

Effects of Shoreline Development on Composition and Physical Structure of Plants in a South Carolina High Marsh

Zofia Noe · Jennifer Jackson · John J. Hutchens Jr. · Keith Walters · James O. Luken · Kevin S. Godwin

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Abstract Increased freshwater and nutrient runoff associated with coastal development is implicated in dramatically altering estuarine communities along eastern US shorelines. We examined effects of three categories of shoreline development on high-marsh environments within Murrells Inlet, South Carolina, USA by measuring sediment nutrients, porewater salinity, plant species diversity, and above- and belowground plant biomass. Effects on new plant growth also were examined in plot clearing and transplantation experiments. Greater nutrient availability in sediments along developed shorelines was reflected in greater aboveground biomass and nitrogen storage in *Juncus roemerianus* plant tissue. Plant species composition was not significantly different among levels of shoreline development. Zinc concentrations were greater in sediments from developed shorelines and may represent an easily measured indicator of shoreline development. Recently accelerating shoreline development in the southeastern USA may alter plant production, nitrogen storage, and sediment metal content in salt marshes.

Keywords Coastal development · *Juncus roemerianus* · Murrells inlet estuary · Zinc

Introduction

Since the early 1600s, about half of the coastal wetlands in the USA have been lost to urban development and agricultural conversion (Dahl and Allord 1999). The influx of European settlers accelerated the exploitation of estuarine marshes by employing practices common worldwide and dating back to Neolithic times (Gedan et al. 2009). In most states the direct ditching, dredging, and filling of coastal wetlands currently are discouraged by existing statutes (e.g., Votteler and Muir 1996). Although the rate of loss has slowed, current trends indicate continued population growth in coastal states (e.g., South Carolina) will affect estuaries and estuarine wetlands primarily through indirect effects (Gedan et al. 2009). The indirect effects of development include cultural eutrophication and additional consequences from pollution (e.g., diseases and toxins), expansion of impervious surfaces (e.g., roads and rooftops) and nonforested areas (e.g., lawns), and alteration of shoreline boundaries (e.g., deforestation and bulkheading).

Altered nutrient dynamics associated with eutrophication have demonstrated negative effects both subtidally (Fisher et al. 2006; Verity et al. 2006; Bowen et al. 2007) and intertidally (Bertness et al. 2002; Wigand et al. 2003, 2009; Deegan et al. 2007). In salt marshes, increased nutrients (e.g., nitrogen) alter competitive interactions among resident plants by changing the limiting resource from nutrients to light (Levine et al. 1998). The shift from below- to aboveground competition facilitates growth of salt-tolerant (e.g., *Spartina alterniflora* Loisel) relative to less-tolerant species (e.g., *Juncus roemerianus* Scheele), transforming high-marsh communities (Emery et al. 2001). In southeastern US marshes, increased nitrogen enables *S. alterniflora* to outcompete the typical high-marsh-dominant *J. roemerianus* (Pennings et al. 2005a). An added influx of nutrients increases the height and

Z. Noe · J. Jackson
Coastal Marine and Wetland Studies Program, Coastal Carolina University, P.O. Box 261954, Conway, SC 29528-6054, USA

J. J. Hutchens Jr. (✉) · J. O. Luken · K. S. Godwin
Department of Biology, Coastal Carolina University,
Conway, SC 29528-6054, USA
e-mail: jjhutch@coastal.edu

K. Walters
Department of Marine Science, Coastal Carolina University,
Conway, SC 29528-6054, USA

biomass of *S. alterniflora*, and the typical high-marsh species *Spartina patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene (Levine et al. 1998). The increased primary production resulting from nutrient loading also affects the carbon balance in marsh sediments with a potential net transfer of soil carbon to the atmosphere and implications for global climate change (Morris and Bradley 1999).

Coastal watershed development, while not directly impacting marsh environments, removes existing upland vegetation (e.g., trees and shrubs) and increases the prevalence of impervious surfaces. Tidal creek physical characteristics are affected adversely with as little as 10–20 % upland impervious coverage, and biological resources experience reduced abundances and altered food webs at levels exceeding increases in 20–30 % impervious coverage (Holland et al. 2004). One consequence of increased impervious coverage in coastal watersheds is an alteration of both sediment and freshwater input into estuarine habitats (Corbett et al. 1997; Byrd and Kelly 2006). Increased freshwater runoff has the potential to decrease soil salinities and alter high-marsh plant assemblages (Pennings et al. 2005b). Growth of *D. spicata*, a fugitive species, in disturbed high-marsh patches is facilitated by reduced soil salinities (Bertness and Ellison 1987; Bertness et al. 1992). Reduced soil salinities along with increased human activity also are implicated in the establishment of the non-native plant *Phragmites australis* (Cav.) Trin. ex Steud. in New England salt marshes (Minchinton and Bertness 2003; Silliman and Bertness 2004; King et al. 2007).

Alteration of the shoreline boundary between estuarine and upland habitats frequently is associated with residential development of coastal watersheds. The local loss of native, terrestrial vegetation along the boundary affects a variety of physical and biological characteristics in southeastern US high-marsh environments (Walters et al. 2010). Predictable, significant increases in sediment surface temperatures and marsh plant height, and a lack of significant differences in marsh plant density or standing crop were observed between developed and undeveloped shorelines (Walters et al. 2010). Either separately or in combination with increased nutrient loading and watershed development, alteration of the native, upland vegetation along shorelines has the potential to affect estuarine environments by changing typical patterns of nutrients, runoff, and insolation.

In this study, we build upon previous work in the same estuary (Walters et al. 2010) addressing impacts of shoreline development on community and ecosystem characteristics by distinguishing among extant patterns in plant assemblages using a transplant approach as well as quantifying shoreline development with geographic databases. We anticipated that boundary development would lead to increased stormwater runoff and nutrient loading resulting in reduced soil salinity and greater soil nutrient availability in the high-marsh environment. Consistent with fertilization studies (e.g., Deegan

et al. 2012; Fox et al. 2012), the effects would be greater nutrient content in plant tissue, increased plant height, and increased aboveground plant biomass. The increased nutrient availability also would affect competitive interactions by changing the limiting resource from nutrients to light resulting in decreased plant diversity, greater occurrence of invasive species such as *P. australis*, and reduced belowground plant biomass. Our study of a southeastern US salt marsh will help assess whether differing species assemblages and different seasonal patterns inherent in southern latitudes alter how anthropogenic activity affects salt marsh plant assemblages.

Materials and Methods

Study Site

Study sites were chosen along the mainland border of Murrells Inlet estuary, South Carolina, USA (33°32' N and 79°07' W). The South Carolina coast is composed of Pleistocene terraces and Pleistocene or Holocene barrier islands (Dame et al. 2000). Murrells Inlet is a bar-built estuary with tidal creeks and marshes forming between the barrier beaches and mainland (Dame et al. 2000). The estuary is kidney-shaped with the mouth of the inlet slightly south of the midline (Fig. 1). The inlet has no major riverine input and experiences a semidiurnal tide (Porter et al. 1997). Average annual salinity is 31.4 and average water temperature is 20 °C (Porter et al. 1997). The mean tidal range is 1.37 m with a maximum spring tide of 1.62 m. Huntington Beach State Park surrounds the southern



Fig. 1 Eleven study sites (indicated by triangles) located in Murrells Inlet, SC. Aerial photograph provided by South Carolina Department of Natural Resources GIS Clearing House (Jackson 2008)

portion of Murrells Inlet and is mostly undeveloped. The rest of Murrells Inlet has extensive upland and shoreline development resulting from urbanization and tourism (Mallin et al. 2000; Porter et al. 1997).

Precipitation and Temperature

Precipitation and temperature data for Sullivan's Island, South Carolina, approximately 129 km south of Murrells Inlet, were provided by the National Weather Service for 2007, 2008, and averaged for 1971–2000. The South Carolina State Climatology Office provided drought status information. Average temperatures did not differ between 2007 and 2008 and were similar to measurements averaged from 1971 through 2000. Total monthly precipitation was below average in 2007 resulting in severe drought conditions for most of South Carolina, including Horry and Georgetown counties. Total monthly precipitation in 2008 was normal and resulted in the removal of Horry and Georgetown counties and most of South Carolina from drought condition status by the end of September (data not shown; see Zaplatynski 2009, for details).

Site Selection and Characterization

The mainland border of Murrells Inlet estuary was measured for total length and divided into 50-m segments using Arc Geographic Information System (GIS) and aerial photography from 2006 available from the US Geological Survey (USGS; Jackson 2008). Eleven shoreline segments (sites) were chosen (Fig. 1) based on accessibility and distance from dredged areas and tidal creeks. Sites on the barrier island side of Murrells Inlet estuary were not chosen because of small upland area and scarcity of undeveloped sites. Sites DVB3, DVB4, and UND4 were at the southern end and closest to the mouth of the inlet with all remaining sites more than 6,000 m from the inlet opening (Table 1). No sites were chosen between these areas because of extensive nearshore dredging. All sites were within 250 m of a road and within 600 m of a tidal creek (Table 1).

Sites were categorized based on the level of shoreline development: (1) undeveloped (UND) sites had extensive woody vegetation abutting the marsh and no housing ($n=4$); (2) developed sites with a riparian border present (DVB) had a 3- to 5-m wide border of trees and shrubs between the marsh and housing ($n=4$); (3) developed sites with no riparian border (DEV) had housing with no vegetation next to the marsh ($n=3$). The three categories were selected to examine the existing range of shoreline development and to suggest possible land management options. Nevertheless, other covarying factors (e.g., slope) may have influenced our findings and we have tried to examine the contribution of these factors in our analyses. Global Positioning System points

Table 1 Slope (in centimeters per meter), impervious cover, lawn cover, and distances to nearest roads, tidal creeks, and inlet (mean \pm SE)

Site characteristic	Shoreline development category		
	UND ($n=4$)	DVB ($n=4$)	DEV ($n=3$)
Slope border to 1 m	-4.3 ± 0.9 a	2.9 ± 1.8 b	-13.1 ± 1.1 c
Slope border to 5 m	-2.9 ± 0.4 a	-0.9 ± 0.5 b	-4.6 ± 0.6 c
Impervious surface (%)	0 ± 0 a	26 ± 5 b	20 ± 10 b
Lawn (%)	0 ± 0 a	18 ± 6 b	9 ± 4
Total development (%)	0 ± 0 a	44 ± 10 b	29 ± 7 b
Distance to nearest road (m)	108 ± 47	79 ± 7	99 ± 16
Distance to nearest tidal creek (m)	200 ± 79	354 ± 113	106 ± 16
Distance to nearest inlet (m)	$5,719\pm 1,017$	$4,962\pm 1,163$	$6,763\pm 230$

Means within each row separated by different letters are significantly different ($\alpha=0.05$) according to the Ryan–Einot–Gabriel–Welsch multiple F test. Lack of letters indicates a nonsignificant difference

UND undeveloped, DVB developed-with-riparian border, DEV developed-without-riparian border

were taken for each site and uploaded into Arc GIS. Levels of development at each of the 11 sites were estimated by calculating the percent cover of impervious surfaces and lawns to a distance of 100 m from the high-marsh/upland border, which included the riparian border (total area of each site was 5,000 m²).

In March 2008, elevation data were collected using a transit and an architect's rod. Slope was estimated by measuring three elevation points at each site: at the upland border and at points 1- and 5-m seaward from the upland border.

Marsh Plant Assemblage

In order to assess differences in plant species richness and abundance among the different shoreline development categories, an area of high-marsh 50-m long parallel to shore and 15-m wide perpendicular to shore was divided into 1-m² quadrats at each of the 11 sites. Randomly chosen quadrats ($n=15$) were sampled in July 2007, and the number of plant species, percent cover of each species, and height of the tallest stem or leaf (i.e., *J. roemerianus* "stems" are leaves) of the dominant species in each quadrat measured.

Aboveground biomass was collected in September 2007 from additional 0.25-m² quadrats ($n=3$) haphazardly chosen at each site. Vegetation was cleared at ground level and separated by species and live and dead tissue (including sorting dead tops of *J. roemerianus* from living bottom sections). Samples were dried for 24 h at 60 °C and weighed to estimate aboveground biomass. Sub-samples were ashed in a muffle furnace for 1 h at 550 °C to calculate ash-free dry mass (AFDM).

Belowground biomass was estimated from 5-cm diameter, 20-cm deep cores ($n=3$) collected at each site in September 2008. Cores were split equally into upper and lower sections. Sections were washed over a 0.5-mm sieve to collect root material (methods modified from Bertness and Ellison 1987). Belowground root and rhizome biomass and AFDM were estimated as described above.

Plant and Soil Chemistry

Nutrient availability was assessed by determining concentrations in aboveground plant tissue (Osgood and Zieman 1993). At each site samples ($n=3$) of only *J. roemerianus*, by far the most abundant high-marsh species, were collected haphazardly in July 2007. The upper 15-cm of each leaf in each sample was sent to the Agricultural Service Laboratory at Clemson University for nutrient content analysis.

Sediment nutrient concentrations and pore water salinity were determined from samples ($n=3$ ea.) collected within quadrats designated for clearing (described below) at each site in July 2007. Soil was collected using a shovel to a depth of 15 cm, dried and sent to the Agricultural Service Laboratory at Clemson University for nutrient content analysis. Additional sediment was collected using a 30-ml syringe to a depth of 2 cm to determine pore water salinity. Samples were weighed before diluting with 30 ml of deionized water. Samples were agitated and allowed to equilibrate for 48 h. Salinity of the supernatant was measured using a hand-held refractometer. Samples were dried for 4 days at 60 °C and weighed again. Pore water salinity was calculated after adjusting for dilution.

Clearing and Transplant Experiment

Effects of upland development on existing and new plant species richness and abundance were investigated in a clearing and *J. roemerianus* transplantation experiment. Vegetation and belowground mass were cleared from three 1-m² quadrats dominated by *J. roemerianus* at each of the 11 sites. A separate Murrells Inlet site with no human development and extensive woody vegetation abutting the marsh was chosen as a source of *J. roemerianus* for transplanting. A haphazardly chosen 0.01-m² plot of *J. roemerianus* was transplanted from the source site into each cleared quadrat ($n=33$) in July 2007. To control for manipulation effects, 0.01-m² plots of *J. roemerianus* ($n=33$) were removed and replanted in place at the source site (Stalter and Batson 1969). Additional 0.01-m² plots of *J. roemerianus* ($n=33$) were chosen haphazardly, marked with a flag, and not manipulated to serve as development treatment controls. At the end of the 2007 and 2008 growing seasons, species richness and abundance, and height and abundance of the *J. roemerianus* transplants were estimated from each cleared quadrat. Soil samples also were

collected to measure pore water salinities and determine if clearing increased salinities and influenced plant growth.

Statistical Analyses

Differences among the UND, DVB, and DEV shoreline development categories were assessed with a nested analysis of variance (ANOVA), sites nested within shoreline development category. Plant height, above- and below-ground biomass, plant chemistry, and soil chemistry were analyzed. If significant, post hoc pairwise comparisons using the Ryan–Einot–Gabriel–Welsch multiple F test were calculated. Initial salinity values were compared with salinity values found in cleared transplant plots using a paired t -test. A one-way ANOVA was used to test for differences among *J. roemerianus* transplants and controls, and a nested ANOVA was used to analyze differences in transplant height and number of leaves among development categories. A one-way ANOVA also was used to analyze differences in shoreline characteristics among development categories. If significant, post hoc pairwise comparisons using the Ryan–Einot–Gabriel–Welsch multiple F test were calculated. All statistical analyses were performed using SPSS v13.0.

Species similarity among shoreline development categories in both the field survey study and the transplantation experiment were analyzed using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001; McArdle and Anderson 2001). Similarity values were calculated using the Bray–Curtis dissimilarity index. Two sites, one each from the UND and DVB shoreline development categories, were selected randomly, and removed to create the PERMANOVA-required balanced design.

A two-tailed Spearman rank correlation was used to examine relationships between above- and below-ground AFDM and between above- and belowground AFDM and slope, impervious cover, lawn cover, and total development. Plant and soil nutrients also were related to slope and percent development with two-tailed Spearman rank correlations.

Results

Shoreline Characteristics

Slopes between the upland border and 1-m seaward were significantly different among all shoreline development categories ($F_{2, 8}=30.097$, $p<0.05$) and were steeper and negative at all the DEV sites (Table 1). The DVB sites had slightly positive slopes, and all four UND sites had slightly negative slopes (Table 1). Slopes between the upland border and 5-m seaward also were significantly different among all development categories ($F_{2, 8}=13.053$, $p<0.05$) and were steeper at the DEV sites with negative values (Table 1). The DVB sites

had significantly smaller slopes than both the UND and DEV sites. All the UND sites had slightly negative slopes (Table 1).

All the UND sites contained significantly less impervious surface than the DVB and DEV sites ($F_{2,8}=6.849, p<0.05$) but impervious surface was similar between the DVB and DEV sites (Table 1). The UND sites also contained significantly less lawn cover than the DVB sites ($F_{2,8}=4.905, p<0.05$; Table 1). Total development (impervious surface + lawn) was greatest at the DVB sites (44 %) but was not significantly different from the DEV sites (Table 1). Distances from a road, tidal creek or the inlet also were not significantly different among development categories (Table 1).

Marsh Plant Assemblages

Seven plant species were found in the 11 sites (Table 2), with the UND, DVB, and DEV containing 5, 6, and 4 species, respectively. *J. roemerianus*, *S. alterniflora*, *Limonium carolinianum* (Walt.) Britt., and *Borrichia frutescens* (L.) DC. were found in all three categories of shoreline development. *Iva frutescens* L. and *S. patens* were found only in the UND and DVB sites. Only DVB3 contained *Scirpus americanus* Pers. (Table 2). *J. roemerianus* and *S. alterniflora* were the dominant species within each sampling area (Table 2). PERMANOVA results indicated that plant assemblages were not significantly different among shoreline development categories ($F_{2,6}=0.7014, p>0.05$) but were significantly different among sites ($F_{2,6}=4.1775, p<0.05$).

All but three of the aboveground biomass samples consisted solely of *J. roemerianus*. Samples from only one site (UND4) contained *B. frutescens*. The collected *B. frutescens* was considered alive, but was not added to live biomass values for statistical analysis because *B. frutescens* was found only in one site. Mean live aboveground AFDM was >250 g/m² greater in the DVB sites than in the DEV and UND sites ($F_{2,8}=4.744, p<0.05$; Fig. 2). Dead AFDM was 500 g/m² greater in the DVB than in the UND or DEV sites ($F_{2,8}=8.641, p<0.05$; Fig. 2). *J. roemerianus* height was ca. 130 cm in the DVB sites versus 118 cm in the UND and

123 cm in the DEV sites, but was not significantly different among shoreline categories ($F_{2,8}=0.260, p>0.05$). Aboveground live and dead AFDM were not significantly correlated with slope over 1 m, total development, impervious cover, or lawn cover (r_s range of 0.378 to 0.697, $p>0.05$). However, dead AFDM was significantly correlated to slope over 5 m ($r_s=0.752, df=9$).

Belowground material only was collected from stands of *J. roemerianus* to facilitate statistical analysis and comparison of aboveground AFDM to belowground AFDM. Roots and rhizomes were very dense at all sites and shoreline categories. The top 10 cm contained the rhizome and a large mass of very fine roots while the lower 10 cm solely contained fine roots. The upper-layer contained 3,000 g/m² more mass than the lower layer (Fig. 2). No significant difference in belowground biomass was found among shoreline categories (Fig. 2). Aboveground AFDM was not significantly correlated with belowground AFDM ($r_s=-0.094$). Belowground upper- and lower-AFDM were not correlated with slope, total development, impervious cover, or lawn cover (r_s range of -0.050 to -0.405).

Combined AFDM (total aboveground AFDM + total belowground AFDM) was approximately 1,000 g/m² greater in either the UND (mean=10,907 g/m²) or DVB (10,785 g/m²) sites than in the DEV sites (9,142 g/m²). No significant difference in combined AFDM was found among shoreline categories ($F_{2,8}=0.341, p>0.05$), and combined AFDM was not significantly correlated with slope or percent development (r_s range of -0.093 to -0.118).

Plant and Soil Chemistry

Percent plant nitrogen content was marginally different among shoreline categories ($F_{2,8}=4.350, p=0.053$; Fig. 3) and was lowest in the DEV sites. Total nitrogen stored in plant tissue was found by multiplying total aboveground AFDM by plant nitrogen content (Fig. 3). The DVB sites exhibited significantly greater nitrogen storage than both the UND and DEV sites ($F_{2,8}=7.526, p<0.05$; Fig. 3). Neither

Table 2 Percent cover of species in three shoreline development categories (\pm SE)

Species	Shoreline development category		
	UND ($n=4$)	DVB ($n=4$)	DEV ($n=3$)
<i>Juncus roemerianus</i>	62 \pm 14	68 \pm 1	61 \pm 14
<i>Spartina alterniflora</i>	20 \pm 5	14 \pm 5	36 \pm 15
<i>Borrichia frutescens</i>	12 \pm 12	5 \pm 3	1 \pm 1
<i>Limonium carolinianum</i>	5 \pm 2	3 \pm 2	2 \pm 2
<i>Iva frutescens</i>	1 \pm 0	0 \pm 0	0 \pm 0
<i>Spartina patens</i>	0 \pm 0	2 \pm 2	0 \pm 0
<i>Scirpus americanus</i>	0 \pm 0	9 \pm 9	0 \pm 0

UND undeveloped, DVB developed-with-riparian border, DEV developed-without-riparian border

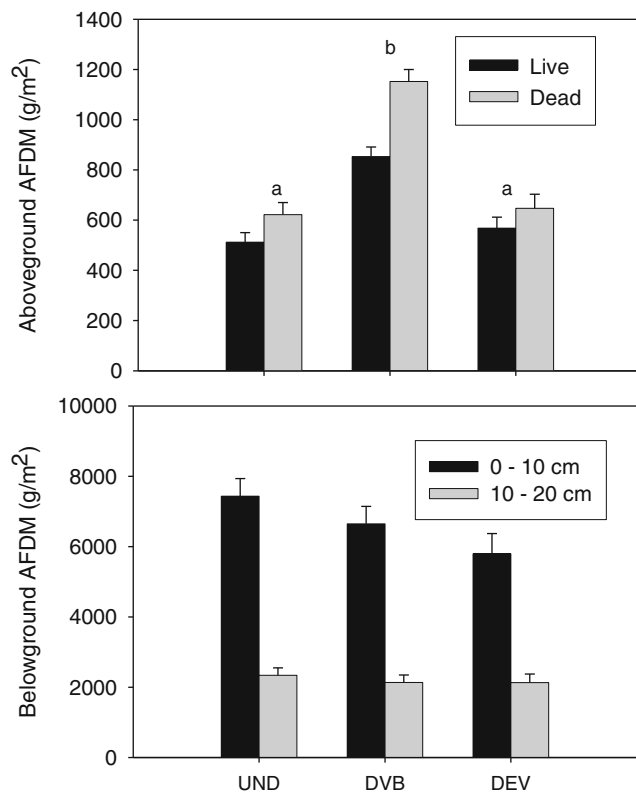


Fig. 2 Above- and belowground ash-free dry mass (AFDM; mean \pm SE). Both live ($F_{2,8}=4.744$, $p<0.05$) and dead ($F_{2,8}=8.641$, $p<0.05$) aboveground AFDM in DVB sites were significantly greater than in UND and DEV sites. UND undeveloped, DVB developed-with-riparian border, DEV developed-without-riparian border. Different letters indicate significant differences among shoreline development categories

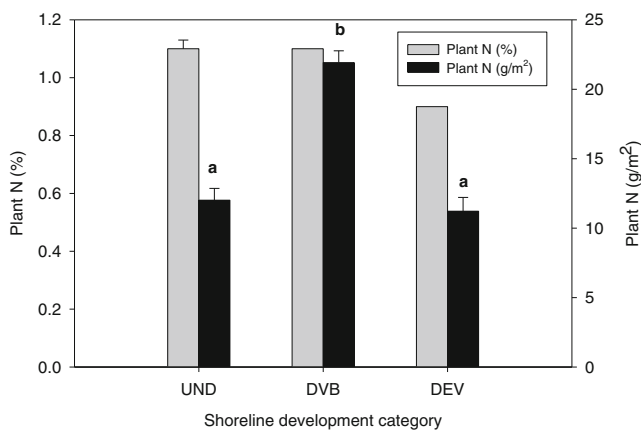


Fig. 3 Plant nitrogen content (in percent) and storage (in grams per square meter) in three shoreline development categories (mean \pm SE). Plant N (in percent) was marginally lower in DEV sites than in UND and DVB sites ($F_{2,8}=4.350$, $p=0.053$). Plant N (in grams per square meter) was significantly greater in DVB sites than in UND and DEV sites ($F_{2,8}=7.526$, $p<0.05$). Error bars not seen have value of SE=0.00. UND undeveloped, DVB developed-with-riparian border, DEV developed-without-riparian border. Different letters indicate significant differences among shoreline development categories

nitrogen content nor nitrogen storage was correlated significantly with slope or percent development (i.e., impervious cover, lawn cover, and total development).

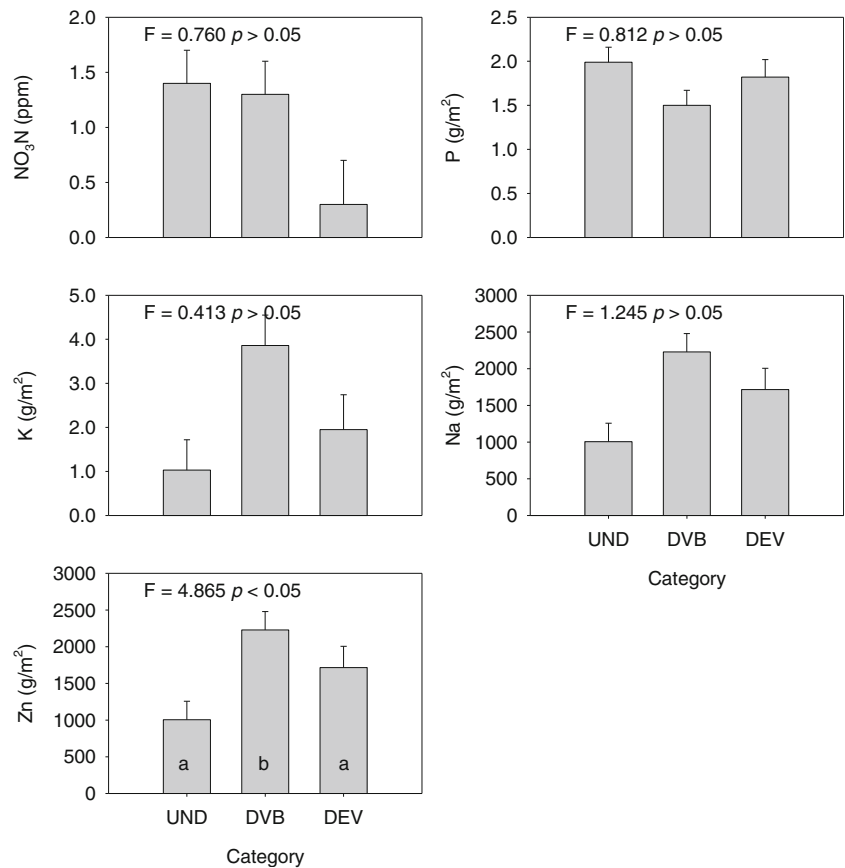
Soil salinity was not significantly different among shoreline categories in 2007 (UND mean \pm SE=4.83 \pm 0.49; DEV=6.44 \pm 0.57; DVB=5.58 \pm 0.49; $F_{2,8}=1.039$, $p>0.05$). Nitrogen (NO₃-N), phosphorus, potassium, and sodium were not significantly different among shoreline categories (Fig. 4) and were not significantly correlated with slope or percent development (i.e., impervious cover, lawn cover, and total development). Calcium, magnesium, manganese, copper, and boron also were not significantly different among shoreline categories and were not significantly correlated with slope or percent development (data not shown; see Zaplatynski 2009 for details). Zinc was the only nutrient found to be significantly different among shoreline categories ($F_{2,8}=4.865$, $p<0.05$) and exhibited the highest concentrations in the DVB sites (Fig. 4). Zinc also was significantly correlated with impervious cover ($r_s=0.777$), lawn cover ($r_s=0.769$), and total development ($r_s=0.730$), but was not correlated with slope.

Clearing and Transplant Experiment

At the end of the first growing season (September 2007) cleared quadrats contained no new plants besides the original *J. roemerianus* transplants. Twenty of the original 33 transplants appeared dead (i.e., brown, broken leaves). The few transplants that survived only had a few green leaves (usually two or three) that were from the original transplant and displayed no new growth. At the end of the second growing season (September 2008), many of the cleared quadrats contained new species and many of the transplants displayed new green leaves. However, comparisons among site types were equivocal for *J. roemerianus* stem recruitment and growth. Comparisons of transplants among site categories revealed no significant differences for total number of leaves ($F_{2,8}=1.159$, $p>0.05$; Fig. 5) and for average leaf height ($F_{2,8}=0.719$, $p>0.05$; Fig. 5). Plants that were manipulated but left in the source site had significantly fewer ($F_{1,64}=27.730$, $p<0.05$), shorter leaves ($F_{1,64}=16.927$, $p<0.05$) than plants left un-manipulated in the source site in 2008 (Fig. 5). The change in number of leaves was equivalent to a density change from 880 to 360 leaves/m².

Five species recruited to and grew within the cleared quadrats (Table 3). *J. roemerianus* was the most prevalent species in cleared quadrats. *J. roemerianus*, *S. alterniflora*, and *L. carolinianum* were found growing in all shoreline categories. *B. frutescens* was found only in the UND and DVB sites and *Aster tenuifolius* L. was found only in the UND sites (Table 3). PERMANOVA results indicated that recruited plant assemblages were not significantly different among the development categories ($F_{2,6}=0.9588$, $p=0.4915$) but were significantly different among sites ($F_{2,6}=2.7365$, $p<0.05$).

Fig. 4 Soil nutrient concentrations in three shoreline development categories (mean \pm SE). Only Zn was significantly different among shoreline development categories ($F_{2, 8}=4.865$, $p<0.05$). *UND* undeveloped, *DVB* developed-with-riparian border, *DEV* developed-without-riparian border. Different letters indicate significant differences among shoreline development categories



Soil salinities in cleared quadrats in September 2008 were not significantly different among shoreline development categories ($F_{2, 8}=1.695$, $p>0.05$) and were lower (mean=3.70, $t=4.288$, $p<0.05$) than salinities found at the beginning of the experiment (mean=5.55, July 2007).

Discussion

We hypothesized that shoreline development would alter plant composition and structure (i.e., plant height and biomass) of a South Carolina high marsh through changes to the abiotic environment. Greater nutrient availability, although not indicated in soil concentrations, was reflected in increased aboveground biomass and increased nitrogen storage in *J. roemerianus* tissue. In addition, zinc, a metal associated with tire wear, was found in greater concentrations in developed sites. However, plant species diversity was not found to be significantly different among shoreline development categories.

Increased freshwater and nutrient loading were not found in developed sites in Murrells Inlet estuary. Soil salinities were low in all high-marsh sites regardless of percent development and were not significantly different among shoreline development categories. Almost all of the soil constituents in this study were not significantly different among shoreline

development categories and were not significantly correlated with upland impervious cover, lawn cover, or total development. Zinc was the only soil component that was significantly different among shoreline development categories and was significantly correlated with increasing development. Zinc is associated with tire wear that is washed from roadways to streams and estuaries (Cole et al. 1984; Maltby et al.

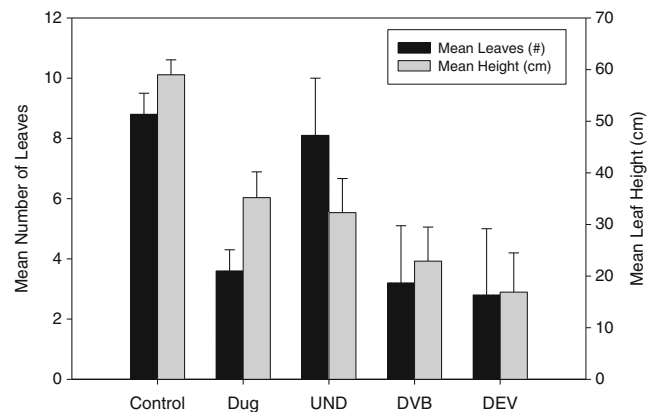


Fig. 5 Transplant success measured by average number of leaves and average leaf height. Control plants were not manipulated in source site; dug plants were control plants manipulated and left in source site. Other plants were manipulated and moved into undeveloped (*UND*), developed-with-riparian border (*DVB*), or developed-without-riparian border (*DEV*) sites. Significant differences are described in text

Table 3 Percent cover of species found in cleared quadrats in three shoreline development categories (\pm SE; September 2008)

Species	Shoreline development category		
	UND ($n=4$)	DVB ($n=4$)	DEV ($n=3$)
<i>Juncus roemerianus</i>	47 \pm 23	57 \pm 25	51 \pm 27
<i>Spartina alterniflora</i>	2 \pm 2	29 \pm 24	40 \pm 20
<i>Borrchia frutescens</i>	19 \pm 19	11 \pm 22	0 \pm 0
<i>Limonium carolinianum</i>	31 \pm 24	4 \pm 4	9 \pm 9
<i>Aster tenuifolius</i>	1 \pm 1	0 \pm 0	0 \pm 0

UND undeveloped, DVB developed-with-riparian border, DEV developed-without-riparian border

1995). Sites in this study were all within 250 m of a road, but had various levels of development that could have influenced zinc input. Greater levels of urbanization in South Carolina have been linked to increased water column and sediment concentrations of trace metals such as Cu and Zn (Sanger et al. 1999). Zinc is an essential plant nutrient, but can have toxic effects at high levels. Many wetland plants, including *Juncus effuses* f. *spiralis*, *S. patens*, and *Zizania latifolia* (Griseb.) Turcz. ex Stapf, can tolerate high levels of zinc and other trace metals and can become more tolerant as they are exposed to greater concentrations for longer durations (Matthews et al. 2004; Liu et al. 2007; Suntornvongsagul et al. 2007). Zinc tolerance or toxicity in *J. roemerianus* has not been studied.

Nutrient enrichment in developed sites was not indicated by significantly different soil nitrogen content or increased plant height but was reflected in high aboveground biomass. *J. roemerianus* did not grow taller in response to increased nutrient input in some studies (Levine et al. 1998; Pennings et al. 2005a), which was attributed to *J. roemerianus* being adapted to low nutrient availability because it is evergreen. However, *J. roemerianus* height increased by 4 % in response to fertilization in a Georgia marsh (McFarlin et al. 2008), although average height with fertilization (<115 cm) was below heights in our study. Pennings et al. (2002) also found a slight increase in *J. roemerianus* height in response to fertilization, but had mixed results for biomass depending on region. *J. roemerianus* was significantly taller in developed sites of Murrells Inlet in an earlier study (Walters et al. 2010), but leaf density and aboveground biomass did not differ between the developed and undeveloped sites.

Total aboveground biomass in our study ranged from 1,100 to 2,000 g/m², but approximately half of the aboveground biomass (600 to 1,100 g/m²) was dead indicating overcrowding and slow decomposition. Total aboveground biomass of *J. roemerianus* in a nontidal, North Carolina salt marsh was dominated by dead leaf tissue, averaging about 1,200 g/m², while living tissue averaged about 500 g/m² (Christian et al. 1990). Total autumn aboveground biomass

values in Georgia were not as great, averaging about 750 g/m² with only about 400 g/m² being standing dead *J. roemerianus* in control plots (McFarlin et al. 2008). Fertilized plots in Georgia contained only 500 g/m² total aboveground biomass with 275 g/m² being composed of standing dead *J. roemerianus* (McFarlin et al. 2008) because of increasing competition with *S. alterniflora* and decreasing *J. roemerianus* leaf density.

Increased aboveground biomass and relatively high plant nitrogen content resulted in increased plant nitrogen storage in the DVB sites. Hence, increased nutrient input may be occurring, but is not seen in soil concentrations because of increased plant uptake as well as other possible processes such as tidal flushing and denitrification by soil bacteria. Other forms of nitrogen, such as ammonium, also may have contributed to the pool of plant nitrogen, but were not measured. Many species, including *P. australis* and *Typha angustifolia* Linn., used in wetland restoration projects or in treatment wetlands are chosen for their fast growth, ability to oxygenate the soil, absorb nutrients, and control erosion (Brix 1997; Craft 2005). Our results from sampling extant plants show that *J. roemerianus* could be used to increase nutrient storage in degraded wetlands because of its ability to increase aboveground biomass to increase total storage. *J. roemerianus* is capable of storing nitrogen up to a point, but its use in remediating degraded marshes is problematic because of possible storage limits, sensitivity to transplant stresses (especially in summer), and low resistance to high levels of petroleum contamination (e.g., Lin and Mendelsohn 2009). Extended studies are needed to evaluate these possible limitations, especially in light of recent long-term studies showing unexpected changes to marsh plant assemblages in response to experimental nutrient addition (e.g., Deegan et al. 2012; Fox et al. 2012).

Belowground biomass was expected to decrease with increased aboveground biomass because increased nutrient availability should have shifted competition from nutrients to light. For example, belowground biomass of *S. alterniflora* and *S. patens* was reduced following 9 years of nutrient enrichment (Deegan et al. 2012). Instead, belowground biomass was extremely high, i.e., at least four times greater below- than aboveground. Similarly, belowground biomass of *J. roemerianus* did not decrease in response to nitrogen addition in Mississippi (Brewer 2003), and preexisting stands and the dense root and rhizome mass of *J. roemerianus* kept *S. alterniflora* from out-competing *J. roemerianus* for nutrients or invading the high marsh. Studies of competition at the *J. roemerianus*/*S. alterniflora* border have shown that fertilization increases *S. alterniflora* biomass while decreasing *J. roemerianus* biomass (Pennings et al. 2002, 2005a). We suspect that a similar reduction in *J. roemerianus* was not found in Murrells Inlet because *J. roemerianus* increased its aboveground biomass in response to nutrient input while maintaining high belowground

biomass. Teasing apart the reasons underlying the differences seen among these studies requires testing whether species-specific or marsh-specific mechanisms are more important.

Plant species diversity in existing assemblages and in recruits in the transplant experiment was similar across shoreline development categories. Considerable above- and belowground *J. roemerianus* biomass likely inhibited the establishment of fugitive species, *S. alterniflora*, and *P. australis* just as *J. roemerianus* inhibits *S. alterniflora* from invading the high marsh in Mississippi (Brewer 2003). Preventing establishment of new species is also enhanced by slow decomposition of standing dead *J. roemerianus* (Christian et al. 1990). Being an evergreen, *J. roemerianus* occupies space year round, takes up and stores nitrogen, and becomes very dense with increased development. Salinity levels and soil nitrogen levels were not different among shoreline development categories so it was unlikely that these parameters explained differences in transplant growth.

A key assumption of this study was that the high marsh would experience freshwater and nutrient loading because of runoff directly from the adjacent upland areas and that the presence of a strip of woody and shrubby vegetation would help mitigate the effects of runoff by filtering nutrients and freshwater. However, soil salinities and most soil nutrients were not different among developed and undeveloped areas indicating that soil conditions did not reflect development categories. Upland-to-wetland slopes at all sites were low, which could have minimized runoff and contributed to the lack of significant differences. Mean slopes at the DVB sites were lowest and may have led to reduced water flushing and increased inundation in the high marsh compared with other site types, although this difference did not lead to a marked change in salinity. Bank slope was positively correlated to dead ADFM, which may be an indication that longer duration of water at the DVB sites affected *J. roemerianus* productivity. Differences in elevation and inundation were important explanatory variables for changing plant productivity in a long-term fertilization study that included the high marsh in Massachusetts, USA (Fox et al. 2012). The DVB sites had borders of shrubby vegetation that were less than 5-m thick, yet the DVB sites had the highest *J. roemerianus* biomass in the marsh. The increased aboveground biomass and increased nitrogen storage indicate that the shrubby border in this study may not have reduced runoff or groundwater flow. Many studies have suggested that a riparian border must be 30 to 100-m wide to reduce runoff and sedimentation, increase nitrogen removal, and maintain species abundance and diversity (Castelle et al. 1994; Lowrance et al. 1997; Wenger 1999), and such widths are recommended in buffer ordinances in several states. It also was possible that flow bypassed these borders. Development in the Grand Strand of South Carolina is accompanied by the creation of storm water detention ponds and roadside and building-side

ditches to catch and divert storm runoff. Potential runoff to wetlands is diverted by these structures to tidal creeks or ocean waters possibly bypassing buffer and marsh vegetation altogether. In that case, tides may be primarily responsible for depositing sediment, nutrients, and pollutants onto the high marsh. The high marsh would then experience infrequent nutrient loading that would cause minimal or slow changes in plant structure and composition compared with the low marsh (Deegan et al. 2007). Examining runoff rates and diversion by roadside ditches and detention ponds in coastal areas could help to elucidate how nutrients and metals (i.e., zinc) are entering salt marshes.

Conclusions

A range of existing shoreline development was associated with different ecological conditions in the high marsh of Murrells Inlet estuary. Greater nutrient availability was reflected in increased aboveground biomass and greater nitrogen storage in *J. roemerianus* plant tissue in developed areas. High above- and belowground biomass of *J. roemerianus* likely inhibited establishment and growth of fugitive marsh species and invasive species such as *P. australis*. Greater soil zinc levels were detected in developed sites and may be a good indicator of development. Identifying ecological effects of anthropogenic activity using existing conditions, even when combined with experimental transplants, was challenged by variation in key factors such as shoreline slope. Nevertheless, recently accelerating shoreline development in the southeastern USA may have increasing effects on high-marsh plant production, nitrogen storage, and sediment metal content.

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