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Abbey Humphreys
William & Mary - Keck Lab

Adrianna L. Gorsky
William & Mary - Keck Lab

Donna Marie Bilkovic
Virginia Institute of Marine Science

Randolph M. Chambers
William & Mary - Keck Lab

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Changes in plant communities of low-salinity tidal marshes in response to sea-level rise

Abbey Humphreys,[1] Adrianna L. Gorsky,[1] Donna M. Bilkovic,[2] and Randolph M. Chambers[1,†]

[1]*Keck Environmental Lab, William & Mary, Williamsburg, Virginia 23187 USA*
[2]*Center for Coastal Resources Management, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062 USA*

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Abstract. As sea-level rises, low-salinity tidal marshes experience greater flooding with more saline water. In the Chesapeake Bay estuary, we compared the 1980 and 2014 tidal marsh inventories (TMIs) of plant communities from James City County, Virginia, USA, with respect to the spatial distribution of two species—the invasive reed *Phragmites australis* and native salt marsh grass *Spartina alterniflora*–plus overall species richness. Since the 1980 TMI, the total area of low-salinity tidal marshes in which *P. australis* occurred increased from 0.46 km^2 to 6.30 km^2 in 2014. Between TMIs, however, the total area of low-salinity marshes occupied by *S. alterniflora* increased by only 0.02 km^2. Species richness in low-salinity tidal marshes decreased from 41 to 25 between TMIs. To assess seedling emergence under increased flooding and salinity, we completed two seed bank germination experiments using soil samples collected from six low-salinity marshes containing established *P. australis* stands. In the first experiment, more seedlings emerged in the two low-salinity (0 vs. 5 ppt) treatments after seven weeks, irrespective of flooding (water 3.75 cm below vs. at soil surface), but no *P. australis* or *S. alterniflora* germinated. For the second experiment, we added seeds of *P. australis* and *S. alterniflora* to soils exposed to the same flooding and salinity treatments to test the impact of these plant competitors on seedling emergence. No difference in number of seedlings was detected among treatments, but the number of species and their relative abundance was significantly affected by flooding (ANOSIM, $R = 0.138$, $P < 0.001$). The presence of *P. australis* and *S. alterniflora* seedlings appeared to shift the physical factor more influential on seedling emergence from salinity to flooding. For both seed bank experiments, more seedlings but not more species emerged from soils collected from marshes where *P. australis* coverage was <50%. High diversity plant communities of low-salinity tidal marshes along the upper reaches of this estuary are gradually being replaced by those dominated by *P. australis* and *S. alterniflora*—a trend expected to continue here and in other riverine estuaries of the Atlantic and Gulf Coasts.

Key words: low-salinity tidal marshes; *Phragmites australis*; sea-level rise; seed bank germination; *Spartina alterniflora*.

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† **E-mail:** rmcham@wm.edu

Introduction

Low-salinity tidal marshes (0–5 ppt) are extensive along the upper reaches of large-river estuaries of many parts of the world, particularly along the Atlantic and Gulf Coasts of the United States (Odum et al. 1984, Perry et al. 2009). While specific plant composition may vary, general community types are similar among low-salinity tidal marshes (Perry et al. 2009). Unlike higher salinity, *Spartina alterniflora* dominated marshes located in mesohaline to polyhaline reaches, low-salinity marshes are characterized by a diverse plant community of scores of species living in freshwater to oligohaline tidal water (Odum 1988, Elsey-Quirk and Leck 2015). In addition to botanical diversity, low-salinity tidal marshes sequester carbon, are proficient at nutrient and sediment assimilation, and provide valuable nurseries for many fish species (Odum et al. 1984, Whigham et al. 2019).

Vegetated, low-salinity tidal wetlands face numerous environmental challenges that largely are associated with sea-level rise (Noe et al. 2013, Beckett et al. 2016, Palinkas and Engelhardt 2016). With sea-level rise, the influx of more water increases wetland hydroperiod, and wetlands that cannot accrete sediment to match rapidly rising waters may drown (Kirwan and Megonigal 2013, Weston 2014). Alternately, wetlands may migrate farther upstream or into adjacent undeveloped uplands if the elevation is gradual, but those opportunities may be limited adjacent to forests (Field et al. 2016) and along incised coastal plain river systems (Torio and Chmura 2013, Mitchell et al. 2020). The encroaching tidal water also brings additional salt, which is a stress to many of the plant species living in low-salinity tidal marshes (Spalding and Hester 2007, Neubauer 2013). The salty water may carry propagules of salt marsh species like *S. alterniflora*, thereby introducing both a physical stress (salt) and a potential plant competitor. Finally, many wetlands in the United States are experiencing expansion of non-native *Phragmites australis*—a competitive dominant species capable of rapid establishment and spread in tidal wetland environments experiencing saltwater intrusion (Chambers et al. 1999, Meyerson et al. 2000, Saltonstall 2002, Vasquez et al. 2005). Collectively, the plant diversity of low-salinity tidal wetlands is expected to change most dramatically with shifts in gradients of hydrology, salinity, and species distributions associated with rapid sea-level rise (Perry and Atkinson 2009, Sharpe and Baldwin 2012).

Seed banks play a critical role in the make-up of plant communities, as seeds persist longer under stress than the standing vegetation (Wang et al. 2008). Recruitment from the wetland seed bank is a primary determinant of plant community composition in low-salinity tidal marshes exposed to sea-level rise (DeBerry and Perry 2000, Sharpe and Baldwin 2012). Both seedling emergence and density are reduced with elevated salinity and prolonged inundation of tidal marsh soils (Baldwin et al. 1996, Baldwin et al. 2001, Peterson and Baldwin 2004). Of course, species first must reach the soil seed bank to germinate, and the pathways to arrival in low-salinity tidal marshes can vary. For example, water-borne *S. alterniflora* seeds may be introduced via saltwater intrusion (hydrochory; Elsey-Quirk et al. 2009), whereas *P. australis* seeds may be carried in by water or by the wind (anemochory; Soomers et al. 2013). The physical vectors of wind and water create opportunities for these species to spread into new wetland environments.

Given the ongoing pressures from sea-level rise, salt water intrusion, and invasive species (Whigham et al. 2019), we completed a study to assess potential changes in plant community structure associated with these pressures in selected, low-salinity tidal marshes of two large-river sub-estuaries of the Chesapeake Bay in southeastern Virginia (VA). Environmental pressures are exacerbated here, as the rate of relative sea-level rise in the Chesapeake Bay (recently measured at 4–6 mm/yr; Boon and Mitchell 2015, Ezer and Atkinson, 2015) is greater than the global average rate (~3.2 mm/yr; Church and White 2011, Ezer 2013). Models of sea-level rise in the region (Hilton et al. 2008, Rice et al. 2012) and qualitative observations (Sutter et al. 2015) suggest ongoing salinity intrusion. We used GIS to compare plant inventories in the 1970s and the 2010s, specifically noting changes in the spatial distribution of *S. alterniflora* and *P. australis* and overall species richness. Additionally, we used low-salinity marsh soils to conduct two seed bank germination experiments in a greenhouse setting. The first experiment examined seed germination as affected by the anticipated physical impacts of sea-level rise, that is, higher water table and higher salinity. The second experiment examined whether seed germination patterns would change in the presence of *S. alterniflora* and *P. australis* as novel plant competitors in low-salinity marshes. Collectively, we hypothesized that both *S. alterniflora* and *P. australis* coverage have increased with sea-level rise and that associated physical factors (increased flooding and salinity) and biological factors (increased novel competitors) negatively affect plant community structure.

Methods

Historical changes in plant distribution

This study was conducted in low-salinity tidal marshes in James City County, VA (465 km^2), bounded to the northeast by the York River and to the southwest by the James River subestuaries of Chesapeake Bay (Fig. 1). Tidal marsh inventories (TMIs) for the county were completed first between 1974 and 1980 (1980 TMI; CCRM 1992) and then more recently between 2010 and 2014 (2014 TMI; CCRM 2014, Mitchell et al. 2017). For both TMIs, we excluded marshes listed as dominated by saltmarsh cordgrass (*S. alterniflora*), saltmeadow hay (*S. patens*), black needlerush (*Juncus roemerianus*), and brackish/mixed communities, assuming the salinity of these marshes was mesohaline. With this operational definition, we designated all other marsh communities identified with freshwater species present as low-salinity tidal marshes, including Arrow Arum-Pickerelweed (*Peltandra virginica-Pontederia cordata*), Cattail (*Typha* spp.), Yellow Pond Lilly (*Nuphar* spp.), Big Cordgrass (*S. cynouroides*), Reedgrass (*P. australis*), and freshwater/mixed communities. ArcGIS 10 was used to determine changes in the areal extent and

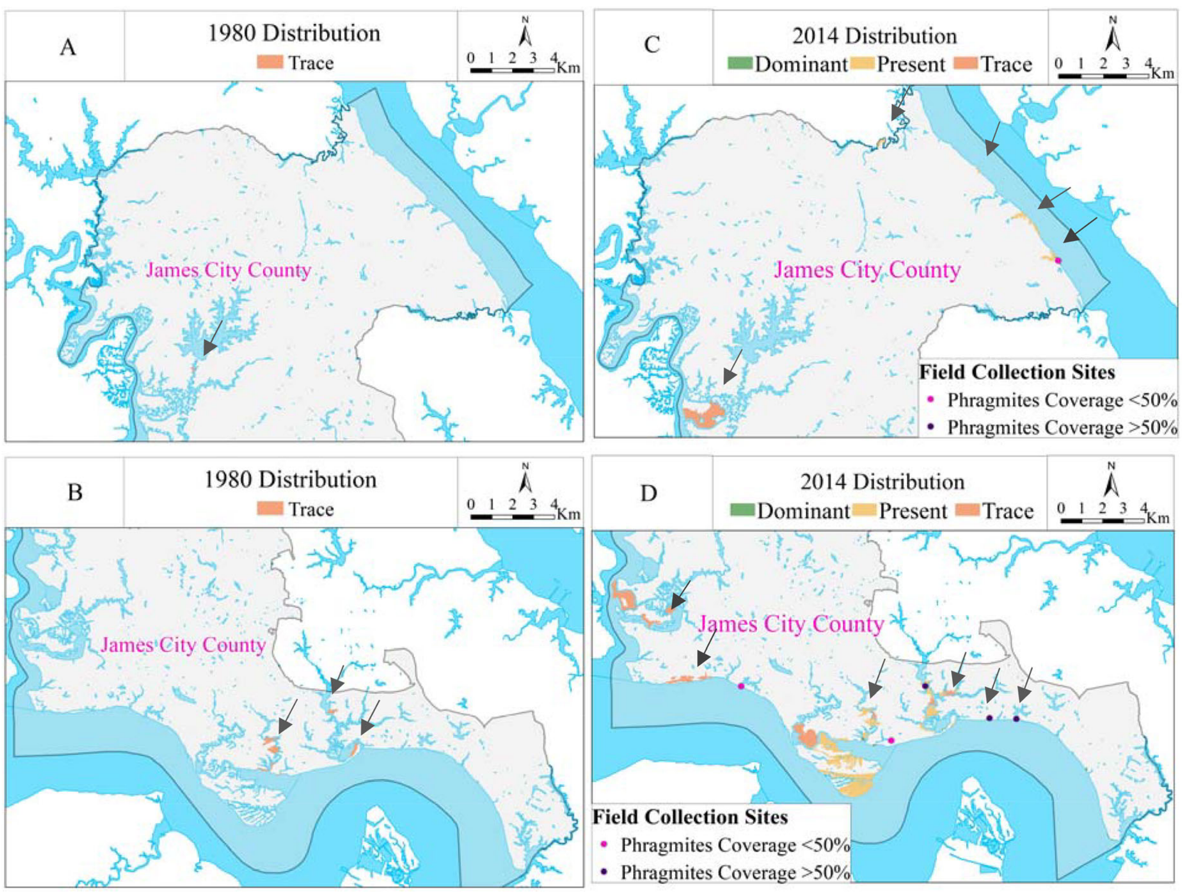

Fig. 1. The distribution of *P. australis* with three levels of occurrence (dominant, present, and trace) within low-salinity tidal marshes of James City County (divided into northern and southern portions) as reported from the 1980 (Maps A and B) and 2014 (Maps C and D) tidal wetland inventories. See Table 2 for the area of coverage in each cover class. Arrows point to smaller marshes in which *P. australis* was observed.

distribution of low-salinity marshes in which the invasive *P. australis* and native *S. alterniflora* occurred. The occurrence data for the invasive *P. australis* and native *S. alterniflora* were collected as cover classes (trace <1%, present 1–50% or dominant >50%); therefore, we reported the total area of low-salinity tidal marshes in which each cover class for *P. australis* occurred and for marshes in which the trace and presence cover classes for *S. alterniflora* occurred (by our definition, *S. alterniflora*-dominant marshes were not considered low-salinity marshes). For the 1980 TMI, species occurrence data were extracted from a hard copy report (Moore and Silberhorn 1980) and added to the GIS shapefile depicting historic marsh extent (CCRM 1992). The historical distribution of *P. australis* and *S. alterniflora* was then mapped by the cover class identified in the 1980 TMI. Similar maps were created for the 2014 TMI to determine changes in relative area of low-salinity marshes in which *P. australis* and *S. alterniflora* occurred.

Physical impacts of sea-level rise on seed germination

Soil samples were collected from six low-salinity tidal marsh sites in James City County. Based on the 2014 TMI, three sites were randomly selected from all low-salinity marshes in JCC with <50% *P. australis* coverage (present) and three sites were randomly selected with >50% *P. australis* coverage (dominant; Table 1). From each site, the top 2–5 cm of marsh soil, that is, the recent seed bank, was collected immediately adjacent to a *P. australis* stand during early March 2016, prior to seed bank germination. Before experimental setup, the soil samples were stored in the dark at 3°C to inhibit premature germination and maintain seed viability. For the experiment, individual 15-cm plastic nursery pots were filled with soil from the field samples and placed inside larger, 27 cm diameter tanks. We employed a 2 × 2 factorial design, with two flooding and two salinity treatments in triplicate for each of the six marsh soils: (1) no salt, no flood (NSNF) treatment: control pots with freshwater to within 3.75 cm of the soil surface; (2) no salt, flood (NSF) treatment: pots with freshwater to the soil surface; (3) salt, no flood (SNF) treatment: pots with brackish water to within 3.75 cm of the soil surface; (4) salt, flood (SF) treatment: pots with brackish water to the soil surface. Seed banks in the no flood treatments were unsaturated at the soil surface, whereas seed banks in the flooded treatments were fully inundated, with the water table at the soil surface. Brackish water for salt treatments (5 ppt salinity—a realistic elevation of salinity during spring when germination occurs) was made from Instant Ocean; freshwater was used for no-salt treatments. Salinity levels were monitored using a YSI handheld salinity meter, and freshwater was added to individual treatment tanks approximately weekly to replace water lost to evapotranspiration. Artificial lighting was set on 12-h periods in the greenhouse, and temperatures were maintained at 23°–24°C throughout the experiment. Each week for seven weeks during spring 2016, sprouted seeds in each pot were identified, counted, and monitored as part of the data collection protocol. For some seedlings, growth had to be extended for longer than seven weeks to allow for taxonomic identification.

Physical and biological impacts of sea-level rise on seed germination

For the second germination experiment, the same setup for testing physical impacts was used. The experimental pots were filled with soil from the same marsh sites, and the same 2 × 2

Table 1. Soil collection sites for seed germination experiments.

Site	River	*Phragmites* coverage	Salinity (ppt)	Latitude, Longitude
John Rolfe Marina	James River	Present (<50%)	0.9	37.239939, −76.810295
Treasure Island Road	James River	Present (<50%)	0.9	37.215163, −76.729937
Airport	James River	Dominant (>50%)	1.1	37.238217, −76.710586
Kingsmill Marina	James River	Dominant (>50%)	2.1	37.223019, −76.661722
Kingsmill Marsh	James River	Dominant (>50%)	4.4	37.223453, −76.676025
Riverview Road	York River	Present (<50%)	3.8	37.388550, −76.684567

Note: For each site, *Phragmites* coverage as listed in the 2014 plant inventory and surface water salinity as measured in spring 2016 is reported.

factorial design was employed, with four replicates per soil and salinity and flooding treatment group. To assess biological impacts, we scattered 20 of the larger *S. alterniflora* seeds and a sprinkling of approximately 50 of the smaller *P. australis* seeds across the surface of each pot of soil. The seeds of both species had been cold-stratified at 3°C prior to use but, neither seed fullness nor viability was tested before the experiment. After setup, the germination of *S. alterniflora*, *P. australis*, and seed bank species was monitored weekly for seven weeks in each of the 96 individual tanks (four replicates of six soils, with two salinity and two flooding treatments).

Data analysis

For both seed germination experiments, the cumulative number of seedlings present within each of the four treatment groups was plotted over seven weeks. Analysis of variance and *t*-tests compared the total number of seedlings present at week 7 by treatment group (salinity and flooding) and by soil source (marshes with <50% or >50% *P. australis* coverage). Analysis of variance compared the number of *P. australis* and *S. alterniflora* seedlings in each treatment group. The coefficient of community (Sorenson 1948) was used for qualitative comparisons of species occurrence between soil and flooding treatment pairs. Finally, an analysis of similarity (ANOSIM) determined the similarity of the seedling communities from each treatment group. Because soils from the York River site yielded no germination from any of the 12 pots in the first germination experiment, those results were not included in the ANOSIM. An additional 10 pots across all treatment types, however, also had no germination. To maintain a balanced sample design and reduce the analytical impact of pots with zero germination, 10 pots were randomly selected for removal from statistical analysis. This adjustment, which yielded the same number of samples in each treatment group, was repeated 10 times in ANOSIM for the first germination experiment. For both germination experiments, the final week's data distribution was normalized using a square root transformation; then, a similarity matrix was created in PRIMER 6.1. ANOSIM was then run on that similarity matrix, testing similarity among plant communities produced under each treatment. A two-way crossed ANOSIM with replicates was used with treatments (N = 4) and soils (N = 6) as factors.

Results

Historical changes in plant distribution

From the 1980 TMI, *P. australis* was found in trace amounts (<1% coverage) in just a few low-salinity tidal marshes in James City County (0.46 km^2). Since then, *P. australis* occurrence has increased dramatically throughout the county (Fig. 1). *P. australis* now is more widespread along the York River and lower portion of the county along the James River (dominant in 0.07 km^2, present in 3.27 km^2, trace in 2.96 km^2). Between TMIs, the total area of marshes in which *P. australis* occurred increased from 0.46 km^2 to 6.30 km^2 (Table 2).

Spartina alterniflora already was found in several low-salinity tidal marshes in the 1980 TMI (Fig. 2; present in 1.93 km^2 and found in trace amounts in 0.16 km^2). In the 2014 TMI, marsh areas with *S. alterniflora* present had increased slightly to 2.10 km^2 and those with trace amounts had decreased to 0.01 km^2. Additionally, the occurrence of *S. alterniflora* in low-salinity tidal marshes along the James River moved farther upstream between 1980 and 2014 (Fig. 2). The total area of low-salinity tidal marshes in which *S. alterniflora* occurred, however, was only 0.02 km^2 higher in the 2014 TMI

Table 2. Total area (km^2) of low-salinity tidal marshes in James City County, VA, in which *Phragmites australis* and *Spartina alterniflora* were found in the 1980 and 2014 tidal marsh inventories, with the difference between dates in total area of each cover class shown.

Species	1980	2014	Difference
Phragmites australis			
Dominant	0	0.07	+0.07
Present	0	3.27	+3.27
Trace	0.46	2.96	+2.50
Spartina alterniflora			
Present	1.93	2.10	+0.17
Trace	0.16	0.01	−0.15
Total area of low-salinity marshes	26.61	22.41	−4.20
Total area of mesohaline marshes	2.53	1.91	−0.62

Note: Total areas of low-salinity and mesohaline salinity marshes are also shown.

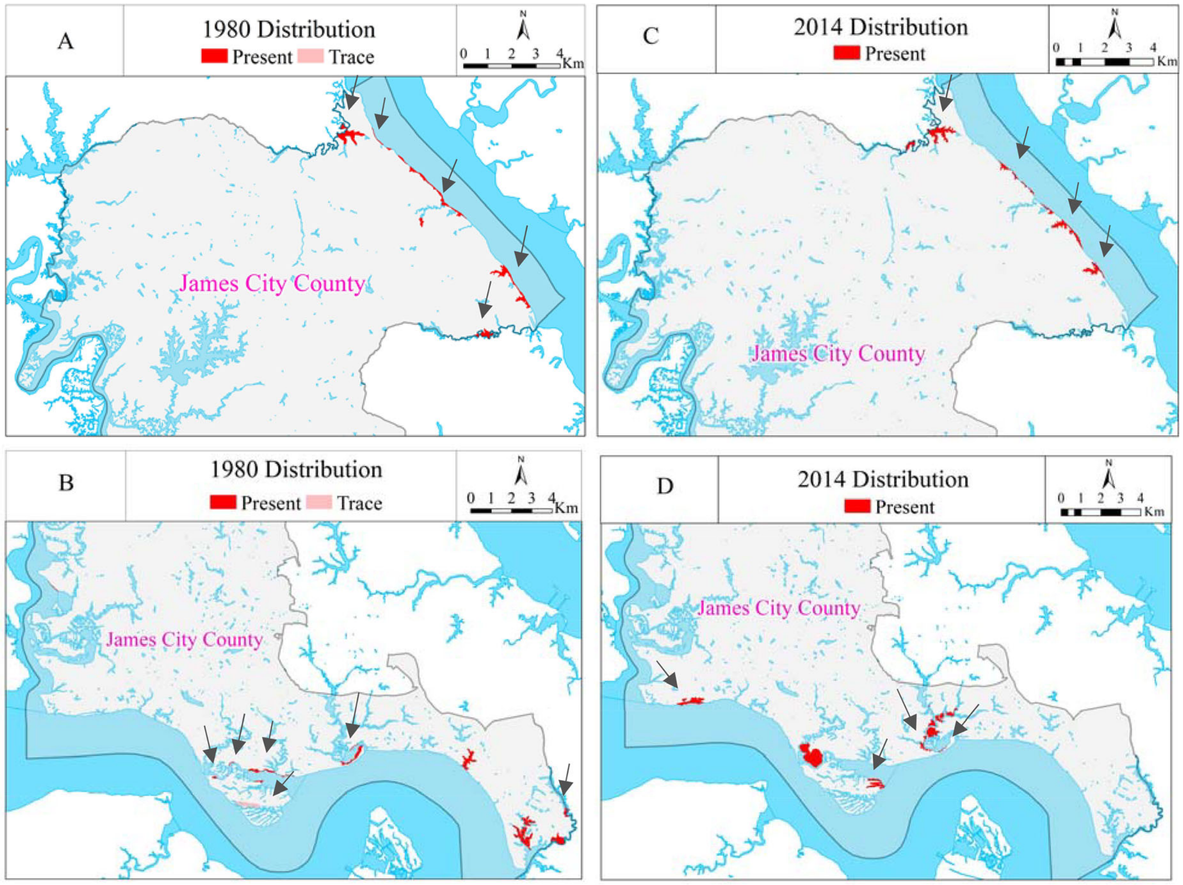

Fig. 2. The distribution of *Spartina alterniflora* with two levels of presence (present and trace) within low-salinity tidal marshes of James City County (divided into northern and southern portions) as reported from the 1980 (Maps A and B) and 2014 (Maps C and D) tidal wetland inventories. See Table 2 for the area of coverage in each cover class. Arrows point to smaller marsh areas in which *S. alterniflora* was recorded.

relative to 1980 (Table 2). The total area of low-salinity tidal marsh in James City County in the 1980 TMI was 26.61 km^2; in the 2014 TMI, the area of marsh was 16.95 km^2 (Table 2).

A total of 41 plant species were recorded from the 1980 TMI, including shrubs, forbs, grasses, rushes, sedges, and trees, with 25 recorded from the 2014 TMI (Table 3). Twenty-three species were common to both TMIs, 18 present in 1980 were absent in 2014, and two new species were listed in 2014.

Physical impacts of sea-level rise on seed germination

Germinating plants were observed in 45 of the 72 pots in the first germination experiment testing the effects of flooding and salinity. Over the seven weeks of the experiment, a total of 251 plants comprising 21 species germinated, of which 242 were alive at week 7, yielding an average of 3.4 ± 0.7 SE seedlings per pot, and 12–16 species per treatment group. *Eleocharis acicularis* was numerically dominant (30.5% of all seedlings) and germinated in 20 of the pots. *Zizania aquatica* was found in 15 pots, and *Persicaria punctata* was found in 10 pots. The rarest species were *Sagittaria subulata*, *Rumex verticillatus*, *Eupatorium perfoliatum*, *Hypericum mutilum*, *Chenopodium album*, and *Amaranthus cannabinus*, occurring separately in just one pot each. Five species were found only in the saline treatments (*Amaranthus cannabinus*, *Hypericum mutilum*, *Bidens laevis*, *Rumex verticillatus, Sagittaria subulata*), and five species were found only in fresh

Table 3. List of species identified in the tidal marsh inventories (TMIs) from 1980 and 2014, plus species identified in the first and second germination experiments.

Species	Group	1980 TMI	2014 TMI	First study	Second study
Acer rubrum	T		X		X
Althaea officinalis	F	X			
Amaranthus cannabinus	F	X	X	X	X
Ambrosia artemisiifolia	F			X	X
Asclepias incarnata	F	X			
Aster tenufolius	F	X			
Atriplex spp.	F	X	X		
Bidens laevis	F	X		X	
Carex spp.	S	X		X	X
Cephalanthus occidentalis	B	X	X		
Chenopodium album	F			X	
Cinna arundinacea	G	X			
Cuscuta spp.	F	X			
Decodon verticillatus	F	X			
Echinochloa walteri	G	X			X
Eleocharis acicularis	S			X	X
Eupatorium perfatolum	F			X	
Hibiscus coccineus	F	X	X		
Hypericum mutilum	F			X	
Impatiens capensis	F	X			
Juncus spp.	R	X	X	X	X
Leersia oryzoides	G	X	X	X	X
Lilaeopsis chinensis	F			X	
Lobelia cardinalis	F	X			
Lythrum lineare	F	X			
Mikania scandens	F	X			
Nelumbo lutea	F	X			
Nuphar spp.	F	X	X		
Nyssa sylvatica	T	X			
Panicum virgatum	G	X	X		
Peltandra virginica	F	X	X	X	X
Persicaria punctata	F	X	X	X	X
Phalaris arundinacea	G				X
Phragmites australis	G	X	X		X
Pluchea odorata	F	X		X	X
Polygonum arifolium	F	X			
Pontederia cordata	F	X	X		
Rosa palustris	B	X			
Rumex verticillatus	F	X	X	X	
Sagittaria spp.	F	X	X	X	X
Schoenoplectus americanus	S	X	X		
Scirpus spp.	S	X	X	X	X
Spartina alterniflora	G	X	X		X
Spartina cynosuroides	G	X	X		
Spartina patens	G	X	X		
Taxodium distichum	T	X	X		
Thelypteris palustris	F		X		
Typha spp.	F	X	X		
Vernonia noveboracensis	F	X	X		
Zizania aquatica	G	X	X	X	
Totals		41	25	18	16

(Table 3. Continued.)

Note: Owing to lack of species-level information for some genera from the TMIs, species within the same genus are combined. Functional groups are abbreviated B, shrub; F, forb; G, grass; R, rush; S, sedge; T, tree.

treatments (*Chenopodium album*, *Carex stricta*, *Pluchea odorata*, *Eupatorium perfoliatum*, *Sagittaria lancifolia*).

Each week over the seven weeks of observation, the cumulative number of seedlings present was consistently higher for the two freshwater treatments than for the saltwater treatments (Fig. 3). By week 7, significantly more seedlings germinated in the freshwater treatments (NSNF + NSF), relative to the saltwater treatments (SNF + SF; ANOVA $F_{(1,14)} = 5.29$, $P = 0.03$). The cumulative number of species present in each treatment group was similar (16, 14, 12, and 13 for NSNF, NSF, SNF, and SF, respectively). More seedlings were produced from soil sites with <50% *P. australis* coverage (13.6 ± 3.9 SE), relative to sites with >50% *P. australis* coverage (6.6 ± 1.9 SE; ANOVA $F_{(1,16)} = 6.32$, $P = 0.013$; Fig. 4). The treatment × site interaction, however, was not significant, indicating that the observed patterns associated with salinity, flooding, and *P. australis* coverage were consistent among sample locations. Across the four treatment groups, the total number of species that emerged from sites with <50% *P. australis* coverage was significantly lower than from sites with >50% coverage (7.5 ± 1.5 SE vs. 9.5 ± 0.4 SE; *t*-test, $P = 0.02$).

The number of common species between flooding and salinity treatment groups ranged from four to nine, and total species observed ranged from 25 to 30 (Table 4). The treatments with the most common species and highest coefficient of community (CoC) were NSF and SNF (CoC = 0.62), followed by NSNF and NSF (CoC = 0.60). The SNF and SF treatments shared the fewest common species and had the lowest community coefficient (CoC = 0.32). Overall, no effect of salinity, flooding, or salinity × flooding was

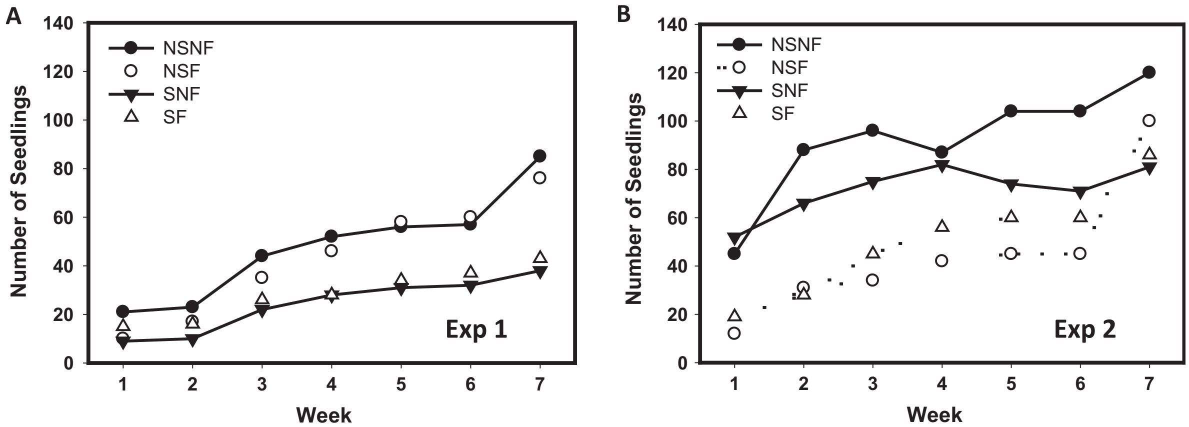

Fig. 3. Cumulative number of seedlings present in the four treatments across the 7 weeks of germination experiments 1 and 2 (A and B, respectively). Abbreviations are NSNF, no salt, no flood; SNF, salt, no flood; NSF, no salt, flood; SF, salt, flood.

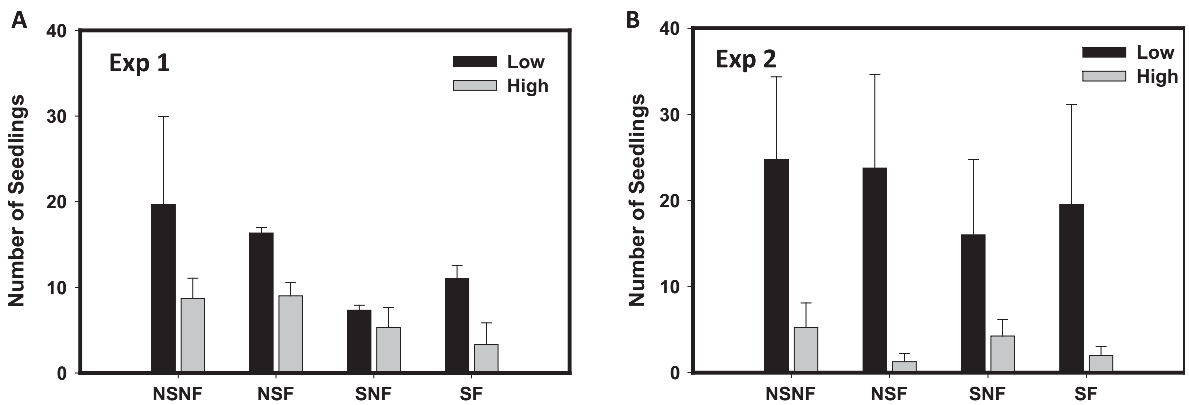

Fig. 4. For germination experiments 1 (N = 3) and 2 (N = 4; A and B, respectively), comparison of average seedling number ± SE after seven weeks in soils collected from marshes with <50% *Phragmites* (low) and >50% *Phragmites* (high). NSNF, no salt, no flood; SNF, salt, no flood; NSF, no salt, flood; SF, salt, flood.

found on the number of species and their relative abundance in week 7 of the germination experiment (ANOSIM, $P > 0.05$).

Physical and biological impacts of sea-level rise on seed germination

Germinating plants were observed in all 96 pots in the second germination experiment, with 1972 germinating plants present at the end of the experiment, representing 16 species (Table 3). Of these seedlings, 513 were *S. alterniflora* and 1072 were *P. australis*. By week 7, *P. australis* was found in 78 out of 96 pots and had germinated at some point in all but five pots (average number of seedlings = 11.8 ± 9.5). Similarly, *S. alterniflora* was found in 79 out of 96 pots and had germinated at some point in all pots (average number of seedlings = 5.3 ± 4.9). The numbers of germinated *P. australis* and *S. alterniflora* seeds were not significantly different among flooding or salinity treatments (*P. australis* $F_{(3,87)} = 0.94$, $P = 0.43$; *S. alterniflora* $F_{(3,92)} = 0.32$, $P = 0.81$).

A total of 387 seedlings from other species were present after week 7, yielding an average of 4.0 ± 0.4 SE seedlings per pot. *Eleocharis acicularis* was overwhelmingly the numerical dominant (79.8% of all seedlings). Relative to the first germination experiment, fewer species

Table 4. Plant community comparison among treatment pairs for the first germination experiment.

Comparison	Common species	Total species	Coefficient of community
NSNF vs. SNF	6	28	0.43
NSNF vs. SF	7	29	0.48
NSF vs. SNF	8	26	0.62
NSF vs. SF	6	29	0.41
NSNF vs. NSF	9	30	0.60
SNF vs. SF	4	25	0.32

Note: Abbreviations are NSNF, no salt, no flood; SNF, salt, no flood; NSF, no salt, flood; SF, salt, flood.

Table 5. Plant community comparison among treatment pairs for the second germination experiment.

Comparison	Common species	Total species	Coefficient of community
NSNF vs. SNF	6	23	0.52
NSNF vs. SF	6	19	0.63
NSF vs. SNF	4	17	0.47
NSF vs. SF	3	13	0.46
NSNF vs. NSF	6	18	0.67
SNF vs. SF	4	18	0.44

Note: *Phragmites* and *Spartina* seedlings are not included in the comparisons. Abbreviations are NSNF, no salt, no flood; SNF, salt, no flood; NSF, no salt, flood; SF, salt, flood.

germinated in these soils seeded with *P. australis* and *S. alterniflora* (Table 3), with 6–12 additional species observed per treatment group. *Persicaria punctata*, *Schoenoplectus robustus*, *Echinochloa walteri*, and *Juncus acuminatus* were found in all the treatments. The forbs *Peltandra virginica* and *Pluchea odorata* were only found in the non-flooded brackish treatment. *Amaranthus cannabinus* was only found in the non-flooded freshwater treatment. *Acer rubrum*, *Sagittaria subulata*, and *Carex albolutescens* were only found in the flooded freshwater treatment.

Over the first six weeks of observation, the cumulative number of these additional seedlings was higher for the two non-flooded treatments (NSNF + SNF) relative to the flooded treatments (NSF + SF; Fig. 3). The ANOVA comparing the average number of seedlings other than *S. alterniflora* and *P. australis* at week 7, however, was not significant between non-flooded and flooded treatments (ANOVA $F_{(1,14)} = 0.004$, $P = 0.948$), but more species germinated from non-flooded vs. flooded treatments (12, 11, 6, and 7 for NSNF, SNF, NSF, and SF, respectively). Significantly more seedlings were produced among soil sites with low *P. australis* coverage (21 $\pm$ 4.7 SE), relative to sites with high *P. australis* coverage (3.2 $\pm$ 0.9 SE; ANOVA $F_{(1,24)} = 11.7$, $P = 0.002$; Fig. 4). The treatment $\times$ site interaction, however, was not significant. Across treatments, the total number of species that emerged from sites with <50% *P. australis* coverage was not significantly different from sites with >50% coverage (4.0 $\pm$ 1.0 SE vs 5.8 $\pm$ 4.8 SE; *t*-test, $P > 0.05$).

With the addition of *P. australis* and *S. alterniflora* seed germination, the number of common species germinating between soil and flooding treatment groups ranged from three to six, and total species observed ranged from 13 to 19 (Table 5). The treatments with the highest coefficient of community were NSNF and NSF (CoC = 0.67). The SF and NSF treatments shared the fewest common species and lowest community coefficient (CC = 0.44). Among treatments, the community differences were significant with respect to flooding (ANOSIM, $R = 0.138$, $P < 0.001$) but not with respect to salinity or the flooding $\times$ salinity interaction.

Eleven species were common to both germination experiments, and six species were common to both tidal marsh inventories and both germination experiments, including five perennial species (*Amaranthus cannabinus*, *Juncus* spp., *Leersia oryzoides*, *Peltandra virginica*, and *Sagittaria* spp.) and one annual species (*Persicaria punctate*; Table 3).

Discussion

Results comparing tidal marsh inventories in James City County from 1980 and 2014 are consistent with the ongoing invasion and spread of non-native *P. australis* into tidal wetlands of North America (Fig. 1; Chambers et al. 1999). Mechanistically, disturbance caused by increased salinity and inundation as stressors to freshwater species (Hazelton et al. 2014) may contribute to the expansion of *P. australis* into low-salinity marshes. The observed decrease in species richness between inventories from 41 to 25 (Table 3) could be due to fewer species adapted to increased salinity and inundation associated with sea-level rise in these low-salinity marshes. *P. australis* is tolerant of both salinity and flooding (Chambers et al. 2003), and results from our second germination experiment showed no difference in *P. australis* seedling germination with respect to salinity or flooding. *P. australis* therefore may be able to exploit windows of opportunity for expansion and spread created by the die-off of other less tolerant species (Sutter et al. 2015).

Alternately, clonal growth of *P. australis* in dense stands may physically inhibit the growth of other species via shading by shoots, by litter, or by direct displacement (Meyerson et al. 2000, Minchintin et al. 2006, Holdredge and Bertness 2011). From both germination experiments, we observed significantly fewer seedlings of other species from marsh soils where *P. australis* was dominant (Fig. 4). More species germinated from those *P. australis*-dominant *soils in the first experiment, but fewer total seedlings were observed in both experiments, perhaps due to smaller seed banks. Low-salinity marshes in James City County are transitioning to increased dominance by P. australis*, for which its invasive ability may be exacerbated by both ongoing recruitment of its seeds to the seed bank (Baldwin et al. 2010) and the inhibitory effects of increased salinity and flooding from sea-level rise on seed germination by native species.

From the 1980 and 2014 TMIs, we did not detect a large difference in the areas of low-salinity marshes where *S. alterniflora* occurred. On the James River, *S. alterniflora* appeared in marshes farther upstream in the 2014 TMI, consistent with the ongoing penetration with sea-level rise of both saltwater and *S. alterniflora* propagules into low-salinity marshes. *S. alterniflora*, however, did not always persist in marshes where it was found in 1980. Our results are similar to another recent study showing that *S. alterniflora* is becoming more prominent in some but not all freshwater tidal marshes regionally (Sutter et al. 2013). The ability of *S. alterniflora* to establish and expand into low-salinity tidal marshes lends little support for the competition stress theory which would predict competitive exclusion of *S. alterniflora* by a more diverse assemblage of plants (Sutter et al. 2013). Our second germination experiment indicated that, similar to *P. australis*, seed germination of *S. alterniflora* was not inhibited by salt, by flooding, or by the presence of seedlings of other species. Sporadic tidal flows of salt water during summer periods of low freshwater runoff may initially increase the salinity level in these low-salinity marshes and convey *S. alterniflora* propagules at the same time. With seed delivery, opportunities exist for germination and establishment of *S. alterniflora* at low marsh elevations, with ample space for *S. alterniflora* to thrive under increased inundation levels. We doubt that *P. australis* as a high marsh species is excluding establishment of the low marsh *S. alterniflora* (but see Medeiros et al. 2013).

The established presence of *S. alterniflora* in many York River and lower James River marshes from the 1980 TMI (Figs. 2 and 3) and its seed distribution via hydrochory would indicate that propagules had previously been carried into these marshes. Some low-salinity marshes experience cyclical, temporal shifts in abundance of *S. alterniflora* versus freshwater perennial species owing to interannual variation in freshwater river flows and/or local groundwater discharge (Davies 2004). We found that the distribution of *S. alterniflora* changed between 1980 and 2014 but did not increase in total marsh area, suggesting the effects of short-term variation may still be a larger influence on *S. alterniflora* occurrence than longer-term forcing by sea-level rise (Perry et al. 2009). Because our second germination experiment showed that *S. alterniflora* seedling emergence was not impacted by salinity or flooding, we suspect that emergence of perennial freshwater species (i.e., not from the seed bank but from established root/rhizome stock) may inhibit emergence of perennial *S. alterniflora* during fresher conditions, but that salt may inhibit freshwater species during more salty conditions. Of six native species common to both TMIs and to both germination experiments (Table 3), five are perennial. These species may be more important than annuals in resisting the spread of *S. alterniflora* into low-salinity marshes, as the germination of annuals is much less consistent in space and time (Hopfensperger et al. 2009).

From the first germination experiment, the physical effect of salinity reduced the number of seedlings emerging from the seed bank more than flooding, with significantly more seeds, but not species, germinating in the two no-salt treatments relative to the two salt treatments (Fig. 3). Further, the coefficient of community was low for the two comparisons for which flooding was held constant (NSNF vs. SNF = 0.43; NSF vs. SF = 0.41; Table 4). This result of a salinity effect greater than flooding has been observed in prior studies of seed germination in low-salinity tidal wetlands (Sharpe and Baldwin 2012, Sánchez-García et al. 2017). For germination studies that tested flooding separately from salinity, however, flooding was also shown to decrease seedling emergence (Peterson and Baldwin 2004, Delgado et al. 2018, Sloey and Hester 2019). Indeed, our measured coefficient of community was lowest between the SNF and SF treatments (0.32; Table 4), so both flooding and salinity are physical factors affecting seed germination and plant success (Middleton 2016).

When both *S. alterniflora* and *P. australis* seeds were added to the seed bank, a different effect was observed with respect to emergence of other species. First, fewer seedlings of other species emerged from flooded treatments over the first six weeks of observation (Fig. 3). During week 7, the effect was altered by the emergence of large numbers of *Eleocharis acicularis* seedlings in both flooded treatments, similar to germination results obtained by Baldwin et al. (1996). Fewer species were observed in the two flooded treatments relative to the two non-flooded treatments, and ANOSIM analysis of seedling species and relative abundance found a significant effect of flooding. The coefficients of community, however, were difficult to interpret, as the most similar treatments were NSNF and NSF (0.67; Table 5), which we thought would have the fewest common species. Also, the average number of other seedlings per pot was not significantly different in the presence or absence of *P. australis* and *S. alterniflora* seedlings (4.0 vs. 3.3 seedlings, respectively).

Schile et al. (2017) suggested that the combined effects of physical stress and competitive stress can create unexpected synergies regarding plant performance. We documented small differences in seed bank germination with the presence of *S. alterniflora* and *P. australis* seedlings (Fig. 3, Table 5), but other factors (salinity, flooding, dominance of *P. australis* in the source marsh) appeared to be more important. The mechanisms behind the observed shift in relative impact of flooding and salinity on the germination and success of other species are unknown. Belowground competition for water and nutrients by *S. alterniflora* and *P. australis* roots, for example, could reduce tolerance of other species to flooding. Biotic interactions appear to alter how physical stresses are manifest in plant performance (Schile et al. 2017).

Over time in these low-salinity marshes, salinity, water level, and the number of introductions of *S. alterniflora* and *P. australis* are expected to rise. We expect *P. australis* will continue to expand clonally and with seed dispersion via anemochory and perhaps also hydrochory (Baldwin et al. 2010), as seeds in our second experiment germinated under all experimental salinity and flooding conditions. Although prior research suggests that *S. alterniflora* coverage in these low-salinity marshes appears to expand and contract in the short term among sampling years (Perry and Hershner 1999, Davies 2004, Perry et al. 2009), conversion to mesohaline plant communities dominated by *S. alterniflora* is expected to occur eventually (Fig. 2). Plant communities in these low-salinity marshes are expected to become less diverse with sea-level rise, with both *P. australis* and *S. alterniflora* becoming more extensive in total area. The short-term persistence of salt-tolerant native species, including *Eleocharis acicularis*, *Persicaria punctata*, *Juncus* spp., *Leersia oryzoides*, *Schoenoplectus americanus,* and *Zizania aquatica,* is also expected.

To preserve diversity in low-salinity tidal marshes along the east coast of the United States, management actions should continue to focus on *P. australis* control. With sea-level rise, low marsh areas exposed to greater inundation, salinity, and *S. alterniflora* propagules will be difficult to manage. As a high marsh species, however, *P. australis* is in competition with native plant species that occur at or above mean high water and can maintain their populations above thresholds of increasing inundation (Delgado et al. 2018). Also, the diversity of seed banks in marshes invaded by *P. australis* remains high (Baldwin et al. 2010; this study), so control of the invader could promote the diversity of native species. Relatively effective methods of *P. australis* management include targeting small stands with herbicides and introducing herbivory (Hazelton et al. 2014). Also, marshes may be more or less susceptible to *P. australis* invasion owing to their relative exposure to wind and water that deliver propagules and increase genetic diversity and expansion rates of invasive stands (Baldwin et al. 2010). Because *P. australis* management can be costly to maintain, simultaneous restoration of disturbed tidal marshes, maintenance of existing tidal marshes in the face of development, and creation of new tidal marshes where possible may aid in preserving the diversity of low-salinity tidal marshes and their ecosystem functions under the increasing threat of sea-level rise.

Conclusion

The physical and biological manifestations of sea-level rise negatively influence plant communities in low-salinity tidal marshes. Physically, the germination and establishment of other species are reduced by increased salinity and flooding regimes. Biologically, the introduction of *P. australis* and *S. alterniflora* reduces the number of other species and, additionally, shifts the relative importance of salinity and inundation on seedling germination and establishment. Further, soils from tidal wetlands dominated by *P. australis* germinate fewer total seedlings relative to soils from wetlands where *P. australis* is not dominant. Without management, low-salinity tidal marshes along the upper reaches of estuarine river systems from the Atlantic and Gulf coasts of the United States will have to migrate upstream in response to sea-level rise as their prior, high diversity plant communities are replaced by those dominated by *P. australis* and *S. alterniflora*.

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