et al. 2011, Silinski et al. 2018, Cao et al. 2020). Avoidance traits are generally described as those that reduce plant exposure to stresses such as increased shoot flexibility (Heuner et al. 2015), reduced shoot height (i.e. in relation to water depth; Rupprecht et al. 2017) and having a streamlined canopy that reduces the area exposed to wave forces (Puijalon et al. 2005). Tolerance traits, on the other hand, are described as those that enhance the ability of plants to endure stresses such as increased shoot density (Peralta et al. 2008, Heuner et al. 2015), increased shoot biomass (Bouma et al. 2010, Heuner et al. 2015), increased shoot stiffness (Ozeren et al. 2014, Rupprecht et al. 2015) and increased rooting depth and production (Balke et al. 2011, Silinski et al. 2018, Cao et al. 2020). These traits may also balance tradeoffs between wave defenses and sediment accretion (Puijalon et al. 2011). For example, stiffer shoots generally result in greater reductions in flow velocity and wave energy (Mullarney & Henderson 2010) which, in turn, can increase sedimentation (Kirwan & Megonigal 2013). Alternatively, sedimentation is generally lower among plants characterized by more flexible stems (e.g. seagrasses), but flexible stems are more likely to adopt a protective 'shielding posture' (i.e. lying flat) during high energy wave events, thereby reducing stem breakage and bed erosion (Rupprecht et al. 2017). The development of these features and magnitude of their effects on several marsh processes can also vary seasonally (Silinski et al. 2018, Schoutens et al. 2019, Schulze et al. 2019, Zhu et al. 2020). As such, plant features that vary seasonally or change in response to various stressors, including waves, have the potential to impact marsh accretion and subsequent persistence.

In comparison to other stressors in tidal wetlands, the ways that plant responses vary in relation to dif-

ferent or changing wave climate conditions remain understudied. Waves occur along a range of both frequency (i.e. how often waves occur) and magnitude (i.e. wave climate; Roland & Douglass 2005), but knowledge of their effects on plant responses has often been limited to laboratory wave tank experiments that offer only limited insight to a set of short-term and specific conditions (Bouma et al. 2010, Mullarney & Henderson 2010, Balke et al. 2011, Silinski et al. 2015, Rupprecht et al. 2017). Field studies have focused on categorical wave exposure gradients (i.e. exposed or sheltered; Keddy 1985, Coops et al. 1994, Silinski et al. 2018) that may limit the elucidation of plant relationships to changing wave environments (Cottingham et al. 2005).

Increased knowledge of plant responses along a gradient of wave conditions is essential to improve the understanding of basic coastal processes and for the effective management of coastal wetlands and the wealth of natural benefits they provide (e.g. Barbier et al. 2011, Sparks et al. 2015). Plant features such as shoot height, diameter and density (e.g. the number of shoots) are constituent parameters in a variety of coastal models (e.g. SLAMM; <https://coast.noaa.gov/digitalcoast/tools/slamm.html>), yet these features have rarely been examined along the range of wave conditions possible in the field. Recently, researchers have argued that including seasonal variation observed in these features would improve the quality of coastal models (Silinski et al. 2018, Schulze et al. 2019, Zhu et al. 2020). Likewise, coastal models could be greatly improved with the inclusion of plant feedbacks or threshold responses. Understanding of these responses could similarly improve the design and installation of coastal restoration and enhancement projects and help maximize the natural benefits they provide.

The main objective of this study was to characterize the effects of increasing wave heights, both in magnitude and frequency of occurrence (i.e. frequency of waves of certain heights), on plant growth and morphological responses in a large-scale field study. Previous efforts to measure waves have been limited due, in part, to the high cost of commercial wave gauges. However, recent technological advances now permit the construction of high-quality wave gauges at a fraction of the cost of commercial gauges (Temple et al. 2020). In this study, these gauges were used to collect wave data from 60 sites within Mobile Bay and surrounding tributaries in Alabama, USA. The data were processed to reflect the magnitude and frequency of occurrence of wave heights experienced at sites (e.g. Roland & Douglass 2005; hereafter, 'wave climate'). We hypothesized that fringing marsh plants

would respond to increasing wave climate by increasing shoot density, biomass per shoot and basal stem diameter aboveground and by increasing the rooting depth belowground. To test these hypotheses, we measured above- and belowground plant responses during the summer months of 2018 (i.e. May to September, when plant productivity in Gulf of Mexico marshes is greatest; Stout 1984) along the measured wave climate gradient.

2. MATERIALS AND METHODS

A comparative regression-based framework was used to explore the potential relationships between site wave climate and plant responses (Cottingham et al. 2005, Temple et al. 2019). Within this framework, sites were selected using proxies to cover a large gradient in wave conditions (e.g. wave height and frequency of occurrence). Wave and plant response data were then collected from each site for comparison using regression models.

2.1. Study site description

Sixty sites including 20 within Mobile Bay (West Mobile Bay and Bon Secour Bay; WMB and BSB, respectively) and 10 each within Bon Secour (BSR), Fish (FiR), Fowl (FoR) and Magnolia (MaR) Rivers in Baldwin and Mobile Counties, Alabama, USA (Fig. 1) were examined. As with other estuarine environments, salinity within bay and river sites varies, creating a gradient of plant species distribution. Salinity is greatest in the waters along the southwestern edge of Mobile Bay (i.e. on average 18 PSU; <https://arcos.disl.org/>), but salinity at all sites within the bay and river sites is generally brackish (0.5–18 PSU) and varies as a function of meteorological events (e.g. rainfall, storms), distance from the Gulf of Mexico (GoM) and, in the case of river sites, distance upstream from the river mouth. Plant communities at the study sites reflect this salinity gradient, as the greatest abundance of salt-tolerant species such as *Juncus roemerianus* and *Spartina alterniflora*

is located in bay sites and at those sites nearest river mouths, while a mix of other species such as *Cladium jamaicense*, *Phragmites australis* and *Typha latifolia* are present or dominant elsewhere where salinity approaches more freshwater conditions. The entire study area experiences a small diurnal tidal cycle (max tidal range ~0.60 m). Maximum channel depth at river sites and average depth across the bay are similar at ~3 m (Noble et al. 1996).

The general location of each study site was selected using a combination of Google Earth, boating activity and wind data (Text S1, Fig. S1.1 in the Supplement at www.int-res.com/articles/suppl/m675_p053_supp.pdf) to establish a wave climate gradient. Once on site, specific plot locations were then refined based on the following selection criterion: including a near monotypic stand of vegetation with patch size measuring at least 3 m² (3 m × 1 m plot size). When no vegetation was found within 100 m in either direction of the relative site location, the Google Earth-generated GPS coordinates were used as a default final site location.

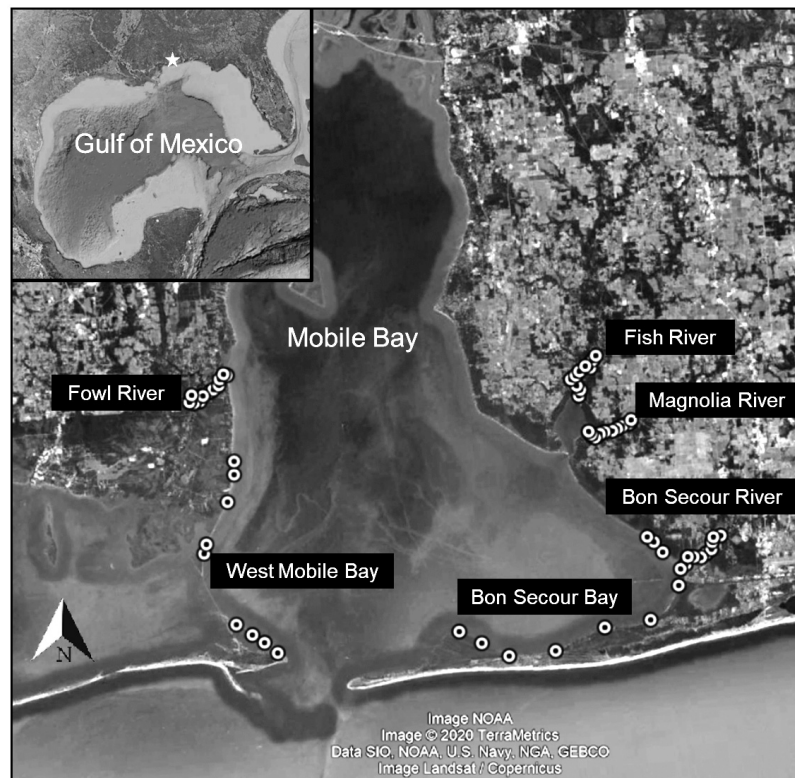


Fig. 1. Study sites (dotted circles) within the different waterbodies in and surrounding Mobile Bay, Alabama, USA (Mobile Bay: 30.4434° N, 87.9923° W). Mobile Bay is a large estuary located within the northern Gulf of Mexico (white star in inset). Ten sites were established within each of the waterbodies examined: West Mobile Bay, Bon Secour Bay, Bon Secour River, Fish River, Fowl River and Magnolia River. Both images accessed via Google Earth Pro

2.2. Wave data collection and processing

A total of 30 pressure sensor-based wave gauges were constructed and deployed in the field during summer 2018 (May to September) following the methods described by Temple et al. (2020). As the number of gauges that could be deployed simultaneously was limited, the specific timing of gauge deployments was selected to maximize potential wave events and comparability between sites, and to reduce potential logistical issues (e.g. excessive boat travel to different sites). Therefore, gauges were deployed according to geographic closeness and to coincide with major US holidays in which boating activity is generally high (e.g. Memorial Day, Fourth of July and Labor Day weekends, Table 1), since waves at several sites are primarily boat-wake driven. In addition, gauges at all sites were deployed for a total of 20 d in 4 consecutive 5 d long deployments within a roughly 1 mo period. This deployment schedule helped to minimize any variability associated with meteorological events that could skew wave data at the different sites (e.g. rain-limited boating activity at river sites). All gauges were programmed to sample continuously at 10 times s^{-1} (10 Hz) which is sufficient to measure the short period waves characteristic of the wind- and boat wake-waves in the study area (Temple et al. 2020). During the study period, some gauges were lost due to debris impact or theft. In such cases, an additional gauge was built and deployed to ensure equal deployment length at each site. Raw pressure data were prepared for statistical wave analyses (discussed in Section 2.4) following the methods described by Temple et al. (2020).

Wave frequency of occurrence and magnitude are particularly important for describing biological responses to disturbance events (e.g. Connell 1978, Roland & Douglass 2005). Therefore, wave statistics including significant wave height (H_s) and period (T_s), and average wave height (H_{avg}) were derived from entire records and within 1 h increments in win-

dowing routines. Windowed wave statistics were then sorted in ascending order, and a frequency of occurrence was calculated by dividing the parameter position by the total number of windowed records (e.g. Roland & Douglass 2005). Windowed wave statistics were then compiled according to the frequency of occurrence into discrete percentile rankings along 25 percentage point increments (i.e. 25th, 50th, 75th and 100th percentile rankings: H_{25} , H_{50} , H_{75} , and H_{100} , respectively) for wave events of varying magnitude during individual deployments.

All wave statistic data (i.e. record-length and windowed wave statistics) at each site were averaged over the 4 deployment sampling periods (i.e. a total of 20 d). All wave data were processed in MATLAB (MATLAB R2017a, The MathWorks, Natick, MA).

2.3. Plant response variables

Following previous research, plant response data were collected at each of the study sites within the same summer period when wave data were collected (i.e. following the approximate end of wave data collection; Table 1). These data include above- and belowground responses that are relevant to plant persistence in the presence of waves (e.g. rooting depth, shoot biomass) and those often considered in models predicting wave movement through marshes (e.g. stem height and diameter; Knutson et al. 1982).

Three 1 m² quadrats were established beginning at the marsh boundary (e.g. pioneer zone) and spaced evenly along the site shoreline within each 3 m × 1 m site plot (i.e. three 1 m² boxes within each site plot). Within each quadrat, an open-ended 0.25 m² subplot marker constructed using PVC was placed haphazardly to delineate subplot boundaries. All aboveground biomass within the boundaries of the 0.25 m² subplot was then removed at the sediment surface using shears, placed in plastic bags and transported in a cooler to the Weeks Bay National Estuarine Research Reserve (WBNERR) for further processing. Cores (~5 cm diameter × 50 cm depth) were collected using a custom corer (Text S2, Fig. S2.1) from within each subplot to assess belowground plant responses. Cores were cut into 4 subsections starting from the top of the core (i.e. at the sediment surface) and every 10 cm along the core depth profile to 40 cm or, in the case of shallow refusal, the maximum depth. Core subsections were placed in plas-

Table 1. Gauge deployment schedule within waterbodies and corresponding US National holidays

Waterbody	Site abbreviation	Approx. start	Approx. end	Major US holiday
Fish River	FiR	24 May	25 June	Memorial Day
Magnolia River	MaR	24 May	25 June	Memorial Day
Bon Secour River	BSR	24 May	25 June	Memorial Day
Bon Secour Bay	BSB	28 June	30 July	Fourth of July
Fowl River	FoR	2 August	3 September	Labor Day
West Mobile Bay	WMB	2 August	3 September	Labor Day

tic bags and transferred in a cooler to WBNERR for further processing.

In this study, plant shoots describe all upright plant materials emanating from the sediment surface. As such, upright leaves of *J. roemerianus* and culms of *S. alterniflora* were counted and measured similarly. This context also forms the basis of functional significance with respect to plant–wave interactions useful for other plant features (e.g. live and dead parts). Shoots collected from each subplot were sorted by species into live (green) and dead (brown) parts. Each stem was measured for length (cm full length) and diameter (mm at 15 cm above the shoot base), dried at 50°C to constant mass and weighed to the nearest 0.1 g.

Core subsections were processed individually as follows. First, cores were rinsed of all sediments and debris using a 2000 micron sieve. All remaining materials were then put in a ~23 cm × 33 cm × 8 cm glass dish which was then filled with water. Roots were sorted by live and dead parts, and by fine roots (≤ 1 mm diameter) and coarse roots/rhizomes. Live roots were identified via elutriation (e.g. Temple et al. 2019) while dead roots were picked free of debris including other inorganic (e.g. glass) and non-root decaying organic materials (e.g. partially decayed invertebrates). Sorted roots were then placed in paper sandwich bags and transported to the Gulf Coast Research Laboratory (GCRL) for further processing. Following the methods described for plant shoots, roots were dried at 50°C to constant mass in a commercial drying oven and weighed to the nearest 0.1 g.

Root:shoot ratios were calculated as the quotient of total live root biomass (i.e. roots and rhizomes from all soil layers on a square meter basis) and above-ground biomass in plots.

2.4. Statistical analyses

Previous work on plant responses to wave events of varying frequency and magnitude is limited (but see Keddy 1982, Roland & Douglass 2005); therefore, both linear and non-linear models were considered to accommodate all potential response patterns. Plant responses were first evaluated graphically following Zuur et al. (2010). Initial exploration of the relationships between plant response variables and wave climate data indicated similarity between plant responses at and above 50th percentile significant wave heights; therefore, 50th percentile significant wave height (i.e. H_{50}) was used as the main wave predictor variable in all plant response models (see

Section 2.2). Average wave height (i.e. H_{avg}) and significant wave height and period (H_s and T_s) were also calculated from the entire record for site type comparisons. Akaike's information criterion (Burnham & Anderson 2002) for linear and non-linear plant response models was used to guide final model selection. Model fit was evaluated using model coefficients and residual plots of log-transformed data, where appropriate (i.e. wave height statistics), to meet model assumptions (Zuur et al. 2007). ANOVAs or non-parametric analogues (i.e. Kruskal-Wallis test of medians) were used to compare wave characteristics within and across study sites. R was used for all statistical analyses (R Core Team 2020).

3. RESULTS

3.1. Wave climate

Wave period data reflected the predominant drivers of wave action at the different sites (i.e. wind and boat wake at bay and river sites, respectively; Webb et al. 2018). Significant wave period (T_s) was, overall, greater in bay sites (Table 2) as compared to river sites (2.67 and 1.63 s median T_s , respectively, Kruskal-Wallis $p < 0.001$). T_s at WMB sites (mean = 3.39 s, Table 3) declined linearly from ~ 4 to ~2.5 s with distance away from the mouth of Mobile Bay ($R^2 = 0.82$, $p < 0.001$). However, T_s within other regions of Mobile Bay (i.e. within BSB sites) averaged 2.5 s, which, while still greater than average T_s at river sites, was well within the range of wave period conditions observed in those areas (Table 3). In addition, within-waterbody T_s variance was minimal in BSB and across each of the river sites (≤ 0.07 s) during the study period as compared to WMB (within site variance = 0.33 s).

Each of the wave height statistics measured, including both record-length (i.e. H_{avg}) and windowed statistics (e.g. H_{50}), showed similar overall trends of varying wave heights at study sites and confirmed the establishment of the wave climate gradient. Record-length average wave height (H_{avg}) conditions were greatest at bay sites as compared to river sites ($p < 0.001$, Table 2). However, differences between individual waterbodies did not necessarily fall in line with differences in waterbody types. For example, mean H_{avg} conditions were nearly identical between FoR and WMB sites, which both averaged 13 cm, and were greater than all other bay and river sites examined ($p < 0.001$; Table 3). Twenty-fifth percentile windowed wave heights (H_{25}) averaged less

Table 2. Record-length bay and river site wave statistics including mean \pm SE, minimum and maximum values. In general, mean values for significant wave period (the average of the top third of all record wave periods, T_s), significant wave height (the average of the top third of all record wave heights, H_s) and average wave height (H_{avg}) were greater in bay sites than in river sites

Waterbody type	Wave statistic	Unit	Mean	Min	Max
Bay	Significant wave period (T_s)	s	2.94 \pm 0.13	2.23	4.2
	Significant wave height (H_s)	m	0.18 \pm 0.02	0.1	0.35
	Average wave height (H_{avg})	m	0.1 \pm 0.01	0.05	0.2
River	Significant wave period (T_s)	s	1.68 \pm 0.5	1.35	3.14
	Significant wave height (H_s)	m	0.13 \pm 0.02	0.03	0.44
	Average wave height (H_{avg})	m	0.06 \pm 0.01	0.02	0.25

than 1 ± 0.14 cm (SE) differences and were statistically similar to mean site H_{avg} conditions (t -test $p = 0.9$; Table 3). All other windowed wave height statistics (i.e. H_{50} , H_{75} and H_{100}) revealed similar trends across study sites but at wave heights of varying magnitude (Table 3). Thus, across all sites, the wave climate gradient was established for both common and rare events. While there were exceptions, bay sites along the northern reaches of the bay (i.e. facing southward) were generally characterized by greater H_{50} wave heights, although these differences were not significant ($p > 0.05$). River site H_{50} data were highly variable and reflected various underlying factors that may control the magnitude and frequency of occurrence for wave events such as the proximity of a site to major boating channels or no-wake zones, the speed of boats passing, the range of boat hull types (Glamore 2008) and the existence

of permanent or temporary obstructive structures (e.g. pier or boathouse pilings and floating tree logs, respectively) that can act to attenuate waves. Predicting the causes and covarying factors driving these wave events was not a focus of this study. However, H_{50} and H_{avg} were predicted to increase from up-river to down-river sites. We found no evidence of this relationship in any of the rivers examined in this study. On the contrary, H_{50} wave heights increased

log-linearly with increasing distance up-river in MaR ($R^2 = 0.59$, $p = 0.01$). However, this trend was not observed elsewhere.

3.2. Plant responses

3.2.1. Diversity across study sites

In total, 10 plant species were found at 51 of 60 sites, including 3 *Spartina* spp. (*S. alterniflora*, *S. cynosuroides* and *S. patens*), *Juncus roemerianus*, *Phragmites australis*, *Cladium jamaicense*, *Alternanthera philoxeroides*, *Sagittaria lancifolia*, *Typha latifolia* and *Panicum repens*. No vegetation was observed at the other 9 sites. In all, the majority (80%) of sites featuring plants were represented by 3 species: *S. alterniflora* (38%), *J. roemerianus* (25%) and

Table 3. Mean \pm SE record wave statistics, windowed wave statistics and environmental characteristics of data collected at each of the study waterbodies (site abbreviations as in Table 1). Record-length wave statistics include significant wave period (the average of the top third of all record wave periods, T_s), significant wave height (the average of the top third of all record wave heights, H_s) and average wave height (H_{avg}). Windowed wave statistics represent significant wave height statistics calculated within 1 h windows through the individual records. The percentile significant wave heights indicate how often wave heights of varying magnitude occur; 25th percentile significant wave height (H_{25}) represents more common events, while 100th percentile significant wave height (H_{100}) represents rarer events. Environmental characteristics include soil bulk density, marsh platform elevation and slope

Sample	Site						
	Unit	WMB	BSB	FoR	FiR	MaR	BSR
Record wave statistics							
Significant wave period (T_s)	s	3.39 \pm 0.17	2.49 \pm 0.04	1.71 \pm 0.16	1.70 \pm 0.03	1.58 \pm 0.03	1.76 \pm 0.09
Significant wave height (H_s)	m	0.22 \pm 0.02	0.14 \pm 0.02	0.24 \pm 0.04	0.06 \pm 0.01	0.13 \pm 0.02	0.08 \pm 0.02
Average wave height (H_{avg})	m	0.13 \pm 0.01	0.08 \pm 0.01	0.13 \pm 0.02	0.03 \pm 0.01	0.06 \pm 0.01	0.04 \pm 0.003
Windowed wave statistic percentiles							
25 th (H_{25})	m	0.15 \pm 0.01	0.08 \pm 0.01	0.12 \pm 0.02	0.03 \pm 0.01	0.05 \pm 0.01	0.03 \pm 0.002
50 th /median (H_{50})	m	0.19 \pm 0.01	0.11 \pm 0.01	0.18 \pm 0.01	0.04 \pm 0.01	0.08 \pm 0.01	0.05 \pm 0.004
75 th (H_{75})	m	0.25 \pm 0.02	0.15 \pm 0.02	0.27 \pm 0.04	0.07 \pm 0.01	0.15 \pm 0.02	0.09 \pm 0.01
100 th (H_{100})	m	0.43 \pm 0.04	0.31 \pm 0.05	0.45 \pm 0.05	0.14 \pm 0.03	0.29 \pm 0.05	0.20 \pm 0.02

Table 4. Regression models relating plant response variables (y) to log-transformed 50th percentile (H_{50}) wave height (x) for both *Juncus roemerianus* and *Spartina alterniflora*. Variables include above- and belowground data collected from each of the study sites in which each of the study species were found. Model fit (R^2) and significance (at $\alpha = 0.05$) is provided for significant relationships between H_{50} wave heights and plant response data; ns: not significant

	<i>Juncus roemerianus</i>			<i>Spartina alterniflora</i>		
	Function	R^2	p	Function	R^2	p
Shoot basal diameter	$y = -1.7x + 7.48$	0.51	<0.01	$y = -1.08x + 8.81$	0.34	<0.01
Shoot height/length	$y = 5.17x + 61.86$	ns	ns	$y = -14.55x + 96.94$	ns	ns
Shoot density	$y = 170.7x + 945$	ns	ns	$y = 66.84x + 61.71$	ns	ns
Plot shoot biomass	$y = 133.9x + 487.1$	ns	ns	$y = 50.3x + 196.58$	ns	ns
Biomass per shoot	$y = 0.13x + 0.39$	ns	ns	$y = -0.46x + 2.97$	ns	ns
Percent live shoots	$y = -6.25x + 97.49$	0.34	0.3	$y = 1.73x + 91.37$	ns	ns
Root biomass	$y = 19.15x - 13.35$	0.26	<0.1	$y = -1.02x + 18.77$	ns	ns
Root:shoot ratio	$y = -0.01x + 0.1$	ns	ns	$y = -0.01x + 0.16$	ns	ns

C. jamaicense (17%); all other species were rare ($\leq 8\%$). While *C. jamaicense* was found at 10 sites, its distribution was limited to upstream FiR and MaR sites, which subsequently limited the exploration of *C. jamaicense* responses along the wave climate gradient. Conversely, both *S. alterniflora* (hereafter, '*Spartina*') and *J. roemerianus* (hereafter, '*Juncus*'), common estuarine marsh plants throughout the southeastern USA (Stout 1984), were found within at least 4 of the waterbodies examined in the study and together accounted for over half (63%) of the plants found at study sites where vegetation was present. Therefore, comparisons of plant responses along the wave climate gradient focused on these 2 species.

3.2.2. Aboveground shoot responses

The diameter of shoots for both species declined in response to increasing wave climate. The basal shoot diameter response was strongest amongst *Juncus* shoots, which declined by nearly 70% (from ~6 to ~2 mm) with increasing H_{50} wave height ($R^2 = 0.51$, $p = 0.004$; Table 4, Fig. 2A), but was also significant for *Spartina* shoots, which declined by nearly 40% from ~8 to ~5 mm ($R^2 = 0.34$, $p = 0.004$; Table 4, Fig. 2B). Declining shoot diameter was not related to changes in shoot density, biomass or height, which remained constant or declined for both species, albeit not significantly, along the wave climate gradient ($p > 0.05$; Table 4).

The percent live and dead shoots in plot canopies was assessed for both species at harvest. There was no observable effect of increasing wave climate on the percentage of live *Spartina* shoots in plot canopies ($p > 0.05$, Table 4). However, the percentage of

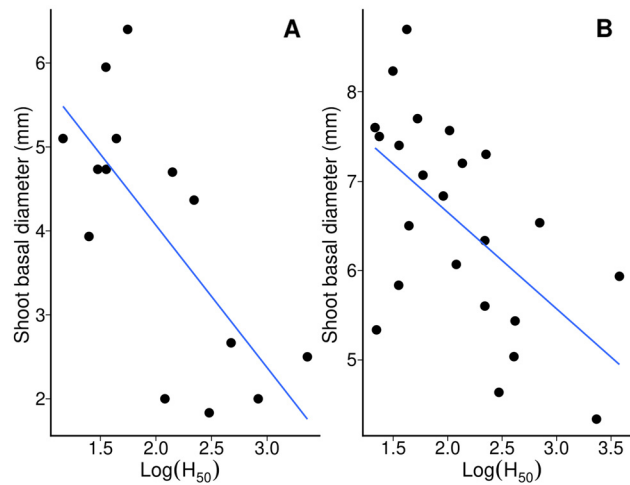


Fig. 2. Regression models relating shoot basal diameter to log-transformed 50th percentile (H_{50}) wave height (m) for both (A) *Juncus roemerianus* ($y = -1.7x + 7.48$) and (B) *Spartina alterniflora* ($y = -1.08x + 8.81$). Basal diameter declined in response to increasing H_{50} wave heights in shoots of both species

live *Juncus* shoots in plot canopies declined linearly by 15% ($R^2 = 0.34$, $p = 0.03$; Table 4, Fig. 3).

None of the other aboveground shoot responses were related to changes in the observed wave climate (Tables 4 & 5).

3.2.3. Belowground root responses

Several belowground responses were measured from cores taken from field plots, including root production within 10 cm increments into the active rooting zone (i.e. ≥ 30 cm; McKee & Cherry 2009), total live and dead roots and rhizomes, and root to shoot ratios comparing potential patterns in above- and

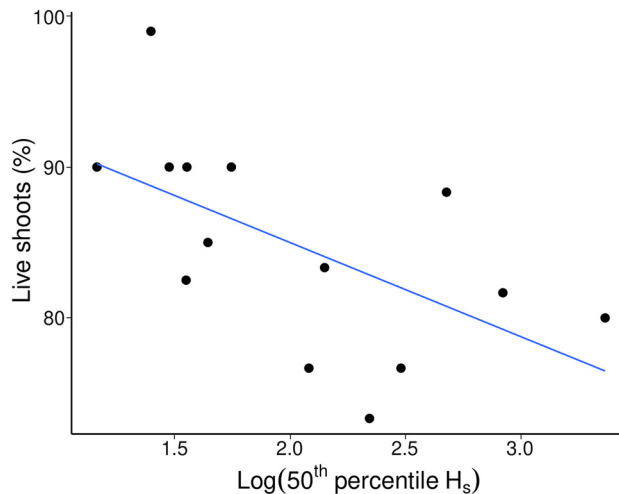


Fig. 3. Regression model relating the percentage of live shoots to log-transformed 50th percentile (H_{50}) wave height (m) in *Juncus roemerianus* marsh canopies ($y = -6.25x + 97.49$). The percentage of live shoots declined in response to increasing H_{50} wave heights

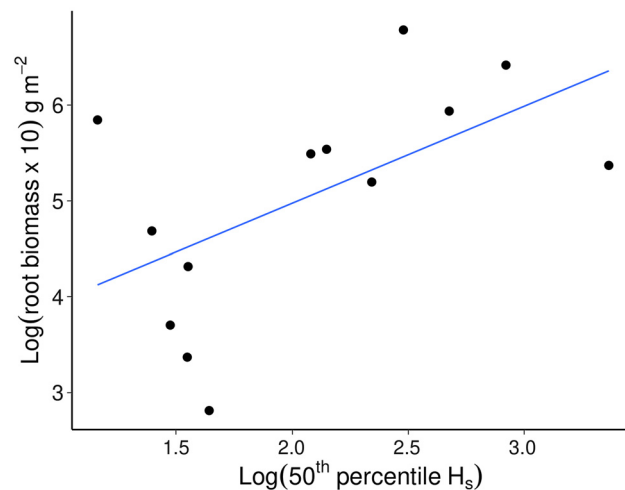


Fig. 4. Regression model relating log-transformed total live root biomass to log-transformed H_{50} wave heights (m) in fringing *Juncus roemerianus* marshes. Total live root biomass of *J. roemerianus* increased in response to increasing H_{50} wave height ($y = 19.15x - 13.35$)

Table 5. Mean and range of aboveground *Juncus* and *Spartina* responses that were not related to wave climate, including shoot density (number m^{-2}), height (m total length) and biomass ($g m^{-2}$)

Species	Response	Average	—Range—	
			Min	Max
<i>Juncus</i>	Density (number m^{-2})	1293	252	2880
	Height (m total length)	0.72	0.50	1.04
	Biomass ($g m^{-2}$)	760	130	1900
<i>Spartina</i>	Density (number m^{-2})	202	52	532
	Height (m total length)	0.66	0.23	1.09
	Biomass ($g m^{-2}$)	302	95	706

belowground resource allocation. However, no patterns were observed for either *Juncus* or *Spartina* roots with respect to various rooting depths, and therefore all live root biomass (i.e. roots and rhizomes) within the first 3 depth increments (i.e. ≤ 30 cm) were integrated to reflect the total root biomass in the active rooting zone (hereafter, 'total live roots'). Regarding resource allocation, analysis of root to shoot ratios for both species revealed belowground production estimates that were substantially less than those observed aboveground. Across all sites, total live roots by *Juncus* and *Spartina* averaged only 8 and 13% of total biomass production, respectively, which is well below other local total production estimates (e.g. 75%; Darby & Turner 2008). Further, root to shoot responses were not related to changes in H_{50} wave heights for either spe-

cies ($p > 0.05$, Table 4). While not observed for *Spartina* belowground responses, *Juncus* total live roots did tend to increase with increasing H_{50} ($r = 0.51$), but these relationships were not statistically significant ($p > 0.05$; Table 4, Fig. 4).

4. DISCUSSION

Coastal marshes are increasingly valued for the many ecosystem services they provide (e.g. Barbier et al. 2011) and increasingly, for their role in coastal defense. This interest has led to numerous studies on the effects of plant features on wave mitigation (e.g. Knutson et al. 1982, Augustin et al. 2009, Möller et al. 2014, Rupprecht et al. 2017). Here, for the first time, above- and belowground fringing marsh plant responses were assessed along a wave climate gradient across a large estuary. We hypothesized that fringing salt marsh plants would respond to increasing wave climate by increasing shoot density, shoot biomass per shoot, basal stem diameter aboveground and rooting depth belowground. Together, these hypotheses would represent a generalized plant response to waves, as suggested by growth strategy theory and the findings of field and laboratory studies conducted previously (e.g. Bouma et al. 2010, Puijalon et al. 2011, Silinski et al. 2018, Cao et al. 2020). However, we found limited evidence to support this generalized response. Instead, we mostly found both general and species-specific plant responses that varied as a function of waves (Table 4) and other

environmental characteristics (i.e. marsh platform elevation and soil bulk density; Text S3, Table S3.2).

Plant responses to wave stress is often described as following either tolerance or avoidance growth strategies. These contrasting strategies could be used to compare the species in this study, since, among other contrasting morphological features, *Juncus* is generally more flexible and has thinner shoots than *Spartina*. Interestingly, however, shoot thickness in both species declined along the wave climate gradient (Fig. 2). This suggests that both species adopt an avoidance strategy in response to larger and more frequent waves. These findings are aligned with those of Schulze et al. (2019), who observed thinner shoots in *S. anglica* in the fringing marsh zone where wave exposure is greatest as compared to interior marsh zones. However, Silinski et al. (2018) found the opposite trend among *Scirpus maritimus* shoots, along a similar wave exposure gradient. Similarly, Carus et al. (2017) observed the thickest shoots of *S. maritimus* (syn. *Bolboschoenus maritimus*) in the fringing marsh zone where current flow velocity was greatest. The similarity in *S. maritimus* responses to coastal stressors, combined with the similarity in *Spartina* spp. shoot diameter responses in previous studies and the differences among responses to waves between *Spartina* and *Juncus* in this study, are further evidence in a growing body of literature illustrating that plant responses to waves are often species-specific (e.g. Rupprecht et al. 2017, Schulze et al. 2019, Zhu et al. 2020).

Other factors may also influence shoot thickness in addition to waves. For example, many plant properties, including shoot thickness, vary seasonally. In this study, plant data were collected in the summer months between June and August. This sampling scheme was mostly a function of logistical constraints but was also designed to control for seasonal influence in plant responses. However, some recent studies have demonstrated seasonal variation in shoot thickness (and several biomechanical properties describing the flexibility of shoots) even in relatively condensed temporal scales (i.e. summer months), but these results are mixed, are often species-specific and are derived using varying sampling schemes that make direct comparisons difficult (Silinski et al. 2018, Schulze et al. 2019, Zhu et al. 2020). For example, Silinski et al. (2018) did observe peak thickness in *S. maritimus* shoots collected at the marsh edge or 'pioneer zone' during July as compared to other sampling months at a protected site, but they also observed virtually no change in the shoot thickness in the same zone at a site exposed to waves during

summer months (i.e. June to September). Schulze et al. (2019) observed a similar trend in *S. anglica* and *Elymus athericus* shoots collected in seaward zones, but their sampling scheme focused on spring and summer comparisons only. However, these results were mostly in line with those of Silinski et al. (2018) at both protected and exposed sites where shoot thickness was smaller in spring as compared to summer. Zhu et al. (2020) found few differences in several plant properties, including the thickness, flexibility (i.e. flexural stiffness and Young's modulus) and strength (i.e. breaking force and flexural strength) of shoots of various plant species, including *S. maritimus* and *S. anglica*, during summer months (i.e. July and September). Combined, these results suggest that seasonal variation was not a significant influence on the results observed in the present study since plant data were only collected at sites exposed to waves and within a relatively tight timeframe in the summer. However, more research is needed to fully assess how *Juncus* and *Spartina* shoot morphology varies across and within seasons.

Salinity also has a strong influence on plant growth and morphological features. For example, salinity is a main driver of ecophenic variation in *Spartina* growth forms (i.e. short and tall; Nestler 1977, Zheng et al. 2018) and influences several biomass features in *Juncus* plants (Eleuterius 1984, Touchette 2006). Salinity was not measured in this study but was accounted for in the study design since the sites were distributed widely and because all sites were located in the fringing zone where tidal flushing is greatest and hence the influence of salinity on plant growth is lowest (i.e. as compared to upland marsh areas; Nestler 1977, Touchette 2006). Still, Zhu et al. (2020) observed a salinity-driven shift in some parameters, including shoot flexibility and strength, that are often related to shoot thickness. Of the species in our study, only *Spartina* was observed in areas where salinity can exceed brackish conditions (i.e. Bon Secour and Mobile Bay sites). However, even at those sites (which account for about a third of sites where *Spartina* was found), the range of observed shoot diameters was representative of those from other sites, and thickness similarly declined with increasing exposure to waves. These findings infer that salinity was also not likely a significant factor driving the observed shoot thickness responses and, as observed in previous studies, provides further evidence of the potential influence of waves on this parameter (e.g. Schulze et al. 2019, Zhu et al. 2020).

A potential mechanism driving observed changes in shoot thickness and dovetailing with the lack of

significant biomass or shoot density (i.e. number of shoots) responses (Table 4) is that it is the result of an indirect positive feedback to increasing wave activity. For example, since wave turbulence increases oxygen saturation in the water column (i.e. air entrainment; Chanson et al. 2006), it is conceivable that increasing wave activity could have a positive effect on soil conditions. If so, increasing wave exposure could lead to a reduction in aerenchyma development since these features are related to oxygen availability in soils (Maricle & Lee 2002). This mechanism could explain why shoot diameters in both species declined with increasing wave climate even while shoot biomass and density responses were similar along the same gradient. More research is needed to investigate this potential mechanism. However, regardless of the mechanism at work, shifting shoot diameters resulting from changing wave conditions may have effects on the wave attenuation capacity of marshes that are not yet accounted for in models, as previously noted by other researchers (Silinski et al. 2018, Schulze et al. 2019).

The only other observable response to waves in either of the study species was a change in the ratio of live and dead aboveground biomass (Fig. 3) and, while limited, in the total live root biomass found in the active rooting zone belowground associated with *Juncus* plants (Fig. 4). The increase in the ratio of live to dead biomass observed in *Juncus* shoots may reflect a decline in the overall vitality of this fringing community or, alternatively, an increase in marsh canopy complexity. If so, this response would reflect more of a tolerance strategy since increasing canopy complexity has been linked to increasing wave tolerance in plant communities (Blackmar et al. 2014, Vuik et al. 2018). Likewise, the increasing rooting activity along the wave climate gradient observed in total biomass of *Juncus* live roots has also been linked to increasing wave tolerance as it relates to the anchoring capacity necessary for successful establishment (e.g. depth or total belowground production; Balke et al. 2011, Cao et al. 2020) or in resistance to uprooting (Balke et al. 2011, Silinski et al. 2018). Neither response was observed in *Spartina* plants, which may reflect the species-specific nature of plant responses to waves reported here and by others (Bouma et al. 2010, Paul et al. 2012, Rupprecht et al. 2015, Vuik et al. 2018, Cao et al. 2020, Zhu et al. 2020). However, combined, the totality of *Juncus* responses demonstrates that plants can, and often do, employ multiple strategies for dealing with environmental stress. Indeed, *Juncus* responses reflected

both tolerance- and avoidance-based strategies for dealing with wave stress.

Other responses of *Juncus* and *Spartina*, such as shoot length, density and biomass, were more correlated with other environmental factors such as soil bulk density or elevation than with wave climate (Text S3). In some respects, these relationships were similar to patterns reported by others, but distinct in other respects. For example, several researchers have illustrated the impact of elevation and/or inundation, and soil bulk density on above- and belowground biomass in both of the study species (e.g. Mendelssohn & Seneca 1980, Snedden et al. 2015, Wang et al. 2016). No significant relationships were observed between the mean aboveground biomass of either species and waves or any other environmental factor (Table S3.1) as has been reported previously (e.g. Silinski et al. 2018). However, overall aboveground biomass estimates (Table 4), like those reported for belowground biomass, were low in comparison to estimates reported by others (Stout 1984, Morris & Haskin 1990, Darby & Turner 2008). We hypothesize that these responses reflect the fringing marsh locations from which samples were taken. While several researchers have examined many of the same plant features investigated in this study, few, even those studying fringing marsh responses, have sampled along the leading edge of the marsh. Among those who did, Silinski et al. (2018) found that aboveground biomass estimates of *S. maritimus* in the pioneer zone amounted to approximately 25% of those reported in the most interior zone. Schulze et al. (2019) reported that *S. anglica* biomass in seaward zones was approximately half of that in landward zones, but sampling in this seaward zone was not exclusive to the marsh–tidal flat boundary (i.e. not necessarily in the fringing zone). Assuming that estimates of aboveground productivity reported by others within the study region (e.g. Stout 1984, Darby & Turner 2008) are representative of the expected biomass estimates at the present study sites, the percentage of biomass observed within these study sites would compare favorably to those reported by Silinski et al. (2018). Unlike Silinski et al. (2018), belowground biomass estimates within the present study sites (i.e. in the pioneer zone) were dwarfed by aboveground estimates and would align closer to the root to shoot ratios reported for more upland zones in their study. However, these differences may also reflect the species-specific responses discussed previously. Moreover, the varying impact of different environmental factors, including soil bulk density, elevation and wave climate, on different plant fea-

tures illustrates the complex interplay of these factors, all with important consequences to plant persistence within the pioneer zone with an array of potential rippling effects on the ecology of these environments. Teasing out the relative effect of these factors on *Juncus* and *Spartina* responses warrants further research.

As with all studies, interpretation may be limited by the constraints of the experimental design and environmental conditions during the study. For example, tidal amplitude in the study area is small compared to other areas, which may further influence the expression of different plant features not controlled for in this study. In particular, the estimation of wave climate parameters examined in this study occurred over a relatively short time period (~20 d). In an effort to compare these short-term measurements to long-term conditions, we explored how wave statistics generated from gauge data collected during this period at bay sites compared to those generated by hindcasted wind-wave models from 10 yr wind records (Text S4), since wave climate at these sites is mostly wind-driven. Results indicated that gauge-generated statistics were similar to those predicted by 10 yr wind records at southern-facing sites (Fig. S4.1), likely due the predominance of winds from the south during this period (Fig. S1.1). Along northern-facing shorelines, gauge-generated statistics tended to underestimate conditions predicted by wind-wave models (Text S4, Fig. S4.2). Only 2 northern-facing sites included the study species *Spartina*, and thus, this short-term wave data accurately reflected longer-term wave conditions across a majority of sites. Regardless, the study period encompassed in the short-term wave climate analyses occurred when plants are actively growing in the northern GoM. Long-term data regarding boat wakes are limited, and modeling is difficult due, in part, to the numerous co-varying parameters involved (Glamore 2008). Therefore, model comparisons to gauge statistics for river site data were not pursued. Boat wake in this study produced waves that were similar to bay sites in height (Table 2) but these data were collected from sites during peak periods of boating activity (i.e. US national holidays; Table 1) and thus may not reflect the wave climate representative of other periods with less boating activity (e.g. during winter months). Even if wave climate parameters collected during these peak boating activity periods were higher, on average, than those collected during slack periods, they would still represent the higher end of the potential wave climate conditions, which often have the greatest

impact on plant responses (e.g. stem breakage and biomass; Connell 1978, Möller et al. 2014, Rupprecht et al. 2017).

More broadly, the wave conditions observed at sites in the present study have strong management implications. Wave conditions were overwhelmingly the result of recreational boating activity and in areas where wave exposure would be near zero in the absence of boats (i.e. 40 riverine sites vs. 20 bay sites). Compared to bay sites, the development of wind-generated waves is extremely limited (Sorensen 2005). However, wave heights at these sites were often comparable to those at bay sites (Table 2). *Juncus* and *Spartina* were the most commonly observed species in this study, but several others were also seen within riverine sites. Many of these plants (e.g. *Sagittaria lancifolia* and *Typha latifolia*) are not typically associated with significant wind-driven wave exposure since they most often occur in historically sheltered areas (e.g. riverine sites in the present study). As such, they may not be able to adjust to a changing wave climate which could open niche space for other species such as the invasives *Phragmites australis* and *Panicum repens* observed at several riverine sites in this study. In addition, the wave-driven changes in marsh morphology observed in this study could also influence specific functions or processes marshes perform that directly benefit humans (i.e. ecosystem services), such as coastal defense, habitat provisioning, nutrient removal capacity and carbon sequestration. However, more research is needed to fully understand the effects of these changes on the ecosystem service capacity of marshes. At any rate, coastal land managers should consider wave protection strategies to maximize the ecosystem services targeted in restoration, conservation or enhancement projects and adaptive management plans, even in riverine systems where wave exposure is often assumed to be non-significant (Hardaway et al. 2010, NOAA 2015).

5. CONCLUSIONS

This study adds to a growing body of research demonstrating shifting plant responses to a varying wave climate, similar to the way plants alter the expression of assorted traits in response to other varying environmental conditions. In particular, both *Juncus* and *Spartina* shoot diameters declined with increasing wave climate exposure. Other responses were not common and were more often related to other environmental factors. In addition to these main

results, we found that surveyed wave climate conditions observed at some river sites were similar, in terms of magnitude and frequency of wave events, to those observed at bay sites. Together, these results have several management implications. For example, boat wake conditions could impact community structure in sheltered brackish marshes locally, while changing wave climate conditions could impact plant features more broadly. Both of these impacts have consequences to most—if not all—of the ecosystem services provided by coastal marshes, including habitat provisioning and coastal defense. However, more research is needed to fully understand the effects of varying wave conditions on coastal marshes and the ecosystem services they provide.

Acknowledgements. We thank Sara Martin and Gillian Palino for help processing plant biomass data, and staff at WBNERR, GBNERR and GCRL for generous use of lab facilities and equipment. We also thank 3 anonymous reviewers for their comments and suggestions which greatly improved the manuscript. Funding for this project was provided by the NOAA NERRS Science Collaborative Program (grant number: NA14NOS4190145), the US EPA Wetlands Program (grant number: CD-00D40115-0), the National Sea Grant College Program (Mississippi–Alabama Sea Grant Consortium, under Grant NA10OAR4170078) and the National Institute of Food and Agriculture, US Department of Agriculture (Hatch project under accession number 1005087 to the Mississippi Agricultural and Forestry Experiment Station).

LITERATURE CITED

- Augustin LN, Irish JL, Lynett P (2009) Laboratory and numerical studies of wave damping by emergent and near-emergent wetland vegetation. *Coast Eng* 56:332–340
- Balke T, Bouma TJ, Horstman EM, Webb EL, Erfteimeijer PLA, Herman PMJ (2011) Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. *Mar Ecol Prog Ser* 440:1–9
- Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Siliman BR (2011) The value of estuarine and coastal ecosystem services. *Ecol Monogr* 81:169–193
- Bilkovic DM, Mitchell MM, Davis J, Herman J and others (2019) Defining boat wake impacts on shoreline stability toward management and policy solutions. *Ocean Coast Manag* 182:104945
- Blackmar PJ, Cox DT, Wu WC (2014) Laboratory observations and numerical simulations of wave height attenuation in heterogeneous vegetation. *J Waterw Port Coast Ocean Eng* 140:56–65
- Bouma TJ, Vries MD, Herman PM (2010) Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. *Ecology* 91:2696–2704
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, NY
- Cao H, Zhu Z, James R, Herman PM, Zhang L, Yuan L, Bouma TJ (2020) Wave effects on seedling establishment of three pioneer marsh species: survival, morphology and biomechanics. *Ann Bot (Lond)* 125:345–352
- Carus J, Heuner M, Paul M, Schröder B (2017) Plant distribution and stand characteristics in brackish marshes: unravelling the roles of abiotic factors and interspecific competition. *Estuar Coast Shelf Sci* 196:237–247
- Chanson H, Aoki S, Hoque A (2006) Bubble entrainment and dispersion in plunging jet flows: freshwater vs. seawater. *J Coast Res* 223:664–677
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Constantin AJ, Broussard WP, Cherry JA (2019) Environmental gradients and overlapping ranges of dominant coastal wetland plants in Weeks Bay, AL. *Southeast Nat* 18:224–239
- Coops H, Geilen N, van der Velde G (1994) Distribution and growth of the helophyte species *Phragmites australis* and *Scirpus lacustris* in water depth gradients in relation to wave exposure. *Aquat Bot* 48:273–284
- Cottingham KL, Lennon JT, Brown BL (2005) Knowing when to draw the line: designing more informative ecological experiments. *Front Ecol Environ* 3:145–152
- Darby FA, Turner RE (2008) Below- and aboveground *Spartina alterniflora* production in a Louisiana salt marsh. *Estuaries Coasts* 31:223–231
- Eleuterius LN (1984) Autecology of the black needlerush *Juncus roemerianus*. *Gulf Caribb Res* 7:339–350
- Glamore WC (2008) A decision support tool for assessing the impact of boat wake waves on inland waterways. In: PIANC-COPEDEC VII: International Conference on Coastal and Port Engineering in Developing Countries, Dubai, UAE, 24–28 February 2008. <https://www.researchgate.net/publication/237735854>
- Green MO, Coco G (2014) Review of wave-driven sediment resuspension and transport in estuaries. *Rev Geophys* 52:77–117
- Hardaway CS Jr, Milligan DA, Duhring K (2010) Living shorelines design guidelines for shore protection in Virginia's estuarine environments. Special Report in Applied Marine Science and Ocean Engineering 421. VIMS, Gloucester Point, VA
- Heuner M, Silinski A, Schoelynck J, Bouma TJ and others (2015) Ecosystem engineering by plants on wave-exposed intertidal flats is governed by relationships between effect and response traits. *PLOS ONE* 10:e0138086
- Howard RJ, Mendelssohn IA (1999) Salinity as a constraint on growth of oligohaline marsh macrophytes. I. Species variation in stress tolerance. *Am J Bot* 86:785–794
- Keddy PA (1982) Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquat Bot* 14:41–58
- Keddy PA (1985) Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. *Can J Bot* 63:656–660
- Kirwan ML, Megonigal JP (2013) Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504:53–60
- Knutson PL, Brochu RA, Seelig WN, Inskeep M (1982) Wave damping in *Spartina alterniflora* marshes. *Wetlands* 2:87–104
- Maricle BR, Lee RW (2002) Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. *Aquat Bot* 74:109–120

- McConchie JA, Toleman IEJ (2003) Boat wakes as a cause of riverbank erosion: a case study from the Waikato River, New Zealand. *J Hydrol N Z* 42:163–179
- ✦ McKee KL, Cherry JA (2009) Hurricane Katrina sediment slowed elevation loss in subsiding brackish marshes of the Mississippi River delta. *Wetlands* 29:2–15
- ✦ Mendelssohn IA, Seneca ED (1980) The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuar Coast Mar Sci* 11: 27–40
- ✦ Möller I, Kudella M, Rupprecht F, Spencer T and others (2014) Wave attenuation over coastal salt marshes under storm surge conditions. *Nat Geosci* 7:727–731
- ✦ Morris JT, Haskin B (1990) A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. *Ecology* 71:2209–2217
- ✦ Mullarney JC, Henderson SM (2010) Wave-forced motion of submerged single-stem vegetation. *J Geophys Res Oceans* 115:C12061
- ✦ Nestler J (1977) Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuar Coast Mar Sci* 5: 707–714
- NOAA (2015) Guidance for considering the use of living shorelines. National Oceanic and Atmospheric Administration, Silver Spring, MD
- ✦ Noble MA, Schroeder WW, Wiseman WJ Jr, Ryan HF, Gelfenbaum G (1996) Subtidal circulation patterns in a shallow, highly stratified estuary: Mobile Bay, Alabama. *J Geophys Res Oceans* 101:25689–25703
- ✦ Nyman JA, Walters RJ, Delaune RD, Patrick WH Jr (2006) Marsh vertical accretion via vegetative growth. *Estuar Coast Shelf Sci* 69:370–380
- ✦ Osland MJ, Griffith KT, Larriviere JC, Feher LC and others (2017) Assessing coastal wetland vulnerability to sea-level rise along the northern Gulf of Mexico coast: gaps and opportunities for developing a coordinated regional sampling network. *PLOS ONE* 12:e0183431
- ✦ Ozeren Y, Wren DG, Wu W (2014) Experimental investigation of wave attenuation through model and live vegetation. *J Waterw Port Coast Ocean Eng* 140:04014019
- ✦ Paul M, Bouma TJ, Amos CL (2012) Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. *Mar Ecol Prog Ser* 444:31–41
- ✦ Pennings SC, Grant MB, Bertness MD (2005) Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *J Ecol* 93:159–167
- ✦ Peralta G, van Duren LA, Morris EP, Bouma TJ (2008) Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. *Mar Ecol Prog Ser* 368:103–115
- ✦ Puijalon S, Bornette G, Sagnes P (2005) Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. *J Exp Bot* 56:777–786
- ✦ Puijalon S, Bouma TJ, Douady CJ, van Groenendael J, Anten NP, Martel E, Bornette G (2011) Plant resistance to mechanical stress: evidence of an avoidance–tolerance trade-off. *New Phytol* 191:1141–1149
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Roland RM, Douglass SL (2005) Estimating wave tolerance of *Spartina alterniflora* in coastal Alabama. *J Coast Res* 2005:453–463
- ✦ Rupprecht F, Möller I, Evans B, Spencer T, Jensen K (2015) Biophysical properties of salt marsh canopies—quantifying plant stem flexibility and above ground biomass. *Coast Eng* 100:48–57
- ✦ Rupprecht F, Möller I, Paul M, Kudella M and others (2017) Vegetation–wave interactions in salt marshes under storm surge conditions. *Ecol Eng* 100:301–315
- ✦ Schoutens K, Heuner M, Minden V, Schulte Ostermann T, Silinski A, Belliard JP, Temmerman S (2019) How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnol Oceanogr* 64:1750–1762
- ✦ Schulze D, Rupprecht F, Nolte S, Jensen K (2019) Seasonal and spatial within-marsh differences of biophysical plant properties: implications for wave attenuation capacity of salt marshes. *Aquat Sci* 81:65
- ✦ Silinski A, Heuner M, Schoelynck J, Puijalon S and others (2015) Effects of wind waves versus ship waves on tidal marsh plants: a flume study on different life stages of *Scirpus maritimus*. *PLOS ONE* 10:e0118687
- ✦ Silinski A, Schoutens K, Puijalon S, Schoelynck J and others (2018) Coping with waves: plasticity in tidal marsh plants as self-adapting coastal ecosystem engineers. *Limnol Oceanogr* 63:799–815
- ✦ Snedden GA, Cretini K, Patton B (2015) Inundation and salinity impacts to above-and belowground productivity in *Spartina patens* and *Spartina alterniflora* in the Mississippi River deltaic plain: implications for using river diversions as restoration tools. *Ecol Eng* 81:133–139
- Sorensen RM (2005) Basic coastal engineering, Vol 10. Springer Science & Business Media, New York, NY
- ✦ Sparks EL, Cebrian J, Tobias CR, May CA (2015) Groundwater nitrogen processing in Northern Gulf of Mexico restored marshes. *J Environ Manag* 150:206–215
- Stout JP (1984) The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. National Coastal Ecosystems Team, Division of Biological Services, Research and Development, Fish and Wildlife Service, US Department of the Interior, Washington, DC
- ✦ Temple NA, Grace JB, Cherry JA (2019) Patterns of resource allocation in a coastal marsh plant (*Schoenoplectus americanus*) along a sediment-addition gradient. *Estuar Coast Shelf Sci* 228:106337
- Temple NA, Webb BM, Sparks EL, Linhoss AC (2020) Low-cost pressure gauges for measuring water waves. *J Coast Res* 36:661–667
- ✦ Touchette BW (2006) Salt tolerance in a *Juncus roemerianus* brackish marsh: spatial variations in plant water relations. *J Exp Mar Biol Ecol* 337:1–12
- ✦ Tweel AW, Turner RE (2012) Watershed land use and river engineering drive wetland formation and loss in the Mississippi River birdfoot delta. *Limnol Oceanogr* 57: 18–28
- ✦ Vasquez EA, Glenn EP, Guntenspergen GR, Brown JJ, Nelson SG (2006) Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. *Am J Bot* 93:1784–1790
- ✦ Vuik V, Heo HYS, Zhu Z, Borsje BW, Jonkman SN (2018) Stem breakage of salt marsh vegetation under wave forcing: a field and model study. *Estuar Coast Shelf Sci* 200: 41–58
- ✦ Wang C, Pei X, Yue S, Wen Y (2016) The response of *Spartina alterniflora* biomass to soil factors in Yancheng, Jiangsu Province, PR China. *Wetlands* 36:229–235

- Webb BM, Smallegan SM, Mazur E, Lamonte L (2018) Incident boat wake energy and implications for restoration design. In: Proceedings of Bays & Bayous Symposium, Habitat Management (Mobile, Alabama), November 29, 2018
- ✦ Weston NB (2014) Declining sediments and rising seas: an unfortunate convergence for tidal wetlands. *Estuaries Coasts* 37:1–23
- ✦ Zheng S, Shao D, Sun T (2018) Productivity of invasive salt-marsh plant *Spartina alterniflora* along the coast of China: a meta-analysis. *Ecol Eng* 117:104–110
- Zhu Z, Yang Z, Bouma TJ (2020) Biomechanical properties of marsh vegetation in space and time: effects of salinity, inundation and seasonality. *Ann Bot (Lond)* 125:277–290
- Zuur A, Ieno EN, Smith GM (2007) *Analyzing ecological data*. Springer, New York, NY
- ✦ Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

*Editorial responsibility: Emily Carrington,
Friday Harbor, Washington, USA
Reviewed by: 3 anonymous referees*

*Submitted: July 12, 2020
Accepted: July 26, 2021
Proofs received from author(s): September 25, 2021*