Climate drivers of *Zizaniopsis miliacea* biomass in a Georgia, U.S.A. tidal fresh marsh

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Abstract

Tidal fresh marshes are at least as productive as nearby salt marshes, but much less is known about controls on primary production in tidal fresh vs. salt marshes. We studied a tidal fresh marsh in Georgia, U.S.A., dominated by the C3 grass *Zizaniopsis miliacea*. We documented seasonal variation in *Z. miliacea* above-ground biomass and below-ground macro-organic matter over 1 yr, and annual variation in end-of-season above-ground biomass over 15 yr in creekbank and midmarsh zones. Aboveground biomass showed a distinct peak in July and October. Belowground macro-organic matter was much greater than aboveground biomass and peaked in October. Overall productivity was similar to that of salt marshes downstream. *Z. miliacea* end-of-season above-ground biomass showed a classic hump-shaped “subsidy-stress” relationship with plot elevation, but on average the creekbank supported about twofold more above-ground biomass than the midmarsh, and both zones varied in biomass about 1.7-fold among years. Annual variation in above-ground biomass was negatively correlated with maximum and mean temperature in both zones, and positively with river discharge in the creekbank zone. Sea level, precipitation and water column salinity showed biologically plausible trends with respect to biomass. The responses of *Z. miliacea* to abiotic drivers were muted compared with the responses of nearby salt marshes dominated by *Spartina alterniflora*. Temperature was more important for *Z. miliacea*, whereas drivers of porewater salinity were more important in the salt marsh. Likely future changes in temperature, precipitation, and river discharge may pose a threat to the high productivity of tidal fresh marshes.

Ecologists have devoted a great deal of attention to determining what controls variation in standing biomass and productivity of macrophytic vegetation in different habitats (Haines and Dunn 1976; Linthurst 1980; Morris and Haskin 1990; Reed et al. 2011; Wang et al. 2012; Morris et al. 2013a,b; Wiśniski and Pennings 2014). Standing biomass is fundamentally important in supporting food webs and in regulating the carbon cycle (Silliman and Zieman 2001; Ewe et al. 2006; Chen et al. 2013). Moreover, many of the factors that affect standing biomass, such as temperature and precipitation, are changing due to human activity (Kharin et al. 2007).

Coastal wetlands are among the most productive habitats on earth (Beck et al. 2001) and provide a variety of important ecosystem services to mankind (Mitsch and Gosselink 2000; Odum and Odum 2000; De Groot et al. 2002; Daily 2003; Craft et al. 2009; Barbier et al. 2011). Coastal wetlands vary in salinity from tidal salt to tidal fresh marshes, but most of the scientific attention has been devoted to salt marshes. For example, a large number of studies have examined productivity of salt marshes dominated by the grass *Spartina alterniflora*, with variation in standing biomass linked to sea level, river discharge, nutrients, and temperature (Valiela and Teal 1979; Morris et al. 2002; Wiśniski and Pennings 2014). In comparison, far less is known about the tidal fresh marshes that occur upstream in estuaries from salt marshes (Batzer and Sharitz 2014). Tidal fresh marshes appear to be more productive, have higher plant species richness and store more blue carbon than salt marshes (Odum et al. 1984; Odum 1988; Craft 2007; Wiśniski et al. 2010; Hopkinson et al. 2012), but little is known about what controls variation in standing biomass in these habitats.
Given that both the abiotic conditions and the dominant vegetation types differ between salt and fresh marshes, it is likely that the controls on biomass also differ.

Almost no long-term comparisons in production of salt and tidal freshwater marshes have been made in single estuarine systems using standardized methods. A review of productivity in tidal salt, brackish, and freshwater marshes in California found that productivity increased up to fivefold from tidal salt to tidal fresh marshes (Palaima 2012). A comparison of tidal fresh and tidal salt marshes in a single year in Georgia found that aboveground biomass of plants, and nitrogen stocks in aboveground biomass and in soils, were greater in stands of tidal fresh marsh dominated by Zizaniopsis miliacea than in stands of salt marsh dominated by S. alterniflora (Wieński et al. 2010). A number of studies have shown that tidal freshwater marshes accumulate more organic matter (OM) in the soil than salt marshes because of greater production and lower decomposition rates (Bowden 1984; Craft et al. 1988; Craft 2007). Because tidal fresh marshes are potentially more important for carbon cycling and nutrient storage than salt marshes, they deserve increased study.

Here, we examined seasonal and annual variation in standing biomass of a tidal fresh marsh in Georgia, U.S.A., dominated by the C₃ perennial grass Z. miliacea. We tested two hypotheses. First, because salt stress is lower, tidal fresh marshes are more productive than tidal salt marshes studied in the same area. Second, because the abiotic regimes differ between tidal salt and fresh marshes, the dominant controls on plant biomass also differ between these habitats.

**Methods**

We worked on a tidal fresh marsh site along the northern bank of Hammersmith Creek at the south end of Carrs Island, on the Altamaha River in Georgia, U.S.A. (Fig. 1). This is study site 7 of the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) program. The tide range at this site is ~3 m. The dominant plant species in the study area throughout the entire intertidal zone was Z. miliacea. A number of other plant species occur at the site (Wieński et al. 2010) but represent <5% of the standing biomass (authors personal observations). Z. miliacea plants growing within a few meters of the creekbank appeared more productive than those growing throughout the marsh platform (authors personal observations). At this site, Z. miliacea is nitrogen but not phosphorus limited (Frost et al. 2009; Ket et al. 2011). Z. miliacea is often

![Fig. 1. Location of study site (A) on the coast of Georgia, U.S.A., (B) on Hammersmith Creek, with hydrographic station nearby in the Altamaha River. Note how Zizaniopsis marsh stands (light gray) occur on the inside of channel meanders. (C) Location of individual plots at the creekbank and in the midmarsh that were used for annual sampling in 2000–2014. The marsh is 50–60 m wide at its widest point. The seasonal sampling was conducted in 1979–1980 in the midmarsh in the same general area as the permanent midmarsh plots.](image)
found on the inside of river meanders, and thus represents an early stage in a long-term succession toward alder and cypress swamp (C. Hopkinson personal observation). It is also common in abandoned rice fields from the 1800’s (C. Hopkinson personal observation). Soils on the marsh platform at the study site had a bulk density of 0.15 g cm$^{-3}$ (0–25 cm depth range) to 0.24 (26–50 cm depth range) g cm$^{-3}$, and were 5–11% sand, 21–22% silt, 41–46% clay, and 27% organic matter by mass (Hopkinson and Schubauer-Berigan, unpublished data).

To understand the phenology of *Z. miliacea*, we examined changes in above- and below-ground live and dead matter of *Z. miliacea* at 2-3-month intervals from December 1979 to December 1980. We sampled five 0.5 m$^2$ plots on the marsh platform (~10 m from the creekbank or about mid-distance between creek and alder) for aboveground live and dead plant mass on each date. All live biomass in the plots was clipped at the soil surface, stripped of dead material, dried at 60°C to constant mass, and weighed. All dead material, either attached to living plants, standing or laying on the surface was also removed, rinsed of any mud, then dried and weighed. To sample belowground matter, we collected a single 16.3-cm diameter core in each clipped plot to a depth of 50 cm on each sampling date except the first. The cores were collected with a thin-walled, highly sharpened, stainless steel core tube. We avoided compressing the marsh soils as much as possible while coring. Compressed air was injected from below to help extract the tube and its contents from the ground. Cores were temporarily stored in a walk-in cold room (< 6°C). Cores were subsequently washed and sorted as quickly as possible. Core sections were placed in plastic cans (ca. 4 liters), filled with a mixture of deionized water and sodium metaphosphate (to disperse the clay: Hopkinson and Dunn 1984), shaken for 30 min on an automatic paint shaker, and then washed through a 1 mm-mesh sieve. The remaining material represented live roots, dead roots, and partially decomposed roots. It was impossible to distinguish live from dead roots on the basis of appearance, even with colorless triphenyl tetrazolium (reduced by living roots to red formazan) or chorozol dyes (stains dead roots), which readily separated live and dead Spartina sp. salt marsh plant roots and rhizomes (Schubauer and Hopkinson 1984), and so we pooled these as “macro-organic matter.” After washing, the macro-organic matter was rinsed with deionized water, oven-dried to a constant mass at 60°C and weighed.

Aboveground productivity for the year-long interval was estimated using the Smalley technique, which accounts for turnover of plant tissues during the annual period (Wiegert and Evans 1964). Belowground productivity was estimated as the difference between maximum and minimum total belowground macro-organic matter (Gallagher and Plumley 1979).

Because a max-min approach underestimates productivity in a system with turnover throughout the year (Schubauer and Hopkinson 1984), we also used a litterbag decomposition approach to quantify belowground macro-organic matter turnover. This approach assumes that the biomass of macro-organic matter remains relatively constant from year to year; if so, the decomposition rate of that material must balance the production rate. To estimate decomposition, we placed 40 10 x 10 cm nylon bags (1 mm mesh) 15 cm and 35 cm deep in the soil where root biomass peaks on June 3, 1981. Bags were placed at least 1 m apart in the area where above and belowground sampling was conducted. Each bag contained 8–12 g of dried macro-organic matter collected and processed in spring 1981 following the same procedure as with belowground macro-organic matter determination. Five bags from each depth were removed from the field at 91 d, 186 d, 304 d, and 415 d following deployment. Organic matter was removed from the bags, washed through a 1 mm screen, and dried to a constant weight at 60°C. Decay rates were estimated for each time interval from the best fit exponential equation (1G model). Productivity was then determined by applying the decay rates for an annual period to the mean belowground macro-organic matter mass.

To document annual variation in productivity, estimated as end-of-year standing biomass, we set up 16 plots (1.0 m x 0.5 m), eight near the creekbank and eight in the middle of the marsh platform (Fig. 1) in October of 2000. In October of every year from 2000 to 2014, we measured the height of every plant in each plot. Plots were replaced if lost (only 1 plot was lost during the study period). We estimated end-of-year standing biomass of *Z. miliacea* in creekbank and midmarsh plots using allometric regression equations that were developed from plants harvested outside the plots in the two zones at this site (creekbank: Ln (Biomass, g) = −15.021 + 3.521 (Ln (Height, cm)); midmarsh: Ln (Biomass, g) = −17.192 + 3.953 (Ln (Height, cm))). All plant data are publicly available (Pennings 2016).

We related end-of-year standing biomass in each marsh zone to abiotic conditions (river discharge, sea level, air temperature, local precipitation, and water column salinity) using multiple regression. We obtained Altamaha River discharge data from the US Geological Survey, sea level data from National Oceanographic and Atmospheric Administration, air temperature and precipitation data from the National Weather Service, and water column salinity data from a nearby station in the Altamaha River maintained by the GCE-LTER (Supporting Information Tables S1–S3). We compiled data for each year’s growing season (April to September), calculated monthly averages, and then calculated annual averages for each variable following Więski and Pennings (2014).

**Results**

Aboveground live biomass displayed a strong seasonal pattern with a peak in late summer and early fall (July and October sampling dates) at around 1100 g dry weight m$^{-2}$ (Fig. 2A). Aboveground dead biomass peaked in December and declined during the growing season to a low in July (Fig. 2B). Below-ground macro-organic matter mass was
considerably greater than aboveground biomass, ranging from 7560 to 8740 g dry weight m$^{-2}$. There was not a clear seasonal cycle, but highest values were observed in October (Fig. 2C).

Given that bulk soils were 26.6% OM by mass and had an average bulk density of 0.20 g cm$^{-3}$, the upper 50 cm of the soils contained approximately 26,600 g OM m$^{-2}$. Belowground macro-organic matter averaged 8044 g m$^{-2}$. Around 13.7% of the belowground macro-organic matter is ash (Hopkinson and Schubauer-Berigan, unpublished data), so the belowground macro-organic matter represented 6945 g OM m$^{-2}$, or about 26% of the total OM to a depth of 50 cm, with the remaining material that passed through the 1 mm screen representing 19,655 g OM m$^{-2}$.

The Smalley method estimated aboveground productivity as 1100 g dry wt m$^{-2}$ yr$^{-1}$. This is an underestimate of true productivity as it does not fully account for death that occurs throughout the year. We calculated two estimates of belowground productivity, one based on the difference between the annual minimum and maximum mass of belowground macro-organic matter (1180 g dry wt m$^{-2}$ yr$^{-1}$) and the other based on the organic matter standing stock and its annual decay rate. There was a gradual decline in incubated mass over time at both 15 cm and 35 cm depths (Fig. 3). Decay rates calculated from these data ranged from 0.0014 d$^{-1}$ during the first 90 d of incubation to 0.00073
d$^{-1}$ for the entire 415-d interval (Fig. 4). In general rates declined when integrating over longer intervals and were higher for material incubated at 35 vs. 15 cm depth. The decline in decomposition rate over time is a common characteristic of organic material decay as the most labile components are rapidly depleted leaving a more recalcitrant residue that degrades more slowly (Berner 1980; Hopkinson et al. 2002). Using the 415-d incubation interval as most representative of annual belowground turnover, we estimate annual belowground decomposition (and belowground production of roots and rhizomes) as 2231 g dry wt m$^{-2}$ yr$^{-1}$. This rate is twice as high as that calculated from the max-min approach, attesting to the year-round turnover of belowground biomass.

Across the permanent plots, end-of-year live aboveground biomass of *Z. miliacea* displayed a hump-shaped relationship with plot elevation (Fig. 5). On average, end-of-year live biomass of in the creekbank zone ($\sim$ 1864 g m$^{-2}$) was about twice that in the midmarsh zone ($\sim$ 898 g m$^{-2}$) (Fig. 6A). Biomass of *Z. miliacea* varied $\sim$ 1.66-fold at the creekbank and $\sim$ 1.65-fold in the midmarsh among years, but both zones showed similar temporal patterns. All six of the abiotic variables studied also varied among years (Fig. 6B–F). Water column salinity was the most variable over time, varying $\sim$ 17.3-fold among years; river discharge varied $\sim$ 9.4-fold among years; and precipitation varied $\sim$ 2.7-fold among years. Several of the abiotic variables were correlated with each other across years (Table 1). In particular, maximum and average temperatures were positively correlated, temperature and water column salinity were positively correlated, and water column salinity was negatively correlated with river discharge.

In the creekbank zone, the best single predictors of *Z. miliacea* biomass were maximum and mean temperature, both of which had negative relationships with plant biomass, and river discharge, which had a positive relationship with plant biomass (Fig. 7A–C; Table 2). In the midmarsh zone, the best single predictors of *Z. miliacea* biomass were maximum and mean temperature, both of which had negative relationships with plant biomass (Fig. 7D, E; Table 2). Sea level, precipitation, and water column salinity tended to correlate with biomass in plausible ways, but the relationships were not significant (Supporting Information Fig. S1). We also explored using monthly and daily maximum water column salinity values as predictors, but these were no better than average salinity at predicting *Z. miliacea* biomass (results not shown).

Because maximum temperature, mean temperature, and river discharge were correlated with each other, when all of them were entered into a multiple regression, only maximum temperature (creekbank) and mean temperature (midmarsh) remained significant (results not shown).

**Discussion**

Our data indicate that aboveground primary production of *Z. miliacea* exceeds 1000 g dry wt m$^{-2}$ yr$^{-1}$ in the midmarsh and 2000 g dry wt m$^{-2}$ yr$^{-1}$ at the creekbank. These values are similar to or greater than those from a site on the Savannah River in Georgia (Birch and Cooley 1982). Our estimates of belowground biomass of *Z. miliacea* were an order of magnitude greater than those of Birch and Cooley (1982), largely because they discarded material that they...
believed to be dead whereas we did not believe that we could reliably distinguish live from dead belowground material, and so pooled them. Using the Smalley method, we estimated aboveground productivity in the midmarsh as 1100 g dry wt m$^{-2}$ yr$^{-1}$, which is comparable to the end-of-year aboveground biomass in the midmarsh (Fig. 5). Both standing biomass and the Smalley method, however, underestimate true primary production because they fail to take into account turnover within the growing season (Schubauer and Hopkinson 1984). Our data indicate that belowground primary production of *Z. miliacea* is between 1180 g dry wt m$^{-2}$ yr$^{-1}$ and 2231 g dry wt m$^{-2}$ yr$^{-1}$, with the latter method accounting for within-season turnover. Given the amount of year-to-year variation in production that occurs (see below) these rates are comparable to past estimates of above- and below-ground production of *Z. miliacea* (Birch and Cooley 1982). They are also similar to estimates of above- and below-ground production of *Spartina alterniflora* and *Spartina cynosuroides* in nearby salt and brackish marshes, respectively, using similar methods in the same year (Schubauer and Hopkinson 1984). End-of-year standing biomass of *Z. miliacea* is greater than that of either *Spartina*

### Table 1. Spearman’s rho correlations among climate factors. Significant relationships are indicated by bold font

<table>
<thead>
<tr>
<th>Spearman’s rho</th>
<th>River discharge</th>
<th>Mean temperature</th>
<th>Maximum temperature</th>
<th>Sea level</th>
<th>Precipitation</th>
<th>Water column salinity</th>
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</thead>
<tbody>
<tr>
<td>River discharge</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean temperature</td>
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<td>1.00</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Maximum temperature</td>
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<td>0.90$^*$</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea level</td>
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<td>−0.21</td>
<td>−0.43</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
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<td>−0.48</td>
<td>−0.43</td>
<td>0.27</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Water column salinity</td>
<td>−0.79$^*$</td>
<td>0.60$^T$</td>
<td>0.56$^T$</td>
<td>0.10</td>
<td>−0.13</td>
<td>1.00</td>
</tr>
</tbody>
</table>

$^*$ Correlation is significant at the 0.01 level (2-tailed).

$^T$ Correlation is significant at the 0.05 level (2-tailed).
suggesting either that we underestimated productivity of *Z. miliacea* or that it has less seasonal turnover than *Spartina*. Thus, our data did not conclusively support our first hypothesis. However, our data do indicate that tidal fresh marshes can be just as productive as tidal brackish and salt marshes, and therefore deserve equal attention when considering the importance of tidal wetlands for the carbon cycle (Neubauer and Craft 2009; Więski et al. 2010; Palaima 2012).

Based on our data, the belowground macro-organic matter mass of *Z. miliacea* was \( \sim 10 \) times higher than the above-ground biomass. This ratio of below- : above-ground biomass was highly buffered among years by underground reserves (Hopkinson and Schubauer 1984; Schubauer and Hopkinson 1984; Wijte and Gallagher 1991). However, we were unable to separate live from dead below-ground macro-organic matter in this study, and so it is likely that the true ratio of below- : above-ground biomass is considerably less than 10. Birch and Cooley (1982) calculated a below- : above-ground biomass ratio for *Z. miliacea* of \( \sim 1.3 \) in October, which is lower than that for the *Spartina* species. This matter deserves future study, because if the below- : above-ground ratio is considerably higher in *Z. miliacea* than in *Spartina* species, it suggests a fundamental life-history difference between the species, may explain why *Z. miliacea* is more stable in above-ground biomass among years than is *S. alterniflora* (see below), and may explain why abiotic variables do a better job explaining year to year variation in aboveground biomass of *S. alterniflora* than of *Z. miliacea* (see below).

Previous descriptions of the phenology of *Z. miliacea* found that minimum aboveground live standing crop occurred

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**Table 2.** Best Single-factor models predicting *Zizaniopsis miliacea* standing biomass in creekbank and midmarsh zones

<table>
<thead>
<tr>
<th>Creekbank</th>
<th>Midmarsh</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Parameter</strong></td>
<td><strong>R^2</strong></td>
</tr>
<tr>
<td>Maximum temperature</td>
<td><strong>0.34</strong></td>
</tr>
<tr>
<td>Mean temperature</td>
<td><strong>0.29</strong></td>
</tr>
<tr>
<td>River discharge</td>
<td><strong>0.28</strong></td>
</tr>
<tr>
<td>Sea level</td>
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</tr>
<tr>
<td>Precipitation</td>
<td>0.26</td>
</tr>
<tr>
<td>Water column salinity</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Bold = \( p < 0.05 \), sign = sign of regression coefficient.
in March with a steady increase thereafter to an October maximum followed by a rapid decline (Birch and Cooley 1982). Our results were very similar, confirming that October is a good time to estimate maximum end-of-season aboveground biomass. Birch and Cooley (1982) also found, as we did, that belowground biomass was high in October, although they saw a decline in January whereas we saw it earlier, in December. They also found, as we did, that belowground biomass reaches its lowest values in summer. The peak in below-ground biomass in the fall that was observed in both studies likely reflects belowground translocation during the onset of aboveground senescence in late summer and early fall, and the dip in belowground biomass in the summer likely represents translocation to rapidly growing aboveground material (Hopkinson and Schubauer 1984; Hopkinson 1992).

Aboveground biomass of *Z. miliacea* showed a classic hump-shaped or “subsidy–stress” relationship (Odum et al. 1979) with elevation. This relationship is expected for intertidal plants (Morris et al. 2002), because plants are stressed at both low and high elevations. Plants low in the intertidal are stressed by flooding and plants high in the intertidal are stressed by a combination of dryer conditions or increased toxins. In contrast, plants at intermediate elevations are subsidized by moderate flooding and porewater drainage, which removes toxins and salt and provides nutrients. For plants that occur low in the intertidal, the lowest part of the elevational niche may be a rare habitat because there is an abrupt transition from low marsh to creek at around this elevation. Consequently, on first inspection it appears that plants are simply larger at lower elevations. Thus, for *S. alterniflora*, the creekbank supports on average ~ five times more biomass than does the midmarsh (Schalles et al. 2013; Więski and Pennings 2014), due to higher levels of salinity and lower levels of available nitrogen in the midmarsh (Mendelsohn and Morris 2002; Schile et al. 2014); these studies and others like them did not separately categorize the few stunted plants growing at extremely low intertidal elevations. In the same way, creekbank *Z. miliacea* stands support on average two times more biomass than midmarsh stands (Fig. 6), and the true subsidy–stress relationship between biomass and elevation (Fig. 5) is often not noted because the lowest-elevation habitat with low-biomass *Z. miliacea* plants is rare.

Biomass of *Z. miliacea* varied ~ 1.6-fold among years. Patterns of variation in the two marsh zones were similar over time. These patterns were simpler and more muted than those of *S. alterniflora* in nearby salt marshes over roughly the same time period, where creekbank and midmarsh biomass showed different temporal patterns, and greater annual variation (~ 2–3 fold among years) (Więski and Pennings 2014; Li and Pennings 2016). In contrast to stands of *S. alterniflora*, which are regularly affected by disturbance from wrack (floating plant debris), creekbank slumping, and herbivory (Li and Pennings 2016, 2017), *Z. miliacea* was almost unaffected by disturbance, with only one plot lost due to creekbank slumping over the entire study period. The absence of wrack disturbance in the *Z. miliacea* marsh is likely due to the lack of seasonal grasses upstream (upstream habitats are floodplain forest) and the steady river flow in this area that prevents wrack produced in salt marshes from moving upstream. What explains differences in creekbank slumping and herbivory between this site and downstream salt marshes deserves further study, but indicates that these controls on primary production may differ in importance between tidal salt and fresh marshes.

Variation of *Z. miliacea* biomass was correlated with several climate drivers in reasonable ways. Both maximum and average temperatures were negatively correlated with *Z. miliacea* biomass. In general, productivity of many terrestrial and wetland grasses (Craine et al. 2012) including *S. alterniflora* (Giurgevich and Dunn 1979; Więski and Pennings 2014) is reduced at high temperatures. A particularly strong relationship between photosynthesis and temperature would be expected for *Z. miliacea* growing in a subtropical climate because it is a C₃ grass (Waller and Lewis 1979), and in general C₃ grasses are favored in cooler climates (Hattersley 1983). River discharge was positively correlated with *Z. miliacea* biomass, likely because years with high river discharge lacked periods when salty water would stress the plants (Guo and Pennings 2012). In the same way, river discharge during the growing season also promoted fall biomass of *S. alterniflora* (Więski and Pennings 2014). We found negative relationships between water column salinity and *Z. miliacea* biomass in both marsh zones, as expected (Supporting Information Fig. S1). This relationship, however, was not as strong as the relationship with river discharge. Because water column salinity was measured in the main channel on a fixed piling, measured salinity values sometimes represented surface water and sometimes represented water 2 or more meters below the water surface, and so may not have strongly correlated with the salinity of the water actually flooding the marsh. It is also possible that short pulses of high salinity are more stressful to plants than the average conditions. We also found positive trends between *Z. miliacea* biomass and sea level, which would tend to promote more flooding of the marsh, and precipitation, which represents an input of freshwater to the marsh (Supporting Information Fig. S1). These trends were not statistically significant at the p < 0.05 threshold given the limited number of years of the study, but are biologically plausible and likely to be increasingly supported over time as the data set grows in length. Because several of the climate variables were correlated with each other, we must be cautious about assigning causation to any one variable; however, all the relationships that we observed were biologically reasonable, and additional years of data should improve our ability to identify their relative importance. Overall, temperature was the strongest predictor of year-to-year variation in *Z. miliacea* biomass because it is a C₃ plant growing in low-salinity
waters. In contrast, factors that mediate salinity were the strongest predictors of year-to-year variation in *Spartina alterniflora* biomass (Wiśni and Pennings 2014) because it is a C₄ plant growing in saline water. Thus, these results support the second hypothesis that the dominant controls on plant productivity differ between tidal salt and fresh marshes.

Our ability to predict the fall biomass of *Z. miliacea* was somewhat lower (R² values of 0.28–0.47) than our ability to predict the fall biomass of *S. alterniflora* in nearby marshes over roughly the same time period (R² values of 0.64–0.93; Wiśni and Pennings 2014), despite using the same abiotic variables as predictors. It is possible that additional, unmeasured variables are important in driving variation in *Z. miliacea* biomass, but it is also the case that statistical analyses of *Z. miliacea* biomass have less power because *Z. miliacea* biomass simply varies less over time than *S. alterniflora* biomass.

In summary, our results indicate that *Z. miliacea* production is reduced in years with warmer temperatures and lower river discharge. Both temperatures and river discharge in the southeastern United States are likely to change in the future. Temperatures are projected to increase, and precipitation (which drives river discharge) to become more variable (Craine et al. 2012; Meehl et al. 2007). Moreover, increasing human populations (Ctr. for Quality Growth 2006) will likely increase freshwater withdrawal from rivers, reducing or altering patterns of river discharge (Metro. North Georgia Planning District 2009). As a result, the high productivity and carbon storage of tidal freshwater marshes in the southeastern United States are at risk without careful management.

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Conflict of Interest
None declared.