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Self-thinning and size-dependent flowering of the grass *Spartina alterniflora* across space and time

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Abstract

1. Plants adjust their size and reproductive effort in response to numerous selection pressures and constraints. The self-thinning law describes a well-known trade-off between size and density. Plants also trade-off investment into growth vs. sexual reproduction, as described by life-history theory.
2. We build on past work on plant allometry and life history by examining both self-thinning and size-dependent reproduction in a single plant species, the saltmarsh grass *Spartina alterniflora*, across a wide range of settings: three landscape positions, two habitats and eight sites, across sixteen years.
3. Plants in different landscape positions and years varied tremendously in size and shoot density. However, all this variation could be explained by a single allometric relationship consistent with the self-thinning law, but with a lower slope. Flowering was size-dependent, and the size at which plants had a 50% probability of flowering varied among habitat, sites and years. Plants that were stressed reproduced at a smaller size than plants that were growing under good conditions, and this pattern was consistent among habitat, sites and years. Finally, reproductive biomass and the proportion of shoots flowering increased with increasing vegetative size (plant height or shoot biomass). Combining these two patterns, *S. alterniflora* plants growing high density are small and reproduce at a smaller size than large plants growing at low density.
4. Although there is tremendous spatial and temporal variation in *S. alterniflora* growth and reproductive patterns, all this variation can be understood as resulting from two simple allometric trade-offs. Because saltmarsh plants often occur in monospecific stands, they may serve as simple, model systems for studies of plant life history.

KEYWORDS
allometry, saltmarsh, self-thinning, sexual reproduction, size-dependent, trade-offs, vegetative growth

1 | INTRODUCTION

The clonal nature of plants means that they can vary tremendously in size, shape and reproductive investment among individuals and populations. This variation presents challenges to any attempt to describe and study plant populations (Harper, 1977; Niklas, 1994). One way to organize our thinking about this variation is the −3/2 self-thinning law (Gorham, 1979; Yoda, Kira, Ogawa, & Hozumi, 1963), which predicts that population density decreases as a power function of plant size (Enquist, Brown, & West, 1998). Thus, populations representing plants that differ greatly in density and size may simply represent different locations along a single allometric relationship. However, it is unclear whether the slope of relationship between shoot density and plant size is a constant (−3/2) or whether it varies depending on environmental conditions (Bai et al., 2010; Dai et al., 2009; Deng et al., 2006; Morris, 2002).

Another way to organize our thinking about variation in plant phenotype is life-history theory, which states that the optimum size for reproduction is a function of trade-offs between survival, fecundity and (for iteroparous species) the costs of reproduction (Berrigan & Koella, 1994; Kachi & Hirose, 1985; Kozłowski & Wiegert, 1987; Stearns & Koella, 1986). For semelparous plants, life-history theory predicts a threshold size or age that must be attained before plants start to flower. This threshold size or age may vary depending on the environment in which populations grow (Clauss & Aarssen, 1994; Wesselingh, Klinkhamer, De Jong, & Boorman, 1997) because this determines both survivorship curves and the fecundity at each size or age (Koons, Metcalf, & Tuljapurkar, 2008; Wesselingh & De Jong, 1995).

For plants that do flower, life-history theory also predicts how plants should allocate biomass between sexual reproduction and growth (Begon, Townsend, & Harper, 2006). The patterns of allocation reflect evolved strategies resulting from different selection pressures and constraints (Weiner, 2004). Allocation patterns have usually been described and analysed as ratios, such as reproductive effort (flowering ratio or percentage of reproductive biomass). However, plant allocation is usually allometric, changing with plant size (Weiner, 2004), so allocation patterns also can be understood using allometric relationships (e.g. plots of reproductive vs. vegetative biomass). A number of studies have examined allometric relationships between reproductive and vegetative investment within populations (Ohlson, 1988; Sugiyama & Bazzaz, 1998; Thompson, Weiner, & Warwick, 1991; Weiner, Campbell, Pino, & Echarte, 2009).

Although a large number of studies have examined self-thinning and life-history variation in plants, many of these have been done in artificial settings or with a limited number of field populations, and few studies have integrated investigations of both topics. Here, we seek to build on past work by examining allometric and life-history variation in a single species of saltmarsh plant, the grass *S. alterniflora*, in natural populations representing three landscape positions, two habitats and eight sites across sixteen years. An advantage of working in saltmarshes is that plants often occur in large, monospecific stands (Pennings & Bertness, 2001), allowing allometric and life-history variation in a single species to be studied without complications arising from interspecific interactions. In addition, saltmarsh habitats contain strong abiotic gradients related to elevation and freshwater input that affect plant growth (Richards, Pennings, & Donovan, 2005; Więski & Pennings, 2014). How these gradients affect allometry and reproduction has not been investigated in detail (but see Ellison, 1987).

We chose to work with *S. alterniflora* because it is the dominant plant at lower elevations in saltmarshes along the Atlantic and Gulf coasts of the United States (Pennings & Bertness, 2001) and represents a powerful invasive species that transforms intertidal landscapes elsewhere in the world where it occurs as an exotic (Strong & Ayres, 2013). *Spartina alterniflora* varies more than 10-fold in height among microhabitats within saltmarshes, with taller plants along creekbanks and shorter plants at higher or saltier locations (Richards et al., 2005). This variation in height has long attracted scientific attention (Chalmers, 1979; Mendelssohn & Morris, 2002), but without much consideration of how height relates to shoot density or flowering. Instead, because saltmarshes are so productive and therefore of interest with respect to support of food webs and mediation of the global carbon cycle, the focus has largely been on how variation in saltmarsh biogeochemistry and other abiotic drivers affects plant productivity (Mendelssohn & Morris, 2002; Morris, Sundberg, & Hopkinson, 2013). A great deal has been learned about these topics, but issues of plant allometry and life-history theory have largely been ignored (but see Xiao, Tang, Qing, Zhou, & An, 2011a, Xiao, Tang, Qing, Zhou, Kong, et al., 2011b; Xiao et al., 2015; Crosby et al., 2015).

Spartina alterniflora grows in the intertidal zone. As a result, plants growing at different intertidal elevations experience different cycles of tidal flooding and exposure; tidal conditions also vary among sites and years. The cycles of flooding and exposure mediate both how salty and how well oxygenated the soil is. Proximity to creekbanks also affects the drainage of porewater at low tide and thus the turnover time of water in the soil. Together, these factors lead through a complex set of hydrological and biogeochemical processes to soils that vary in water content, salinity, oxygen content, sulphide concentration and nitrogen availability (Mendelssohn & Morris, 2002), all of which lead to variation in *S. alterniflora* productivity over space (Kirwan, Guntenspergen, & Morris, 2009; O'Donnell & Schalles, 2016; Zheng, Shao, & Sun, 2018) and among years (Morris et al., 2013; Więski & Pennings, 2014). Different locations and years also vary in shoot density (Gleason, Elmer, Pien, & Fisher, 1979; Morris & Haskin, 1990) and flowering (Crosby et al., 2015; Qiu et al., 2018), but these variables have not been systematically linked together in the context of ecological theory.

We took advantage of the monitoring programme of the Georgia Coastal Ecosystems Long-Term Ecological Research programme to examine relationships between *S. alterniflora* height, shoot density and flowering across landscape positions, habitats (creekbank vs. mid-marsh elevations), sites and years. Past work at this site has documented variation in plant biomass across habitats, sites and years (Więski & Pennings, 2014). We tested the hypotheses that (a) the relationship between shoot density and shoot size of *S. alterniflora* conforms to the −3/2 self-thinning law, (b) this relationship is the same (slopes and intercepts do not differ) across landscape position and years, (c) size at which plants had a 50% probability of flowering (henceforth, F_{50}) is the same across habitats, sites and years, and (d) plants that flower invest a constant proportion of their biomass in sexual reproduction.

2 | MATERIALS AND METHODS

We worked within the domain of the Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) programme (http://gce-lter.marsci.uga.edu/). The GCE-LTER includes 8 permanent sites (GCE 1–6, 9,10) where either creekbank or mid-marsh habitats or both are dominated by the grass *S. alterniflora* (Figure 1). Tides are mesotidal, with a range of 2–3 m. To assess the possibility that results would vary as a function of landscape position, we followed Li and Pennings (2016) in categorizing sites as mainland (GCE 1, 4), intermediate (GCE 2, 5, 9, 10) and barrier island (GCE 3, 6), speculating that mainland sites might have more freshwater input and therefore taller plants. At each site, we measured shoot height and flowering status of all shoots each October in 8 permanent plots (0.5 × 0.5 m) along the creekbank and 8 permanent plots (0.25 × 0.25 m) in the mid-marsh, from 2000 to 2015. About 13% of the were disturbed or lost each year due to deposition of floating wrack, creekbank slumping, heavy herbivory or other causes (Li & Pennings, 2016); these were omitted from the analysis in the year that they were disturbed. Plots that were lost were replaced each year. Because there was some turnover in plots among years, we could not use repeated-measures approaches to analyse the data; instead, we treated data from each year as independent even though many of the plots were resampled in multiple years. We calculated shoot density in each plot based on the number of shoots and the plot area, and the flowering ratio as the number of shoots flowering divided by the total number of shoots in each plot. We used shoot heights and flowering status of *S. alterniflora* every October from 2000 to 2015 and allometric relationships to estimate standing biomass (Więski & Pennings, 2014).

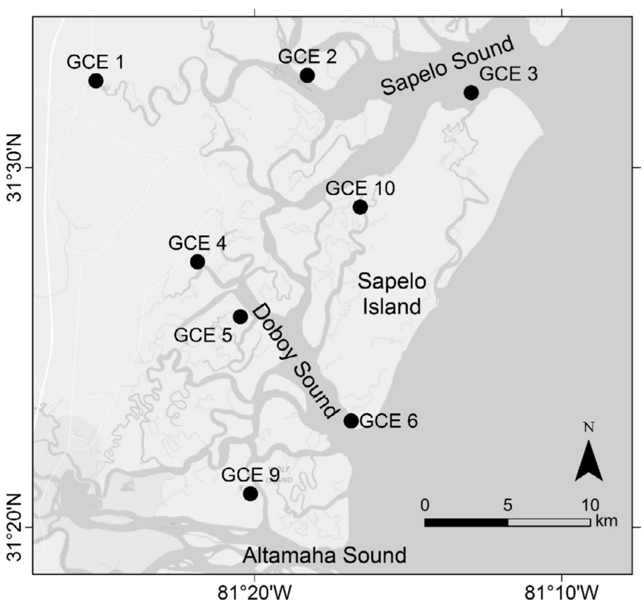

FIGURE 1 Map of the study site on the coast of Georgia, USA. Georgia Coastal Ecosystems Long-Term Ecological Research (GCE-LTER) permanent monitoring sites that were included in this study are marked with filled circles. GCE 3 and GCE 6 were coded as barrier island sites; 2, 5, 9 and 10 as intermediate; and 1 and 4 as mainland sites

In order to determine the mass invested into vegetative growth and sexual reproduction, we clipped 5 flowering shoots near each of the creekbank plots at GCE 1 and near each of the creekbank and mid-marsh plots at GCE 4 on 12–18 October 2017. At the same time, we similarly clipped 5 flowering shoots at eight plots (spaced ~10 m apart) in the creekbank and in the mid-marsh zones of two additional sites on the south end of Sapelo Island. For each shoot, we measured the total shoot height (including the inflorescence) and the inflorescence length. We cut each shoot into the inflorescence and the vegetative portion and determined dry mass of both after drying at 70°C for 72 hr.

To assess how abiotic conditions might affect plant allometry and reproduction, we examined eight abiotic drivers likely to be important to *S. alterniflora* growth: pore water salinity, elevation of each plot, temperature, precipitation, the Palmer Drought Severity Index (PDSI), sea level, tide range and river discharge. Porewater salinity was measured adjacent to permanent plots in October of 2010–2015. Plot elevation was measured using real-time kinematic GPS. For climate data, we used average air temperature and precipitation at the Malcolm McKinnon Airport in Brunswick, Georgia (Wade & Sheldon, 2019), and the Palmer Drought Severity Index (PDSI) drought index for Georgia Division 9 (National Oceanic & Atmospheric Administration, 2018). Sea level and tide range data were obtained from the National Oceanographic and Atmospheric Administration (station 8,670,870, Fort Pulaski, Georgia, http://www.noaa.gov/) (Wade & Sheldon, 2018a). Discharge of the Altamaha River was measured at Doctortown gauging station on the Altamaha River by USGS (Wade & Sheldon, 2018b). Predictors that varied during each year (precipitation, temperature, river discharge, sea level, tide range and PDSI) were averaged over the growing season (April-September) to provide a single value per year.

For analysis of variation in plant height and density among landscape positions, all the plots representing a particular landscape position were averaged within a year to yield a single data point for each landscape position in each year. We used *t*-tests to test for differences in plant height and shoot density between landscape positions. We used linear regression to analyse the relationships between plant traits (height and shoot density) and abiotic factors, with years as replicates, for each landscape position separately. To explore the relationship between shoot height and shoot density, we analysed data with individual plots from each year as replicates. We first analysed the entire dataset using a mixed model with log (shoot density) as the predictor variable, year as a random effect, landscape position as a fixed factor and the interaction of log (density)*landscape in order to see whether the relationship between shoot height and density varied among landscape positions. We then analysed data for each landscape position separately, to see whether the relationship between shoot height and density varied among years in each landscape position. To this end, we fit the regression model with density (continuous independent variable), year (main effect) and density * year (interaction effect). To explore the relationships between shoot mass and shoot height, and between shoot mass and shoot density, we analysed data with individual plots from each year as replicates. We used a mixed model, with year as a random factor and shoot height (or density) as a fixed factor. For the mass–density relationship, we tested for deviation from the expected value under the self-thinning law (−3/2; Yoda et al., 1963) using the R library smart (Warton, Duursma, Falster, & Taskinen, 2012). To analyse variation in plant height and proportion flowering among different sites, years and habitats, plots were averaged within a site for each year to yield a single data point for each site and year per habitat. We used *t*-tests to test for differences in plant height and proportion flowering between habitats. We similarly used linear regression to analyse the relationships between plant traits (height and proportion flowering) and abiotic factors. To describe the relationship between plant size and flowering probability and to test for differences between groups, we used binomial logistic regression (function lmer in R; Bates & Maechler,) with individual shoots as the unit of replication, and plant size as the explanatory variable where *x* is plant size and *y* is the flowering probability. We also determined the size at which a plant had a 50% probability of flowering (F_{50}) among different sites, years and habitats. We used linear regression to analyse the relationships between F_{50} and abiotic factors. We also used linear regression to determine the relationships between vegetative growth and sexual reproduction. We performed all analyses with R statistical software (R Development Core Team, 2016) and provide our R code in the Appendix.

3 | RESULTS

3.1 | Variation in plant height, shoot density and allometry

Plant height (creekbank and mid-marsh combined) varied among years and landscape positions (Figure S1a,b). Shoot density also varied among years and landscape position (Figure S1c,d), but in the opposite direction, such that years or locations with tall shoots had a low shoot density, and years or locations with short shoots had a high shoot density. Different abiotic factors were the best univariate predictors of plant height and shoot density at the different landscape positions. At mainland sites, plant height was positively correlated with river discharge, PDSI and decreased with increasing temperature (Figure S3a–c). At intermediate sites, plant height was positively correlated with river discharge and tidal range and decreased with temperature; shoot density decreased with tidal range (Figure S3d–g). At barrier island sites, plant height was positively correlated with river discharge and PDSI, and decreased with temperature; shoot density decreased with sea level (Figure S3h–k).

Within the mainland, intermediate and barrier island sites, plant height declined as shoot density increased (Figure 2a, Table S2); this relationship did not differ among landscape positions. Similarly, within each landscape location, the negative relationship between plant height and shoot density did not differ among years in the mainland or intermediate landscape positions, but did differ among years in the barrier island landscape position (Figure 2b–d, Table S2).

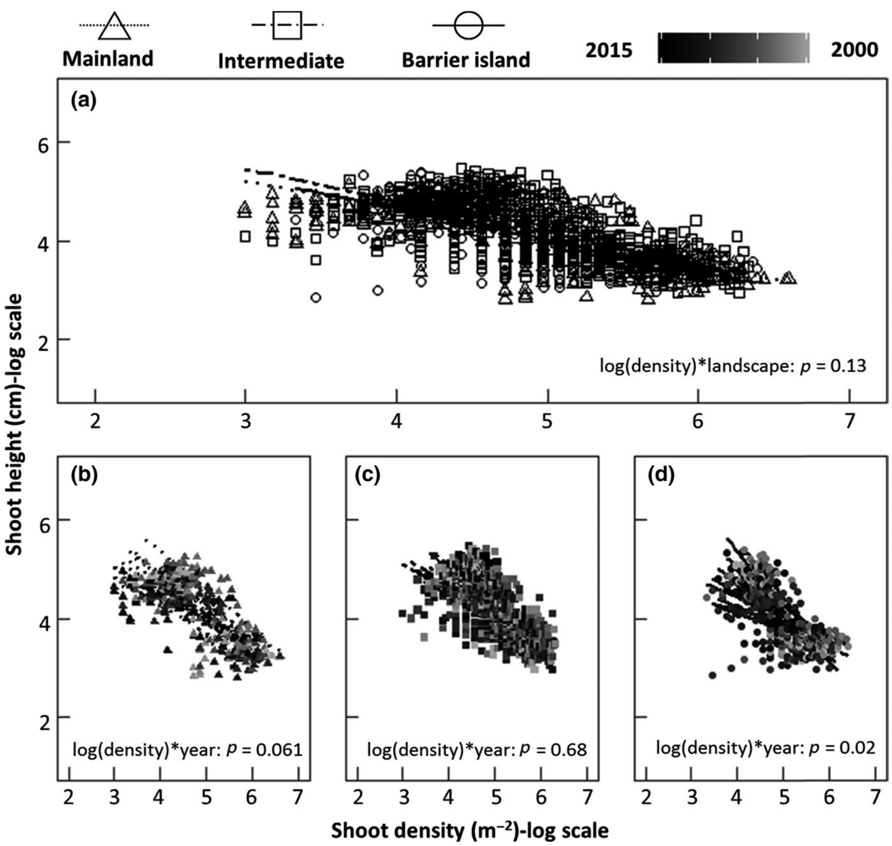

FIGURE 2 Relationships between shoot height and density in different landscape positions (all years combined) (a), and among years at mainland (b), intermediate (c) and barrier island (d) landscape positions. There were no differences in the slopes among landscape positions or years, detailed statistical results in Table S2

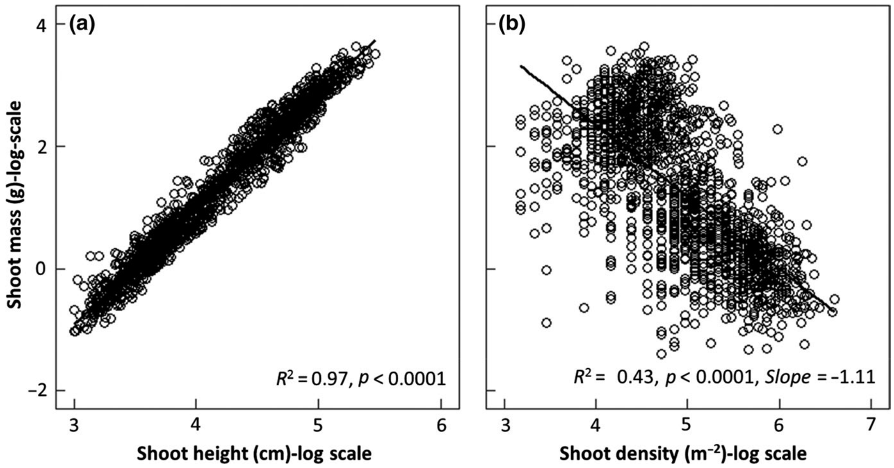

FIGURE 3 Relationships between shoot mass and shoot height (a), and between shoot mass and shoot density (b)

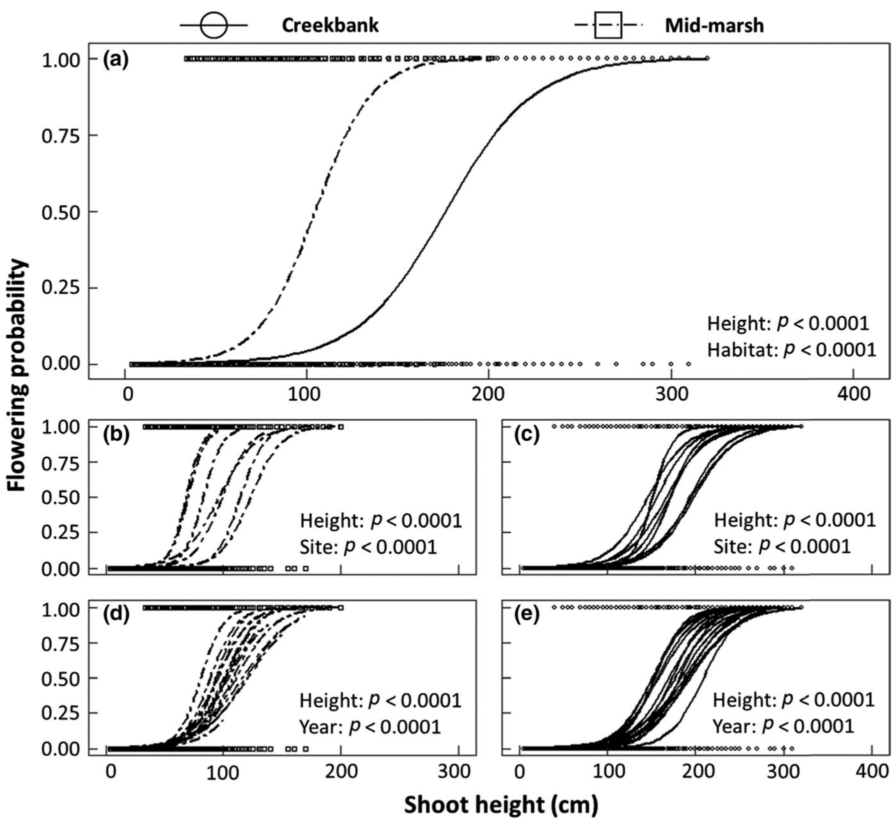

FIGURE 4 Binomial regression models predicting the probability that an individual shoot of *Spartina alterniflora* will flower based on shoot height in creekbank vs. mid-marsh habitats for all sites and years combined (a), among 8 different GCE sites in the creekbank (c) and mid-marsh (b) habitats for all years combined, and across years in the creekbank (e) and mid-marsh (d) habitats for all sites combined

Shoot height was a strong predictor of shoot biomass (Figure 3a), allowing us to estimate shoot biomass in all the monitoring plots from the shoot height data. With all the monitoring data combined, shoot mass decreased with shoot density with a slope of −1.11 on a log–log scale (R^2 = 0.43, p < 0.0001), which differs (p < 0.0001) from the canonical slope of −3/2 expected under the self-thinning law (Yoda et al., 1963).

3.2 | Variation in proportion flowering and F_{50}

Plants were ~170% taller, and the proportion of shoots flowering was ~400% greater at the creekbank vs. the mid-marsh plots (Figure S2b,d,f,h). Height varied among years (Figure S2a) and among sites (Figure S2c) in both the creekbank and mid-marsh habitat. The proportion of shoots flowering also varied among years (Figure S2e) and sites (Figure S2g) in both the creekbank and mid-marsh habitat. Marsh zones, sites and years with taller plants tended to have a higher proportion of shoots flowering; we address this point more rigorously below. Different abiotic factors were the best univariate predictors of plant height and shoot density at the different sites and among years. Variation in height among sites in both the creekbank and mid-marsh habitats was predicted by soil salinity (Figure S4a) and plot elevation (Figure S4b). Neither variable predicted variation in the proportion of shoots flowering among sites (Figure S4c,d). Variation in both height and proportion flowering among years in the creekbank habitat was predicted by temperature and river discharge (Figure S5c,d,g,h). In the mid-marsh, variation in both height and the proportion of stems flowering among years was predicted by precipitation, river discharge and PDSI (Figure S5a,b,e,f,i,j).

We measured 31,352 shoots between 2000 and 2015 in undisturbed plots. The probability of any given shoot flowering increased with plant height, but this relationship differed between marsh zones, sites and years (Figure 4). The F_{50} was 176 cm at the creekbank vs. only 105 cm in the mid-marsh (Figure 4a). The F_{50} at the mid-marsh varied from 68 to 123 cm among sites (Figure 4b) and from 81 to 120 cm among years (Figure 4d). The F_{50} at the creekbank varied from 146 to 195 cm among sites (Figure 4c) and from 151 to 209 cm among years (Figure 4e). Among sites, the F_{50} increased with average plant height (Figure S6a), decreased with soil salinity (Figure S6b) and decreased with elevation (Figure S6c). Among years, the F_{50} at the creekbank increased with tide range (Figure S6d). In the mid-marsh habitat, temperature (marginally significant, $p = 0.057$) and river discharge predicted annual variation in F_{50}.

3.3 | Relationship between vegetative growth and sexual reproduction

Across the sixteen years of data at all the sites, the proportion of shoots flowering was positively related to average plant height (Figure 5a). For the plants sampled in 2017, inflorescence length was positively related to shoot height (Figure 5b), and inflorescence mass was positively related to shoot mass (Figure 5c).

4 | DISCUSSION

Ecologists have long remarked on the tremendous variation in *S. alterniflora* height and shoot density across the landscape. Here, we show that 14-fold variation in shoot height and 37-fold variation in density among plots are explained by the self-thinning law. Variation in flowering was more complex: the probability that an individual shoot at a given location would flower was a simple function of plant height, but the F_{50} varied among microhabitats, sites and years, with plants flowering at a shorter height when conditions were more stressful.

Saltmarshes have long been a model system for studies of plant ecology (Chapman, 1974), in part because the simplicity of their low-diversity plant communities makes ecological patterns more obvious. One of the most obvious patterns in saltmarshes on the East and Gulf Coasts of North America is that the dominant plant in these habitats, *S. alterniflora*, varies tremendously in height, from <25 cm to >200 cm, among different microhabitats (Richards et al., 2005; Schalles, Hladik, Lynes, & Pennings, 2013). In particular, plants are shorter at higher marsh elevations and taller along the creekbank (Proffitt, Travis, & Edwards, 2003; Schalles et al., 2013).

Consistent with these previous studies, we found variation in plant height and shoot density both across the landscape and among microhabitats. Plant height increased but shoot density decreased from barrier island to mainland sites. As has been found previously (Bertness, 1992; Nestler, 1977), this spatial variation was correlated with porewater salinity, with plants shorter in more saline soils (Bertness & Pennings, 2002; Richards et al., 2005).

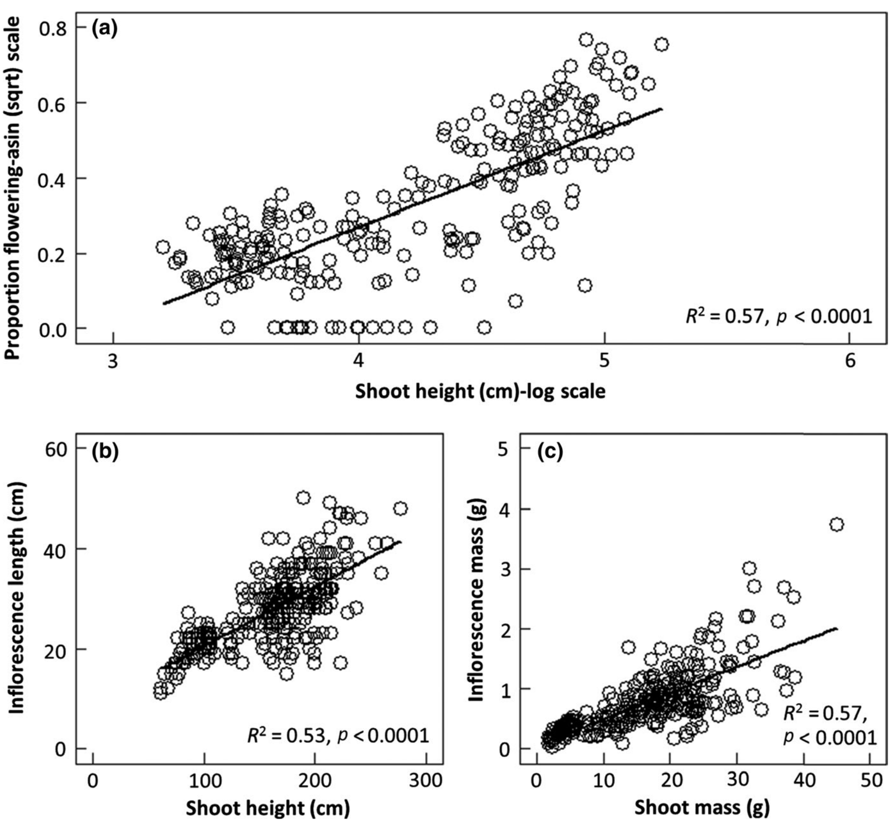

FIGURE 5 Relationships between the proportion of shoots flowering and shoot height (a), inflorescence length and shoot height (b), and inflorescence mass and shoot mass (c)

There are fewer studies of temporal variation in *S. alterniflora* (Teal & Howes, 1996; Visser, Sasser, & Cade, 2006), but we found that shoot height and density (pooled across creekbank and mid-marsh habitats) again varied inversely among years. Plant height was positively affected by river discharge, which reduces porewater salinities, and negatively by temperature, which concentrates salts by increased evapotranspiration (Więski & Pennings, 2014). The PDSI, which incorporates both precipitation and temperature, also was a good predictor of plant height. At the intermediate sites, plant height was also positively related to tide range, consistent with previous geographical comparisons that have found that tide range positively affects *S. alterniflora* (Liu, Maung-Douglass, Strong, Pennings, & Zhang, 2016; Mckee & Patrick, 1988; Turner, 1976). Fewer significant relationships were found for variation in shoot density among years, but the best predictors were tide range and sea level.

For any subset of these data, plant height was negatively related to shoot density. This result is consistent with a vast body of work showing that density is one of main components in determining plant size due to competition for resources (Deng et al., 2006; Harper, 1977; Roscher & Schumacher, 2016; Sugiyama & Bazzaz, 1998). The relationships between plant height and shoot density did not differ among landscape positions or, for any given landscape position, among years, suggesting that there was a universal underlying relationship for all sites and dates. Because *S. alterniflora* naturally occurs as monocultures at all the locations sampled, we were able to test the hypothesis that this universal underlying relationship was the −3/2 self-thinning law.

The self-thinning law is generally understood to reflect the effects of intraspecific competition within a monoculture, creating a negative relationship between plant size and density (Watkinson, 1980; Yoda et al., 1963). We found a strong negative relationship between log shoot mass and log density that held across all landscape positions and years. The slope of −1.11 was different than the canonical self-thinning slope of −3/2, but there is increasing evidence that the self-thinning slope is variable among species and conditions (Wade, 2018). In particular, the self-thinning slope is often shallower than −3/2 for plants growing in stressful conditions (Deng et al., 2006; Morris, 2002), which is consistent with our finding from the saltmarsh. Regardless of the exact slope, the important finding is that the tremendous variation in *S. alterniflora* height and variation observed among microhabitats and sites actually reflects a single size–density relationship, with stands of plants located at different point along the relationship depending on local environmental conditions.

This single size–density relationship, however, did not fully explain spatial or temporal variation in flowering. The proportion of stems in a plot that were flowering varied tremendously, from 0 to 0.85. As has been previously reported (Bertness, 1985; Gallagher, Somers, Grant, & Seliskar, 1988), *S. alterniflora* were both taller and more likely to flower in creekbank vs. mid-marsh habitats; however, as we will discuss below, the relationship between height and flowering varied among habitats. *Spartina alterniflora* stems also varied in height among sites, due in part to variation among sites in plot elevation and soil salinity. Plant height decreased with plot elevation and soil salinity in both the mid-marsh and creekbank habitats (Figure S4a,b), which is consistent with many previous results showing that *S. alterniflora* height decreases with elevation and salinity (Linthurst & Seneca, 1981; Pearcy & Ustin, 1984; Peng, Chen, Pennings, & Zhang, 2018). Across sites, however, these same variables did not predict the proportion of stems flowering, suggesting that the relationship between plant height and flowering differed among sites. Finally, *S. alterniflora* stems at both the creekbank and the mid-marsh varied in height and flowering among years. The same variables predicted annual variation in both height and proportion flowering; however, as we discuss below, this superficial similarity obscures important differences in the relationship between height and flowering among years.

In most plant species, the probability of flowering increases with size (Pickering & Arthur, 2003; Reekie, 1998; Sun & Frelich, 2011). Similarly, we found an overall relationship across the entire dataset (31,352 stems) for *S. alterniflora* in which the probability of flowering increased with stem height. Moreover, the 2017 field survey clarified that the height–flowering relationship was a simplified version of a positive relationship between somatic mass and reproductive mass, with heavier shoots producing heavier flowers. This relationship is consistent with the general finding that larger plants invest more in reproduction (Aarssen & Taylor, 1992; Bolmgren & Cowan, 2008; Du & Qi, 2010; Hoyo & Tsuyuzaki, 2015). This relationship can be interpreted as a result of the modular architecture of plants. Within a population, larger individuals have more vegetative and reproductive modules (Niklas, 1995; Weiner, 1988). Large plants can thus allocate more biomass to both vegetative and sexual reproduction than smaller plants, resulting in a positive correlation between plant size and sexual reproduction rather than the expected negative one (Weiner et al., 2009).

However, the average size at which plants flowered varied ~170% among habitats, 25%–50% among sites and 10%–50% among years, as a function of abiotic stress. In particular, the size at which plants had a 50% probability of flowering was greater when abiotic conditions were less stressful, as indicated by taller shoots (Figure S6a). Because variation in *S. alterniflora* height is directly or indirectly a function of river discharge, porewater salinity, temperature, tide range and plot elevation, variation in these factors also affected the F_{50}, with porewater salinity as the best single predictor (Figure S6b–d).

Life-history theory shows that the optimum size for reproduction is a function of trade-offs between survival, fecundity and (for iteroparous species) the costs of reproduction (Berrigan & Koella, 1994; Kachi & Hirose, 1985; Kozłowski & Wiegert, 1987; Stearns & Koella, 1986). A clone of *S. alterniflora* is iteroparous, but an individual shoot—the focus of this study—lives for only a single year and can be treated as semelparous. At the growing edge of a clone invading a salt pan, young shoots are supported by the translocation of resources from older shoots, but the benefits of clonal integration in *S. alterniflora* were minor for shoots growing in monospecific stands (Pennings & Callaway, 2000). If we consider individual shoots as semelparous organisms, theory predicts that sexual reproduction should be delayed under conditions in which plants grow better (Hesse, Rees, & Müller-Schärer, 2008). This is exactly what we found. The F_{50} was greater (i.e. plants delayed reproduction), at the creekbank, where plants were taller, vs. the mid-marsh, where plants were shorter. Similarly, the F_{50} was greater at sites and in years when plants grew taller.

A number of other studies have compared the threshold for flowering of plants growing in different conditions, with results consistent with ours. For example, Wesselingh et al. (1997) compared three sites and found that the threshold size for flowering of the facultative biennial herb *Cynoglossum officinale* increased with habitat suitability. Similarly, Méndez and Karlsson (2004) compared 11 populations of the perennial herb *Pinguicula ulgaris* and found that flowering probability varied among sites, with populations in better abiotic conditions (low altitudes and wet soils) having a significantly higher threshold size for reproduction. Similarly, Guo et al. (2012) compared 44 naturally occurring populations representing 24 species of *Pedicularis* in the Tibetan Plateau and found that plants invested less in reproduction at more stressful, higher elevations. Our study extends these previous findings by comparing a single species across two habitats, eight sites and sixteen years in a single study, thereby providing the most comprehensive understanding of size-dependent flowering variation across space and time to date.

This extensive dataset provided an unprecedented opportunity to explore how natural populations of plants conform to general theories of allometry and reproduction. Plant phenotype varied tremendously across the dataset, with height varying 14-fold, shoot density varying 35-fold, the proportion of stems in a plot flowering varying from 0 to 0.85 among plots and the size at which plants had a 50% probability of flowering varying ~170% among habitats, 25%–50% among sites and 10%–50% among years. This remarkable phenotypic variation, however, could be explained by general ecological theory. Variation in plant height and shoot density was mediated across sites and dates by abiotic conditions, but conformed across the entire dataset to the self-thinning law. Both the proportion of stems flowering and the resources allocated to flowering increased with plant height, but the F_{50} for flowering also increased with plant height, consistent with general life-history theory. Because of their strong abiotic gradients and low species diversity, saltmarshes have long been a productive study system for studies of community ecology (Bertness, 1992; Chapman, 1974; Pennings & Bertness, 2001); our work suggests that they also offer an excellent model system for studies of plant life history.

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AUTHORS' CONTRIBUTIONS

W.W.L. and S.C.P. conceived the ideas and designed the analysis; S.P.C. conceived the monitoring programme and led data collection over the years with assistance from many parties including W.W.L.; W.W.L. analysed the data; W.W.L. led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Plant monitoring data collected by our group are available at the Georgia Coastal Ecosystems Long-Term Ecological Research. Plant monitoring survey data deposited in the Georgia Coastal Ecosystems Long-Term Ecological Research Repository at 2000: https://doi.org/10.6073/pasta/0a82de490612fd997260349572b95704 (Pennings, 2003a); 2001: https://doi.org/10.6073/pasta/fb7d782b7f9e5d91b2346faff623c99a (Pennings, 2003b); 2002: https://doi.org/10.6073/pasta/3124fd475a71ac2e8b23dfc4e87f4542 (Pennings, 2003c); 2003: https://doi.org/10.6073/pasta/45680d2b15b34154d496022967fc0496 (Pennings, 2004); 2004: https://doi.org/10.6073/pasta/674fec2640e4ff3ad5f96a3303f7f0c3 (Pennings, 2006a); 2005: https://doi.org/10.6073/pasta/1a781e75d57b0f999090c42032b3a52d (Pennings, 2006b); 2006: https://doi.org/10.6073/pasta/beafc321d556c6a408013f200a5334f4 (Pennings, 2007); 2007: https://doi.org/10.6073/pasta/a7d25d256f23e3427752229cf736a3a6 (Pennings, 2009a); 2008: https://doi.org/10.6073/pasta/43c93615a18bc464c7468069e718ffe7 (Pennings, 2009b); 2009: https://doi.org/10.6073/pasta/729095532fdc5549c3a3625b1eba4a90 (Pennings, 2011a); 2010: https://doi.org/10.6073/pasta/f5d79a9722572c7c2a10b8cba4a85a58 (Pennings, 2011b); 2011: https://doi.org/10.6073/pasta/11609e84864f1dfc390fd3e82b975d2d (Pennings, 2012); 2012: https://doi.org/10.6073/pasta/7c952f82f698c6a731759ad497bc8889 (Pennings, 2013a); 2013: https://doi.org/10.6073/pasta/8bdad996ac2923367d99724ae9b0dfea (Pennings, 2014a); 2014: https://doi.org/10.6073/pasta/618f9ec979aca6669d92646f7271a30f (Pennings, 2015a); 2015: https://doi.org/10.6073/pasta/980d41234ea67c2eacd6bcc69d4b877f (Pennings, 2016). Soil salinity at GCE-LTER vegetation monitoring plots from October 2010–2015: 2010: https://doi.org/10.6073/pasta/03ed725daf81ce3ae0735932b5e0f38a (Pennings, 2011c); 2011: https://doi.org/10.6073/pasta/e53d69beecaa3a6832dc8dc8205d623b (Pennings, 2013b); 2012: https://doi.org/10.6073/pasta/f940e82462b8964242eec9cb531c440d (Pennings, 2013c); 2013: https://doi.org/10.6073/pasta/24d15af4f2dab97aff5148d5ae17d3aa (Pennings, 2014b); 2014: https://doi.org/10.6073/pasta/c8ca5865d19b3de6d6b70d53dc0833db (Pennings, 2015b); 2015: http://dx.doi.org/10.6073/pasta/d0e55b8da9bb0e71d4a8b893fc9a0c7a (Pennings, 2017). Climate and hydrological data collected by other group are available throw the GCE-LTER data portal as follows. Climate data (air temperature and precipitation) at the Malcolm McKinnon Airport in Brunswick, Georgia, 1948–2019: https://gcelter.marsci.uga.edu/portal/stations/nws_brunswick_ap/historic/data/nws_brunswick_ap_monthly_aug1948-jun2019.xml (Wade & Sheldon, 2019); The Palmer Drought Severity Index (PDSI) drought index data at Georgia Division 9, 1895–2018: http://gce-lter.marsci.uga.edu/portal/stations/noaa_drought/historic/data/noaa_pdsi_ga_div9_jan1895-jan2018.xml (National Oceanic and Atmospheric Administration, 2018); Sea level and tide range data at the National Oceanographic and Atmospheric Administration, 1935–2018: http://gce-lter.marsci.uga.edu/portal/stations/nos_fort_pulaski/historic/data/nos_fort_pulaski_monthly_jul1935-jan2018.xml (Wade & Sheldon, 2018a); Discharge of the Altamaha River data at Doctortown gauging station on the Altamaha River by USGS, 1932–2017: http://gce-lter.marsci.uga.edu/portal/stations/usgs_doctortown/historic/data/usgsdoctortown_yearly_jan1932-dec2017.xml (Wade & Sheldon, 2018b).

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REFERENCES

Aarssen, L. W., & Taylor, D. R. (1992). Fecundity allocation in herbaceous plants. *Oikos*, *65*, 225–232. https://doi.org/10.2307/3545013

Bai, Y. Y., Zhang, W. P., Jia, X., Wang, N., Zhou, L., Xu, S. S., & Wang, G. X. (2010). Variation in root: Shoot ratios induced the differences between above and belowground mass-density relationships along an aridity gradient. *Acta Oecologica*, *36*, 393–395. https://doi.org/10.1016/j.actao.2010.03.007

Bates, D., & Maechler, M. (2009). *lme4: Linear mixed-effects models using S4 classes*. R package version 0.999375-32. Available from http://CRAN.R-project.org/package=lme4

Begon, M., Townsend, C. R., & Harper, J. L. (2006). *Ecology: From individuals to ecosystems*, 4th ed. Oxford, UK: Blackwell Publishing.

Berrigan, D., & Koella, J. C. (1994). The evolution of reaction norms: Simple models for age and size at maturity. *Journal of Evolutionary Biology*, *7*, 549–566. https://doi.org/10.1046/j.1420-9101.1994.7050549.x

Bertness, M. D. (1985). Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, *66*, 1042–1055. https://doi.org/10.2307/1940564

Bertness, M. D. (1992). The ecology of a New England salt marsh. *American Scientist*, *80*, 260–268.

Bertness, M. D., & Pennings, S. C. (2002). Spatial variation in process and pattern in salt marsh plant communities in eastern North America. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 39 –57). Dordrecht, The Netherlands: Springer. https://doi.org/10.1007/0-306-47534-0_4

Bolmgren, K., & Cowan, P. D. (2008). Time-size tradeoffs: A phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. *Oikos*, *117*, 424–429. https://doi.org/10.1111/j.2007.0030-1299.16142.x

Chalmers, A. G. (1979). The effects of fertilization on nitrogen distribution in a *Spartina alterniflora* salt marsh. *Estua Rine and Coastal Marine Science*, *8*, 327–337. https://doi.org/10.1016/0302-3524(79)90050-1

Chapman, V. J. (1974). Salt marshes and salt deserts of the world. In R. J. Reinold & W. H. Queen (Eds), *Ecology of halophytes* (pp. 3–19). New York, NY: Academic Press.

Clauss, M. J., & Aarssen, L. W. (1994). Phenotypic plasticity of size-fecundity relationships in *Arabidopsis thaliana*. *Journal of Ecology*, *82*, 447–455. https://doi.org/10.2307/2261254

Crosby, S. C., Ivens-Duran, M., Bertness, M. D., Davey, E., Deegan, L. A., & Leslie, H. M. (2015). Flowering and biomass allocation in US Atlantic coast *Spartina alterniflora*. *American Journal of Botany*, *102*, 669–676. https://doi.org/10.3732/ajb.1400534

Dai, X. F., Jia, X., Zhang, W. P., Bai, Y. Y., Zhang, J. Y., Wang, Y., & Wang, G. X. (2009). Plant height-crown radius and canopy coverage-density relationships determine above-ground biomass-density relationship in stressful environments. *Biology Letters*, *5*, 571–573. https://doi.org/10.1098/rsbl.2009.0228

Deng, J. M., Wang, G. X., Morris, E. C., Wei, X. P., Li, D. X., Chen, B. M., … Wang, Y. (2006). Plant mass-density relationship along a moisture gradient in north-west China. *Journal of Ecology*, *94*, 953–958. https://doi.org/10.1111/j.1365-2745.2006.01141.x

Du, G. Z., & Qi, W. (2010). Trade-offs between flowering time, plant height, and seed size within and across 11 communities of a QingHai-Tibetan flora. *Plant Ecology*, *209*, 321–333. https://doi.org/10.1007/s11258-010-9763-4

Ellison, A. M. (1987). Density-dependent dynamics of *Salicornia europaea* monocultures. *Ecology*, *68*, 737–741. https://doi.org/10.2307/1938480

Enquist, B. J., Brown, J. H., & West, G. B. (1998). Allometric scaling of plant energetics and population density. *Nature*, *395*, 163–165. https://doi.org/10.1038/25977

Gallagher, J. L., Somers, G. F., Grant, D. M., & Seliskar, D. M. (1988). Persistent differences in two forms of *Spartina alterniflora*: A common garden experiment. *Ecology*, *69*, 1005–1008. https://doi.org/10.2307/1941255

Gleason, M. L., Elmer, D. A., Pien, N. C., & Fisher, J. S. (1979). Effects of stem density upon sediment retention by salt marsh cord grass, *Spartina alterniflora* Loisel. *Estuaries*, *2*, 271–273. https://doi.org/10.2307/1351574

Gorham, E. (1979). Shoot height, weight and standing crop in relation to density of monospecific plant stands. *Nature*, *279*, 148–150. https://doi.org/10.1038/279148a0

Guo, H., Weiner, J., Mazer, S. J., Zhao, Z. G., Du, G. Z., & Li, B. (2012). Reproductive allometry in *Pedicularis* species changes with elevation. *Journal of Ecology*, *100*, 452–458. https://doi.org/10.1111/j.1365-2745.2011.01884.x

Harper, J. L. (1977). *Population biology of plants*. London, UK: Academic Press.

Hesse, E., Rees, M., & Müller-Schärer, H. (2008). Life-history variation in contrasting habitats: Flowering decisions in a clonal perennial herb (*Veratrum album*). *The American Naturalist*, *172*, E196–E213. https://doi.org/10.1086/591683

Hoyo, Y., & Tsuyuzaki, S. (2015). Sexual and vegetative reproduction of the sympatric congeners *Drosera anglica* and *Drosera rotundifolia*. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *210*, 60–65. https://doi.org/10.1016/j.flora.2014.10.003

Kachi, N., & Hirose, T. (1985). Population dynamics of *Oenothera glazioviana* in a sand-dune system with special reference to the adaptive significance of size-dependent reproduction. *Journal of Ecology*, *73*, 887–901. https://doi.org/10.2307/2260155

Kirwan, M. L., Guntenspergen, G. R., & Morris, J. T. (2009). Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Global Change Biology*, *15*, 1982–1989. https://doi.org/10.1111/j.1365-2486.2008.01834.x

Koons, D. N., Metcalf, C. J. E., & Tuljapurkar, S. (2008). Evolution of delayed reproduction in uncertain environments: A life-history perspective. *The American Naturalist*, *172*, 797–805. https://doi.org/10.1086/592867

Kozłowski, J., & Wiegert, R. G. (1987). Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology*, *1*, 231–244. https://doi.org/10.1007/BF02067553

Li, S., & Pennings, S. C. (2016). Disturbance in Georgia salt marshes: Variation across space and time. *Ecosphere*, *7*, e01487. https://doi.org/10.1002/ecs2.1487

Linthurst, R. A., & Seneca, E. D. (1981). Aeration, nitrogen and salinity as determinants of *Spartina alterniflora* Loisel. growth response. *Estuaries*, *4*, 53–63. https://doi.org/10.2307/1351542

Liu, W. W., Maung-Douglass, K., Strong, D. R., Pennings, S. C., & Zhang, Y. H. (2016). Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. *Journal of Ecology*, *104*, 173–181. https://doi.org/10.1111/1365-2745.12487

Mckee, K. L., & Patrick, W. H. (1988). The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datums: A review. *Estuaries*, *11*, 143–151. https://doi.org/10.2307/1351966

Mendelssohn, I. A., & Morris, J. T. (2002). Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. In *Concepts and controversies in tidal marsh ecology* (pp. 59–80). Dordrecht, The Netherlands: Springer.

Méndez, M., & Karlsson, P. S. (2004). Between-population variation in size-dependent reproduction and reproductive allocation in *Pinguiculavulgaris* (Lentibulariaceae) and its environmental correlates. *Oikos*, *104*, 59–70. https://doi.org/10.1111/j.0030-1299.2004.12335.x

Morris, E. C. (2002). Self-thinning lines differ with fertility level. *Ecological Research*, *17*, 17–28. https://doi.org/10.1046/j.1440-1703.2002.00459.x

Morris, J. T., & Haskin, B. (1990). A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. *Ecology*, *71*, 2209–2217. https://doi.org/10.2307/1938633

Morris, J. T., Sundberg, K., & Hopkinson, C. S. (2013). Salt marsh primary production and its responses to relative sea level and nutrients in estuaries at Plum Island, Massachusetts, and North Inlet, South Carolina, USA. *Oceanography*, *26*, 78–84. https://doi.org/10.5670/oceanog.2013.48

National Oceanic and Atmospheric Administration (2018). *Georgia Division 9 Palmer Drought Severity Index (PDSI) from Jan-1895 to Jan-2018*. Retrieved from http://gce-lter.marsci.uga.edu/portal/stations/noaa_drought/historic/data/noaa_pdsi_ga_div9_jan1895-jan2018.xml

Nestler, J. (1977). Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuarine and Coastal Marine Science*, *5*, 707–714. https://doi.org/10.1016/0302-3524(77)90043-3

Niklas, K. J. (1994). *Plant allometry: The scaling of form and process*. Chicago, IL: University of Chicago Press.

Niklas, K. J. (1995). Size-dependent allometry of tree height, diameter and trunk-taper. *Annals of Botany*, *75*, 217–227. https://doi.org/10.1006/anbo.1995.1015

O'Donnell, J. P., & Schalles, J. F. (2016). Examination of abiotic drivers and their influence on *Spartina alterniflora* biomass over a twenty-eight year period using Landsat 5 TM satellite imagery of the Central Georgia Coast. *Remote Sensing*, *8*, 477. https://doi.org/10.3390/rs8060477

Ohlson, M. (1988). Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. *Journal of Ecology*, *76*, 1007–1016. https://doi.org/10.2307/2260629

Pearcy, R. W., & Ustin, S. L. (1984). Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia*, *62*, 68–73. https://doi.org/10.1007/BF00377375

Peng, D., Chen, L. Z., Pennings, S. C., & Zhang, Y. H. (2018). Using a marsh organ to predict future plant communities in a Chinese estuary invaded by an exotic grass and mangrove. *Limnology and Oceanography*, *63*, 2595–2605. https://doi.org/10.1002/lno.10962

Pennings, S. C. (2003a). Fall 2000 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/0a82de490612fd99726034957 2b95704

Pennings, S. C. (2003b). Fall 2001 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/fb7d782b7f9e5d91b2346faff623c99a

Pennings, S. C. (2003c). Fall 2002 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/3124fd475a71ac2e8b23dfc4e87f4542

Pennings, S. C. (2004). Fall 2003 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/45680d2b15b34154d49602296 7fc0496

Pennings, S. C. (2006a). Fall 2004 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/674fec2640e4ff3ad5f96a3303f7f0c3

Pennings, S. C. (2006b). Fall 2005 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/1a781e75d57b0f999090c4203 2b3a52d

Pennings, S. C. (2007). Fall 2006 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/beafc321d556c6a408013f200a5334f4

Pennings, S. C. (2009a). Fall 2007 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/a7d25d256f23e3427752229cf 736a3a6

Pennings, S. C. (2009b). Fall 2008 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/43c93615a18bc464c7468069e 718ffe7

Pennings, S. C. (2011a). Fall 2009 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/729095532fdc5549c3a3625b1 eba4a90

Pennings, S. C. (2011b). Fall 2010 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/f5d79a9722572c7c2a10b8cba4a85a58

Pennings, S. C. (2011c). Soil salinity and water content at GCE-LTER vegetation monitoring plots in October 2010. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/03ed725daf81ce3ae0735932b 5e0f38a

Pennings, S. C. (2012). Fall 2011 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/11609e84864f1dfc390fd3e82b975d2d

Pennings, S. C. (2013a). Fall 2012 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/7c952f82f698c6a731759ad49 7bc8889

Pennings, S. C. (2013b). Soil salinity and organic content at GCE-LTER vegetation monitoring plots in October 2011. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/e53d69beecaa3a6832dc8dc82 05d623b

Pennings, S. C. (2013c). Soil salinity at GCE-LTER vegetation monitoring plots in October 2012. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/f940e82462b8964242eec9cb531c440d

Pennings, S. C. (2014a). Fall 2013 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/8bdad996ac2923367d99724ae9b0dfea

Pennings, S. C. (2014b). Soil salinity at GCE-LTER vegetation monitoring plots in October 2013. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/24d15af4f2dab97aff5148d5ae17d3aa

Pennings, S. C. (2015a). Fall 2014 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/618f9ec979aca6669d92646f7271a30f

Pennings, S. C. (2015b). Soil salinity at GCE-LTER vegetation monitoring plots in October 2014. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/c8ca5865d19b3de6d6b70d53dc0833db

Pennings, S. C. (2016). Fall 2015 plant monitoring survey – biomass calculated from shoot height and flowering status of plants in permanent plots at GCE sampling sites 1–10. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/980d41234ea67c2eacd6bcc69d4b877f

Pennings, S. C. (2017). *Soil salinity at GCE-LTER vegetation monitoring plots in October 2015*. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/d0e55b8da9bb0e71d4a8b893fc9a0c7a

Pennings, S. C., & Bertness, M. D. (2001). Salt marsh communities. In M. D. Bertness, S. D. Gaines, & M. E. Hay (Eds.), *Marine community ecology* (pp. 289–316). Sunderland, UK: Sinauer Associates.

Pennings, S. C., & Callaway, R. M. (2000). The advantages of clonal integration under different ecological conditions: A community-wide test. *Ecology*, *81*, 709–716. https://doi.org/10.1890/0012-9658(2000)081[0709:TAOCIU]2.0.CO;2

Pickering, C., & Arthur, J. M. (2003). Patterns of resource allocation in the dioecious alpine herb *Aciphylla simplicifolia* (Apiaceae). *Austral Ecology*, *28*, 566–574. https://doi.org/10.1046/j.1442-9993.2003.01313.x

Proffitt, C. E., Travis, S. E., & Edwards, K. R. (2003). Genotype and elevation influence *Spartina alterniflora* colonization and growth in a created salt marsh. *Ecological Applications*, *13*, 180–192. https://doi.org/10.1890/1051-0761(2003)013[0180:GAEISA]2.0.CO;2

Qiu, S. Y., Xu, X., Liu, S. S., Liu, W. W., Liu, J., Nie, M., … Li, B. (2018). Latitudinal pattern of flowering synchrony in an invasive wind-pollinated plant. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20181072. https://doi.org/10.1098/rspb.2018.1072

R Development Core Team (2016). *R: A language and environment for statistical computing, version 3.3.2*. Vienna, Austria: R Project for Statistical Computing. www.r-project.org.

Reekie, E. G. (1998). An explanation for size-dependent reproductive allocation in *Plantago major*. *Canadian Journal of Botany*, *76*, 43–50. https://doi.org/10.1139/b97-160

Richards, C. L., Pennings, S. C., & Donovan, L. A. (2005). Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology*, *176*, 263–273. https://doi.org/10.1007/s11258-004-0841-3

Roscher, C., & Schumacher, J. (2016). Positive diversity effects on productivity in mixtures of arable weed species as related to density-size relationships. *Journal of Plant Ecology*, *9*, 792–804. https://doi.org/10.1093/jpe/rtw013

Schalles, J. F., Hladik, C. M., Lynes, A. A., & Pennings, S. C. (2013). Landscape estimates of habitat types, plant biomass, and invertebrate densities in a Georgia salt marsh. *Oceanography*, *26*, 88–97. https://doi.org/10.5670/oceanog.2013.50

Stearns, S. C., & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. *Evolution*, *40*, 893–913. https://doi.org/10.1111/j.1558-5646.1986.tb00560.x

Strong, D. R., & Ayres, D. R. (2013). Ecological and evolutionary misadventures of *Spartina*. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 389–410. https://doi.org/10.1146/annurev-ecolsys-110512-135803

Sugiyama, S., & Bazzaz, F. A. (1998). Size dependence of reproductive allocation: The influence of resource availability, competition and genetic identity. *Functional Ecology*, *12*, 280–288. https://doi.org/10.1046/j.1365-2435.1998.00187.x

Sun, S. C., & Frelich, L. E. (2011). Flowering phenology and height growth pattern are associated with maximum plant height, relative growth rate and stem tissue mass density in herbaceous grassland species. *Journal of Ecology*, *99*, 991–1000. https://doi.org/10.1111/j.1365-2745.2011.01830.x

Teal, J. M., & Howes, B. L. (1996). Interannual variability of a salt-marsh ecosystem. *Limnology and Oceanography*, *41*, 802–809.

Thompson, B. K., Weiner, J., & Warwick, S. I. (1991). Size-dependent reproductive output in agricultural weeds. *Canadian Journal of Botany*, *69*, 442–446. https://doi.org/10.1139/b91-061

Turner, R. E. (1976). Geographic variations in salt marsh macrophyte production: A review. *Contributions in Marine Science*, *20*, 47–68.

Visser, J. M., Sasser, C. E., & Cade, B. S. (2006). The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts*, *29*, 328–339. https://doi.org/10.1007/BF02782001

Wade, M., & Sheldon, J. R. (2018a). *Monthly mean water level data were acquired from the NOAA/NOS Center for Operational Oceanographic Products and Services (CO-OPS) database* (http://www.co-ops.nos.noaa.gov/). Selected date/time and data columns were extracted from the CO-OPS web pages, standardized and documented using metadata templates. Retrieved from http://gce-lter.marsci.uga.edu/portal/stations/nos_fort_pulaski/historic/data/nos_fort_pulaski_monthly_jul1935-jan2018.xml

Wade, M., & Sheldon, J. R. (2018b). *Monthly Summary of Daily Summary of Data from the USGS gaging station on the Altamaha River at Doctortown from 01-Jan-1932 to 30-Aug-2018*. Retrieved from http://gce-lter.marsci.uga.edu/portal/stations/usgs_doctortown/historic/data/usgsdoctortown_monthly_oct1931-aug2018.xml

Wade, M., & Sheldon, J. R. (2019). *Monthly Summary of Daily climatological observations from the National Weather Service weather station at the Malcolm McKinnon Airport in Brunswick, Georgia from 01-Aug-1948 through 12-June-2019*. http://gce-lter.marsci.uga.edu/portal/stations/nws_brunswick_ap/historic/data/nws_brunswick_ap_monthly_aug1948-jun2019.xml

Wade, R. K. (2018). Models for plant self-thinning. *Ecosphere*, *9*, e02219. https://doi.org/10.1002/ecs2.2219

Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3-an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, *3*, 257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Watkinson, A. R. (1980). Density-dependence in single-species populations of plants. *Journal of Theoretical Biology*, *83*, 345–357. https://doi.org/10.1016/0022-5193(80)90297-0

Weiner, J. A. C. O. B. (1988). The influence of competition on plant reproduction. *Plant Reproductive Ecology: Patterns and Strategies*, 228–245.

Weiner, J. (2004). Allocation, plasticity and allometry in plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*, 207–215. https://doi.org/10.1078/1433-8319-00083

Weiner, J., Campbell, L. G., Pino, J., & Echarte, L. (2009). The allometry of reproduction within plant populations. *Journal of Ecology*, *97*, 1220–1233. https://doi.org/10.1111/j.1365-2745.2009.01559.x

Wesselingh, R. A., & De Jong, T. J. (1995). Bidirectional selection on threshold size for flowering in *Cynoglossum officinale* (hound's-tongue). *Heredity*, *74*, 415–424. https://doi.org/10.1038/hdy.1995.59

Wesselingh, R. A., Klinkhamer, P. G., De Jong, T. J., & Boorman, L. A. (1997). Threshold size for flowering in different habitats: Effects of size-dependent growth and survival. *Ecology*, *78*, 2118–2132.

https://doi.org/10.1890/0012-9658(1997)078[2118:TSFFID]2.0.CO;2

Więski, K., & Pennings, S. C. (2014). Climate drivers of *Spartina alterniflora* saltmarsh production in Georgia, USA. *Ecosystems*, *17*, 473–484. https://doi.org/10.1007/s10021-013-9732-6

Xiao, Y., Tang, J. B., Qing, H., Zhou, C. F., & An, S. Q. (2011a). Effects of salinity and clonal integration on growth and sexual reproduction of the invasive grass *Spartina alterniflora*. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *206*, 736–741. https://doi.org/10.1016/j.flora.2010.12.003

Xiao, Y., Tang, J. B., Qing, H., Zhou, C. F., Kong, W. J., & An, S. Q. (2011b). Trade-offs among growth, clonal, and sexual reproduction in an invasive plant *Spartina alterniflora* responding to inundation and clonal integration. *Hydrobiologia*, *658*, 353–363. https://doi.org/10.1007/s10750-010-0505-3

Xiao, Y., Zhao, H., Yang, W., Qing, H., Zhou, C. F., Tang, J. B., & An, S. Q. (2015). Variations in growth, clonal and sexual reproduction of *Spartina alterniflora* responding to changes in clonal integration and sand burial. *Clean–soil Air, Water*, *43*, 1100–1106. https://doi.org/10.1002/clen.201300868

Yoda, K., Kira, T., Ogawa, H., & Hozumi, K. (1963). Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University*, *14*, 107–129.

Zheng, S. Y., Shao, D. D., & Sun, T. (2018). Productivity of invasive saltmarsh plant *Spartina alterniflora* along the coast of China: A meta-analysis. *Ecological Engineering*, *117*, 104–110. https://doi.org/10.1016/j.ecoleng.2018.03.015

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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