Wetlands Ecol Manage (2025) 33:64
https://doi.org/10.1007/s11273-025-10079-8

ORIGINAL PAPER

# Efficacy of stress acclimation techniques in coastal wetland plants (*Spartina alterniflora* and *S. patens*): implications for restoration and nursery production

**Taylor M. Sloey · Kylie D. Gieser · Kaitlyn Pounders · Sofía E. Báez · Jennifer L. Whytlaw**

Received: 12 June 2025 / Accepted: 8 August 2025 / Published online: 20 August 2025
© The Author(s) 2025

**Abstract** The implementation of coastal nature-based features, created wetlands, and wetland restoration has increased globally over recent years. Many of these projects have been successful in meeting their goals, however, when projects fail, it is often attributed to mortality of transplanted vegetation. Transplant mortality may be due to inappropriate timing, poor site selection, or abiotic stressors associated with transplant shock. Science-backed guidelines have been well established in many coastal regions regarding site specifications and species selection, but nursery practices for reducing transplant shock remain inconsistent. In this study, we tested a combination of four salinity acclimation treatments and two inundation acclimation treatments on nursery-grown *Spartina alterniflora* and *S. patens* plugs. We measured a suite of plant functional traits to determine tradeoffs in plant response with a focus on traits associated with plant marketability, indicators of stress acclimation, and desired traits for restoration goals. A subset of plants was transplanted to a restoration site for analysis of their survival in situ. Exposure to salinity and inundation resulted in traits associated with both marketability and restoration goals (e.g., increased stem height, reduced dead to live stem ratio, and increased biomass), as well as evidence of acclimation to field stressors. However, trait differences did not translate to differences in field performance as survival and expansion of transplanted individuals showed no difference between acclimation treatments. The future of coastal wetland creation and restoration will require plant material that is produced using a science-based approach to ensure plants are robust, long-lived, and marketable to achieve the needs to restoration and nursery practitioners alike.

**Keywords** Living shoreline · Plant functional trait · Salinity · *Spartina alterniflora* · *Spartina patens* · Stress acclimation

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11273-025-10079-8.

T. M. Sloey (✉) · K. D. Gieser · K. Pounders · S. E. Báez
Department of Biological Sciences, Old Dominion University, 5115 Hampton Blvd, Norfolk, VA 23529, USA
e-mail: tsloey@odu.edu

S. E. Báez · J. L. Whytlaw
Department of Political Science and Geography, Old Dominion University, 5115 Hampton Blvd, Norfolk, VA 23529, USA

## Introduction

Coastal wetlands provide valuable ecosystem services and functions, including water quality enhancement, nutrient cycling, flood risk reduction, and carbon storage (Costanza et al. 2021; Hagger et al. 2022; Temmerman et al. 2023). Unfortunately, three centuries of land use change, erosion, subsidence, sea level rise (SLR), altered hydrology, and other anthropogenic

influences have resulted in notable loss of the world's wetlands (Lee et al. 2006; White and Kaplan 2017). Estimated rates of global loss range from 21 to 87% (Davidson 2014; Fluet-Chouinard et al. 2023). Holmquist et al. (2021) found that up to 48% of coastal wetlands through the United States are currently vulnerable to loss, and Fant et al. (2022) estimated up to 10.7 million acres of coastal wetlands may be lost within this century depending on SLR scenarios. To combat wetland loss and mitigate climate change through carbon sequestration, coastal wetland restoration (i.e., the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004)) and habitat creation (i.e., create a marsh where it had not previously existed) efforts have increased worldwide. These efforts include the emerging field of coastal nature-based solutions which aim to use natural systems, such as salt marshes, to provide shoreline protection as well as ecological co-benefits (O'Leary et al. 2023). Despite increasing willingness and financial investment in coastal restoration and habitat creation projects, the ability for practitioners and planners to meet ambitious goals and ecosystem trajectories remains a challenge.

Habitat recovery through revegetation is one of the most implemented salt marsh restoration strategies; and plant-centered metrics such as species diversity, vegetation cover, plant biomass, and stem density are among the most often used indicators of salt marsh restoration success (Billah et al. 2022). When wetland restoration or habitat creation projects fail to meet their goals, it is often attributed to low survival of transplanted vegetation (Zedler et al. 2003). Planting projects located in salt marshes have noted < 15% survival success of transplanted vegetation; these low survival rates were partially attributed to physical wave and sediment dynamics (Ge et al. 2019) and herbivore pressure (Temmink et al. 2022). A global meta-analysis of salt marsh plantings found that the mean survival rate of transplanted vegetation is only ~ 53%, and in 23% of the 1,038 observed projects recorded survival rates were less than 5% (Liu et al. 2024). To improve transplant survival, restoration ecologists and practitioners emphasize the importance of establishing appropriate site conditions and understanding species' tolerance thresholds to abiotic stressors (Duggan-Edwards et al. 2020). Even as the practice of coastal restoration becomes increasingly informed by science, high mortality of transplanted vegetation still occurs (Wodehouse and Rayment 2019; Macy et al. 2021; Pausch 2024).

Vegetation transplanted in restored coastal salt marshes encounter several stressors that may explain their high rates of mortality. These stressors include natural processes that are difficult to ameliorate at large scales, such as hypersaline soils, sedimentation and burial, algal smothering, and animal herbivory (Zedler et al. 2003). Failures of project implementation, such as planting at inopportune times or locations, may cause mortality (Liu et al. 2024). The transplantation process itself (i.e., removing young plants from plastic pots) can damage roots and root hairs (Zedler et al. 2003; Di Benedetto 2011). When field conditions differ from nursery conditions, transplanted plants will experience physiological stress characterized by decreased growth rate or mortality during the acclimatization period; this is known as transplant shock and may last days to weeks (Reitveld 1989; Close et al. 2005). Salinity and tidal inundation are two dominant abiotic stressors in coastal wetlands that nursery-reared plants may first encounter only after transplantation.

Cordgrasses (Genus *Spartina*) are the most commonly used genus in coastal marsh restoration projects worldwide due to their role as a strong biotool for creating marsh habitat (Castillo and Figueroa 2009; Strong and Ayres 2009; Curado et al. 2020; Rohal et al. 2025). In the U.S., *S. alterniflora* (Loisel) and *S. patens* (Aiton) Muhl. are native to and commonly used throughout the Gulf of Mexico and Atlantic coast plantings, whereas *S. foliosa* (Trin.) is native to and used on the west coast (Rohal et al. 2025). Halophytic species, such as *Spartina* spp., have evolved means to concentrate and excrete salt through specialized pores, but salinity presents a stressor, nonetheless. In *Spartina* spp., high salinity (> 20 ppt) has been shown to reduce plant biomass (Mooring et al. 1971; Parrondo et al. 1978), nutrient uptake (Chambers et al. 1998), and growth (Phleger 1971); however, high salinity has little effect on photosynthesis (Longstreth and Strain 1977), and has been shown to increase leaf dry mass (Longstreth and Strain 1977) and leaf thickness (Poljakoff-Mayber 1975). Previous work shows that traits (e.g., leaf area, SLA, thickness, leaf toughness, leaf strength) of *Spartina alterniflora* correlate with soil salinity (Liu et al. 2022), and hydrology (Shao et al. 2020). While many studies

show high levels of salinity reduce plant survival and vigor, Zhang et al., (2024) showed that moderate levels of salinity increase live leaf production, leaf area, and leaf mass compared to freshwater or higher salinities. They indicate this is evidence of plant shift from rapid growth to more efficient nutrient conservation strategies. Halophytes that have not been exposed to salinity at young life stages show decreased ability to cope with salinity stress later in life (Touchette et al. 2009). The salinities of coastal marsh planting sites may exist beyond the optimal range for *Spartina* spp. and thus create additional transplanting stress. For example, in coastal Virginia, approximately one third of living shorelines are located in areas with average summer salinities ranging from 15–30 ppt (Bever et al. 2021; St-Laurent and Friedrichs 2024; Virginia Marine Resources Commission 2025).

Inundation can create plant stress by limiting gas exchange and creating anoxic soils. Increased inundation has been shown to decrease above- and belowground biomass in *Spartina* spp. (Visser and Peterson 2015), decrease root tensile strength (Hollis and Turner 2021), and decrease photosynthetic performance (Mao et al. 2023). Extreme precipitation events that are accompanied by pulses of inundation by freshwater are associated with causing sudden vegetation dieback in *Spartina* spp. dominated marshes (Stagg et al. 2021). Further, in many field settings, *Spartina* spp. productivity is determined by a variety of interacting factors that are influenced by inundation, including soil anoxia, soluble sulfide concentration, and plant nitrogen assimilation (Mendelssohn and Morris 2000). Several studies have investigated the role of inundation and elevation on *Spartina* spp. distribution. For example, residual biomass of transplanted *S. alterniflora* following a tropical storm event was positively correlated with elevation (Hill et al. 2020). However, few studies have investigated the effectiveness of inundation acclimation on transplant survival. Baldwin and Mendelssohn (1998) recommended allowing one month for *Spartina* plants to acclimate to increased inundation. To improve outcomes of wetland restoration plantings, and protect the financial investments of these efforts, creative approaches aimed at rearing stress-tolerant and robust plants are needed.

Plant functional traits, defined as morpho-physio-phenological traits which impact fitness (Violle et al. 2007), comprise a suite of metrics that can serve as indicators of plant evolutionary adaptation, plant performance, species niche, resource acquisition strategy, and response to environmental change (Violle et al. 2007). The use of plant functional traits to understand ecosystem function and response has increased in recent years. While some studies have specifically evaluated the use of plant functional traits in evaluating wetland restoration (Charles et al. 2022), connecting plant functional traits to specific concerns in wetland restoration remains a research gap (Sloey et al. 2023). Plant functional traits are frequently correlated along a plant economic spectrum, from resource acquisition (rapid growth) to resource conservation (slow growth) (Díaz et al. 2016). Traits that are indicative for assessing health and growth status of the plant (e.g., rapid growth, aboveground biomass, number of stems, live stem:dead stems, total biomass, plant height) are directly related to marketability from the grower's perspective. Leaf traits related to photosynthesis (e.g., leaf number, leaf length, leaf area, leaf dry mass, specific leaf area (SLA), total biomass, and photosynthetic assimilation of $CO_2$ (A)) are informative about the plant's resource acquisition and adaptive strategy, but also indicative of environmental stress (Zhang et al. 2024; Liu et al. 2022). High SLA indicates fast resource acquisition and rapid primary production (Lavorel and Garnier 2002). Other traits indicate response to environmental stress or damage to the plants (e.g., dead leaf number, ratio of dead leaves to live leaves, stem height (etiolation, or rapid stem growth, is evidence of flooding stress response), area of emergent roots (evidence of soil anoxia stress response), or low A) (Zhang et al. 2024). Finally, some traits may be more important indicators of ecosystem services, function, and resilience (De Battisti 2021), and therefore prioritized by coastal restoration practitioners. These may include traits associated with rapid revegetation and habitat creation (aboveground biomass, stem number, stem height), soil stability and cohesion (belowground biomass, root to shoot ratio), wave attenuation (stem density and stem rigidity), elevation accretion (belowground biomass and stem density), and persistence of the plant community (rapid clonal growth, quantity of viable seed) (De Battisti 2021). Studying plant functional traits in coastal restoration species with wide abiotic tolerance

ranges, such as *Spartina* spp., is important for both understanding trait linkages (Zhang et al. 2024) and for more applied trait-function relationships. We propose that a trait-based framework can also be employed to inform plant production decisions with the goal of maximizing marketability and resilience of coastal plant species transplanted in restoration sites.

Nursery grown coastal plant species are commonly reared under benign conditions (i.e., soils kept moist with freshwater) to maximize growth. However, benign nursery conditions may exacerbate transplantation shock in the field. Plant rearing techniques that incorporate abiotic stress acclimation have potential to reduce mortality caused during these vulnerable transition phases. Carrion (2016) compared *S. alterniflora* reared in 0 ppt and 15 ppt and found the saline treatment had greater shoot production when transplanted in the field. Some commercial growers of coastal grass species have anecdotally used plant hardening techniques (such as gradual salt acclimation) (personal communication, Sloey et al 2023). Salinity acclimation, or salt hardening, is even noted in some *Spartina* spp. plant preparation guides (Biber et al., ND), but the efficacy of abiotic stress acclimation in nursery-raised wetland plant species has not been rigorously studied. Sloey et al. (2025) identified that determining best practices for developing robust plant material is a key knowledge gap needed to improve the efficacy of coastal nature-based solutions.

The goal of this study was to determine if salinity and inundation acclimation treatments (1) result in the development of traits that indicate plant acclimation and adaptation to abiotic stressors, and (2) improve transplant survival in *S. alterniflora* and *S. patens*. Additionally, we sought to determine (3) whether these acclimation treatments influenced traits associated with marketability of the plants. We combined a greenhouse experiment, performed at a commercial plant nursery, with a field transplant experiment, performed at a recently installed living shoreline site, to provide feasible techniques for stress acclimation practices. The ultimate goal of this work was to determine best practices to reduce transplant shock and increase survival rates following transplantation for two of the most heavily demanded coastal wetland plant species.

## Materials and methods

### Plant preparation and experimental design

Plugs (5 cm × 5 cm pots) of freshwater-reared *S. alterniflora* and *S. patens* were purchased from a commercial plant nursery (Virginia, USA) in May 2024. On 20 May 2024, plants were selected for similar sizes (stem number) and repotted into plastic pots (8 cm diameter × 20 cm height). Each pot was perforated at the bottom to allow for exchange of water. A piece of cotton fabric was placed at the bottom of each pot to prevent loss of soil. Each pot was filled with commercial topsoil (Scotts™ Topsoil) and bound roots were loosened upon repotting. All planted pots were watered, but not inundated, with freshwater from an adjacent pond and kept in a greenhouse until the experiment began on 17 June 2024.

This fully factorial study consisted of two species (*S. alterniflora* and *S. patens*), two flooding treatments (inundated and non-inundated), four salinity treatments (freshwater, gradual salinity increase, pulsed salinity exposure, and salinity press), two destination treatments (harvest and transplant), and ten replicates of each combination for a total of 320 experimental plants. Plants were placed in each of four fiberglass tanks (H:1.0 m, L: 2.0 m, W: 1.0 m) corresponding to their respective salinity treatment. All four tanks were located within 1 m of one another within a hoop house covered with white visquene (~ 20% shading). Although plants were potted independently and randomized within their tank, salinity treatment was confounded with the random effect of tank assignment. While we acknowledge this is simple pseudoreplication, this choice was a necessity due to space and resource limitations. Additionally, this approach allowed for greater control of uniform salinity within a treatment, given potential hourly evaporative differences that would have otherwise occurred in separate smaller replicates. We acknowledge the design error of pseudoreplication, but advocate the outcomes are nonetheless valuable given the increased control of treatment groups (e.g., Davies and Gray 2015). The plants were placed at one of two elevations within the tank to achieve the flooding treatments with non-inundated plants elevated so that the soil level was 10 cm above the water and inundated plants were submerged 5 cm below the water. Salinity treatments were achieved using Instant

Ocean® to create each of the four following salinity exposure treatments: freshwater (0 ppt salinity was maintained throughout the experiment), gradual salinity increase (salinity was increased 3 ppt every week starting at 3ppt on 17 June and ending at 27 ppt on 12 August), pulsed salinity exposure (plants were kept in freshwater (0 ppt) and moved into saltwater (25 ppt) for 72 h every two weeks (on 17 June, 1 July, 15 July, 29 July, 12 Aug)), and salinity press (25 ppt salinity was maintained throughout the experiment). Although nursery practices vary widely, the freshwater, non-inundated treatment combination was the treatment most similar to standard wetland plant rearing practices that do not use salinity or inundation stress acclimation practices. Water level (depth) and salinity was checked every two days using a ruler and handheld refractometer respectively. Freshwater and salt were added as needed to counter evaporative loss and maintain desired salinity.

## Measurements

Growth traits (i.e., number of live and dead stems and stem heights) were measured for all plants (both harvested and transplanted) throughout the experiment on 12 June (pre-experiment baseline), 03 July, 29 July, and 19 August. Photosynthesis (A) was measured using a LI-6800 (LICOR, Lincoln, NE) every two weeks in five replicates of the *S. alterniflora* assigned to the harvest group. Photosynthesis measurements were taken concurrently with adjustments made to the pulse salinity treatments for all treatment combinations of *S. alterniflora*. Photosynthesis was measured again 72 h after salinity treatment adjustments for the gradual increase and pulse exposure treatments only. Photosynthesis could only be measured in *S. alterniflora* because limited leaf number and width in *S. patens* made it impossible to fill the LI-6800's 2 cm chamber aperture. For *S. alterniflora*, multiple live leaves were placed together, but not overlapping, to fill the chamber. Replicates were limited to 5 to complete measurement of all treatment groups within the photosynthetic maximum window (~8:30–13:00) on the same day. Light (600 µmol $m^{-2}$ $s^{-1}$) and $CO_2$ (420 ppm) were kept consistent each reading, but temperature and humidity settings were adjusted to match ambient conditions on the day of measurement. All plants assigned to the harvest group were harvested for final plant trait measurements on 19 August 2024. Stem number, individual stem heights of live stems, and maximum plant heights were measured using a metric ruler. Three representative leaves were removed from each plant, kept on ice, and processed for leaf traits (e.g., leaf length, area, maximum width) within 24 h in the lab using a LI-3000C leaf area meter and LI-3050 conveyor belt (LICOR, Lincoln, NE). After, each leaf was placed in an individual paper envelope and dried for 72 h in a convection oven (Thermo Scientific) at 60° C. The dry mass of each individual leaf was collected (accuracy of 0.0001 g) using an analytical balance (Sartorius). Specific leaf area (SLA) was calculated for each leaf by dividing the leaf area by the dry mass. All aboveground biomass was cut at the soil surface, bagged and dried, and dry biomass weighed using the analytical balance. After aboveground plant material was removed, a photo of the pot's soil surface, including soil and emergent roots, was taken using a Samsung Galaxy A54 5G. A metric ruler was placed in each photo for scale. The area ($cm^2$) of emergent root material was measured using Image J Fiji (Schneider et al. 2012). Finally, all belowground biomass was removed from the soil, rinsed clean, bagged, dried at 60° C for 8 days, and dry mass was collected using an analytical balance.

## Transplants

All plants assigned to the transplant group remained in the greenhouse in their respective salinity treatments until they could be planted at a living shoreline marsh restoration project site on 10 October, 2024. The transplanting site was located at an urban intertidal shoreline adjacent to an Oyster Castle™ breakwater in the Lafayette River in Norfolk, VA, USA (36.889418, − 76.297583) that had been recently graded and filled with sand. Experimental plants were placed at elevations ideal for their species tolerance thresholds with *Spartina alterniflora* arranged in three rows closest to the oyster reef breakwater and *S. patens* were placed at the highest elevation (still intertidal) furthest from the shoreline. All plants were arranged in a blocked randomized order with one replicate of each treatment in each block. To best standardize elevation variability at the site *Spartina alterniflora* were arranged in three rows (consisting of 3, 4, and 3 replicated blocks) and *S. patens* were arranged in one row. Plants were spaced 40 cm apart

and hand planted in the sand. Plants were monitored for survival using binary categorization (i.e., alive vs. dead) at one month (14 November 2024) and 6 months (3 April 2025) after transplanting. Transplant expansion was measured at 6 months by measuring two perpendicular directions of areal spread, with X being the largest distance of area coverage and Y being the distance 90° from X.

### Statistical analysis

All data were analyzed using R version 4.4.3 (R Core Team 2024). Data was analyzed for each species separately using a two-way analysis of variance (ANOVA). The ANOVAs tested for the main effects (i.e., salinity and inundation treatments) and their interaction on response variables. Response variables for the harvest group included stem height, stem number, maximum plant height, aboveground biomass, belowground biomass, leaf area, leaf length, leaf dry mass, leaf maximum width, SLA, and area of emergent roots. The effects of salinity and inundation treatments on photosynthetic assimilation of $CO_2$ (A) were analyzed over time using a linear mixed-effects model using the lme4 package (Bates et al. 2015). Treatment influence on plant survival and growth post-transplant was analyzed with a binomial generalized linear mixed model (GLMM) with logit link function. Full results of statistical analyses are available in Table S1.

## Results

### Harvest subgroup

#### *Spartina alterniflora*

All plants survived the full growing season in the nursery. Stem height was greater in *S. alterniflora* plants that were exposed to the gradual salinity treatment ($p = 0.037$, Fig. 1). Dead to live stem ratio was greatest in the freshwater treatment ($p = 0.005$, Fig. 1). Leaf maximum width was greatest in freshwater treated plants ($p < 0.001$, Table S2) and SLA was greatest in plants exposed to the press salinity or freshwater treatments ($p < 0.001$, Fig. 1). Emergent root production was greater in flooded plants compared to their non-flooded counterparts, but only for the gradual and pulse salinity treatments ($p < 0.001$, Fig. 1). Total biomass showed an interaction between salinity and inundation ($p = 0.036$, Fig. 1). Aboveground biomass was greatest in the gradual salinity treatment ($p = 0.023$, Fig. 1). Root to shoot ratio was greatest in the freshwater treatments ($p < 0.001$, Fig. 1). *Spartina alterniflora* showed no significant impact of salinity or inundation treatments on number of live stems, maximum plant height, average leaf area, average leaf length, average leaf dry mass, belowground biomass, or dead to live aboveground biomass ratio. The LMER model showed a significant effect of date ($p = 0.001$) on photosynthesis, with greatest A values occurring on 29 July, but no effect of treatments. Separate ANOVAs conducted at each photosynthesis measuring date revealed that plants exposed to the gradual and pulse salinity treatment groups had greater A values compared to other treatments on 12 June, 15 July, and 29 July (Fig. 2, Table S1).

#### *Spartina patens*

All plants survived the growing season in the nursery. Number of live stems was greater in flooded plants exposed to freshwater and pulse salinity treatments, but in plants exposed to the press salinity treatment, stem production was greater in non-flooded treatments ($p = 0.012$, Fig. 3). Maximum plant height was greatest in the non-flooded gradual salinity treatment as well as the flooded pulse salinity treatment (interaction $p < 0.001$, Table S2). Average stem height showed an interaction between salinity and inundation treatments ($p = 0.012$), with inundated stems being significantly taller than their non-flooded counterparts for pulse and press salinity treatment groups only (Fig. 3). Leaf area was greater in non-flooded compared to flooded treatments, but only in the gradual and pulse salinity treatments ($p = 0.012$, Table S2). Leaf maximum width was greater in the gradual salinity treatment ($p < 0.001$, Table S2). Leaf length was significantly greater in the pulse salinity treatment ($p = 0.005$). Leaf dry mass was impacted by salinity treatment ($p = 0.001$) with greatest length occurring in press salinity treatments. Also, whereas leaf length was greater in non-flooded plants exposed to gradual and pulse salinity treatments, the opposite pattern occurred in freshwater treatments (Table S2). SLA showed significant effects of both salinity

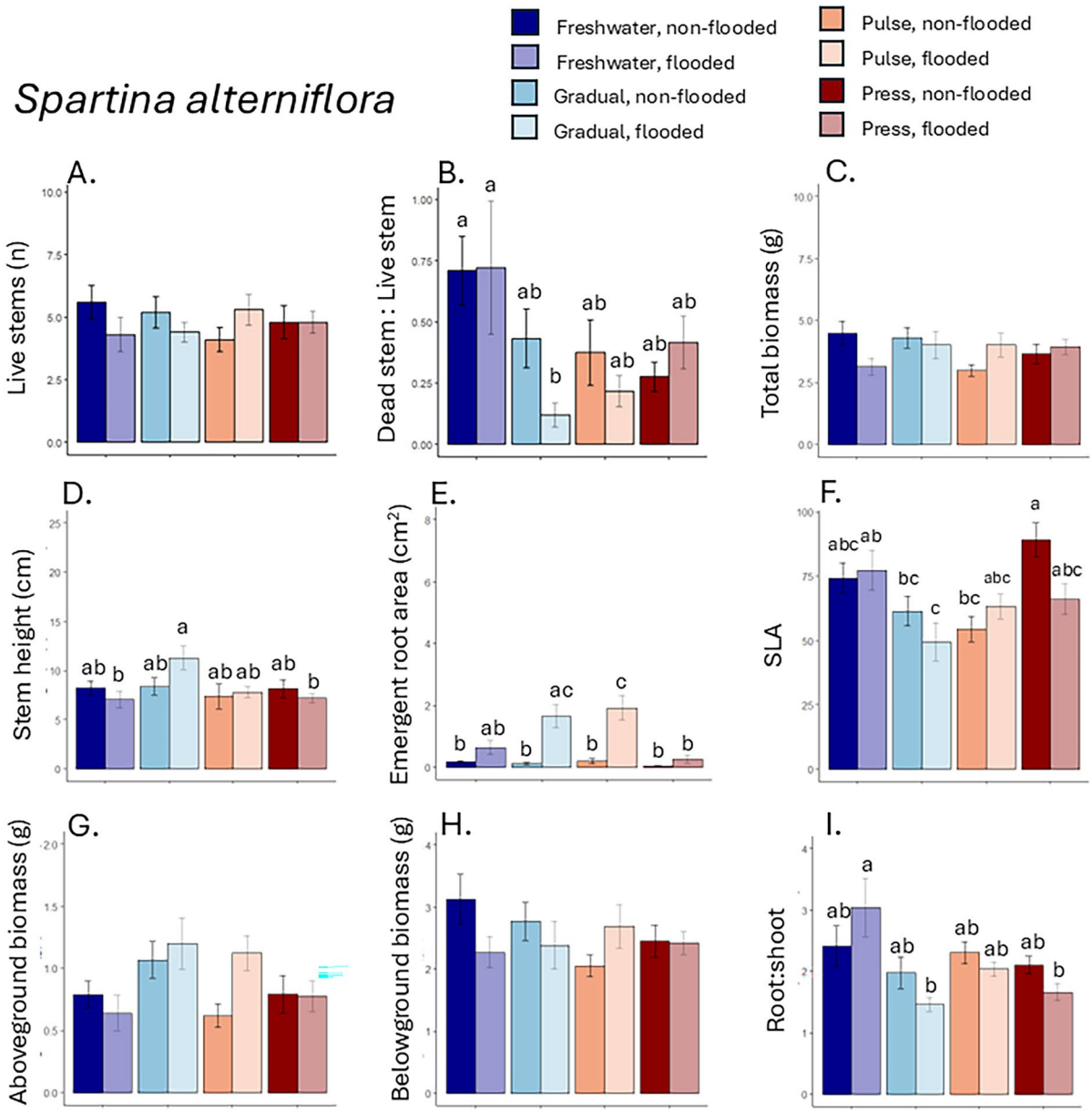



**Fig.1** Plant traits of *Spartina alterniflora* exposed to combinations of four salinity treatments (freshwater, gradual, pulse, and press; grouped by color) and two inundation treatments indicated by shading (non-flooded = opaque, flooded = transparent). All data presented are means ± stderr for plants assigned to the harvest group. Letters indicate statistically significant differences within trait determined by Tukey HSD

(0.0005) and inundation ($p = 0.048$) with SLA being greatest in plants receiving the pulse and press salinity treatment and non-flooded treatments (Fig. 3). Emergent root area showed an interaction between salinity and inundation treatments ($p < 0.001$) with flooded plants exhibiting more emergent roots, especially in freshwater and pulse salinity treatments (Fig. 3). Total plant biomass showed an interaction between salinity and inundation treatments ($p = 0.031$) with greatest biomass occurring in the gradual salinity and non-flooded combination and lowest occurring in the press salinity non-flooded

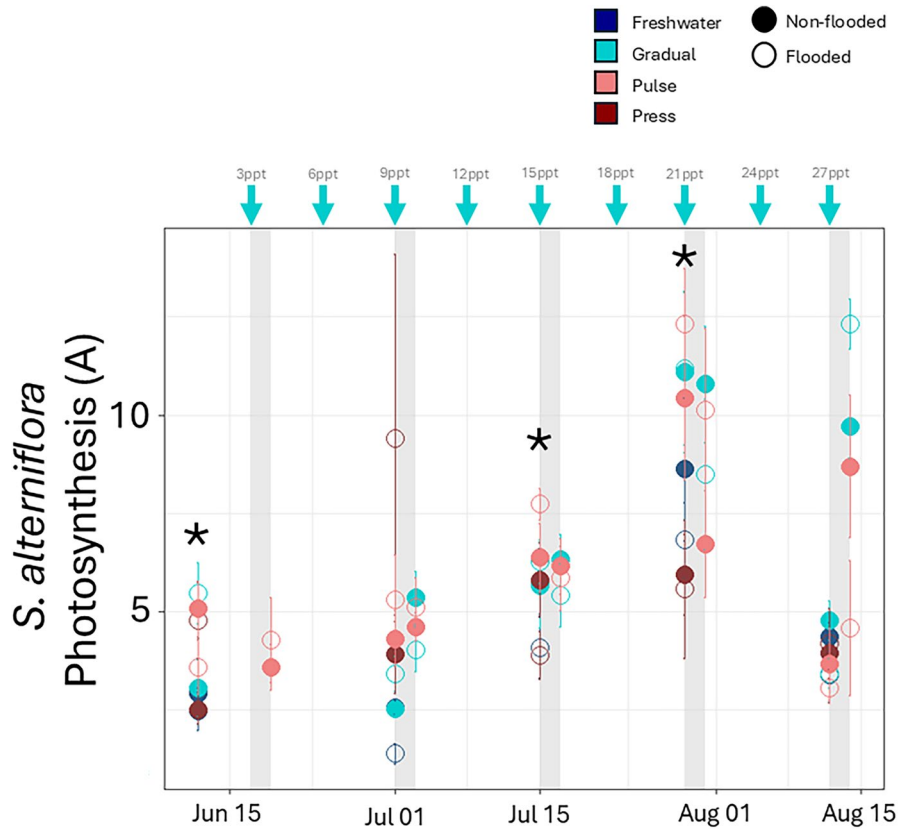



**Fig. 2** Photosynthetic assimilation of $CO_2$ (A) by *S. alterniflora* exposed to combinations of four salinity treatments (freshwater, gradual, pulse, and press; grouped by color) and two inundation treatments (flooded, non-flooded; grouped within color indicated by point fill). All data presented are means ± stderr for plants assigned to the harvest group. Arrows indicate the time points and corresponding salinity levels for the gradual salinity increase treatment. The gray shaded areas show the time windows that salinity was elevated from 0 to 25 ppt for the pulse salinity treatment. Only pulse and gradual treatment groups were measured two days following each salinity increase point. Asterisks indicate time points at which significant differences occurred between salinity treatment groups

treatment combination (Fig. 3). Belowground biomass was greatest in the gradual salinity and non-flooded combination ($p = 0.019$) and lowest in the press salinity flooded combination (Fig. 3). Root to shoot ratio showed an interaction between salinity and inundation treatments ($p = 0.006$) with greatest R:S occurring in non-flooded pulse treatment combinations, and R:S generally being lesser in the flooded treatments compared to their non-flooded counterparts (Fig. 3). *Spartina patens* showed no effect of treatments on dead to live stem ratio, aboveground biomass, or dead to live aboveground biomass ratio.

*Transplants*

At the end of the growing season (August 2024), the plants assigned to the transplant subgroup showed no significant differences between treatments on stem production (number of live stems) (Table S1). Stem height was significantly greater in *S. alterniflora* plants exposed to the gradual salinity treatment ($p < 0.001$). In *S. patens*, stem height was significantly reduced in the non-flooded-pulse treatment compared to all other treatment combinations ($p = 0.001$, Table S1). Overall, plant survival at six months after transplanting was high (97.5% in *S. alterniflora* and 92.5% in *S. patens*). The GLMM showed no significant effect of time or treatment on survival (Fig. S1). An ANOVA conducted on plant survival and vegetative expansion after six months also showed no significant effect of treatment on either variable (Table S1).

## Discussion

The growing fields of coastal marsh restoration and creation requires sustainable plant material. In many cases these projects depend on successful transplantation and survival of nursery-grown plants (plugs), rather than taking the risk of waiting on natural vegetation colonization. The current standard practice is to acquire these plants from commercial nurseries. While marsh creation project contracts may specify the number of stems or plant height required

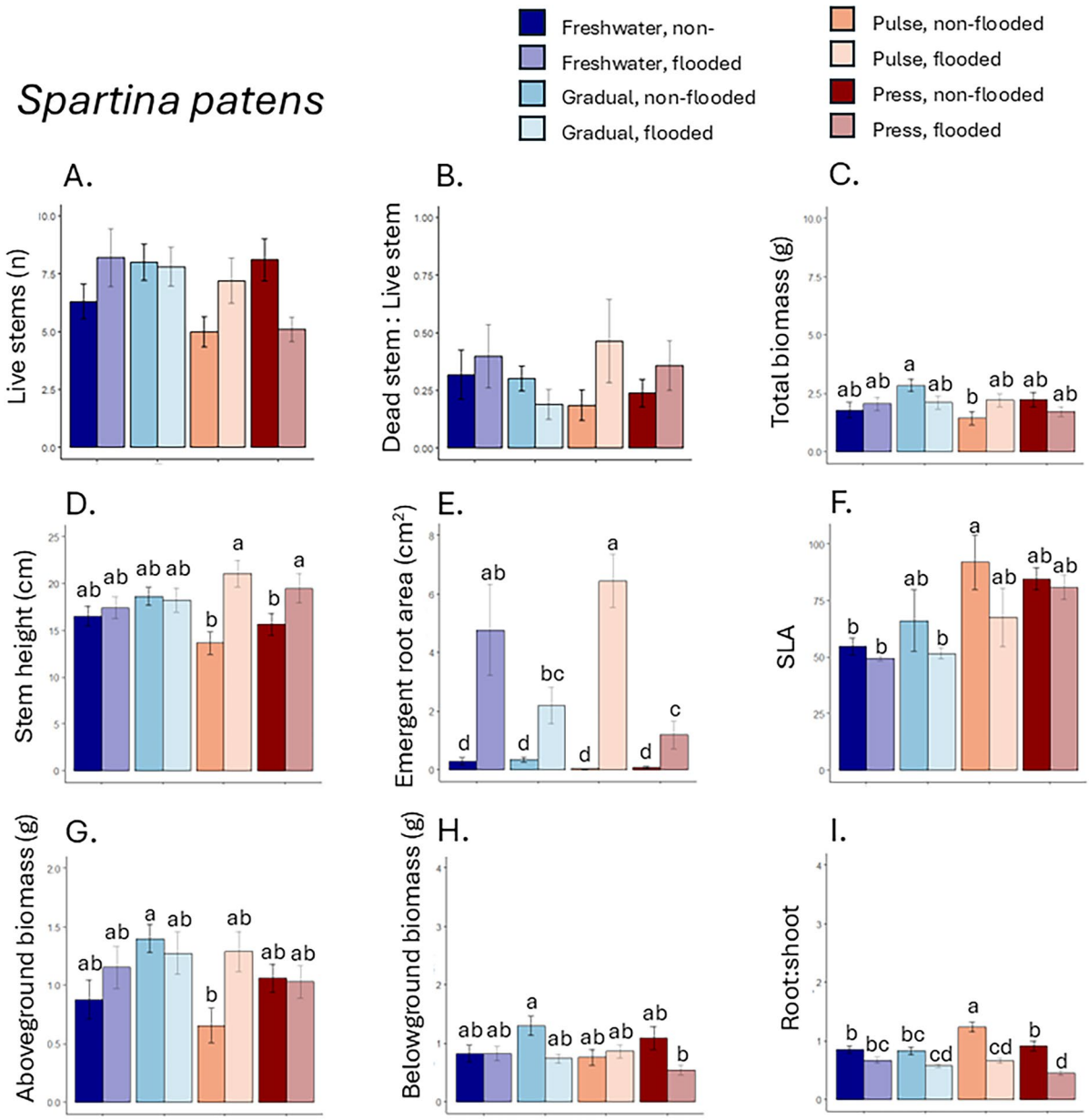



**Fig. 3** Plant traits of *Spartina patens* exposed to combinations of four salinity treatments (freshwater, gradual, pulse, and press; grouped by color) and two inundation treatments indicated by shading (non-flooded = opaque, flooded = transparent). All data presented are means ± stderr for plants assigned to the harvest group. Letters indicate statistically significant differences within trait determined by Tukey HSD

from the plant provider, there remain inconsistencies regarding best practices for nursery-rearing. Although marsh plantings have occurred for decades, and some growers anecdotally report practices of salt-hardening plants to reduce transplant shock and mortality, there are few scientific reports of the efficacy of these practices, both in terms of transplant survival response, but also in terms of the effects of stress acclimation practices of plant trait responses. This study conducted rigorous testing of four salinity acclimation treatments and two inundation treatments on the two salt marsh species most commonly planted

in the U.S. to determine the effect of stress acclimation practices on plant growth, plant functional traits, and survival post-transplantation.

### Marketability of stress acclimated plants

Plant nurseries are unlikely to adopt practices that reduce the quality of their product. We found that salinity and inundation treatments had no effect on number of live stems or total biomass in *S. alterniflora.* Although *S. alterniflora* stem height showed a statistically significant difference between flooded freshwater and flooded press (lower) and gradual flooded (higher) treatments, the total range in average stem height (i.e., 7 cm–12 cm) may not be economically or ecologically significant. Interestingly, there was a significant difference between treatments in terms of the dead to live stem ratio. The highest ratio was observed in both freshwater treatments, suggesting that although more stems may have been produced in freshwater treatments in total, many died. To maximize the presence of live stems compared to dead, the gradual, flooded treatment combination was superior for *S. alterniflora*. *Spartina patens* showed minimal effect of stress acclimation treatments on total biomass with no effect on number of live stems or dead to live stem ratio. With live stem production and total biomass relatively similar across all treatments, our data show that incorporating salinity and inundation stress acclimation techniques will not reduce product supply for a nursery provider, though adding salinity may come at an additional cost (both financial and time) to the grower depending on accessibility of salt water.

### Plant functional traits indicate stress acclimation

We were particularly interested in functional traits that are indicative of flooding and salinity stress acclimation (i.e., increased stem height due to etiolation, increased emergent root production due to anoxia, and lower SLA indicating response to resource-limited environments). While shifts in these traits do not necessarily correspond with increased growth rates, research has demonstrated that these trait shifts are important for assessing the plant's ability to cope with stressors to survive. Etiolation allows the plant to escape poor conditions to access light and air. Etiolation due to shading and flooding has been documented in *Spartina* spp. previously (Hubbard 1969; Logan et al. 2018; Mao et al. 2023).Consistent with Hubbard (1969), Logan et al. (2018), and Mao et al. (2023), *Spartina alterniflora* stem length showed an increase in the flooded-gradual treatment combination, whereas *S. patens* stems were tallest in all flooded treatments, as well as freshwater and gradual non-flooded treatments.

Root adaptations to soil waterlogging are important autecological factors controlling plant distribution in wetlands (Sorrell et al. 2000). A variety of wetland plant adaptations to soil anoxia have been observed in *Spartina* spp., including adventitious root production, rhizosphere oxygenation, root radial oxygen loss, and aerenchyma formation (Granse et al. 2022). To escape waterlogged anoxic soil conditions, plants may produce surface roots, or as we observed, emergent roots where roots grow at or above the soil surface level. Emergent root production was significantly greater in the flooded treatments compared to non-flooded plants for both *Spartina* species, except for the freshwater *S. alterniflora* salinity treatment. This is strong evidence that plants had acclimated to flooded conditions, and although aerenchyma wasn't measured in this study, other studies have documented positive relationships between surface rooting and aerenchyma production (Burdick 1989; Maricle and Lee 2002; Granse et al. 2022). Thus, we expected these plants would not experience additional transplant shock from tidal flooding. Although, it is possible that emergent roots may be more subject to physical damage during transportation. Emergent roots are not a desirable trait for field transplants as plants would not be secured in the sediment; however, if planted below the soil surface in a location that is not continuously flooded, emergent roots are not expected to persist.

In *S. alterniflora*, SLA was greatest in plants exposed to the press—non-flooded treatment combination followed by both the freshwater treatments (Fig. 1). These observations may indicate that constant salinity exposure, either freshwater or saline, may allow for the plant to fully acclimate. The lower SLA values found in the gradual and pulse non-flooded treatment may indicate the plant was in a state of stress response and had not reached a point to maximize energy allocation toward leaf growth. In *S. patens*, SLA was greatest in both pulse and press treatments as well as the non-flooded—gradual

salinity treatment. Lower SLA observed in all flooded treatments indicates an expected negative influence of constant inundation on *S. patens*.

Photosynthesis was greatest in the gradual and pulse salinity treatment groups at three time points (12 June, 15 July, and 29 July), and remained lower in static freshwater or saline treatments. The observed transient increase in A in the gradual and pulse treatments may be attributed to upregulation of Rubisco, accumulation of osmolytes like proline, and activation of salt-mediated osmotic stress pathways (Yang and Guo 2018). These changes reduce the cell osmotic potential to stabilize proteins and cellular structures (Blumwald 2003), thereby improving carbon fixation in the presence of stress. Previous research has shown that moderate levels of salinity increase photosynthetic performance in *Spartina* spp. (Mallot et al. 1975; Naidoo et al. 2012; Zhou et al. 2015), but exceeding an upper threshold (20% in *S. maritima* (Naidoo et al. 2012), 30% in *S. patens* and *S. alterniflora* (Maricle et al. 2007; Hwang and Morris 1994) Hester et al., (2001) found that the effect of salinity exposure on *S. alterniflora* and *S. patens* photosynthesis was short-lived as differences between the salinity-treatment and freshwater control groups were reduced over a 5-week growing period, with the largest differences occurring only after 1 week of salinity exposure. As halophytic species that can exclude or secrete salt, the physiological stress of sub-lethal salinity exposure may not persist long term (Bradley and Morris 1991). Our observations showed a gradual increase in photosynthetic assimilation of $CO_2$ over time across all treatments with greatest A in the gradual and pulse treatments. No detected effect of treatments on photosynthesis at the end of the study may indicate that physiological acclimation of photosynthetic machinery occurred by the end of the study. Additional investigation of the effects of salinity and inundation on photosynthesis is needed in more intensive frequencies over shorter time frames to understand plant stress and recovery responses.

### Traits associated with restoration goals

Goals for projects where *Spartina* spp. is planted may include rapid revegetation of an area to promote primary productivity, provide habitat, secure sediments, and eventually sequester and store carbon (Moritsch et al. 2021). Plant functional traits indicative of these services include increased aboveground biomass production (correlated with primary productivity), belowground biomass, and high root to shoot ratio (correlated with soil strength and carbon storage). In *S. alterniflora*, biomass was not significantly affected by treatments, though there was a slight trend toward increasing aboveground biomass in the gradual salinity treatment. Root to shoot ratio was lowest in the gradual flooded and press flooded treatment combinations, thus these treatments may be less ideal for securing sediments. In *S. patens*, the gradual non-flooded treatment combination resulted in most desirable biomass production traits. The highest root to shoot ratio was shown in the pulse non-flooded combination, but this may be due to reduction in aboveground biomass and not promotion of roots. Thus, the gradual salinity non-flooded treatment may be the best for producing restoration-ready *S. patens*. Although biomass production is certainly an indicator of many other restoration goals, there remains room for further research on how acclimation treatments may correlate with desired physical services of vegetation to dampen wave energy and accrete sediments. For example, previous research showed that *S. alterniflora* pre-acclimated to freshwater showed increased tissue rigidity as a result of osmotic adjustment when exposed to high salinity (Touchette et al. 2009).

### Field transplant survival

Ultimately, the primary metric of success for vegetation transplanted into restoration sites is continued survival and expansion (Menges 2008; Drayton and Primack 2012). Our transplant study showed equal field performance, in terms of plant survival and expansion, regardless of nursery acclimation treatment. The period observed was six months (October to April), which captured survival and re-sprouting after winter senescence. By this point, we assume all plants are similarly acclimated to their site conditions, thus diminishing future effects of nursery treatment. With > 90% survival across both species, the transplant site location is suitable for these species with or without acclimation. Importantly, our plants were only transplanted at one living shoreline project location. Heterogeneity between sites may provide results different from ours. For example, perhaps the effect of stress acclimation would have been more apparent

if plants were transplanted to a more stressful field site. Continued field testing of the efficacy of stress acclimation techniques is warranted.

## Conclusions

Stress acclimatization has been inconsistently practiced among coastal plant providers, with some choosing to introduce plants to salinity prior to selling and others maintaining plants in freshwater. As implementation of coastal nature-based solutions and restoration projects rise, so does the need for science-informed plant preparation guidelines. Our research shows that exposing young plugs of *S. alterniflora* and *S. patens* to salinity and flooding in a nursery setting can activate plant stress acclimation responses without compromising desirable traits associated with marketability and restoration performance. In fact, salinity exposure resulted in lower dead to live stem ratio in *S. alterniflora* and increased biomass production in *S. patens*. Observation of plants transplanted at a living shoreline project site showed no benefit or cost of nursery acclimation treatment on plant survival or initial expansion. Our study shows some benefits of stress acclimation practices, but also that plants produced without any acclimation treatments can be similarly robust in terms of number of stems, total biomass, and field survival. The *Spartina* spp. tested in this study are inherently good stress tolerators as evidenced by their adaptations and observed niche position. This may explain why some traits showed minimal effect of acclimation treatments. We encourage continued research on the tradeoffs between stress acclimation and plant trait responses in additional species, particularly those found at higher elevations that may be less adapted to coastal stressors but potentially impacted by periodic salinity and flooding events.

**Acknowledgements** The authors thank Kori Carr, Etinosa Igunbor, Muriel Draper, Jada Ray, and Dr. Erik Yando for their assistance with data collection. Greenhouse facilities were kindly provided by Mike and Anne Hilton of Knotts Creek Nursery. Living shoreline site access for the transplant experiment was provided by Lafayette Wetlands Partnership, Ruth Martin, and the City of Norfolk, VA. The authors thank the anonymous reviewers for their review and suggestions for enhancement of this article.

**Author contributions** Taylor M. Sloey and Jennifer L.Whytlaw conceptualized the study and acquired funding. Taylor M. Sloey, Kylie D. Gieser, and Kaitlyn Pounders maintained the greenhouse experiment and collected data. Sofía E. Báez conducted literature review and conducted watershed salinity data collection. Taylor M. Sloey and Kylie D. Gieser analyzed the data and created the figures. Taylor M. Sloey wrote the original draft of the manuscript, all authors contributed to editing and revisions gave final approval for publication.

**Funding** This research was supported by the Institute for Coastal Adaptation & Resilience (ICAR) Joan P. Brock Endowment and the Office of Enterprise Research and Innovation within the Division of Research and Economic Development at Old Dominion University, Norfolk, Virginia, USA. Funding of student researchers provided by NSF: Grant 2142348.

**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

### Declarations

**Conflicts f interest** The authors have no relevant financial or non-financial interests to disclose.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

## References

Baldwin AH, Mendelssohn IA (1998) Effects of salinity and water level on coastal marshes: an experimental test of disturbance as a catalyst for vegetation change. Aquat Bot 61:255–268. https://doi.org/10.1016/S0304-3770(98)00073-4

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Bever AJ, Friedrichs MAM, St-Laurent P (2021) Real-time environmental forecasts of the Chesapeake Bay: model setup, improvements, and online visualization. Environ Model Softw. https://doi.org/10.1016/j.envsoft.2021.105036

Biber P, Caldwell JD, Caldwell SR, Marenberg M (2025) Smooth cordgrass, Spartina alterniflora. Center for plant

restoration, propagation guide. https://sites.google.com/site/coastalplantrestoration/home Last accessed: 17 August 2025

Billah MM, Bhuiyan MKA, Islam MA, Das J, Hoque AR (2022) Salt marsh restoration: an overview of techniques and success indicators. Environ Sci Pollut Res 29(11):15347–15363. https://doi.org/10.1007/s11356-021-18305-5

Blumwald E (2003) Engineering salt tolerance in plants. Curr Opin Biotechnol 13:261–275. https://doi.org/10.1080/02648725.2003.1064804

Bradley PM, Morris JT (1991) Relative importance of ion exclusion, secretion and accumulation in *Spartina alterniflora* Loisel. J Exp Bot 42:1525–1532. https://doi.org/10.1093/jxb/42.12.1525

Burdick DM (1989) Root aerenchyma development in *Spartina patens* in response to flooding. Am J Bot 76(5):777–780. https://doi.org/10.1002/j.1537-2197.1989.tb11373.x

Carrion SA (2016) Determining factors that influence smooth cordgrass (Spartina alterniflora Loisel) transplant success in community-based living shoreline projects. Honors Undergraduate Theses, 68

Castillo JM, Figueroa E (2009) Restoring salt marshes using small cordgrass, *Spartina maritima*. Restor Ecol 17(3):324–326. https://doi.org/10.1111/j.1526-100X.2008.00465.x

Chambers RM, Mozdzer TJ, Ambrose JC (1998) Effects of salinity and sulfide on the distribution of *Phragmites australis* and *Spartina alterniflora* in a tidal saltmarsh. Aquat Bot 62(3):161–169. https://doi.org/10.1016/S0304-3770(98)00095-3

Charles B, Chase MH, Pociask G, Bhattarai R, Matthews JW (2022) Can functional leaf traits be used for monitoring wetland restoration? A comparison between commonly used monitoring metrics and functional leaf traits. Ecol Indic 140:109032. https://doi.org/10.1016/j.ecolind.2022.109032

Close DC, Beadle CL, Brown PH (2005) The physiological basis of containerised tree seedling 'transplant shock': a review. Aust for 68(2):112–120. https://doi.org/10.1080/00049158.2005.10674954

Costanza R, Anderson SJ, Sutton P, Mulder K, Mulder O, Kubiszewski I, Wang X, Liu X, Pérez-Maqueo O, Luisa Martinez M, Jarvis D, Dee G (2021) The global value of coastal wetlands for storm protection. Glob Environ Chang 70:102328. https://doi.org/10.1016/j.gloenvcha.2021.102328

Curado G, Gallego-Tévar B, Figueroa E, Castillo JM (2020) Effects of removal of alien *Spartina densiflora* and restoration of native *S. maritima* on succession and zonation in European salt marshes. Estuar Coast Shelf Sci 244:105815. https://doi.org/10.1016/j.ecss.2018.04.011

Davidson NC (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar Freshw Res 65(10):934–941. https://doi.org/10.1071/MF14173

Davies GM, Gray A (2015) Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecol Evol 5:5295–5304. https://doi.org/10.1002/ece3.1782

De Battisti D (2021) The resilience of coastal ecosystems: a functional trait-based perspective. J Ecol 109(9):3133–3146. https://doi.org/10.1111/1365-2745.13641

Di Benedetto A (2011) Root restriction and post-transplant effects for bedding pot plants. Ornamental plants: types, cultivation and nutrition, pp 47–80. Nova Science Publishers, Inc, Hauppauge

Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Cornelissen JHC, Reu B, Kleyer M, Wirth C, Colin Prentice I, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Joseph Wright S, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD (2016) The global spectrum of plant form and function. Nature 529(7585):167–171

Drayton B, Primack RB (2012) Success rates for reintroductions of eight perennial plant species after 15 years. Restor Ecol 20(3):299–303. https://doi.org/10.1111/j.1526-100X.2011.00860.x

Duggan-Edwards MF, Pagès JF, Jenkins SR, Bouma TJ, Skov MW (2020) External conditions drive optimal planting configurations for salt marsh restoration. J Appl Ecol 57(3):619–629. https://doi.org/10.1111/1365-2664.13550

Fant C, Gentile LE, Herold N, Kunkle H, Kerrich Z, Neumann J, Martinich J (2022) Valuation of long-term coastal wetland changes in the US. Ocean Coast Manage 226:106248. https://doi.org/10.1016/j.ocecoaman.2022.106248

Fluet-Chouinard E, Stocker BD, Zhang Z, Malhotra A, Melton JR, Poulter B, Kaplan JO, Goldewijk KK, Siebert S, Minayeva T, Hugelius G, Joosten H, Barthelmes A, Prigent C, Aires F, Hoyt AM, Davidson N, Finlayson CM, Lehner B, Jackson RB, McIntyre PB (2023) Extensive global wetland loss over the past three centuries. Nature 614(7947):281–286

Ge ZM, Li SH, Tan LS, Li YL, Hu ZJ (2019) The importance of the propagule-sediment-tide "power balance" for revegetation at the coastal frontier. Ecol Appl 29:e01967. https://doi.org/10.1002/eap.1967

Granse D, Titschack J, Ainouche M, Jensen K, Koop-Jakobsen K (2022) Subsurface aeration of tidal wetland soils: Root-system structure and aerenchyma connectivity in *Spartina* (Poaceae). Sci Total Environ 802:149771. https://doi.org/10.1016/j.scitotenv.2021.149771

Hagger V, Waltham NJ, Lovelock CE (2022) Opportunities for coastal wetland restoration for blue carbon with co-benefits for biodiversity, coastal fisheries, and water quality. Ecosystem Serv 55:101423. https://doi.org/10.1016/j.ecoser.2022.101423

Hester MW, Mendelssohn IA, McKee KL (2001) Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: morphological and physiological constraints. Environ Exp Bot 46(3):277–297. https://doi.org/10.1016/S0098-8472(01)00100-9

Hill JM, Petraitis PS, Heck KL Jr (2020) Submergence, nutrient enrichment, and tropical storm impacts on *Spartina alterniflora* in the microtidal northern Gulf of Mexico.

Mar Ecol Prog Ser 644:33–45. https://doi.org/10.3354/meps13342
Hollis LO, Turner RE (2021) The tensile root strength of *Spartina patens* declines with exposure to multiple stressors. Wetl Ecol Manage 29:143–153. https://doi.org/10.1007/s11273-020-09774-5
Holmquist JR, Brown LN, MacDonald GM (2021) Localized scenarios and latitudinal patterns of vertical and lateral resilience of tidal marshes to sea-level rise in the contiguous United States. Earths Future 9:Article e2020EF001804. https://doi.org/10.1029/2020EF001804
Hubbard JCE (1969) Light in relation to tidal immersion and the growth of *Spartina townsendii* (sl). J Ecol. https://doi.org/10.2307/2258500
Hwang Y-H, Morris JT (1994) Whole-plant gas exchange responses of *Spartina alterniflora* (Poaceae) toa range of constant and transient salinities. Am J Bot 81(6):659–665
Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. Funct Ecol 16(5):545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x
Lee SY, Dunn RJK, Young RA, Connolly RM, Dale PER, Dehayr R, LeMckert CJ, McKinnon S, Powell B, Teasdale PR, Welsh DT (2006) Impact of urbanization on coastal wetland structure and function. Austral Ecol 31:149–163. https://doi.org/10.1111/j.1442-9993.2006.01581.x
Liu W, Wang W, Zhang Y (2022) Differences in leaf traits of *Spartina alterniflora* between native and invaded habitats: implication for evolution of alien species competitive ability increase. Ecol Indic 138:108799. https://doi.org/10.1016/j.ecolind.2022.108799
Liu Z, Fagherazzi S, He Q, Gourgue O, Bai J, Liu X, Miao C, Hu Z, Cui B (2024) A global meta-analysis on the drivers of salt marsh planting success and implications for ecosystem services. Nat Commun 15(1):3643
Logan JM, Voss S, Davis A, Ford KH (2018) An experimental evaluation of dock shading impacts on salt marsh vegetation in a New England estuary. Estuar Coasts 41(1):13–24
Longstreth DJ, Strain BR (1977) Effects of salinity and illumination on photosynthesis and water balance of *Spartina alterniflora* Loisel. Oecologia 31:191–199
Macy A, Osland MJ, Cherry JA, Cebrian J (2021) Effects of chronic and acute stressors on transplanted black mangrove (*Avicennia germinans*) seedlings along an eroding Louisiana shoreline. Restor Ecol 29(5):e13373. https://doi.org/10.1111/rec.13373
Mallot PG, Davy AJ, Jefferies RL, Hutton MJ (1975) Carbon dioxide exchange in leaves of *Spartina anglica* Hubbard. Oecologia 20:351–358. https://doi.org/10.1007/BF00345525
Mao L, Mishra DR, Hawman PA, Narron CR, O'Connell JL, Cotten DL (2023) Photosynthetic performance of tidally flooded *Spartina alterniflora* salt marshes. J Geophys Res Biogeosci 128(3):e2022JG007161. https://doi.org/10.1029/2022JG007161
Maricle BR, Lee RW (2002) Aerenchyma development and oxygen transport in the estuarine cordgrasses *Spartina alterniflora* and *S. anglica*. Aquat Bot 74(2):109–120. https://doi.org/10.1016/S0304-3770(02)00051-7
Maricle BR, Lee RW, Hellquist CE, Kiirats O, Edwards GE (2007) Effects of salinity on chlorophyll fluorescence and CO 2 fixation in C 4 estuarine grasses. Photosynthetica 45:433–440
Mendelssohn IA, Morris JT (2000) Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. Concepts Controversies Tidal Marsh Ecol. https://doi.org/10.1007/0-306-47534-0_5
Menges ES (2008) Restoration demography and genetics of plants: when is a translocation successful? Aust J Bot 56:187–196. https://doi.org/10.1071/BT07173
Mooring MT, Cooper AW, Seneca ED (1971) Seed germination response and evidence for height ecophenes in *Spartina alterniflora* from North Carolina. Am J Bot 58:48–55. https://doi.org/10.1002/j.1537-2197.1971.tb09944.x
Moritsch MM, Young M, Carnell P, Macreadie PI, Lovelock C, Nicholson E, Raimondi PT, Wedding LM, Ierodiaconou D (2021) Estimating blue carbon sequestration under coastal management scenarios. Sci Total Environ 777:145962. https://doi.org/10.1016/j.scitotenv.2021.145962
Naidoo G, Naidoo Y, Achar P (2012) Ecophysiological responses of the salt marsh grass *Spartina maritima* to salinity. Afr J Aquat Sci 37(1):81–88. https://doi.org/10.2989/16085914.2012.666377
O'Leary BC, Fonseca C, Cornet CC, de Vries MB, Degia AK, Failler P, Furlan E, Garrabou J, Gil A, Hawkins JP, Krause-Jensen D, Le Roux X, Peck MA, Pérez G, Queirós AM, Różyński G, Sanchez-Arcilla A, Simide R, Sousa Pinto I, Trégarot E, Roberts CM (2023) Embracing nature-based solutions to promote resilient marine and coastal ecosystems. Nature-Based Solut 3:100044. https://doi.org/10.1016/j.nbsj.2022.100044
Parrondo RT, Gosselink JG, Hopkinson CS (1978) Effects of salinity and drainage on the growth of three salt marsh grasses. Bot Gaz 139(1):102–107
Pausch R (2024) Testing strategies to enhance transplant success under stressful conditions at a tidal marsh restoration project. Restor Ecol 32(4):e14117. https://doi.org/10.1111/rec.14117
Phleger CG (1971) Effects of salinity on growth of a salt marsh grass. Ecology 52:908–911. https://doi.org/10.2307/1936042
Poljakoff-Mayber A (1975) Morphological and anatomical changes in plants as a response to salinity stress. In: Poljakoff-Mayber A, Gale J (eds) Plants in saline environments, Ecological studies, vol 15 , pp 97–117. Springer, Berlin. https://doi.org/10.1007/978-3-642-80929-3_8
R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Reitveld WJ (1989) Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. North J Appl for 6:99–107. https://doi.org/10.1093/njaf/6.3.99
Rohal CB, Yu X, Crawford JM, Montgomery O, Reynolds LK, Adams CR (2025) Sediment stability is optimized by manipulating planting design during coastal marsh establishment. Sci Rep 15(1):19854
Schneider C, Rasband W, Eliceiri K (2012) NIH image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

SER (Society for Ecological Restoration International Science and Policy Working Group) (2004) The SER International Primer on Ecological Restoration. Tucson, AZ: Society for Ecological Restoration International SOURCE: http://www.ser.org/content/ecological_restoration_primer.asp

Shao D, Zhou W, Bouma TJ, Asaeda T, Wang ZB, Liu X, Cui B (2020) Physiological and biochemical responses of the salt-marsh plant Spartina alterniflora to long-term wave exposure. Ann Bot 125(2):291–300. https://doi.org/10.1093/aob/mcz067

Sloey TM, Ellis VS, Kettenring KM (2023) Using plant functional traits to inform wetland restoration. Wetlands 43(7):92

Sloey TM, Hildebrandt S, Morris RL, Bilskie MV, Bland A, Bushek D, DiPetto G, Elefant D, Encomio V, Familkhalili R, Hladik C, Kreeger D, Paxton AB, Palinkas CM, Steele LaTina, Scheld A, Taira D, Toft JD, Ubeda AJ, Whitcraft C, Bilkovic DM (2025) A blueprint to greener shorelines: advancing the effectiveness, sustainability, and widespread adoption of coastal nature-based solutions through transdisciplinary research. Estuaries Coasts 48(5):133. https://doi.org/10.1007/s12237-025-01571-8

Sorrell BK, Mendelssohn IA, McKee KL, Woods RA (2000) Ecophysiology of wetland plant roots: a modelling comparison of aeration in relation to species distribution. Ann Bot 86(3):675–685. https://doi.org/10.1006/anbo.2000.1173

St-Laurent P, Friedrichs MAM (2024) On the sensitivity of coastal hypoxia to its external physical forcings. J Adv Model Earth Syst. https://doi.org/10.1029/2023MS003845

Stagg CL, Osland MJ, Moon JA, Feher LC, Laurenzano C, Lane TC, Jones WR, Hartley SB (2021) Extreme precipitation and flooding contribute to sudden vegetation dieback in a coastal salt marsh. Plants 10:1841. https://doi.org/10.3390/plants10091841

Strong DR, Ayres DR (2009) Spartina introductions and consequences in salt marshes. Human impacts on salt marshes: a global perspective. University of California Press, Berkeley, pp 3–22

Temmerman S, Horstman EM, Krauss KW, Mullarney JC, Pelckmans I, Schoutens K (2023) Marshes and mangroves as nature-based coastal storm buffers. Annu Rev Mar Sci 15(1):95–118. https://doi.org/10.1146/annurev-marine-040422-092951

Temmink RJ, van den Akker M, van Leeuwen CH, Thöle Y, Olff H, Reijers VC, Bakker ES (2022) Herbivore exclusion and active planting stimulate reed marsh development on a newly constructed archipelago. Ecol Eng 175:106474. https://doi.org/10.1016/j.ecoleng.2021.106474

Touchette BW, Smith GA, Rhodes KL, Poole M (2009) Tolerance and avoidance: two contrasting physiological responses to salt stress in mature marsh halophytes *Juncus roemerianus* Scheele and *Spartina alterniflora* Loisel. J Exp Mar Biol Ecol 380(1–2):106–112. https://doi.org/10.1016/j.jembe.2009.08.015

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116(5):882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Virginia Marine Resources Commission (2025). Habitat management permits and applications. webapps.mrc.virginia.gov/public/habitat/ Last accessed: 2025 05 01

Visser JM, Peterson JK (2015) The effects of flooding duration and salinity on three common upper estuary plants. Wetlands 35:625–631

White E, Kaplan D (2017) Restore or retreat? Saltwater intrusion and water management in coastal wetlands. Ecosyst Health Sustain. https://doi.org/10.1002/ehs2.1258

Wodehouse DC, Rayment MB (2019) Mangrove area and propagule number planting targets produce sub-optimal rehabilitation and afforestation outcomes. Estuar Coast Shelf Sci 222:91–102. https://doi.org/10.1016/j.ecss.2019.04.003

Yang Y, Guo Y (2018) Elucidating the molecular mechanisms mediating plant salt-stress responses. New Phytol 217(2):523–539. https://doi.org/10.1111/nph.14920

Zedler JB, Morzaria-Luna H, Ward K (2003) The challenge of restoring vegetation on tidal, hypersaline substrates. Plant Soil 253:259–273

Zhang D, Shi X, Lie X, Wand S, Tian J, Wand T, Zhang M (2024) Leaf traits of Spartina alterniflora in response to soil salinity. Appl Ecol Environ Res. https://doi.org/10.15666/aeer/2205_41374153

Zhou C, Shen W, Lu C, Wang H, Xiao Y, Zhao Y, An S (2015) Effects of salinity on the photosynthesis of two poaceous halophytes. CLEAN-Soil Air Water 43(12):1660–1665. https://doi.org/10.1002/clen.201300840

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.