Seawater intrusion mediates species transition in low salinity, tidal marsh vegetation

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ABSTRACT

In a transitioning tidal freshwater marsh (TFM) experiencing relative sea-level rise, the native vegetation community has been introduced to both an abiotic stressor (salt) and a new plant competitor (*Spartina alterniflora*). Within a narrow salinity range (0–3), we examined the interplay between salt stress and plant interactions by comparing growth and nutrient status of *S. alterniflora* grown alone and in the presence of one of three TFM species (*Leersia oryzoides*, *Peltandra virginica*, and *Phragmites australis*). We conducted a mesocosm study pairing *S. alterniflora* with a TFM plant or a conspecific and subjecting the pairs to sub-lethal levels of salinity (0, 1.5, and 3). Measured plant traits included net photosynthesis (A_{net}), aboveground and belowground biomass and tissue carbon (C), nitrogen (N), phosphorus (P), and their corresponding ratios. Relative to *S. alterniflora* grown alone, the presence of either TFM grass (*L. oryzoides* and *P. australis*): (1) altered *S. alterniflora* A_{net}, (2) suppressed *S. alterniflora* biomass accumulation aboveground and belowground in all salinity treatment levels, and (3) altered aboveground and belowground tissue nutrient content. Regardless of neighbor, *S. alterniflora*'s growth and nutrient status was greatest at the lowest salinity and remained largely unchanged in the presence of *P. virginica*. These results suggest that *S. alterniflora* can successfully expand into TFM communities. Once established, salt stress eventually may hasten the transition to a *S. alterniflora*-dominated marsh community. The success of *S. alterniflora* may allow these marshes to maintain vegetation and increase their likelihood of maintaining elevation with rising sea level.

1. Introduction

Many species of tidal marsh plants are tolerant of temporal variation in salinity (interannual, seasonal, and even tidal), and individual species have general ranges of salinity tolerance that determine where in the estuary they are typically found. *Spartina alterniflora* Loisel., for example, is the dominant salt marsh species throughout Eastern and Gulf coasts of the U.S., forming expansive monospecific stands in oligohaline to polyhaline marshes (Mitsch and Gosselink, 2000). In contrast, a diverse assemblage of species adapted to low salinity occurs in tidal freshwater marshes (TFMs) (Odum et al., 1984; Odum, 1988; Perry and Atkinson, 1997). With rising sea level, the TFM plant community transition is especially dynamic, as even small amounts of seawater intrusion into TFMs

can lead to changes in species distributions (Perry and Atkinson, 1997; Swarth et al., 2013).

Plant species found in stressful environments like saline wetlands have physiological tolerance or adaptations to salt stress. In higher salinity environments, plants use energy for maintaining osmotic balance rather than for growth. Crain et al. (2004) demonstrated that *S. alterniflora* accumulated more biomass in freshwater relative to saltwater. Plant distribution in more benign, low-salinity, environments is believed to be dictated not by physiological tolerance, but by biotic factors such as competition (Grime, 1977). Pennings et al. (2005) determined that *S. alterniflora*'s upper estuarine range distribution (*i.e.*, at low salinity) was established by competition, and Crain et al. (2004) found more *S. alterniflora* biomass in the absence of competition. Vegetation zones often correlate well with salinity tolerances (Callaway et al., 1990; Greiner La Peyre et al., 2001).

Previous work generally found that plants are poorer competitors in the presence of salt (*e.g.*, Cooper, 1982; Hellings and Gallagher, 1992); studies investigating the interaction between salinity and competition mostly looked at higher levels of salinity,

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but even low salinity treatments (0, 2, 4, and 8) have been shown to influence species abundance (Greiner La Peyre et al., 2001). Greiner La Peyre et al. (2001) found that as the species were more stressed by salt, competition became less important. A recent study of competition between *S. alterniflora* and *Phragmites australis* (Cav.) Trin. Ex Steud. found both salinity and competition negatively affected biomass of both species, although *P. australis* had a disproportionate decline in biomass relative to *S. alterniflora* in salinity treatments of 10 and 28 (Medeiros et al., 2013). Plants that can withstand a more saline environment can shift individual plant traits, such as tissue C:N and N:P, which may have implications for speed of growth (Eskalinen et al., 2012), system nutrient pools or limitations (Baldwin, 2013), and herbivory (Couture et al., 2010).

Vegetation changes in tidal marshes in the eastern U.S. and Europe have been attributed to seawater intrusion facilitated by sea-level rise (Perry and Hershner, 1999; Engels and Jensen, 2010; Sharpe and Baldwin, 2012). Local hydrodynamics at Sweet Hall Marsh (Virginia, USA; 37°34′N, 76°53′W) have created areas of the marsh where salinity is higher than other areas, with pore water salinity ranging from 0.4 to 4.9 with a mean just over 2 (Sutter, 2014). Water column salinity at a nearby water-quality monitoring station spanned 0–15.4 and averaged 2.8 between 2009 and 2012, with annual means ranging from 1.4 in 2011, 2.8 in 2009 and 2012, to 4.0 in 2010 (NOAA, 2013). Vegetation composition in the area undergoing greater seawater intrusion has been documented since 1981; historically, species with high importance values (*sensu* Mueller-Dombois and Ellenberg, 1974) include *Peltandra virginica* (L.) Schott (a C3 broad-leafed freshwater plant) and *Leersia oryzoides* (L.) Sw. (a freshwater C3 freshwater grass; Perry and Hershner, 1999; Davies, 2004). We observed large, monospecific stands of *S. alterniflora* in a section of Sweet Hall Marsh for the first time in the fall of 2010 after dominant TFM vegetation senescence.

Moving downstream through estuarine environments, a vegetative transition occurs where freshwater moves into saltwater as rivers flow to the ocean. Sea-level induced salinity intrusion, however, has reversed that perspective as the salt front moves upstream and alters the tidal freshwater environment. Given the recent expansion of *S. alterniflora* into Sweet Hall Marsh (Sutter, 2014), a TFM transitioning to oligohaline marsh, our objective was to test in a controlled mesocosm experiment how interactions between *S. alterniflora* (at the putative competitive limit to its distribution) and three TFM species (two at the salinity-imposed physiological limit to their distribution and one cosmopolitan species found in freshwater to lower polyhaline environments, including TFM) varied along a small-range, salinity-stressor gradient between fresh and oligohaline water. Focusing research on a narrow range of salinity can help identify mechanisms behind the ongoing shift in species distributions. Our overall goal was to determine the relative influence of biotic and abiotic stressors on the observed species transition to *S. alterniflora* in a TFM.

2. Methods

2.1. Experimental design

We obtained nursery-raised individuals (Naturescapes Wetland Plants; Suffolk, VA) of three perennial, wetland vascular plant species: *S. alterniflora* (a C4, facultative halophytic grass), *P. virginica*, and *L. oryzoides*. *P. australis* (a C3, salt-tolerant grass) rhizomes were excavated from Sweet Hall Marsh in late winter, cut to approximately 5 cm across the nodes and potted until sprouts emerged. We did not test the haplotype of the specific *P. australis* rhizomes selected, but seven samples taken in the vicinity were genetically identified as the native haplotype (L.A. Meyerson, pers.

Table 1
Mean salinity achieved over the study period for each treatment in the experimental unit (tub) and within each pot containing a species mixture.

Salinity treatment		Tub		Pot (porewater)	
		Mean	SE	Mean	SE
0	Low	0.2	0.005	0.35	0.01
1.5	Medium	1.6	0.04	2.1	0.06
3	High	2.8	0.06	3.5	0.1

comm.). Propagules of the same height of each plant were chosen to create similar baseline conditions. Each *S. alterniflora* propagule was potted in sand outdoors in a 7.5 L container (220 cm top diameter; 215 cm height) and paired with one of the other species or with another *S. alterniflora* plant. Seedlings were spaced equally between the pot edge and another individual and fertilized with slow release fertilizer (15 mL Osmocote® 19-6-12; Scotts Sierra Co., Marysville, OH). Three pots containing the same species combination (*S. alterniflora vs P. virginica*, *S. alterniflora vs L. oryzoides*, or *S. alterniflora vs S. alterniflora*) and one pot of *S. alterniflora vs P. australis* (until week 6 when a second pot was added) were placed in a 129 L shallow plastic tub. The tubs were randomly organized in a block and replicated three times; each block contained a total of 12 tubs with all unique combinations of species and salinity represented. Taxonomy used throughout this manuscript follows USDA (2013).

After initial transplant outdoors in May 2011, plants acclimated in pots for approximately two weeks in ambient conditions as the level of de-chlorinated fresh (tap) water level was slowly raised to approximately 10 cm, thereby filling the tubs to a standard flooding level below the soil surface. Because an earlier study investigating physiological responses to low salinity treatment found *L. oryzoides* and *P. virginica* to have a negative response by a salinity of 4 (Sutter et al., 2014), salinity treatments were established at 0, 1.5 and 3. After the initial two week acclimation period, tubs were brought to a salinity of 1.5 with Instant Ocean® Sea Salt (Cincinnati, OH), a commercially available synthetic sea salt. The final salinity adjustment to 3 was made after an additional 4 days. We chose to use a synthetic salt to minimize variability of sulfate and nutrients found in naturally-derived seawater. Salinity was measured in both the tub (biweekly) and pore water (weekly) using a YSI conductivity meter (Yellow Springs, OH) and adjusted with de-chlorinated freshwater or salt additions. The actual salinities maintained are shown in Table 1. For the remainder of the manuscript, salinity treatments of the intended 0, 1.5, and 3 will be referred to as low, medium, and high treatments, respectively.

2.2. Plant response measurements

Photosynthesis, measured as net carbon dioxide (CO_2) assimilation (A_{net}) was measured weekly during peak sunlight using a TPS-2 portable infrared gas analyzer with a leaf cuvette (PP Systems, Amesbury, MA). For the grasses, the third fully expanded leaf on an arbitrary stem was measured every ten seconds for 30 s. *P. virginica* rarely had more than one leaf from which to select; when it did, the youngest fully expanded leaf was used. Measurements not meeting the instrument tolerances (Bergweiler pers. comm.) were discarded; those remaining were averaged over the sampling interval to represent the experimental unit of the tub. Data were recorded for weeks 1–4 and 6–7.

Individual plants were harvested eight weeks after establishing the final salinity treatment levels. Aboveground and belowground plant material was separated, rinsed, and dried at 60 °C to constant mass, and individual plant material was milled for nutrient analyses. Total phosphorus (P) was determined using a modified ashing/acid extraction process and colorimetric analysis (Chambers