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# Effects of saltwater intrusion on candidate restoration species in coastal agricultural fields

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ABSTRACT

Sea level rise (SLR) and saltwater intrusion (SWI) along the Eastern Seaboard of the U.S. are reducing crop productivity and driving farmland abandonment. However, planting native marsh species can accelerate the transformation of these degraded fields into thriving tidal marshes, enhancing their ecosystem services. This study evaluates the productivity and element dynamics of six native warm-season grasses, including *Panicum amarum*, *Panicum virgatum*, *Paspalum floridanum*, *Spartina patens*, *Spartina pectinata,* and *Tripsacum dactyloides* on two abandoned agricultural fields in Somerset County, Maryland, USA. Aboveground biomass and plant tissue element concentrations were analyzed to evaluate their potential for use on field edges (buffers) or whole-field restoration efforts. Additionally, soil samples were collected to measure electrical conductivity (EC, as a proxy for salinity) and sodium (Na) concentrations. We found *T. dactyloides* to be an ideal candidate for salt-affected fields due to its high biomass productivity, efficient phosphorus uptake, and eligibility for several federally-funded conservation practice standards (CPS), including conservation cover (CPS 327) and field borders (CPS 386). Similarly, both *Spartina* species performed well and exhibited the highest Na accumulation in their tissues, making them ideal candidates for transitional restoration efforts due to their ability to thrive in both saline and non-saline conditions. Moreover, *Spartina patens* and *Spartina pectinata* are currently recommended for some conservation practice standards, including CPS 580 (Streambank and shoreline stabilization) and CPS 390 (Riparian herbaceous cover). Collectively, these native grasses offer versatile strategies to mitigate the environmental impacts of SLR and SWI, while supporting ecosystem services essential for maintaining the resilience and long-term sustainability of coastal regions.

## 1. Introduction

Climate change is driving profound transformations in coastal environments in the form of rising sea levels, more frequent storms, and prolonged droughts (IPCC, 2023). As sea levels rise, saltwater advances into upland areas - a process known as saltwater intrusion (SWI) - threatening freshwater sources and increasing salinity levels in groundwater and soil (Tully et al., 2019a, 2019b). Globally, the total area of salt-affected soils amounts to 1381 million hectares (FAO, 2024), posing a significant threat to food production. Saltwater intrusion occurs when storm surges or high tides overflow into low-lying areas, infiltrating surficial soil, or when saltwater infuses into freshwater aquifers, which can also elevate the groundwater table below the soil surface (Guimond and Michael, 2021). Prolonged droughts exacerbate this impact by depleting freshwater availability and increasing evaporation, which further concentrates salts in affected soils (Ardón et al., 2013; Tully et al., 2019a, 2019b).

Saltwater intrusion sets off a series of ecological changes, including increased soil salinity, yield declines, forest loss, and the transition of farmland into salt marshes (de la Reguera et al., 2020; Kirwan and Gedan, 2019; Tully et al., 2019a, 2019b; Zörb et al., 2019). It may also contribute to nutrient enrichment in nearby water bodies by mobilizing legacy phosphorus (P). As saltwater alters soil chemistry, it increases ionic strength and disrupts nutrient retention mechanisms (Tully et al., 2019a, 2019b). For instance, sulfate ($SO_4^{2-}$) introduced through saltwater can displace phosphate ions bound to soil particles, increasing P

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availability in surface runoff (Tully et al., 2019a, 2019b; Weissman and Tully, 2020). These processes elevate the risk of P loss from soils to adjacent aquatic ecosystems, ultimately contributing to eutrophication (Lucas et al., 2023; Steinmuller and Chambers, 2018; Tully et al., 2019a, 2019b).

The Mid-Atlantic region of the United States is among the areas most affected by sea-level rise (SLR) in the world (Goddard et al., 2015; Sallenger et al., 2012), as for many decades, rates of SLR have been double the global average (NOAA, 2021). Projections indicate that by 2050, sea levels will rise in the Mid-Atlantic Coastal Plain by 28–65 cm, effectively drowning several coastal counties (Miller et al., 2013). Accelerated SLR makes the coastal counties in Delmarva Peninsula (Delaware, Maryland, and Virginia) increasingly vulnerable to high-tide flooding and SWI, damaging agricultural systems by reducing crop productivity as salinity levels increase (Bhattachan et al., 2018; Gedan and Fernández-Pascual, 2019). Between 2011 and 2017, approximately 20,000 ha of farmland on the Delmarva Peninsula were converted to marshland due to rising salinity levels, resulting in an estimated annual loss of $39.4 million (in soybean) to $107.5 million (in corn) (Mondal et al., 2023). A study in coastal New Jersey identified over 18,000 ha of farmland that will be affected by SWI in this decade, worth approximately $18 million in losses (Shope et al., 2022). Our research will fill an important knowledge gap by providing guidance for how to manage coastal fields as they transition out of agriculture.

Saltwater intrusion elevates soil concentrations of chloride, sodium (Na), calcium (Ca), potassium (K), and $SO_4^{2-}$, significantly altering biogeochemical processes (Setia et al., 2010; Tully et al., 2019a, 2019b; Weston et al., 2011). For example, the increase in ionic strength enhances ion exchange, which affects the release and availability of essential nutrients to plants, such as nitrogen (N) and P (Weston et al., 2006). Alkalinization raises soil pH, reducing nutrient uptake (e.g. P, molybdenum (Mo), zinc (Zn), boron (B)) and inhibiting microbial processes necessary for nutrient cycling (e.g., soil organic matter decomposition) (Barrow and Hartemink, 2023; Wang and Kuzyakov, 2024). Additionally, as saltwater increases $SO_4^{2-}$ concentrations, soils undergo sulfidation, shifting microbial respiration pathways from methane production to sulfate reduction. This shift can reduce soil carbon (C) storage, further destabilizing ecosystem functions (Neubauer et al., 2013; Weston et al., 2011). Together, these changes disrupt interactions among plants, soils, and microbial communities, destabilizing ecological balance and decreasing the resilience of affected ecosystems (Mazhar et al., 2022). Saltwater intrusion also alters osmotic potentials in the soil, which limits water and nutrient uptake, and can lead to ion toxicity in crop plants not adapted to saline conditions. These stresses lead to stunted growth, reduced leaf expansion, and nutrient deficiencies, particularly in potassium (K) (Kumari et al., 2021; Mahajan and Tuteja, 2005). Thus, high salinity not only restricts productivity but, in severe cases, can force the abandonment of farmlands (Diome and Tine, 2015; Mazhar et al., 2022; Sambou et al., 2016).

On abandoned or unmanaged fields and field edges, SWI can lead to a proliferation of invasive and weedy species (e.g., *Phragmites australis*) and a shift toward woody plant communities, rather than a natural transition to native marsh vegetation (Gedan and Fernández-Pascual, 2019). However, active restoration efforts, such as planting native marsh species, may effectively guide these degraded fields back toward productive tidal marshes. This intentional approach not only promotes native vegetation but also enhances ecosystem services, including C storage, water quality maintenance, shoreline stabilization, habitat creation, and food resources for various species (Barbier et al., 2011; Duarte et al., 2013). Therefore, the goal of this study was to investigate the performance and response of several potential restoration species to increasing SWI on previously abandoned agricultural fields.

The selection of candidate species for restoration and conservation buffers is a critical decision, as these plants play a fundamental role in the stability and functionality of restored ecosystems (Butterfield et al., 2016; Jackson, 2017). Edge-of-field projects, or buffers, are also shown to reduce nutrient runoff, improve water quality, and enhance soil health (Jackson, 2017; Lowrance et al., 1997). Additionally, they support biodiversity by providing wildlife habitat and enhancing soil microbial activity, which, in turn, improves soil structure and promotes carbon sequestration (Mitchell et al., 2023).

In this study, six native warm-season grasses were selected for coastal restoration based on their ability to thrive in salt-affected soils and their adaptability to local environmental conditions (Table 1). These species include: *Spartina patens* and *Spartina pectinata* are highly salt-tolerant grasses commonly found in brackish marshes (Belt and Miller, 2021). *Panicum amarum* and *Panicum virgatum* are highly adapted to saline and drought conditions (Snell, 2020; Belt and Miller, 2021), with dual potential as forage and biofuel crops (David and Ragauskas, 2010; Snell, 2020), making them ideal for cultivation on saltwater-intruded marginal lands (Belt and Miller, 2021). Moreover, *P. virgatum* demonstrates high efficiency in soil P uptake, effectively reducing porewater P concentrations through biomass assimilation, thereby mitigating farm-level P losses that contribute to eutrophication (Schulenburg et al., 2024). ***Tripsacum dactyloides*** is typically found at the edges of salt marshes (Native Plant Trust, 2023), and *Paspalum floridanum*, naturally occurs along saline ditches on farms in the Lower Eastern Shore of the Chesapeake Bay, demonstrating potential for use in riparian buffers that are periodically inundated by brackish water (Table 1). Together, these species perform a diverse range of ecological functions, including stabilizing streambanks and shorelines, enhancing riparian buffers, improving water and air quality, offering wildlife food and cover, and serving as drought-tolerant forage for livestock (Belt and Miller, 2021).

The Mid-Atlantic region is one of the first in the world to lose farmlands so quickly, and the region's landowners and agricultural advisors are requesting science-based management strategies to adapt to and mitigate the effects of SWI and SLR on salt-intruded fields (Dubow et al., 2024). Our study objectives were to (1) quantify the effects of SWI on the productivity of the candidate restoration species; and (2) determine the effect of SWI on tissue elements (Ca, Mg, Na, K, and P) concentrations and accumulation. Results of this research will help inform land management policies that are actively being developed in this region to respond SWI and SLR effects on farmland. This research helps fill both basic and applied scientific knowledge gaps in how to respond to climate change in coastal agricultural regions.

## 2. Materials and methods

### 2.1. Study sites

In 2021, a field experiment was established on two privately-owned agricultural fields affected by SWI in Somerset County, Maryland, on the Lower Eastern Shore of Chesapeake Bay, USA. This region's dominant agricultural crops are corn (*Zea mays*) and soybean (*Glycine max*); however, these crops are highly sensitive to saline and saturated soil conditions (de la Reguera et al., 2020). The area has been experiencing significant losses in viable farmland, with a 2 % reduction in agricultural land between 2009 and 2017, largely due to the conversion of farmland to marsh habitat (Gedan et al., 2020). The farms, hereafter called Oriole Farm and Venton Farm, are both approximately 1 km from a waterbody that drains into the Chesapeake Bay (38.0862° N, 75.8534° W; Fig. 1). Most soils in Somerset Co. are Quindocqua silt loams with little to no slope. Oriole Farm has a mixture of Quindocqua silt loam (mesic Typic Endoaquults) and Manokin silt loam (mesic Aquic Hapludults), while the soils at Venton Farm are a mixture of Quindocqua and Othello silt loams (mesic Typic Endoaquults). The area receives an average of 1085 mm of precipitation annually, and the mean annual temperature is 19 °C. During the study period (2021–2023), total annual precipitation ranged from 993 to 1028 mm. Mean high temperatures ranged from 20.4° to 21.1°C, and mean low temperatures ranged from 9.3 to 10.2°C (NOAA -NCEI, 2025). Although soil salinity levels were not above 1 dS $m^{-1}$, the ditches that border both agricultural fields ranged from 5 to 10

**Table 1**
Site conditions and salt adaptation strategies of six restoration species.

| Species | Common name | Site conditions | | | Adaptations to Saline Conditions | References |
|---|---|---|---|---|---|---|
| | | Drought tolerance | Flooding tolerance | Salt tolerance | | |
| *Panicum amarum* | Coastal panicgrass | ★★ | ★ | ★★ | Adapted to dune systems, can withstand salt spray, brief storm surges, and drought. | (DiCara and Gedan, 2023; Lonard and Judd, 2011) |
| *Panicum virgatum* | Switchgrass | ★ | ★★ | ★★ | Tolerant to salt and alkali soils and drought. Has salt excretion glands and synthesizes organic compounds to maintain osmotic balance. | (DiCara and Gedan, 2023; Kobayashi, 2008) |
| *Paspalum floridanum* | Florida paspalum | ★ | ★★ | ★ | Common in brackish ditches adjacent to crop fields (authors' observations). | (DiCara and Gedan, 2023) |
| *Spartina patens* | Saltmeadow cordgrass | ★ | ★★ | ★★ | Secretes salt through specialized glands and accumulates organic solutes (e.g., proline, glycine betaine) for osmotic adjustment, allowing survival in high-salinity environments. | (Hester et al., 2001) |
| *Spartina pectinata* | Prairie cordgrass | ★ | ★★ | ★★ | Secretes excess salt through specialized salt glands, allowing it to survive in saline and brackish environments, making it an effective option for salt remediation | (Litalien et al., 2020; Morris et al., 2019) |
| *Tripsacum dactyloides* | Eastern gamagrass | ★ | ★ | ★ | Typically found at the edges of salt marshes; can withstand brief saltwater inundation during storm surges but is not highly tolerant of prolonged exposure to saline soils. | (Florida Native Plant Society, 2023; Native Plant Trust, 2023) |
| ★ Acceptable | ★★ Optimal | | | | | |

Modified from Belt and Miller (2021).

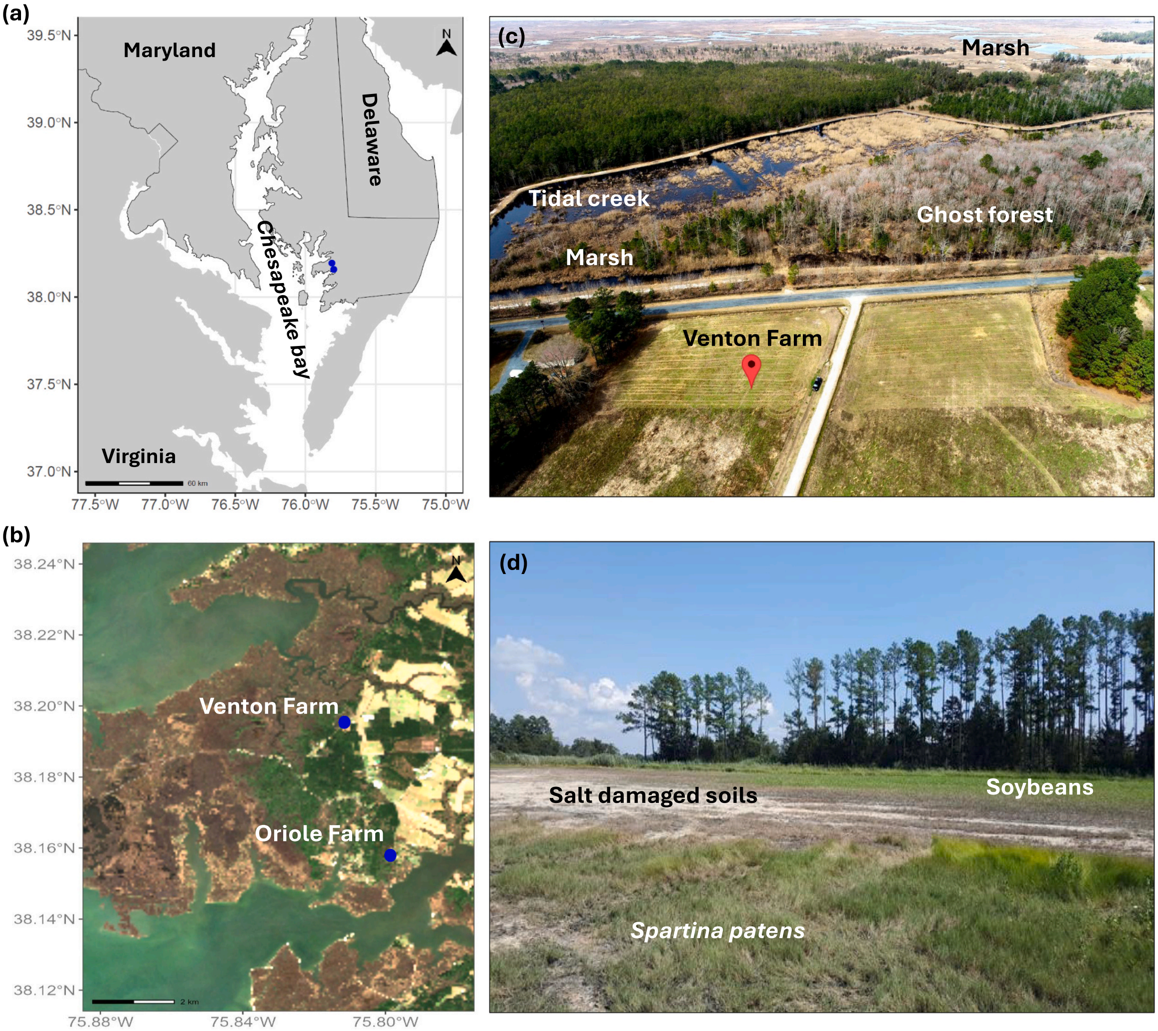

**Fig. 1.** (a) Map of the Chesapeake Bay region in the United States, where the blue dots depict the location of our two saltwater-intruded farms; (b) Map of the study area showing site locations (blue dots) and proximity in Somerset County, Maryland; (c) Drone image of Venton Farm; (d) Image of a nearby farm field showing a salt-damaged area transitioning to marsh vegetation, dominated by *Spartina patens*.

dS $m^{-1}$ because of their proximity and connectivity to saline water bodies. These fields are typical of the region (Weissman and Tully, 2020).

### 2.2. Experimental design

This study identified six candidate restoration species for the saline field restoration planting: (1) *Panicum amarum;* (2) *Panicum virgatum*; (3) *Paspalum floridanum*; (4) *Spartina patens*; (5) *Spartina pectinata*; and (6) *Tripsacum dactyloides*. More information about these perennial native warm-season grasses can be found in Table 1. At the start of the study, Venton Farm had been fallow for two years (agricultural activities ceased in 2019) and Oriole Farm for six years (agricultural activities ceased in 2015). Weeds, primarily dog fennel (*Eupatorium capillifolium)* and crab grass (*Digitaria sanguinalis*), dominated the fields. They were sprayed with glyphosate and mowed in early March 2021 in preparation of restoration planting.

Following spraying and mowing, treatments were installed in a randomized complete block design. Each farm field was divided into four blocks (replicates), each containing six plots. We obtained bare rootstock of each species from the Natural Resources Conservation Service (NRCS) Plant Material Center in Cape May, NJ. Species were grown in monoculture production fields and harvested using a seedling undercutter. During harvest, efforts were made to collect as much root biomass as possible while the aboveground biomass remained intact to protect the bare rootstock. One day after excavation, the plants were transported by box truck to the site for planting. In each plot, one of the six candidate species was planted. Plots were 3 m wide and 15 m long, with at least 1 m between plots and 2 m between blocks. All six species were planted within each plot evenly spaced on a grid 50 cm between plants and 50 cm between rows (3 rows x 60 plants per row = 180 plants per plot). Individuals were planted using a power auger to dig a shallow hole about 4 cm wide, carefully laying the roots below ground and backfilling the hole with removed soil. Plots were rainfed and not irrigated to mimic natural conditions.

### 2.3. Soil sampling and analyses

Soil samples were collected from each site prior to any field activities in March 2021 (baseline collection) and at the end of the study in November 2023 using a 22-mm diameter push probe (AMS, Idaho Falls, ID, USA). During baseline sampling, we randomly selected five locations within each block and collected soil at four depths (0–10 cm, 10–20 cm, 20–30 cm, and 30–60 cm), which were composited at the block level (n = 4 per farm). In November 2023, five soil samples were collected lengthwise across the plot and composited at the plot level (n = 36 per farm). Soils were transported to the University of Maryland Agroecology Laboratory, where they were air-dried for one week and then ground using a Dyacrush Soil Crusher to pass through a 10-mesh sieve. We analyzed soil samples for electrical conductivity (EC) and sodium (Na) concentrations, as these are widely used indicators of salinity in soils. EC provides a general measure of soil salinity, capturing the presence of multiple soluble salts, while Na is a dominant ion in saline water and plays a key role in altering soil structure, plant ion balance, and nutrient availability. To quantify exchangeable Na, a subsample of ground soil was extracted for plant-available nutrients using Mehlich-3 (Mehlich, 1984). The extracts were analyzed using an Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES, PerkinElmer Optima 7000DV). Solution concentrations were converted to milligrams per kilogram using initial soil weight and solution volume. The EC of the soil was determined on a sub-sample of soil in a 1:5 soil:water slurry using a Thermo Scientific Orion Versa Star Pro probe (Thermo Fisher Scientific, Hampton, NH).

### 2.4. Plant sampling and analyses

Plant samples from each treatment were collected in August 2021 (Year 1) and July 2023 (Year 3) at the plot-level. Four quadrats of 0.25 m x 0.25 m were sampled from each plot at Oriole and Venton Farms. All aboveground biomass within the quadrat was collected using a scythe. Fresh plant material was placed in a bag, transported to George Washington University laboratory, and placed in a freezer until processing. Samples were sorted to the species-level and dried in an oven with forced air circulation at a temperature of 60 ºC until a constant weight was achieved. Plant material was then weighed, ground (Wiley Mill, Swedesboro, NJ), and digested in nitric acid (Huang and Schulte, 1985). The digestion solutions were analyzed to determine the concentrations of Na, potassium (K), calcium (Ca), phosphorus (P), and magnesium (Mg) using ICP-OES as above. Solution concentrations were converted to grams per kilogram using initial soil weight and solution volume. Element concentrations in aboveground biomass were calculated by multiplying ion concentrations (g $kg^{-1}$) by the aboveground biomass (g $m^{-2}$) collected from the plots.

### 2.5. Statistical analysis

We used a linear mixed-effects (LME) model (*lme4* package for R; (Bates, 2007) to determine the effect of plant species on plant tissue Na, K, Ca, P, and Mg concentrations and accumulation. We examined each site individually, with plant species (treatment) as the main effect and block as the random effect. We also used LME to determine the effect of plant species (treatment) on Na concentration and EC in the soil. We examined each site individually, with species, year and soil depth as the main effect and block as the random effect. When a significant main factor was identified, pairwise comparisons were performed with Tukey's *post-hoc* test (function glht, package *multcomp*). All data were examined using the Shapiro–Wilk test ($p < 0.05$) to check for normal data distribution. Where data failed the Shapiro–Wilk test, a Box–Cox transformation was performed to obtain a normal distribution of data (Box and Cox, 1964). We ran a Pearson correlation matrix to evaluate the relationships among soil Na, soil EC, plant Na, K, Mg, P, and Ca concentrations. All statistical analyses were performed using the R statistical software version 4.0 (R Core Team, 2020).

## 3. Results

### 3.1. Soil electricity conductivity and soil Na concentration

Overall, we observed increases in soil EC and Na concentrations from 2021 (baseline) to 2023 at both Venton and Oriole Farms, indicating that these soils are salinizing over time (Fig. 2). There was a significant effect of soil depth on EC and Na in both years, with the lowest values in the topsoil (0–10 cm) and highest values in the deeper soil (30–60 cm) depth ($p < 0.05$) (Fig. 2). We found no differences in EC or soil Na concentrations under the different plant restoration species.

### 3.2. Plant element concentration and accumulation

We analyzed the concentration and accumulation of elements (Na, K, P, Ca, and Mg) in plant leaf tissue at Venton and Oriole Farms in 2021 and 2023. Plant element concentrations did not change at either site over time, but we observed many significant differences in tissue concentrations among plant restoration species for elements at the farm-level (Fig. 3; $p < 0.05$ in all cases). At both sites, *Spartina* species exhibited the highest sodium concentrations ([Na]) in both years. All other species had lower [Na], with *T. dactyloides* and *P. floridanum* showing the lowest concentrations (Fig. 3b). In contrast, *Spartina* species had the lowest tissue potassium concentrations ([K]) (Fig. 3b), while *P. floridanum* and *T. dactyloides* consistently exhibited the highest [K] ($p < 0.05$ in all cases; Fig. 3b). *T. dactyloides* had the highest phosphorus

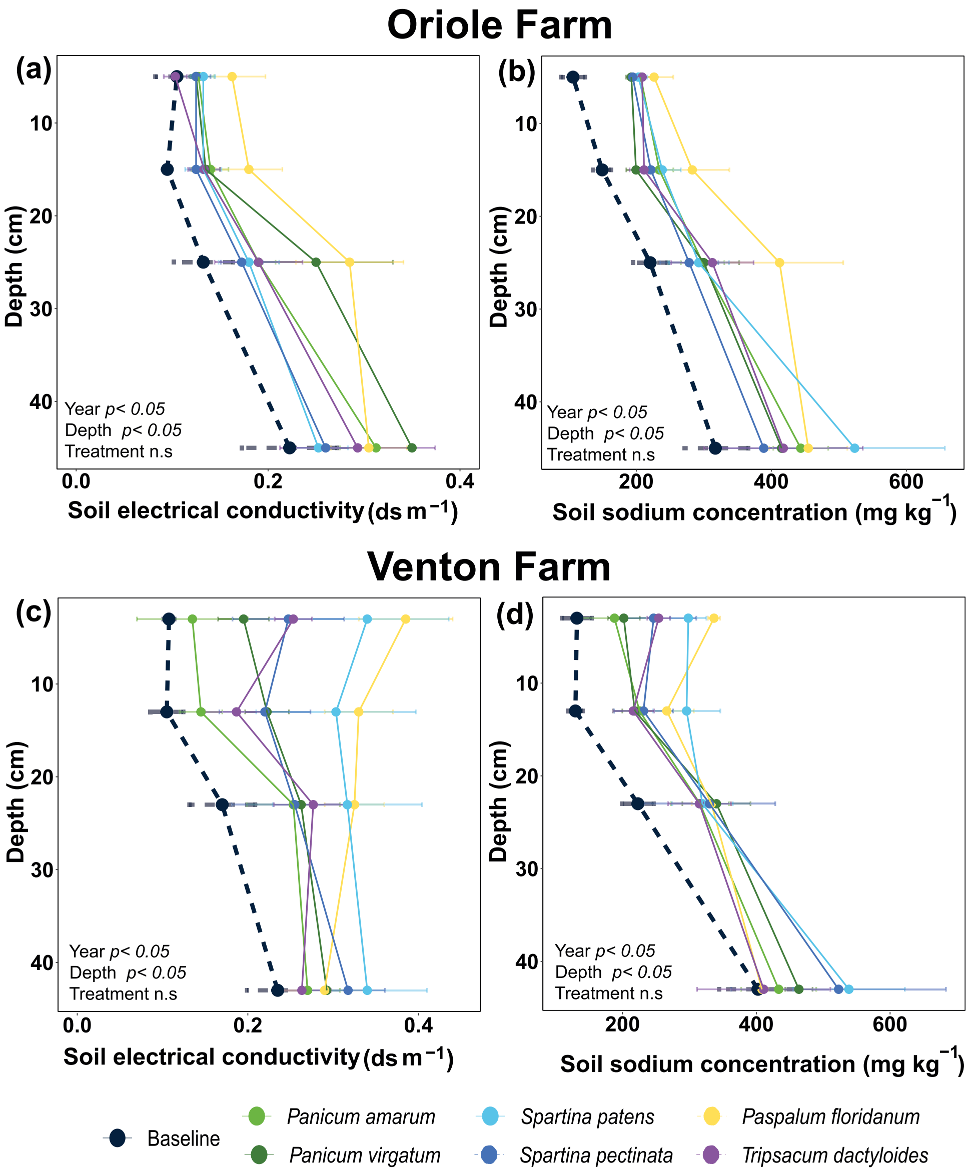

**Fig. 2.** (a,c) Soil electrical conductivity (EC) and (b,d) soil sodium (Na) concentrations at two focal farms in Somerset County, Maryland. Baseline soils collected in 2021 are represented by black dashed lines. Colored lines indicate EC and Na concentrations in the soil below different plant species in 2023. Error bars are standard error of the mean.

concentration ([P]) at both farms in 2021 ($p < 0.05$ in all cases; Fig. 3c), but there was no effect of species at Oriole Farm in 2023. Plant tissue calcium concentrations ([Ca]) were relatively similar between Venton and Oriole Farms (Figure S2). At both sites in 2023, *Spartina* species and *P. floridanum* had the highest [Ca] ($p < 0.05$ in all cases; Figure S2).

Plant biomass influenced the distribution of element accumulation across sites. In 2021, element pools for most of the studied species showed no significant differences, as biomass among restoration species remained similar due to the small size of the plants. By 2023, at both sites, *Spartina* species exhibited the highest Na accumulation, whereas *T. dactyloides* had the highest K and P accumulation in their plant tissues ($p < 0.05$ in all cases; Fig. 4).

### 3.3. Biomass

Biomass production of the planted species during the first year of the experiment was generally low (with most species below 100 $m^{-2}$) and showed variability across sites and species (Fig. 5). At Oriole Farm in 2021, *S. pectinata* produced the highest biomass (~250 $g\ m^{-2}$) and *P. virgatum* had the lowest biomass (below 20 $g\ m^{-2}$). In 2023, *T. dactyloides* produced the highest biomass (~300 $g\ m^{-2}$), followed by *S pectinata* ($p < 0.05$; ~200 $g\ m^{-2}$; Fig. 6a). At Venton Farm in 2021, no significant differences were observed among restoration species because the plants were small. Two years later, in 2023, *S. patens* produced the highest biomass (~200 $g\ m^{-2}$), and *P. floridanum* and *P. amarum* the lowest ($p < 0.05$).

Plant [Na] exhibited significant negative correlations with [K] (r = -0.48, $p < 0.001$), [Mg] (r = -0.40, $p < 0.05$), and [P] (r = -0.31, $p < 0.01$) in plant tissue. Conversely, a positive correlation was observed between plant [Na] and [Ca] (r = 0.40, $p < 0.05$). Plant [K] showed a positive correlation with plant [Mg] and [P]. Additionally, plant [Mg] had a strong correlation with plant [P] (r = 0.42; $p < 0.005$). As expected, soil [Na] was strongly correlated with soil EC (r = 0.82; $p < 0.001$).

## 4. Discussion

This study aimed to understand how biomass and element uptake

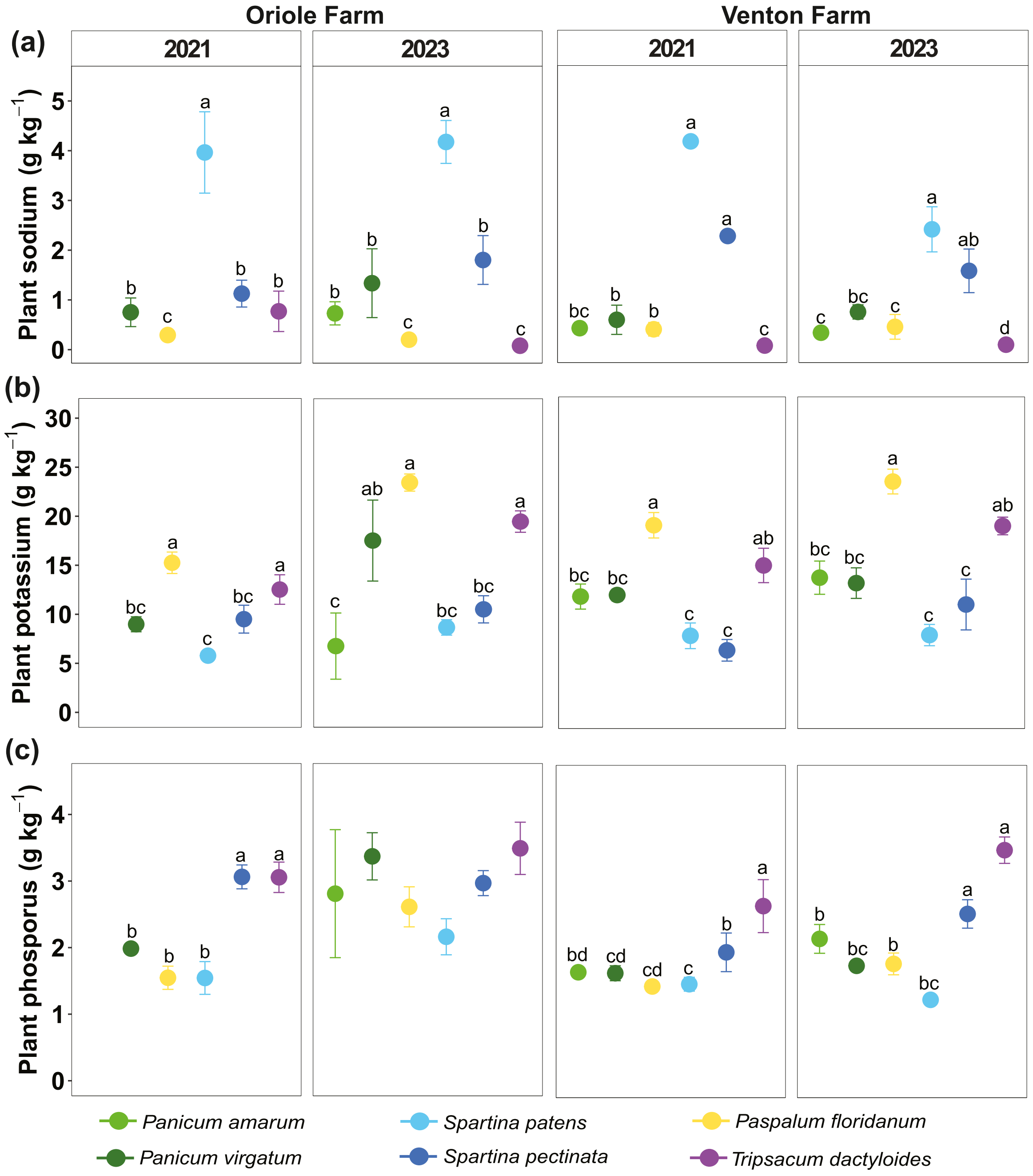

**Fig. 3.** (a) Sodium (Na), (b) potassium (K), and phosphorus (P) plant tissue concentrations of six restoration species at two focal farms in Somerset County, Maryland. Different letters indicate a significant effect ($p < 0.05$) of species in Tukey *post hoc* pairwise comparisons within a farm and year. Error bars are standard error of the means.

differed among candidate restoration species in salt-intruded farms. Our results indicate that *Spartina* species, which are commonly associated with saline environments, exhibit a notable ability to accumulate Na in their tissues. Conversely, these species showed low tissue K accumulation, highlighting their capacity to co-regulate cations and adapt to elevated salinity conditions. Among the species studied, *T. dactyloides* demonstrated the highest biomass accumulation over time and a capacity to accumulate P in their tissues, which suggests that it may be a good candidate for remediating high P soils. Finally, we observed a small but significant increase in soil salinity over the study period and higher soil Na and EC in deeper soil layers, suggesting that SWI in these soils occurs primarily below the surface, influenced by a shallow, groundwater table, which is salinizing over time.

### *4.1. Soil salinity increases with depth and over time*

Our results demonstrate that the focal farms are salinizing (Fig. 2). This trend, along with the observed increase in salt concentrations with soil depth, suggests a primarily “bottom-up” mode of saltwater intrusion (Mondal et al., 2025) at these sites (e.g., salinization of groundwater tables) rather than a “top-down” mode of SWI intrusion (e.g., overtopping of saline ditches) (Kirwan et al., 2024). The bottom-up intrusion process may be driven by rising groundwater levels or pressure from adjacent saline bodies, which push saltwater into lower soil horizons over time (Tully et al., 2019a, 2019b). In contrast, top-down intrusion is typically caused by surface flooding from storm surges and ditch overtopping, high tides, or even irrigation with salty water (Guimond and Michael, 2021). Because overtopping is intermittent by nature, the study

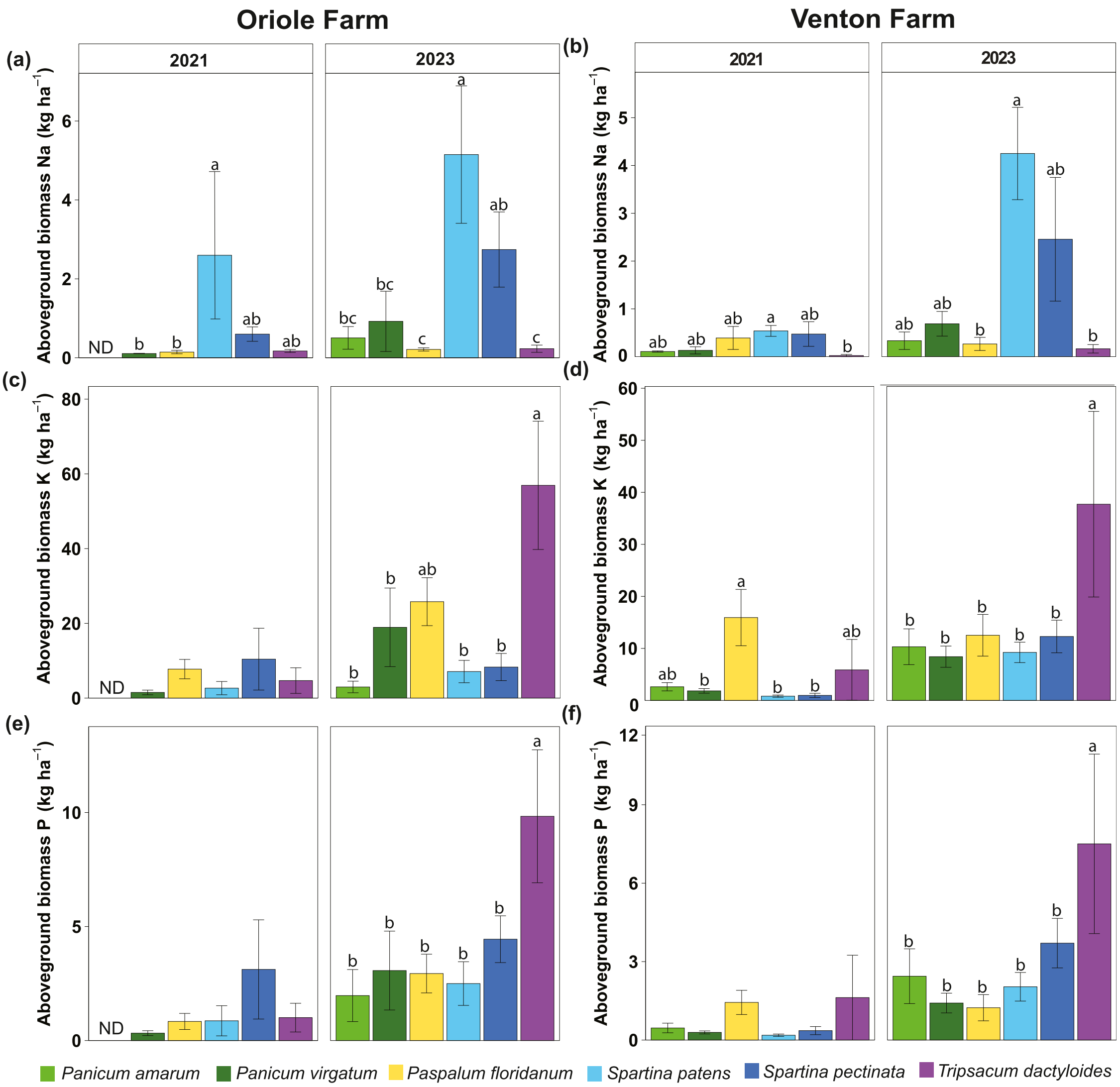

**Fig. 4.** Plant aboveground element pools (kg ha$^{-1}$) in the six restoration species at two focal farms in Somerset County, Maryland. Different letters indicate a significant effect of species in Tukey *post hoc* pairwise comparisons. Bars represent the means ± standard error.

years may have occurred between major flooding events during which top-down modes may be more important. "Bottom-up" SWI, however, can be particularly insidious and present distinct challenges for agricultural management because it is happening below the soil surface, making it difficult to diagnose and remediate (Mondal et al., 2025; Tully et al., 2019a, 2019b). Thus, it impacts the root zones and progressively undermines soil health, leading to ongoing issues for agricultural productivity in coastal environments (Mazhar et al., 2022; Zörb et al., 2019). Agricultural activities ceased at Venton Farm in 2019 and at Oriole Farm in 2015, leaving the lands fallow. Both sites sit at a low elevation (0.9 m above sea level), which facilitates the movement of saltwater across the landscape and increases the frequency and severity of flooding, particularly during high tides and storm events. This flooding not only exacerbates saltwater intrusion but also accelerates the degradation of soil and water resources, compromising the usability of agricultural lands (Anderson et al., 2020; Ponting et al., 2021). The vulnerability of low-lying farm fields is further intensified by the network of drainage ditches originally designed to manage excess water for agricultural purposes (Bhattachan et al., 2018). Over time, these ditches have begun to channel saltwater inland, especially during high tides or storm surges. Salinity measurements in the ditches were 9 dS m$^{-1}$ and 5 dS m$^{-1}$ at Venton Farm and Oriole Farm, respectively, which falls within typical ranges found in agricultural ditches and tidal creeks in the region (Weissman and Tully, 2020). Although our data indicate that soil salinity levels in these areas are not excessively high, they also fluctuate over time due to periodic storm-induced flooding and precipitation events, which may temporarily dilute salts.

### *4.2. Spartina species exhibit the highest Na and lowest K accumulation*

*S. patens* and *S. pectinata*, as facultative halophytes, can thrive in both saline and non-saline environments (Halvorson and Singer, 1974). Our study demonstrated that *Spartina* species accumulated the largest amount of Na in aboveground biomass compared to other candidate restoration species. Salt tolerance in halophytes is largely attributed to cellular mechanisms that prevent metabolic disruption by sequestering $Na^+$ and chlorine ($Cl^-$) in vacuoles, while compatible organic solutes (e.g., proline, glycine betaine) accumulate in the cytoplasm to maintain osmotic balance (Flowers and Colmer, 2015). Additionally, *Spartina* species excrete excess salts through specialized salt glands, depositing Na on leaf surfaces as an added means of ion regulation (Maricle et al., 2009; Morris et al., 2019). We found a negative correlation between plant Na and K concentrations, with the lowest K levels found in *S. patens* and *S. pectinata* tissues compared to the other species studied (Fig. 6). High Na concentrations in the soil can limit the availability of essential nutrients like K, suggesting competition between these ions, where

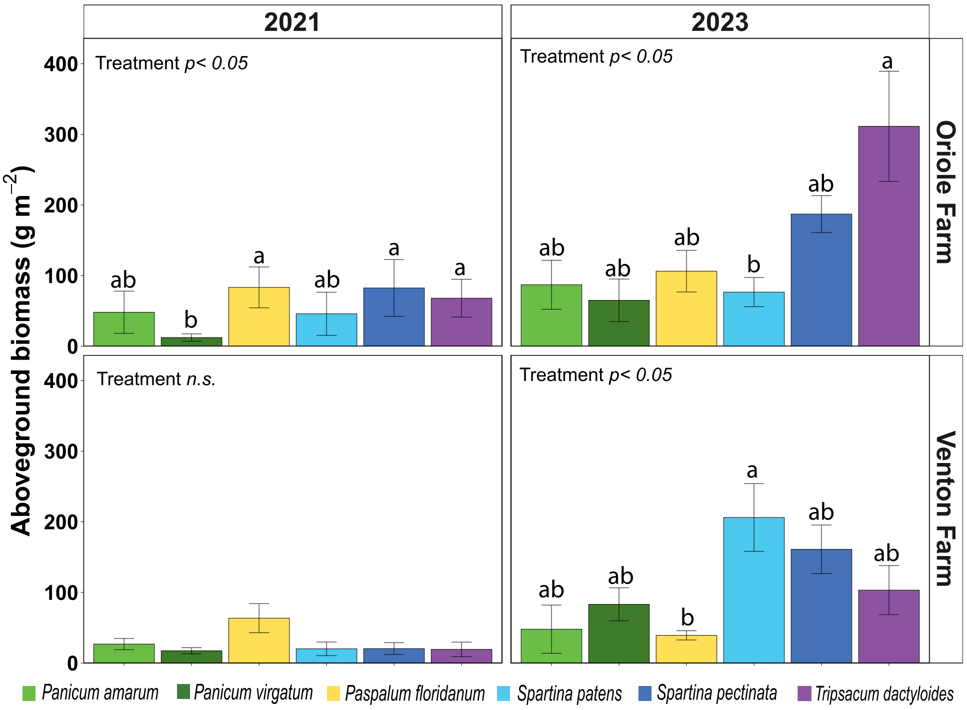

**Fig. 5.** Aboveground biomass (g m$^{-2}$) in the six restoration species at two focal farms in Somerset County, Maryland. Different letters indicate a significant effect of species in Tukey *post hoc* pairwise comparisons. Bars represent the means ± standard error.

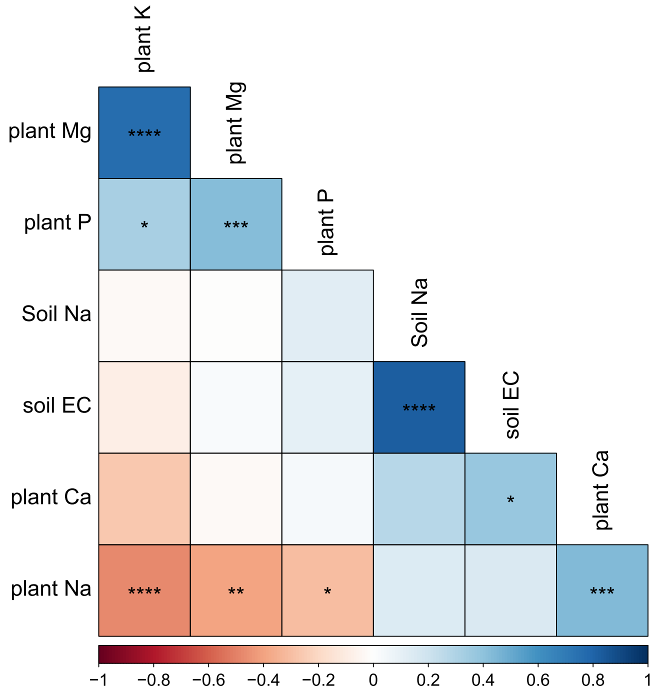

**Fig. 6.** Pearson correlation matrix among ions concentration in plant leaf tissue of six restoration species (*Panicum amarum*; *Tripsacum dactyloides*; *Spartina pectinata*; *Spartina patens*; *Panicum virgatum*; and *Paspalum floridanum*). Soil Na concentration and electrical conductivity (EC). Red colors indicate a negative correlation, and blue colors indicate a positive correlation. Significant correlations are indicated as follows: *= $p < 0.05$, ** = $p < 0.01$, ***= $p < 0.005$, **** = $p < 0.001$.

increased Na in the soil may reduce K uptake capacity (Shabala and Cuin, 2008). However, in salt-tolerant plants, Na can replace K in osmotic functions such as cell expansion and osmotic regulation, enabling these species to maintain cellular homeostasis under saline conditions (Assaha et al., 2017; Wakeel et al., 2011; Yamada et al., 2016). This substitution is particularly advantageous for salt-tolerant plants, as it allows them to maintain cellular turgor and water balance in saline conditions, ensuring growth and survival despite reduced K availability (Wakeel et al., 2011). A reduced dependency on $K^+$ in favor of $Na^+$ likely enables resilience in saline environments and explains why *S. patens* and *S. pectinata* maintain elevated Na levels in their tissues while accumulating biomass (Fig. 4).

### 4.3. *Tripsacum dactyloides* is efficient at taking up phosphorus

Our study showed that *T. dactyloides* can accumulate large quantities of biomass and biomass P in its tissues. Excessive applications of P from poultry litter or commercial fertilizers have led to elevated soil P levels that can persist for decades in the mid-Atlantic region, and especially on the Lower Eastern Shore of Maryland (Kleinman et al., 2015; Lucas et al., 2023). This legacy P in soils poses ongoing environmental challenges, because if released, it can contribute to nutrient runoff and eutrophication in nearby water bodies (Carpenter, 2008; Lucas et al., 2023). In these coastal areas, SWI may exacerbate P loss by essentially scraping soils across the fields and into ditches (Tully et al., 2019a, 2019b; Weissman and Tully, 2020) and as high-P soils are inundated with salty waters due to exchange of phosphate ($PO_4{}^{3-}$) for sulfate ($SO_4{}^{2-}$) on iron oxides (Hartzell and Jordan, 2012; Tully et al., 2019a, 2019b). Nutrient runoff in these areas is a significant environmental concern as it promotes algal blooms, depleting oxygen levels and harming aquatic life (Lan et al., 2024).

Our data suggest that planting *T. dactyloides* on coastal agricultural fields (especially field edges) could be a strategic approach to remove soil or at least bind up P in biomass, ultimately decreasing the amount available to runoff into Chesapeake Bay. Additionally, planting *T. dactyloides* in these areas serves as a natural filter, absorbing nutrients and stabilizing soil with its deep root system, which enhances water infiltration and reduces erosion (Table 2; Clark et al., 1998). Its extensive root system also contributes to C storage, provides drought

**Table 2**
Biomass and Sodium (Na) accumulation over time in native warm grass species and their potential applications in Conservation Practice (CPS).

| Species | Δ Biomass (g $m^{-2}$) | Δ Na accumulation (kg $ha^{-1}$) | Conservation practice / Potential uses | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 327 – Conservation Cover | 386 - Field borders | 390 - Riparian Herbaceous Cover | 420 - Wildlife habitat | 422 - Hedgerow/ wind barrier | 512 - Pasture and Hay | 512 - Biomass | 580 - Stream/ Shore stabilization |
| *Panicum amarum* | ↑ 79.90 | ↑ 0.27 | ★ | ★ | ★★ | ★ | ★★ | | ★ | ★★ |
| *Panicum virgatum* | ↑ 30.58 | ↑ 0.70 | ★ | ★ | ★★ | ★ | ★ | | | ★★ |
| *Paspalum floridanum* | ↓ −11.40 | 0 | ★★ | ★ | ★★ | ★★ | | ★★ | ★ | ★ |
| *Spartina patens* | ↑ 119.93 | ↑ 2.97 | | | ★ | ★★ | | | | ★★ |
| *Spartina pectinata* | ↑ 93.01 | ↑ 2.07 | | | ★★ | ★ | | | ★ | ★★ |
| *Tripsacum dactyloides* | ↑ 184.18 | ↑ 0.09 | ★★ | ★★ | ★★ | ★★ | | ★★ | | ★★ |
| ★ Acceptable | ★ Optimal | | | | | | | | | |

The values presented in the table represent the average data from both study farms (Oriole and Venton Farm). Arrows indicate trends in biomass and Na accumulation over time: ↑ for an increase and ↓ for a decrease
Modified from Belt and Miller (2021).

tolerance, and offers resilience against flooding, making it well-suited for frequently inundated soils (Henson, 2012; Blanco-Canqui, 2016). Furthermore, *T. dactyloides* has the potential to provide high-quality forage throughout the summer grazing season and can serve as a perennial substitute for corn silage (Keyser et al., 2020; Roberts and Kallenbach, 1999).

### 4.4. Incorporating warm-season grasses into conservation practices

The Mid-Atlantic region, particularly the Delmarva Peninsula, faces significant challenges due to SLR. Over 20,000 ha of farmland have been converted to marshland within just seven years (Mondal et al., 2023). Many farm fields in salt-affected areas are no longer viable for traditional crop cultivation, and practices are needed to support farmers who wish to adopt alternative strategies, such as planting restoration species better-suited to high-salt conditions. The native warm-season grasses selected for this study are ideal components of conservation practices throughout the Mid-Atlantic region (Table 2).

The species in this study were selected because of their ability to provide significant ecosystem services of shoreline stabilization, riparian protection, wildlife habitat creation, and carbon storage, making them valuable assets for addressing environmental challenges in vulnerable regions (Table 2; Belt and Miller, 2021). Among the species studied, *T. dactyloides* exhibited the highest biomass production and demonstrated efficiency in P uptake, suggesting that it can also improve water quality by reducing nutrient runoff. Furthermore, its high palatability and forage productivity make it a highly valuable option for agricultural systems (Keyser et al., 2020). *T. dactyloides* can be used in several federally-funded conservation practice standards (CPS) through the Natural Resources Conservation Service (NRCS), including conservation cover (CPS 327), field borders (CPS 386), riparian herbaceous buffer (CPS 390), and others (Table 2). Its eligibility for these programs can provide an alternative income to coastal farmers whose fields are no longer suitable for conventional crops. Our findings further demonstrate that it is a good candidate species for transitioning coastal agricultural fields due to its capacity for P uptake.

Unsurprisingly, of the candidate species studied, the *Spartina* species were the most effective Na-accumulators. *Spartina* species thrive in saline environments and can play a crucial role in shoreline stabilization and wildlife habitat creation, providing essential shelter and food for diverse wildlife (Table 2). Further, although the soil EC in the focal fields never reached saline levels (> 4 dS $m^{-1}$; Richards, 1954), both *Spartina* species performed well on abandoned agricultural fields (Fig. 1d), suggesting that they should be considered for coastal restoration projects in agricultural areas even prior to severe salinization. Currently, these species are not eligible for several on-field CPS, but our data suggest that policy should be modified to include these species for conservation practices such as riparian herbaceous cover (CPS 390), wetland restoration (CPS 657), and field borders (CPS 386) on salt-intruded farm fields. Of note, *Spartina* species do not establish well when planted from seed and require the planting of root stock, so there exists technical constraints to scaling *Spartina* plantings to the field-level. Local nurseries could grow salt-tolerant plants such as *Spartina* to support the installation of conservation projects on salt-affected farmland.

Our study demonstrated that *Panicum amarum* and *Panicum virgatum* were successfully established and accumulated biomass over time. Both species are widely utilized in various conservation practices, including conservation cover (CPS 327), field borders (CPS 386), riparian herbaceous cover (CPS 390), wildlife habitat (CPS 390), and shore stabilization (CPS 580). Additionally, Schulenburg et al. (2024) reported that *P. virgatum* efficiently uptakes P from soil and porewater, reducing P loss to water bodies and mitigating eutrophication risks. Furthermore, both species have potential as bioenergy crops (David and Ragauskas, 2010; Yue et al., 2017; Snell, 2020). Their tolerance to saline conditions suggests they could be ideal for cultivation on marginal agricultural lands affected by saltwater inundation (Snell, 2020).

Finally, our study showed that *P. floridanum*, established well initially but did not continue to accumulate biomass. This species often acts as a foundational species that facilitates the establishment of slower-growing native grasses, enhancing restoration outcomes during the early stages (pers. comm. Chris Miller*). Paspalum floridanum* is eligible for many conservation programs (Table 2) and contributes to shoreline stabilization efforts when included in mixtures with native grasses, enhancing the diversity of conservation plantings. Furthermore, it offers additional benefits by providing wildlife habitat and forage value to warm-season grass stands. Together, these native grasses provide a multifunctional approach to addressing the environmental challenges posed by SLR and SWI delivering essential ecosystem services that are critical for the resilience and sustainability of coastal landscape.

### 4.5. Study limitations and considerations

This study provides a valuable contribution to understanding how native warm-season grasses perform under SWI in coastal agricultural fields. Salinity levels at the study sites remained moderate throughout the experiment, which may be partially explained by the timing of soil sampling. As noted in the discussion, periodic storm-induced flooding and precipitation events may have temporarily diluted salts, potentially underestimating the long-term salinization trend. Future research conducted in sites with higher and more persistent salinity, as well as through longer-duration experiments, would provide a clearer understanding of species responses under more extreme salinity conditions. Although *T. dactyloides* demonstrated high P uptake, presenting soil P data was outside the scope of this work and will be presented as part of a future study. Longer-term studies examining changes in different forms of soil P would be useful to assess the species' potential for remediating legacy P in degraded soils. Nevertheless, this study establishes a strong foundation for the development of climate-adaptive conservation practices in salt-intruded landscapes and highlights promising candidate species for ecological restoration and farmland transition.

## 5. Conclusion

As sea levels continue to rise, SWI will expand across coastal agricultural regions, and ultimately lead to field abandonment. In this study, we observed a gradual increase in soil salinity over time at both farms, particularly in deeper soil layers. Our data suggest that salinization occurs from groundwater intrusion rather than surface water overtopping at these sites. We demonstrated that among the six species evaluated, *T. dactyloides* showed strong potential for ecological restoration, demonstrating high biomass production, efficient P uptake, and eligibility for federally-funded conservation programs. Similarly, *Spartina* species exhibited notable Na accumulation, reflecting its resilience to saline conditions and suitability for transitional restoration projects, such as shoreline stabilization and wildlife habitat creation. These traits can support the natural transition of degraded farm fields or field edges into wetlands. As sea levels keep rising, driving salty waters further into rural areas, data are needed to inform management strategies at the field-level. This study provides key information on species selection for transitioning fields or field edges out of agriculture in salt-affected areas. Studies such as this are important to inform conservation policy, technical support, and entrepreneurial efforts.

## CRediT authorship contribution statement

**Alison N. Schulenburg:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Patricia Ramalho de Barros:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Keryn Gedan:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Katherine L. Tully:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Christopher Miller:** Writing – review & editing, Methodology, Conceptualization.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109757.

## Data availability

All data used in the manuscript is available within the manuscript and supplement.

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