

RESEARCH ARTICLE



Sexual reproduction is light-limited as marsh grasses colonize maritime forest

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Abstract

Climate change is driving abiotic shifts that can threaten the conservation of foundation species and the habitats they support. Directional range shifting is one mechanism of escape, but requires the successful colonization of habitats where interspecific interactions may differ from those to which a species has adapted. For plants with multiple reproductive strategies, these range-edge interactions may alter the investment or allocation toward a given reproductive strategy. In this study, we quantified sexual reproduction of the clonal marsh grass *Spartina patens* across an inland colonization front into maritime forest being driven by sea-level rise. We find that flowering is variable across *S. patens* meadows, but consistently reduced in low light conditions like those of the forest understory. Observational surveys of *S. patens* flowering at four sites in the Delmarva Peninsula agreed with the results of two experimental manipulations of light availability (shading experiment in *S. patens*-dominated marsh and a forest dieback manipulation). These three approaches pinpointed light limitation as a principal control on *S. patens* flowering capacity, suggesting that light competition with taller upland species can suppress *S. patens* flowering along its upland migration front. Consequently, all propagation in shaded conditions must occur clonally or via seeds from the marsh, a reproductive restriction that could limit the potential for local adaptation and reduce genetic diversity. Future research is needed to determine whether the lack of flowering is the result of a trade-off between sexual and clonal reproduction or results from insufficient photosynthetic products needed to achieve either reproductive method.

KEYWORDS

ecotone, high marsh, intraspecific variation, maritime forest, marsh migration, Poaceae, range edge, sea-level rise, *Spartina*

Climate change is driving shifts in environmental conditions that directly impact the fitness, physiological function, and geographic distribution of plant species (Parmesan and Yohe, 2003; Walther, 2003). Plants can respond to rapid environmental change by adapting to new selection pressures in situ (Jump and Peñuelas, 2005) or by dispersing in ways that shift their range extent (Chen et al., 2011). If they are unable to respond to environmental change, plants are forced to persist in conditions that are suboptimal to their phenotype. This leads to negative fitness repercussions and the risk of extinction (Fordham et al., 2011). On a broad scale, climate-driven range shifts move plants into environmental conditions similar to their area of origin, such as the expansion of temperate plants upward in latitude and altitude in concert with temperature shifts along those same

gradients (Beckage et al., 2008; Gottfried et al., 2012). However, heterogeneity in biotic and abiotic conditions over smaller spatial and temporal scales can place constraints on plant fitness, limiting the rate of climate-driven habitat expansion (HilleRisLambers et al., 2013).

One aspect of plant function that can be highly variable at range edges is reproduction. The remarkable diversity of reproductive strategies within the plant world incorporates different dispersal vectors, relative frequencies of mating with other individuals (outcrossing) (vs. self-fertilization [selfing]), and degrees of sexual (vs. asexual [i.e., vegetative clonal]) reproduction (Barrett and Harder, 2017; Orive and Krueger-Hadfield, 2021). Plants that have evolved multiple reproductive strategies can have high intraspecific variation in the relative allocation of resources to different

reproductive modes. This variation can be genetically encoded (Kleunen et al., 2002) or plastically induced by environmental conditions (Cheplick, 2007). For example, clonal plants often limit floral output when faced with environmental stress because producing clonal offspring can be less energetically costly than producing seeds, and clonality entails lower risk because it avoids the bottleneck of seed dispersal and establishment (Jonsdottir et al., 1996). In species that reproduce both clonally and sexually, sexual reproduction decreases at range limits that coincide with environmental gradients (Dorken and Eckert, 2001; Beatty et al., 2008).

Around the world, accelerated sea-level rise is driving the migration of tidal wetland habitats into upland coastal habitats (Kirwan and Gedan, 2019; Taillie et al., 2019; Carr et al., 2020). In the coastal Mid-Atlantic region of the United States, brackish and salt marsh plants are rapidly moving into coastal pine forests that are dying due to a combination of chronic salt-stress and periodic storm events (Smith, 2013; Fagherazzi et al., 2019; Gedan et al., 2020). This process has affected large areas of coastal habitat; Schieder et al. (2018) found that fully one third of today's marshland in the Chesapeake Bay was created through upland-to-marsh conversion during the last 200 years. In areas where migration is inhibited by factors such as a steeper topography or impermeable natural or anthropogenic barriers, wide-scale marsh losses have been recorded (Gedan et al., 2009; Smith, 2009). These losses are predicted to worsen in coming decades (Enwright et al., 2016; Raposa et al., 2017). For this reason, the process of marsh migration can be seen as a vital part of marsh habitat resilience and of preserving the ecosystem services provided by marshes.

The ecological processes at this shifting ecotone are understudied. However, recent work has found that marsh plants appear before edaphic changes (Anisfeld et al., 2017) and are observed in the soil seed bank of upland forests (Kottler and Gedan, 2020). The species comprising this migration front are a relatively small number of salt-tolerant shrubs and grasses that are adapted to high-light environments. These are also found in the low-lying coastal forest understory (Shaw et al., 2021). To better understand the community processes at this ecotone border, we investigated how marsh plants are responding to biotic and abiotic shifts at this range edge. Abiotic conditions change dramatically across the marsh migration front: salinity decreases and shading by trees and shrubs increases (Kottler and Gedan, 2020; Jobe and Gedan, 2021). Although the reduced salinities of uplands translate into less salinity stress for marsh endemics, the introduction of light limitation strongly reduces plant photosynthetic resources and restricts net carbon gain (Pearcy et al., 1987).

One of the key high-marsh native species undergoing this migration process into the coastal forest understory is *Spartina patens* (W. Aiton) G.H. Muhlenberg [synonymous with *Sporobolus pumilis* (Roth) P.M. Peterson & Saarela; Poaceae]. *Spartina patens*, also known as salt marsh hay, is

the dominant plant species that typifies the irregularly flooded high-marsh zone of tidal salt and brackish marshes in the eastern United States (Bertness, 1991b; Lonard et al., 2010). Salt marsh hay is a foundation species whose conservation is of critical importance to the maintenance of ecosystem services. Its presence on the landscape reduces evapotranspirative water loss and hypersalinization of marsh soils (Pennings and Bertness, 2014), provides food and hunting grounds for a diversity of arthropods and arachnids and, critically, serves as the only suitable nesting habitat for many native and endangered shorebirds (Wilson et al., 2007).

In recent years, the high-marsh habitat of *S. patens* has been declining throughout much of its native range due to the additive stressors of sea-level rise, drought, invasive species, and land development (Watson et al., 2016). With sea-level rise, *S. patens* is experiencing encroachment by its more flood-tolerant sister species, *Spartina alterniflora* (Donnelly and Bertness, 2001), and is also being replaced by non-native *Phragmites australis* that establishes at upland marsh borders (Amsberry et al., 2000). This narrowing of the high-marsh zone, referred to as coastal squeeze, threatens to eliminate high-marsh habitat altogether in many regions experiencing future sea-level rise scenarios (Raposa et al., 2017; Smith et al., 2017; FitzGerald et al., 2021). For this reason, upland migration of *S. patens*, where possible, is critical to maintaining high-marsh habitat.

We observed that flowers were rare in *S. patens* living on this climate-driven migration front. This phenomenon raised the question, “Does light availability limit sexual reproduction of this grass species?” Therefore, we conducted a series of flowering surveys of *S. patens* along the habitat transition from high marsh to coastal forest; we performed a shading experiment; and we surveyed areas where forest canopy was experimentally removed to facilitate marsh migration. We hypothesized that, given the high-light conditions to which this species is accustomed, flowering density would be inhibited by decreased light availability across the marsh-forest ecotone and that this effect could be experimentally induced with shading in open marsh conditions.

MATERIALS AND METHODS

Study sites

We employed a multifaceted approach that incorporated observational surveys of *S. patens* flowering stem densities at multiple sites and experimental manipulations of light availability in areas of *S. patens*-dominated marsh and forest understory. Observational flowering surveys and a shading experiment were conducted at four saline marsh sites on the Mid-Atlantic coast of the United States. Each site has an ecotone in which a high-marsh plant community, dominated by *S. patens*, *Schoenoplectus americanus*, *Juncus*

roemerianus, and *Distichlis spicata*, transitions into a heterogeneous distribution of salt-tolerant shrubs and short trees (*Iva frutescens*, *Baccharis halimifolia*, and *Juniperus virginiana*) as well as grasses (*Festuca rubra*, *Panicum virgatum*, and *Phragmites australis*) amid dead and stressed loblolly pine (*Pinus taeda*) trees. Farther inland, this ecotone transitions into a maritime forest dominated by loblolly pine. This shift in vegetation occurs in a heterogeneous manner. There is little to no change in elevation associated with the vegetation shift (Kottler and Gedan, 2020).

Observational surveys were conducted at Phillips Creek, Box Tree, Cushman's Landing, and Moneystump Marsh (Figure 1A). Phillips Creek Marsh is a mainland salt marsh on the eastern side of the Delmarva Peninsula and is tidally connected to the Atlantic Ocean via Hog Island Bay. Marsh accretion and sedimentation dynamics have been studied extensively at this site (Christiansen et al., 2000; Thomas and Christian, 2001; Kirwan and Blum, 2011; Blum et al., 2020). Our surveys were conducted in the upper portion of Phillips Creek where *S. patens* high marsh transitions into loblolly pine forest. Box Tree and Cushman's Landing are also situated on the Virginia seaside of the Virginia Eastern Shore, to the south of Phillips Creek. They are tidally connected to the Atlantic Ocean via

Ramshorn Bay and Magothy Bay, respectively. These three sites have been protected by The Nature Conservancy within the Virginia Coast Reserve for the past 50 years and represent a unique opportunity to study sea-level rise impacts without the many confounding impacts of intensive land development.

The final site of observational surveys was Moneystump Marsh, a tidal brackish marsh within the Blackwater National Wildlife Refuge in Dorchester County, Maryland. The marsh is connected to the Chesapeake Bay via a series of tidal creeks that flow past Taylors Island. This site also served as the location of the marsh shading and forest-disturbance experiments (Figure 1B). Once a continuous marsh, the marshes at Blackwater Refuge have experienced habitat loss due to subsidence and sea-level rise. They now contain an expansive tidal lake and extensive ghost forest where a coastal loblolly pine forest has receded (Stevenson et al., 1985; Kern and Shriver, 2014; Ganju et al., 2015).

Flowering survey

At each site, we surveyed points spaced 5 m apart along five transects, each 40 m in length. Surveys were conducted

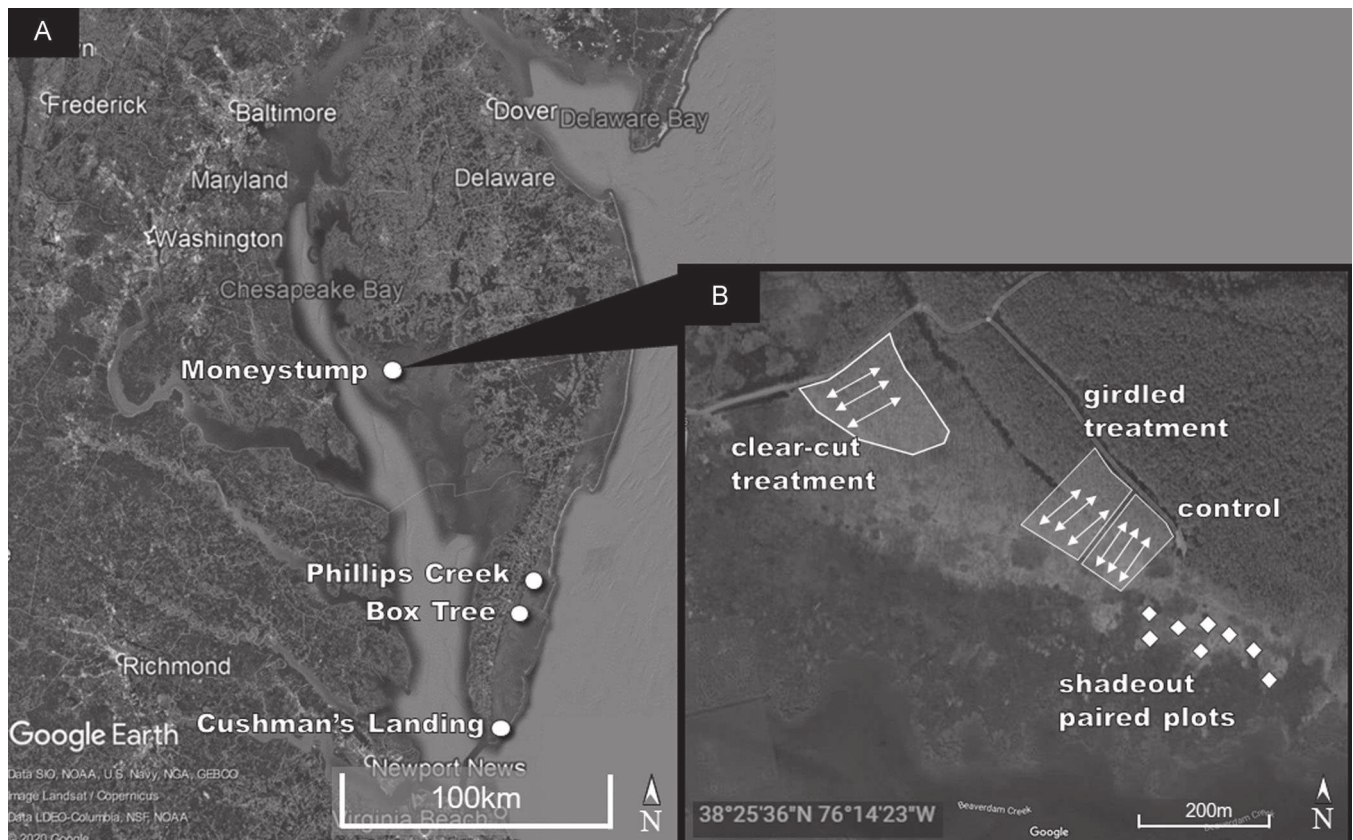


FIGURE 1 Map of study sites. (A) Regional map with dots that represent sites at which observational transects were surveyed: Moneystump Marsh (38°25'36"N, 76°14'23"W); Phillips Creek Marsh (37°27'44"N 75°49'47"W); Box Tree Marsh (37°23'48"N 75°52'312"W); and Cushman's Landing (37°10'42.5"N 75°56'35.8"W). (B) Inset map of Moneystump Marsh with positions of the paired plots in the shading experiment and of the USGS forest-disturbance treatments.

between 28 June and 1 August 2019. All transects began close to the marsh–forest ecotone in high-marsh habitat dominated by *S. patens* and *D. spicata* and progressed into the forest, perpendicular to the forest edge. At each point, we estimated the percentage cover of *S. patens* within a 1-m² PVC quadrat and the number of flowering stems within a 25 × 25 cm quadrat. This survey of flowering density per unit area provided a rapid assessment of floral capacity, since this species grows in a continuous mat rather than individual tussocks (Lonard et al., 2010). To quantify available light at the subcanopy level, we took the average of six readings of photosynthetic photon flux density (PPFD) in $\mu\text{mol m}^{-2} \text{s}^{-1}$ using a LI-250A light meter (LI-COR Biosciences, Lincoln, NE, USA) positioned approximately 30 cm above the plot, just above the grass canopy. Simultaneously, we measured ambient light data using a HOBO light pendant (Onset Computer Corp., Bourne, MA, USA), which logged the total available light in lumens per square foot in 15-min intervals in an area of open sun. The same transects were surveyed twice during the flowering season, both at and after peak bloom. Surveys were timed to capture the maximum number of flowers or seed heads and to ensure that differences between transect locations were not confounded by potential phenological differences in flowering across the marsh migration front. During the second sampling, we collected 12 × 5 cm (diameter × depth) soil cores to measure soil salinity. These were brought to the lab and mixed in a 1:1 dilution with distilled water. Salinity was measured using a salinity/conductivity meter (EC-170, Extech Instruments, Waltham, MA, USA).

Forest dieback survey

To address the flowering potential of migrating *S. patens* under different forest dieback scenarios, we surveyed transects within a pre-existing forest-disturbance experiment (also at Moneystump Marsh, MD) established by U.S. Geological Survey (USGS) researchers in 2014 (Walters et al., 2021). The experiment was designed to assess the effects of forest mortality on ecological and biophysical processes across the marsh–forest ecotone. Forest areas represent three disturbance levels: a control area naturally undergoing forest dieback with sea-level rise; a clear-cut treatment, in which trees were removed by a logging company in a conventional timber harvest; and a girdling treatment, in which a full ring of bark and cambium was stripped from tree trunks, inducing a slow mortality which resembles the impact of major storm events in coastal forests (Sah et al., 2010). Five years after the treatments, the areas were surveyed as described for the flowering survey but with three transects per experimental treatment. Transect length (40 m) and spacing (30–50 m apart) remained the same. We collected the same data at the dieback experimental sites as were collected in the observational flowering surveys, with the exception of salinity, which was not measured due to concerns about collecting soil samples from another researcher's active experiment.

Additional percentage cover data for co-occurring species were also collected within the 1-m² plots.

Shading experiment

At Blackwater NWR, pairs ($n = 8$) of 4-m² plots were established in the open marsh in early March 2019. Plots were sited haphazardly within the high-marsh zone, away from the forest dieback survey sites described below, and where *S. patens* areal cover was 50% or greater. Pairs were separated by approximately 15 m to assure independence. Within each pair of adjacent plots, one plot was randomly assigned to the shaded treatment and the other to the control treatment. There was no significant difference in percentage cover of *S. patens* between control and shaded plots. On each square plot, we placed a 2 × 2 m PVC frame, elevated approximately 60 cm above the marsh platform, which was left open in control plots and covered with shade cloth (10% light transmission) in shaded plots. There was no structure-free control; control plots, like shaded plots, received a PVC frame to reduce plot differences that could have been attributed only to the presence of a structure. Around the boundary of each plot, roots and rhizomes were severed with a knife to a 15-cm depth to prevent sharing of resources between grasses inside and outside of plots. This depth was considered sufficient given evidence that the majority of *S. patens* belowground biomass occurs within the top 10 cm of soil (Windham, 2001). Twice during the flowering season, flowering heads were counted in four randomly selected 25 × 25 cm quadrats in each plot. Total percentage cover of *S. patens*, light availability, and salinity were also measured in each plot at these times, using same methods as described above.

Statistical analyses

All statistical analyses were performed in R version 4.0.2 (2020-06-22). Unless specified otherwise, data conformed to the statistical assumption of homoscedasticity. Light availability is presented as a percentage value, with light availability at plant height in PPFD normalized by ambient light under open conditions. Ambient light values were originally measured in Lux and were converted to $\mu\text{mol m}^{-2} \text{s}^{-1}$ using the standard calibration factor 0.0185 under sunlit conditions (Moheimani et al., 2013). A few sampling points arrived at a percentage available light greater than 100, likely attributable to a difference in cloud cover in the minutes between PPFD and ambient HOBO light data collection. These observations were omitted, after confirming that all analyses returned the same statistical conclusion with and without their presence in the data set.

To predict flowering density as a function of environmental conditions, we ran a generalized linear model (GLM) with a negative binomial distribution (Table 1). All GLMs were run using the package MASS version 7.3-54

TABLE 1 Statistical models of *Spartina patens* flowering. Full and reduced models relating environmental factors and *S. patens* traits are presented, fitted to data from one of the three data sets in this study. All models are generalized linear models (GLMs) with a negative binomial distribution unless marked with a †, in which case they are GLMs. The goodness of fit of each model is quantified using the Akaike information criterion (AIC) estimator. Variables that were significant within each model are bolded with asterisks to indicate threshold of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Experiment	Model	AIC	Variable	Estimate	SE
Observational surveys	$f \sim l + t + s + c$	1148.2	l^{***}	7.337	0.4872
			c^{**}	1.6826	0.5342
			t	0.1244	0.26
			s_{MS}	0.5831	0.3778
			s_{CL}	0.5759	0.382
			s_{PC}	0.7123	0.3778
Forest dieback surveys	$f \sim d$	1102.6	d^{***}	-0.1391	0.01047
	$f \sim x$	1172.8	y^{***}	0.8267	0.1126
	$f \sim l + t + y + c$	852.72	l^{***}	2.3605	0.688
			c^{***}	3.6488	0.4315
			y_g^{**}	-0.9774	0.3258
			y_c^*	-0.6265	0.3099
			t	-0.2171	0.2923
	$f \sim d$	886.13	d^{***}	-0.04189	0.01118
	$l \sim d^* y^\dagger$	-	d^{***}	-0.00806	0.00227
			y_g	0.15208	0.07813
			y_c	-0.11173	0.07565
			$d^* y_g$	-0.00085	0.01118
			$d^* y_c^{**}$	0.0096	0.0031
	$c \sim d^* y^\dagger$	-	d	0.24274	0.31338
			y_g	20.3736	10.7747
			y_c	-11.6302	10.4315
			$d^* y_g^{***}$	-1.51912	0.43714
			$d^* y_c$	-0.05844	0.42788

Abbreviations: f = flowering stems/m², l = light availability, t = sampling time point, s = site, d = distance across transect, x = soil salinity, y = forest dieback treatment, y_g = contrast of control vs. girdled treatment, y_c = contrast of control vs. clear cut treatment, c = *S. patens* percentage cover.

(Ripley et al., 2013). To account for time since colonization (which will impact the belowground resources available for producing flowers), we included percentage ground cover of *S. patens* within our 1-m survey plots as a covariate in our full statistical models. The variables of distance along transect, light availability, and salinity were significantly correlated with one another, and as such, all could not be included as predictors in the same model. Because we were interested in the relationship between light availability and flowering, we included light availability as a predictor in the full model along with site, percentage cover of *S. patens* and sampling time point, then ran separate univariate models of salinity and distance vs. flowering (Table 1). Continuous predictor variables (light and *S. patens* cover) were scaled as proportions (range of 0–1).

To model the maximum flowering potential under limited light conditions, we ran a nonlinear quantile regression on the subset of data from 0 to 50% available light. A quantile regression allowed us to empirically characterize the maximal flowering response across a variety of light conditions, while allowing that most plants are unlikely to reach full floral output due to unmeasured limiting factors such as nutrient availability and hydrology (Cade and Noon, 2003). We used the `nlrq` function from the `quantreg` package to fit a nonlinear quantile regression for a 95% quantile (Koenker et al., 2018). The nonlinear function took the form of a logistic (sigmoid) curve with the equation $y \sim a / \{1 + \exp[-b(x - c)]\}$ where y is the predicted flowering density, x is light availability, a is the upper asymptote, b is the slope parameter, and c is the inflection point. For the

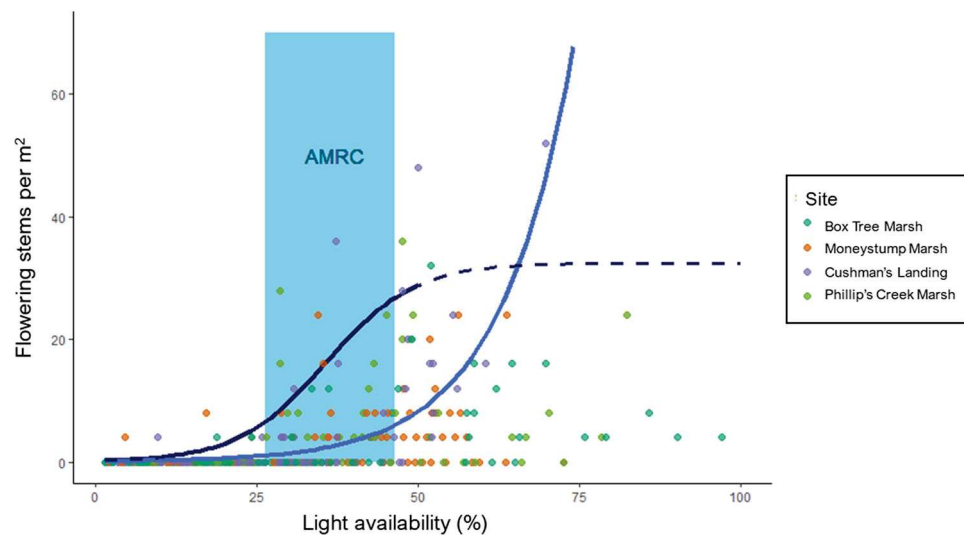


FIGURE 2 Flowering density for *Spartina patens* across a light gradient. Points represent sampled quadrats across observational transects that are color-coded by site. The x-axis displays percentage available light at vegetation height relative to total light under open conditions (both in $\mu\text{mol m}^{-2} \text{s}^{-1}$), and the y-axis displays flowering density in flowering stems per meter squared. The cobalt blue curve models the negative binomial GLM relationship between the x and y variables. The navy blue logistic (sigmoid) curve shows a 0.95 nonlinear quantile regression fitted to the data curve (a [upper asymptote] estimate: 32.469, SE: 12.936, $P < 0.05$; b [slope parameter] estimate: 0.144, SE: 0.064, $P < 0.05$; c [inflection point] estimate: 35.721, SE: 8.512, $P < 0.0001$). The area of maximum rate of change (AMRC; shaded blue), determined by finding the local maxima of the second derivative, occurs between 26.3% and 46.4% light availability. The dashed blue line indicates the threshold of 26.3% light availability; when light availability is less than 26.3%, flowering is strongly light-limited.

derived curve, we determined the inflection point and the area of maximum rate of change (AMRC) (Frasier and Wang, 2013). For light availability values below the AMRC, the slope of the sigmoidal curve does not change meaningfully; thus, below this threshold, floral capacity is effectively null (Figure 2).

To assess the relationship between light and forest treatment on *S. patens* flowering, we ran a GLM with a negative binomial distribution, with flowering density as the response variable; with light availability, forest treatment, *S. patens* cover (%) and sampling time point as predictors in the model (with continuous variables scaled as proportions) (Table 1). Once again, we modeled the univariate relationship between distance along transects and flowering density separately due to the collinearity of distance and light availability. Additionally, we modeled the additive effects of distance from the marsh and dieback treatment on light availability and *S. patens* cover using linear models. To assess the species composition along the marsh to forest gradient under different forest-disturbance conditions, we used nonmetric multidimensional scaling (NMDS) from the vegan package (Oksanen et al., 2020). After this variable reduction process, we ran an analysis of similarity (ANOSIM) to test whether there was a significant difference in species composition under different dieback treatments, and we ran a vector analysis of our continuous variables of light availability, distance, and *S. patens* flowering density. We also identified indicator species for each treatment group using a multilevel pattern analysis from the indicpecies R package (Cáceres and Legendre, 2009; Cáceres et al., 2016).

In the analysis of the shading experiment data, flowering density, light availability, and salinity data were transformed with a log10 function to account for issues of homoscedasticity. There was greater variance in flowering density in the control plots than in the shaded plots, as a result of a large difference in their means and the lower bound of flower density at zero. After transformation, the relationship between shade treatment and sampling time point on these response variables were assessed with linear models.

RESULTS

Flowering survey

We observed positive relationships between available light and flowering density (Figure 2) and between *S. patens* cover and flowering density, with light explaining a greater proportion of variance in the model (Table 1). There was a slight correlation of 0.342 between light availability and *S. patens* cover (Appendix S1). The other factors (time point, site) in the full model were not significant. The univariate model of distance along transect vs. flowering density was also significant and had a somewhat better fit than the full model ($\text{AIC } \Delta 45.9$) (Table 1). Our nonlinear 95% quantile regression arrived at a logistic (sigmoid) curve with an estimated inflection point of 35.7% and with an area of maximum rate of change (AMRC) between 26.3 and 46.4% light availability.

Forest dieback survey

Five years after the USGS implemented their forest-disturbance treatments, we observed significant differences in plant community composition between the clear-cut, girdled, and natural dieback zones. The control and girdled plots had similar communities in the marsh and ecotone, but differed at the most upland portions of the transects. The shrub *Morella cerifera* dominated in the girdled area, whereas *P. taeda* dominated in the control area. In the clear-cut area, the plant community differed significantly from control and girdled communities (ANOSIM statistic R : 0.264; $P < 0.001$). Observationally, the clear-cut area also had greater heterogeneity in microtopography associated with remnant tree stumps.

We observed significant positive relationships between available light and flowering density and *S. patens* cover and flowering density, and a negative relationship between the two forest dieback treatments (as compared with control transects) and flowering density (Table 1; Appendix S2). While we found lower flowering density in clear-cut and girdled forest treatments compared to the control, this pattern was largely driven by three samples of especially high flowering density in the control (Figure 4). Light availability was negatively correlated with distance from the marsh in the girdled and natural dieback (control) zones where vegetation cover shifted from marsh grasses to shrubs and trees, respectively (Figure 4A). The girdled treatment also showed a negative relationship between distance from the marsh and *S. patens* cover that was not present in the other treatment zones (Figure 4B). In the clear-cut zone, light availability had no relationship with distance from the marsh (Figure 4A). Correspondingly, the clear-cut zone did not exhibit the negative relationship between flowering and distance from the marsh that was observed in the other treatments and in the observational plots (Figure 4C, Table 1). In all dieback treatments, including the clear-cut zone where the relationship between light and distance from the marsh broke down, *S. patens* flowering density was significantly correlated with light availability (Table 1; Appendix S1).

Shading experiment

The shading treatment significantly reduced light availability ($\sim 12.16\%$ available light $\pm 0.75\%$ SE) in the marsh plots (ANOVA, $F_{1,26} = 126.9$, $P < 0.0001$). This treatment is comparable to what is found in the forest understory, with data from other work indicating 23.6% light availability when canopy cover is 50%, the value we use to delineate the marsh–forest ecotone (Shaw et al., 2021). We found no difference in soil salinity between control and shaded conditions (ANOVA, $F_{1,14} = 3.19$, $P = 0.0957$). We observed a 7-fold reduction in mean floral density in shaded relative to control plots (Figure 3) (ANOVA, $F_{1,26} = 114.2$, $P < 0.0001$), and there was no difference in flowering between time points (ANOVA, $F_{1,26} = 0.1451$, $P = 0.7064$).

DISCUSSION

In our study, flowering by *S. patens* was highly variable in the open conditions of the high marsh, but uniformly decreased to zero or nearly so in the low light conditions typical of the forest edge. Light intensity had a significant effect on flowering density when percentage cover of *S. patens* was included as a covariate, revealing that the negative effect of shade on reproduction cannot simply be explained by a decline in abundance (Table 1). This positive correlation between light availability and flowering density was consistent across multiple marsh sites, at different times in the flowering phenology of *S. patens* and under different upland management scenarios. In the shading experiment, we found that well-established high-marsh populations of *S. patens* were unable to flower under shaded conditions. When distance across the marsh migration front was decoupled from light availability (in the clear-cut forest treatment), we still saw a significant relationship between light availability and flowering density. Using nonlinear quantile regression of flowering under low-light conditions, we identified a threshold of 26.3% light availability, below which flowering rarely occurs. Thus, floral capacity is effectively light-limited below this value. These observational and experimental results support the hypothesis that, unless there is significant seed rain from the adjacent marsh, light limitation prevents sexual reproduction of *S. patens* along its upland migration front.

Our data show a consistent pattern of decreased *S. patens* flowering across the environmental gradient from high marsh to maritime forest. Across the marsh-to-forest ecotone, there is a reduction in soil salinity and a shift in species composition (from grasses and forbs to shrubs and trees) that prevents light from reaching marsh plants of smaller stature such as *S. patens* (Kottler and Gedan, 2020). In the USGS experimental forest dieback experiment, we found that under alternative management strategies of girdling and clear-cutting pine trees, *S. patens* flowering was still impacted by shading of taller species that were beginning to take advantage of the newly opened canopy. In the clear-cut zone, there was heterogeneous variability in the regeneration of juvenile *Pinus taeda* saplings that shaded *S. patens* and growth of some shrubs and even other grasses such as *Panicum virgatum* that had sufficient height to shade *S. patens*. Areas of girdled forest farthest from the marsh had a lower percentage cover of *S. patens* (Figure 4B) and were dominated by *Morella cerifera* shrubs. This result suggests that the wide and dense shrub habit competitively inhibits *S. patens* establishment in newly girdled forest. Light limitation of marsh grasses by maritime tree species has been documented before (Brinson et al., 1995); however, identifying the ecophysiological drivers underpinning this interaction is crucial to predicting changes in species composition during marsh migration. Especially in the current crises of marsh loss due to sea-level rise,

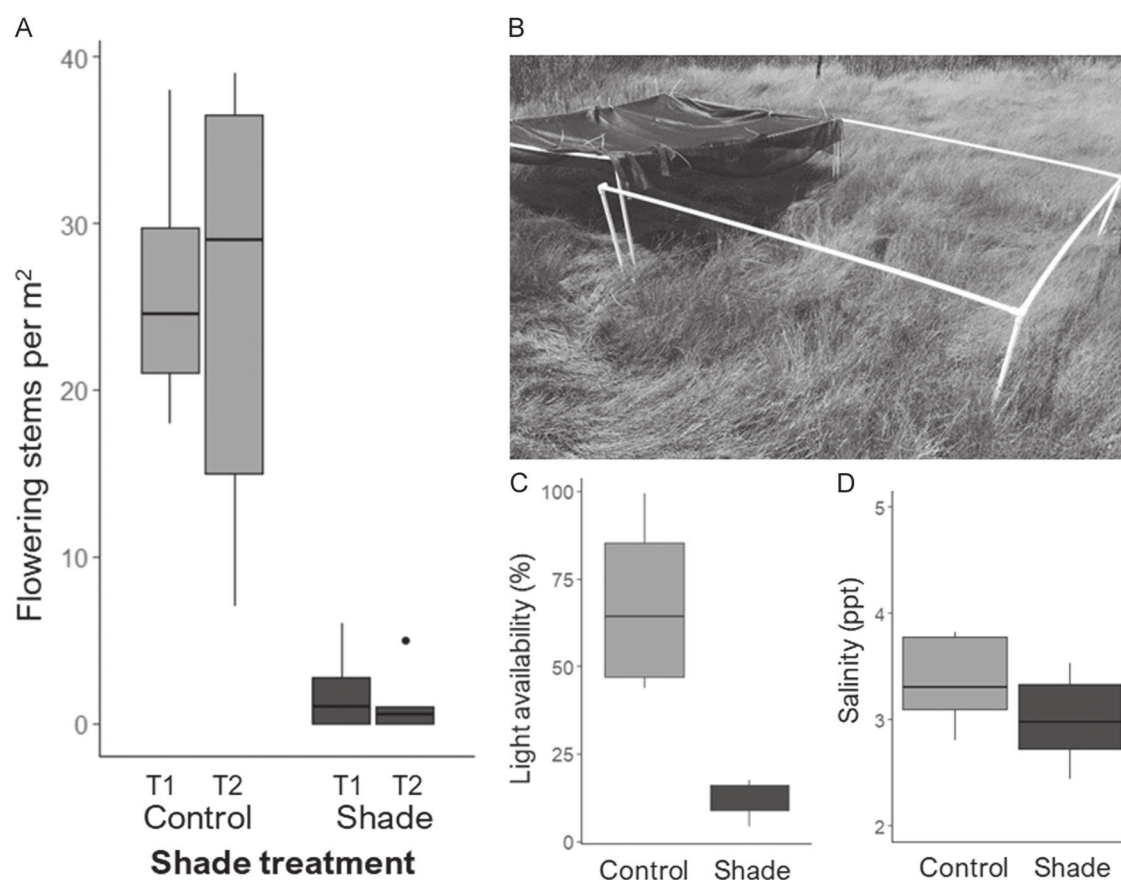


FIGURE 3 Flowering of *Spartina patens* and light availability in shading experiment. (A) Box and whisker plot of flowers per meter squared in control (gray) vs. shaded (dark gray) plots. Shaded boxes display the range between the upper (75%) and lower (25%) quartile for each group, the dark line inside each box indicates the median value, and the lines above and below each box denote values beyond 1.5 times the interquartile range (IQR). T1 and T2 indicate collection times (28 June 2019 and 16 July 2019, respectively). (B) Photograph of paired 2 × 2 m shade and control plots, July 2019. (C) Box and whisker plot of mean percentage available light, at vegetation height relative to total light under open conditions (both in PPFD: Photosynthetically Active Radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)) in control (light gray) vs. shaded (dark gray) plots. (D) Box and whisker plot of mean soil salinity (ppt) collected on 16 July 2019 in control (light gray) vs. shaded (dark gray) plots.

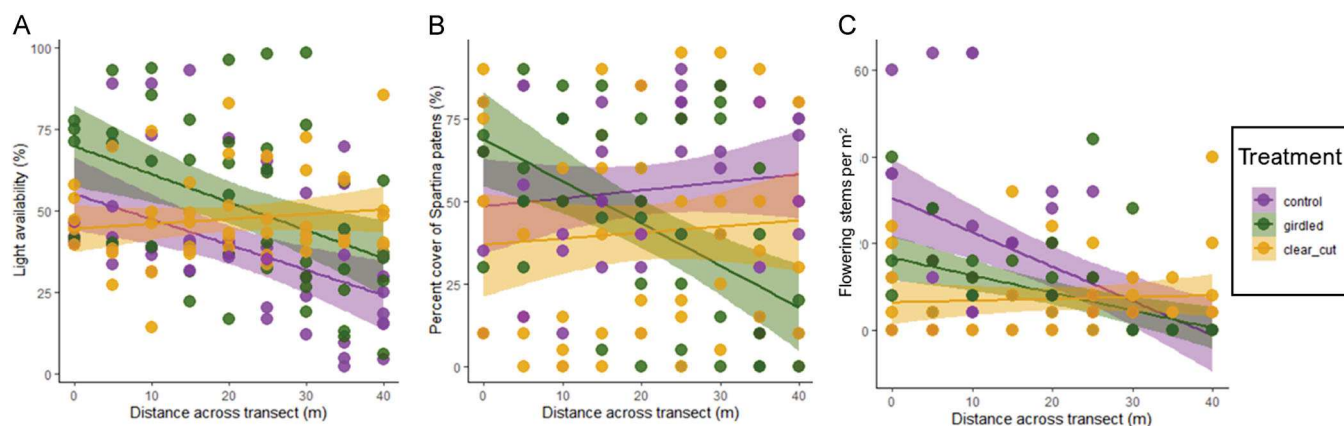


FIGURE 4 Light availability and percentage cover and flowering of *Spartina patens* across forest dieback transects. Points represent sampled quadrats across observational transects that are color-coded by forest dieback treatment (clearcut, control, girdled). Regression lines with standard error margins display linear modeling of the relationship between the x and y variables which was modeled separately for each dieback treatment. In each graph, the x -axis displays distance from high marsh along sampled transects. (A) The y -axis displays percent available light at vegetation height relative to total light under open conditions (both in $\mu\text{mol m}^{-2} \text{s}^{-1}$). (B) The y -axis displays percentage cover of *S. patens* within a 1-m² quadrat. (C) The y -axis displays flowering density in flowering stems per meter squared.

accurate prediction of marsh migration patterns is more important than ever.

While we have used a multifaceted approach to identify light limitation as a causal driver of floral capacity in *S. patens*, there are other abiotic factors and gradients in our study sites that may have affected the abundance and distribution of *S. patens* flowering and merit consideration. Most importantly, light and salinity gradients run counter to one another along this marsh migration front, which means that *S. patens* flowering density is statistically associated with both higher light and higher soil salinity in our study sites. It is unlikely that higher soil salinity contributes to floral capacity in *S. patens*, since low salinity conditions release *S. patens* from osmotic stress (Hester et al., 2001) and increase reproductive fitness in its sister species *Spartina alterniflora* (Xiao et al., 2011). A more feasible alternative explanation for the observed shift in flowering density is the confounding factor of time since colonization. Given the successional role of *S. patens* as the dominant species of a climax high-marsh habitat (Crain et al., 2008), the more contiguous populations of *S. patens* in or near the high marsh are likely to be older and more established than those in the forest understory. Older populations are more likely to have greater stored resources in their belowground biomass (Wigand et al., 2004), resources that can provide for flower and seed production even in adverse conditions. Therefore, time since colonization may account for the slightly better fit of the model of distance and flowering density in our observational surveys.

The loss of sexual reproduction under shaded conditions means that the migration of *S. patens* into upland habitats is dependent upon lateral clonal expansion or seed dispersal from marsh (open-sun) populations. *Spartina patens* seeds can be found in the soil seed banks of a forest understory up to 15 m from the marsh–forest ecotone; but they are less abundant than the seeds of non-halophytes, such as *Panicum virgatum*, found in the same seed bank samples (Kottler and Gedan, 2020). Germination of these seeds is also likely inhibited by the low light conditions of the forest understory, as *S. patens* germination has been shown to be highly photosensitive (Plyler and Proseus, 1996). In the absence of sexual reproduction, migration by *S. patens* will be solely driven by clonal expansion. *Spartina patens* can spread moderately quickly; the species is able to colonize 0.25-m², high-salinity bare patches or dredge spoil piles within a single growing season (Burger and Shisler, 1983; Bertness, 1991a). However, its rhizomatous colonization of upland habitats may be impeded by light competition with taller plant species, such as the invasive *Phragmites australis*, which can supplant it along the migration front (Smith, 2013; Shaw et al., 2021). Therefore, it is unclear whether the clonal migration of *S. patens* will be able to keep pace with movement of the marsh–forest boundary, which is moving at a pace of several meters per year (e.g., 0.5 m/yr from the late 1800s to 2013 in the Chesapeake Bay [Schieder et al., 2018]; 1.8 m/yr from 1930 to 2006 in Delaware Bay [Smith, 2013]). Furthermore,

without sexual reproduction, the species will lose the adaptive advantage of genetic recombination that typically provides the allelic variation necessary for natural selection. Thus, the potential for local adaptation of *S. patens* to upland conditions is limited before forest dieback and associated increases in light availability.

In the absence of sexual reproduction generating new allelic diversity, species can acclimate to suboptimal conditions through phenotypic plasticity or altered gene expression. *Spartina patens* has exceptional phenotypic plasticity in response to different abiotic conditions (Castillo et al., 2017; Kirschner and Zinnert, 2020). When we moved *S. patens* plants from the open marsh to the shaded forest understory, we observed that it significantly altered its phenotype and resource allocation within a single growing season (Kottler and Gedan, 2022). But there is also some evidence to suggest that this phenotypic variation is genetically encoded (Silander and Antonovics, 1979). Future research on the genotype by environment interactions of this species is needed to determine its potential for plastic response to upland light limitation.

Another question raised by these findings is whether minimal flowering under light limitation is the result of a trade-off between clonal and sexual reproduction or simply a lack of the necessary resources to allocate toward any mode of reproductive fitness. Clonal propagules may maintain a physical connection with their progenitor plant via underground tillers and receive resources from said plant through the process of clonal integration (Liu et al., 2016). For this reason, clonal reproduction can facilitate migration into more stressful environments (Amsberry et al., 2000). We know that *S. patens* can send nitrogen to clonal offspring to help their establishment (Hester et al., 1994) and that clonal reproduction is the mode by which *S. patens* recovers from disturbance (Gedan et al., 2009). But as this species has never been studied under light-limited conditions, the level of light resources required to produce either clonal ramets or flowers remains to be seen. It is possible that, rather than a trade-off, clonality is a persistence mechanism employed when sexual reproduction is limited by resource availability or environmental stress (Herben et al., 2015). Whether or not the loss of flowering in migrating *S. patens* populations will impact genetic diversity and resilience will depend on the relative rates of multiple comingled ecological processes including marsh migration, the dieback of maritime forests, and marsh habitat loss due to increased flooding regimes with sea-level rise (Gedan et al., 2020).

We have detailed light as a limiting factor in the reproduction of a dominant marsh grass at a range edge that is responding to climate change. Our findings of limited seedling establishment at the migration front present another challenge to this species that is already being squeezed in several ways. Whether or not *S. patens* will fulfill the same ecological function as a foundation species in tidal marshes in the future, as the maritime forest retreats, remains to be seen. The reproductive consequences of biotic

interactions for resources during the response of *S. patens* to sea-level rise may also apply more generally to other plant interspecific interactions along ecotones that are being shifted by climate-driven factors.

AUTHOR CONTRIBUTIONS

E.K. designed and performed the surveys and experiment and analyzed the data in consultation with K.G. E.K. and K.G. both contributed to writing the manuscript.

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DATA AVAILABILITY STATEMENT

All are publicly available on Dryad Digital Repository at <https://doi.org/10.5061/dryad.t1g1jw44> (Kottler and Gedan, 2022).

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SUPPORTING INFORMATION

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

Appendix S1. *Spartina patens* percentage cover across a light gradient at different locations. Points represent sampled quadrats across observational transects that are color-coded by site. The x -axis displays percentage available light at vegetation height relative to total light under open conditions (both in $\mu\text{mol m}^{-2} \text{s}^{-1}$), and the y -axis displays percentage cover of *S. patens* within a 1-m quadrat. The black line denotes a linear regression between the two variables that were correlated with one another ($0.342, P > 0.0001$).

Appendix S2. Flowering density across forest dieback gradients. Points represent sampled quadrats across observational

transects that are color-coded by forest treatment (clear-cut, control, girdled). The x -axis displays percentage available light at vegetation height relative to total light under open conditions ($\text{mol m}^{-2} \text{s}^{-1}$), and the y -axis displays flowering density in flowering stems per square meter. The black curve models the negative binomial GLM relationship between the x and y variables.

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