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Edges of opportunity: tidal creek edge processes drive pioneer marsh vegetation establishment

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Tidal marshes provide many critical ecosystem services, yet extensive losses have occurred due to human land use change. This has created a demand for tidal marsh restoration. A key challenge in tidal marsh restoration projects is providing the conditions for early establishment of pioneer algae and plants, which are often limited by unfavorable environmental conditions. Observations reveal that pioneer species preferentially establish along tidal creek edges, yet the mechanisms causing this colonization pattern remain poorly understood. Here, we investigated the drivers of pioneer vegetation colonization along tidal creeks edges in a brackish marsh in the Scheldt estuary (Belgium). First, we characterized the spatio-temporal colonization pattern using geospatial analyses and seedling survival (via a field transplantation experiment). Then, we tested potential mechanisms underlying this pattern through field assessments of seed deposition and retention (via seed traps and seed bank sampling), and sediment characteristics. Higher seed retention (around 3 to 4 times higher near tidal creek edge compared to interior tidal flat) and improved seedling survival were found near tidal creeks. Furthermore, increased sediment shear strength (around 4 to 10 times higher near tidal creek edge compared to interior tidal flat) was measured in the superficial sediment layer near tidal creeks. In contrast, other sediment properties measured at greater depth (up to 5 cm), such as dry bulk density, did not consistently explain these spatial patterns. Instead, we hypothesize that enhanced surface drainage and evaporation-driven consolidation near tidal creeks increase sediment erosion resistance of the thin sediment surface layer, which enhances seed retention and seedling survival. Overall, our results show that the superficial sediment bed of creek edges forms a hotspot for pioneer algal and plant establishment, demonstrating the importance of tidal creek networks to promote tidal marsh development in restoration projects.

KEYWORDS
pioneer vegetation establishment, sediment erosion-resistance, spatio-temporal colonization pattern, surface drainage, tidal creek edges, tidal marsh restoration, *Vaucheria* algae

1 Introduction

Tidal wetlands are valuable ecosystems that provide a range of essential ecosystem services, including carbon sequestration and shoreline protection (e.g. Barbier et al., 2011; Rogers et al., 2019; Temmerman et al., 2023). However, large tidal wetland areas have been lost historically due to conversion of human land use, and successful restoration of these valuable habitats requires informed and effective management strategies. A crucial aspect of tidal marsh restoration is understanding the process of pioneer vegetation colonization, which initiates the transition from a bare intertidal mudflat to a stable and resilient marsh (Brückner et al., 2019; van Belzen et al., 2017; Wang and Temmerman, 2013; Zhu et al., 2014).

Successful recruitment and establishment of vegetation on intertidal mudflats is a complex process influenced by multiple factors, including habitat suitability and the availability of propagules (Erfanzadeh et al., 2010a; Liu et al., 2024; van Regteren et al., 2019). Plant colonization typically occurs through two mechanisms: (1) seed or propagule dispersal, driven by vectors such as wind and tides, or via deposition of rhizome fragments, and (2) in case of perennial species, lateral clonal expansion, whereby new shoots emerge from laterally outgrowing root systems (Huiskes et al., 1995; Silinski et al., 2016; Steinigeweg et al., 2023; Zhu et al., 2022). The proximity of mature marshes is essential for colonization through seed dispersal, as they serve as sources for propagules (Mossman et al., 2012; Wolters et al., 2005; Zhu et al., 2014). However, the mere arrival of propagules is insufficient for successful establishment. The environmental conditions must also be favorable for a specific period to enable seed germination, seedling survival and growth into mature plants.

Such favorable periods, often referred to as "Windows of Opportunity", are characterized by minimal physical disturbance from tidal currents, waves and sediment bed erosion, which allow seed retention, germination, and seedling survival (Balke et al., 2011, 2014; Hu et al., 2015, 2021). During the early stages of tidal marsh development, however, intense sediment dynamics -such as rapid sediment accretion- can produce soft, fluid sediment beds that hinder root anchorage and reduce seed retention (Cao et al., 2021; Oosterlee et al., 2020). For seedlings to establish successfully, the sediment must eventually transition to a more consolidated and erosion-resistant state (Cao et al., 2018). This state can develop through abiotic processes such as consolidation, sediment drainage, and evaporation (Brooks et al., 2021; Colosimo et al., 2023; Grabowski et al., 2011) or through biotic processes like vegetation growth (Brooks et al., 2021; Chen et al., 2012). Consolidation strengthens the sediment as porewater is expelled either under the weight of accumulating sediment (Torfs et al., 1996; Zhou et al., 2016) or through drying (Dong et al., 2020), which is often enhanced by drainage and evaporation (Cao et al., 2022; Colosimo et al., 2023). Vegetation can further enhance erosion resistance by modifying sediment properties and through its belowground biomass. In particular, increased root biomass improves aggregate stability and cohesion, which leads to an increase in erosion resistance (Brooks et al., 2021; Feagin et al., 2015). Furthermore, the vegetation canopy can reduce hydrodynamic forces such as flow and waves, consequently reducing shear stress (e.g. Möller et al., 2014; Möller and Spencer, 2002; Schoutens et al., 2024).

Observations from several tidal marshes - including the Tollesbury marsh restoration site in southeastern England (Garbutt et al., 2006), Petaluma Marsh in California, USA (Sanderson et al., 2000), and tidal marsh restoration sites in Belgium such as Fassaatpolder, Zennegat, and Lillo Potpolder (Supplementary Figures 1, 2; Mertens et al., 2024) - reveal a distinct spatio-temporal vegetation colonization pattern. In these systems, pioneer species (e.g. *Vaucheria* algae and *Aster tripolium* plants in the Belgian sites) initially establish along creek edges before gradually spreading across the mudflat. This vegetation zone then facilitates colonization of other marsh species. Our understanding of the mechanisms driving this creek-edge focused colonization pattern is rather limited but will be instrumental to inform successful tidal marsh restoration projects.

Several hypotheses may explain why vegetation colonization often begins near tidal creek edges. One possibility is that seed availability is higher alongside creeks, due to enhanced seed supply by tidal flows, giving more opportunities for pioneers to attempt to successfully establish. Alternatively, tidal creeks may enhance seedling survival by locally enhancing sediment erosion resistance. For instance, we expect higher dry bulk density and lower sediment water content near tidal creeks due to increased subsurface drainage and sediment consolidation (Stoorvogel et al., 2024; Ursino et al., 2004; Xin et al., 2010), which are expected to reduce the sediment's vulnerability to erosion.

In this study, we first demonstrate the effects that tidal creek proximity has on the establishment of pioneer vegetation and algae using (1) geospatial analysis and (2) a field transplantation experiment in the managed realignment site of Lillo Potpolder in the brackish zone of the Scheldt estuary, Belgium. We then pursue a mechanistic explanation of this effect by evaluating the effects of a number of environmental parameters that depend on creek proximity. These include: (1) seed deposition and seed retention, measured using seed traps and by sampling the seed bank in the superficial sediment layer, (2) sediment shear strength measured by shear vane, and (3) changes in sediment characteristics, including grain size distribution, dry bulk density, and organic matter content.

2 Materials and methods

2.1 Study area

This study was conducted at Lillo Potpolder (51°18'14.3" N, 4° 17'50.5" E), a tidal marsh restoration site along the brackish portion of the Scheldt estuary in northeastern (NE) Belgium (see Figure 1a). The mean tidal range in this part of the estuary is approximately 5.2 meters (van den Hoven et al., 2022) and the salinity of the water varies between 5.5 and 8 PSU (Erfanzadeh et al., 2010b). Lillo Potpolder was a formerly embanked polder, i.e. low-lying land adjacent to the estuary that was protected from tidal flooding by historical dike construction. This 13-hectare restoration site was de-embanked in late 2012 as part of the ongoing Belgian Sigmaplan, which aims to enhance flood protection combined with restoring tidal ecosystems by managed realignment of dikes.

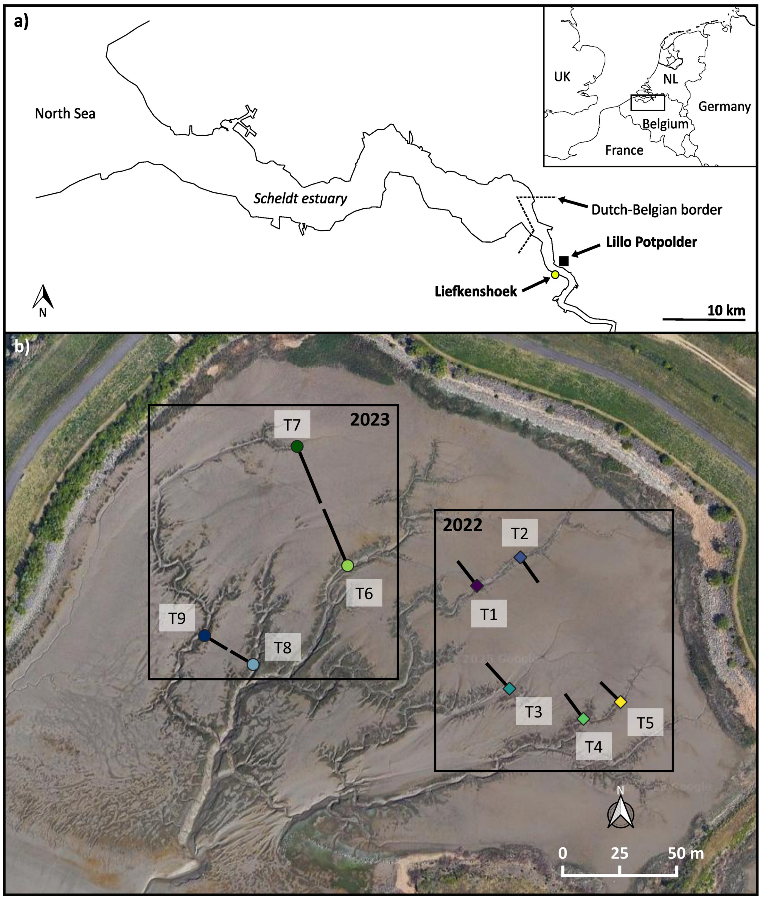

FIGURE 1
(a) Overview of the study site (Lillo Potpolder) and tidal gauge station (Liefkenshoek) located along the Scheldt estuary (NE Belgium, see inset map); **(b)** Overview of all transects that were used for the tests and field experiments. The rectangular box "2022" (referring to the year of fieldwork) includes five transects (T1 - T5) where we tested for spatial variation in seed deposition and retention along a gradient of increasing distance to the creek edge. Additionally, a field experiment testing the spatial variation in seedling survival along a creek edge distance gradient was carried out in three of the five transects (T1, T2 and T3). The four transects (T6 - T9) in the rectangular box "2023" were used to test the spatial variation in sediment drainage and erosion resistance in relation to creek edge distance. Map data obtained from © Google Earth, 28 April 2022.

The polder was de-embanked by constructing a new landward dike in 2011, along with the construction of a dike that separated the area in two compartments, after which the pre-existing dike was breached in late 2012 (Peeters et al., 2014). Furthermore, the area was leveled to an elevation of 4 to 4.5 m TAW (i.e. Belgian reference level), while the local mean low and high water levels are at about 0.5 and 5.2 m TAW (Vandenbruwaene et al., 2022). All field research in this study was conducted in the largest compartment of 5.2 ha (Mertens et al., 2024). Following de-embankment and the reintroduction of tidal flooding by brackish water, the study site's original terrestrial vegetation and biota were killed and tidal deposition of mud started, creating a bare intertidal mudflat that was subsequently colonized by estuarine biota.

2.2 Geospatial analysis of vegetation establishment during the early developmental stages of brackish tidal marshes

In this study, we performed a geospatial analysis to identify the spatio-temporal patterns of vegetation establishment by two marsh pioneer species: (1) the filamentous algae, *Vaucheria* sp., and (2) the halophyte, *Aster tripolium* L. (also known as *Tripolium pannonicum*), during the early developmental stages of brackish tidal marshes. *Vaucheria* are yellow-green algae that can form thick filamentous mats on intertidal mudflats which can trap and bind sediment particles, creating elevated sediment hummocks (Gallagher and Humm, 1981; van de Vijsel et al., 2020, 2021). By acting as a biostabilizer, these algae can facilitate pioneer plant establishment. *Aster tripolium* (is a biennial marsh plant species of the *Asteraceae* family that flowers from July to October. The plants primarily reproduce through seeds, which are dispersed by wind and water flow from October to December (Hill et al., 2004; Huiskes et al., 1995; van Regteren et al., 2019).

We analyzed digital terrain models (DTMs) and vegetation maps constructed for every year from 2016 to 2020 by the Research Institute for Nature and Forest (Mertens et al., 2024). The DTMs were derived from annual aerial lidar surveys (1 x 1 m resolution; vertical accuracy = 5 cm RMSE) which were commissioned by the Flemish Waterways plc and acquired by the Digital Flanders Agency during spring (March-May). Annual vegetation mapping was conducted by visually delineating homogeneous vegetation units on the aerial images, complemented by field verification of vegetation types. The delineated units were classified into formations based on physiognomy and structural complexity. Per unit, the abundance of species with at least 10% vertical cover was recorded in the field using standardized cover classes (Van Ryckegem et al., 2020). The polygons were rasterized and the resulting raster maps (1 x 1 m resolution) for *Vaucheria* and *Aster* were resampled to the same spatial resolution as the DTMs to allow analysis (see below).

The inundation frequency was calculated from water level time series of the Liefkenshoek tidal gauge station (https://www.waterinfo.be; measured every low and high tide) and the Lidar-derived DTMs (every year from 2016 to 2020) of the intertidal study area. These were used to map the spatial variations in the frequency of tidal inundations in the study area over the 1 x 1 m resolution grid. Following Fivash et al. (2023), the inundation frequency (i.e. the proportion of high tides that flood a specific intertidal elevation) was calculated and mapped by dividing the number of high tides that reached elevations above the local sediment surface elevation by the total number of tidal cycles within the measured period.

To determine how the proximity of tidal creeks correlates with the probability of vegetation presence, we computed the distance of each grid cell to the nearest tidal creek. Tidal creek delineation based on local relative differences in elevation resulted in inaccurate delineation of creek edges. Tidal creeks were therefore first visually delineated using a polyline shapefile. The Euclidean distance (m) from each grid cell to the nearest point on this polyline was then computed as the distance from that cell to the nearest tidal creek.

2.3 Effect of inundation frequency and proximity to creek edges on vegetation presence

Next, we conducted a geospatial analysis to assess the combined effect of tidal inundation frequency and proximity to creeks on the presence of marsh pioneers, differentiating between *Vaucheria* algae and *Aster* seedlings using the vegetation map. Both explanatory variables (inundation frequency and distance to creek edge) were binned into categories as follows. Vegetation presence was binned across tidal inundation and creek distance categories, creating a 2D array where each bin represented a specific combination of these explanatory variables. The likelihood of vegetation presence within each bin was then determined as the proportion of vegetated cells relative to the total cells within each bin.

We found that tidal creek influence on pioneer establishment diminishes significantly beyond 7 m (see Supplementary Material - Section S1 for detailed explanation). Therefore, further analysis focused on distances within that range.

2.4 Effect of creek edge proximity on seedling survival probability

A field experiment was conducted in June 2022 to investigate the survival probability of the pioneer plant species *Aster tripolium* at varying distances from a creek edge. *Aster* seedlings were transplanted into 1 x 1 m plots arranged along three transects at three distances from the creek edge (see Figure 1b, T1 - T3 in box 2022): 0 m, i.e. directly adjacent to the creek edge (n = 6 plots), 5 m (n = 3 plots), and 10 m (n = 3 plots). A greater number of plots were selected at the creek edge because this was the only location where both areas with and without *Vaucheria* algae were present. Therefore, we set up three plots with and three plots without *Vaucheria* directly adjacent to the creek edge. The seedlings were germinated in the lab from seeds collected from plants in late 2021 in the Lillo Potpolder. Once the *Aster* seedlings reached an average height of 7.5 cm (approximately two months old), 15 individuals were transplanted into each field plot on June 8 and 10, 2022. Seedling survival was monitored throughout the growing season, with observations conducted weekly until the end of July, biweekly until the end of October, and approximately monthly until the end of November 2022.

A binomial regression was fitted to determine the effect of distance from the creek edge on the survival probability of *Aster* seedlings using a Chi-squared test. This was followed by pairwise comparisons with Bonferroni correction.

2.5 Effect of creek edge proximity on seed deposition and retention

Spatial variation in seed deposition relative to creek edge distance was assessed using AstroTurf® seed traps (45 x 45 cm), a synthetic mat consisting of a dense network of 18 mm high grass tufts (Wolters et al., 2004). The mats were positioned along five transects at three distances from the creek edge (see Figure 1b, T1 - T5 in box 2022): 0 m, 5 m, and 10 m. The traps were securely anchored at each corner with steel pegs and deployed during the seed rain period (October 2022 - January 2023). To prevent sediment accumulation and seed loss due to tidal currents, the traps were replaced with fresh ones every three weeks, and the collected traps were stored in plastic bags at 4 °C. After collection, the mats were rinsed upright on a 1 mm mesh sieve to retrieve the seeds. The seeds were then dried at 40 °C for temporary storage before species identification and counting.

The spatial variation in seed retention (i.e. the actual seed bank in the sediment surface layer) was quantified at the same locations by scraping the upper 1 cm of the sediment surface over a 40 x 40 cm area at the end of the seed rain period (i.e. in January 2023). The sediment samples were stored in plastic bags and kept in a cooling cell until further processing.

One month after all seeds were collected (i.e. February 2023), a germination experiment was conducted in a greenhouse under controlled conditions, including adequate light and a temperature of approximately 16 °C. After three weeks, the number of germinated *Aster tripolium* seedlings was recorded.

A negative binomial model was fitted to assess the effect of proximity to creek edge on the number of germinated seeds resulting from the seed deposition and seed retention samples using a Chi-squared test. Afterwards, pairwise comparisons were made.

2.6 Effect of creek edge proximity on sediment erosion resistance

Further we quantified environmental conditions that may vary with distance from creek edges and that may affect the seed deposition, retention and seedling survival and growth. In November 2023, sediment surface erosion resistance was tested using a pocket shear vane device (Eijkelkamp, the Netherlands) along four transects with increasing distance from creeks (see Figure 1b, T6 - T9 in box 2023). Shear strength values were recorded by pressing the device into the superficial sediment layer up to a depth of maximum 1 cm and rotating it clockwise until sediment movement was observed. New transects with bare mud were selected for this test, as the previous transects were nearly entirely covered by vegetation by November 2023, making them unsuitable for measurements. For each transect, multiple measurements ($n \geq 3$) were taken at regular distance intervals and recorded using an RTK GPS (Leica Zeno GG04 plus).

To account for the variability in sample size, a generalized linear model with a gamma distribution was used to assess the effect of distance from the creek edge on sediment shear strength. The significance of the model was assessed using a Chi-squared test. Furthermore, the relationship between sediment shear strength and distance from the creek edge was characterized by using an exponential decay model with nonlinear least-squares regression.

2.7 Effect of creek edge proximity on sediment properties and nutrient content

Sediment samples up to a depth of 5 cm were collected using a Kopecky ring (∅ = 53 mm, height = 50 mm) in June 2022 to investigate the spatial variation in sediment properties in the field locations where the seed deposition and retention was assessed (Figure 1b, T1 - T5 in box 2022) and in May 2024 along the transects where the sediment erosion resistance was measured (Figure 1b, T6 - T9 in box 2023). In both cases, the transects consisted of a vegetated creek edge and a bare interior tidal flat (≥ 5 m). Three replicates were taken per location (0 m, 5 m, and 10 m from the creek edge for T1 - T5; 0 m, 1 m, 2 m, 4 m, 6 m, and 10 m from the creek edge for T6 - T9). Before grain size analysis, the sediment samples were pre-treated with H_2O_2 and HCl to remove organic matter and disperse aggregates. The treated sediment was analyzed for its grain size distribution using a Mastersizer 2000 (Malvern) and classified according to the standard grain-size distribution categories: clay:< 2 µm, silt: 2-63 µm, sand: 63-2000 µm. Dry bulk density and sediment water content were calculated by weighing the fresh wet sediment mass and dry sediment mass after oven-drying the samples at 70 °C for 72 hours (until complete dryness was achieved). Finally, organic matter content was estimated by performing the loss on ignition (LOI) method (Heiri et al., 2001), which involves the combustion of sediment at 550 °C for four hours in a muffle furnace. The total nitrogen and phosphorus content of sediment was analyzed along the same five transects used for sediment property measurements (Figure 1b, T1 - T5 in box 2022). The analysis was conducted in November 2023 using the previously collected sediment samples. These samples were first dried in an oven at 70 °C, then subjected to sulfuric acid (H_2SO_4) digestion for nutrient determination.

A linear mixed-effects model using restricted maximum likelihood estimation, with transect as a random effect was used to assess the effect of creek edge proximity (0 m, 5 m, and 10m) on the measured sediment properties in transects 1 to 5. These include dry bulk density, median grain size, the fraction below 63 µm (i.e. mud content) and organic matter content. A similar approach was used for the measured sediment water content and dry bulk density in transects 6 to 9.

A generalized linear model with gamma distribution was used to assess the effect of distance from the creek edge (0 m, 5 m, and 10 m) on total phosphorus and nitrogen content in transects 1 to 5. The significance of the model was assessed using a Chi-squared test.

2.8 Statistical analysis

Before every analysis, we conducted Shapiro-Wilk tests to check for normality of the residuals and Levene's tests to check the homogeneity of variances. All analyses were performed in R version 4.2.2 (R Core Team, 2022), applying a significance level of $\alpha = 0.05$.

3 Results

3.1 Algae and pioneer plants prefer to establish along creek edges

Our geospatial analysis showed that vegetation establishment is strongly influenced by tidal inundation frequency, and that this relationship is affected by proximity to tidal creeks (see spatial context of the study site in Supplementary Figure 3). Specifically, pioneer species are more likely to establish under higher inundation frequencies when they are closer to the creek edge. This effect declines with distance from creeks and becomes negligible beyond 7 meters, corresponding to the unvegetated interior tidal flat (as seen in Supplementary Figure 4 and explained in S1).

We observed this pattern for both *Vaucheria* and *Aster* (Figure 2; Supplementary Figure 5), but with a key distinction: *Vaucheria* proved to be a more robust pioneer, establishing at higher inundation frequencies (i.e. lower elevations in the tidal frame) than *Aster* near the creek edge (see detailed analysis and statistics in S1). This suggests *Vaucheria* is less sensitive to inundation stress and more suited to early colonization under challenging conditions.

3.2 *Aster* seedlings have higher survival probabilities closest to the creek edge

The transplantation experiment showed that *Aster* seedlings have higher survival probabilities when located closer to the creek edge (Figure 3). A significant effect of distance on survival was found (likelihood-ratio $\chi^2(2) = 18.14$, $p < 0.001$). Pairwise comparisons indicated significant differences in survival between seedlings located closest to the creek edge (0 m) and those located at 5 m from the creek edge ($z = 3.68$, $p < 0.001$), as well as between 0 m and 10 m

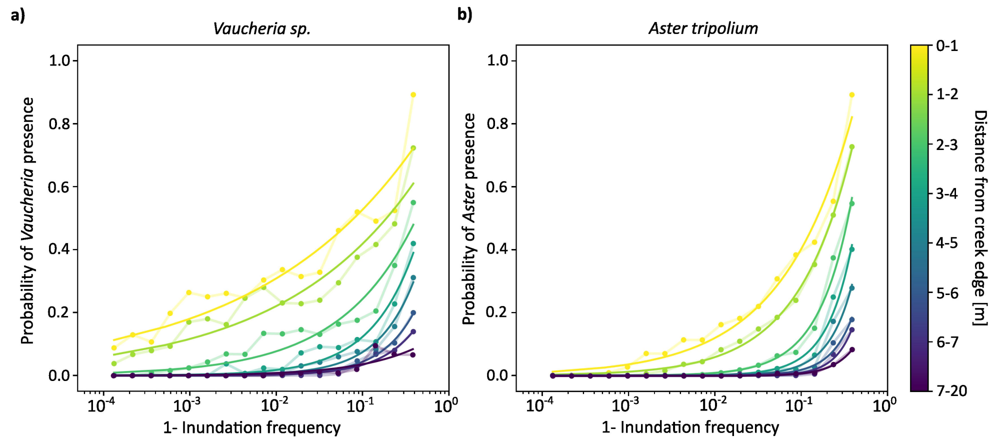

FIGURE 2
Relationship between the probability of **(a)** *Vaucheria* sp. algae and **(b)** *Aster tripolium* presence, inundation frequency, and distance from the creek edge. The probability of pioneer presence (y-axis) is shown in relation to "1 - Inundation frequency", the proportion of tidal cycles that the area is not submerged at high tide (x-axis) for a series of binned groups at various distances from the nearest creek edge (different colors). The points represent the observed proportion of vegetated cells at each inundation frequency and distance bin, while the lines represent the model fits.

(z = 3.23, p = 0.004). No significant difference was found between seedlings located 5 m and 10 m from the creek edge (z = -0.42, p = 0.91).

3.3 Creek edge proximity influences seed retention but not deposition

Seed deposition (i.e. measured by germinating seeds collected on AstroTurf® mats) did not show significant differences along the creek edge distance gradient (Figure 4). However, the results from the seed retention samples (i.e. seeds present in upper 1 cm of sediment surface) showed significant differences. Seed retention appears to be highest closest to the creek edge (0 m) and decreases with increasing distance (Figure 4).

Significant differences in seed retention were found across distances from the creek edge (likelihood-ratio χ^2 (2) = 12.598,

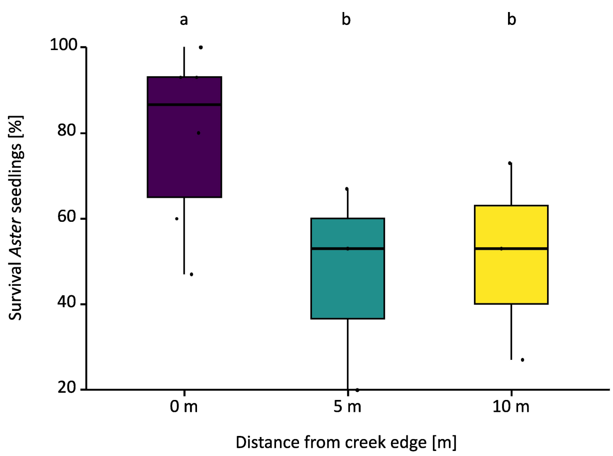

FIGURE 3
Aster seedling survival probability along varying distances from the creek edge (0 m, 5 m and 10 m), based on three transects (T1 - T3 in box 2022). Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

p = 0.002). Specifically, a significant difference was found between 0 m and 5 m (z = -3.62, p< 0.001), while the difference between 0 m and 10 m was not statistically significant (z = -1.9, p = 0.057). In contrast, no significant differences in seed deposition were detected along the creek edge distance gradient (likelihood-ratio χ^2 (2) = 3.841, p = 0.147).

3.4 Creek edge proximity enhances sediment erosion resistance

The sediment shear strength measurements revealed differences in sediment erosion resistance in relation to distance from the creek edge across all four transects. The highest shear strength values were found near the creek edge, gradually decreasing with distance (Figure 5). A significant negative relationship was observed between shear strength and distance from the creek edge (β = -0.096, t = −12.24, p< 0.001), confirming that shear strength decreases with increasing distance. Model comparison (likelihood $\chi^2(2)$ = 69.58, p< 0.001) showed that a quadratic model provided a significantly better fit than a linear model. The quadratic model suggests that shear strength initially decreases sharply with distance, but the rate of decline slows at greater distances ($\beta_1 = -8.94$, $\beta_2 = 8.24$, both p< 0.001).

Complementing this, an exponential decay model, fitted via nonlinear least-squares regression, captured the decreasing trend in shear strength with distance (R^2 = 0.81, $F_{3,205}$ = 289.4, p< 0.001). This model supports the interpretation that sediment erosion resistance declines asymptotically with increasing distance from the creek edge.

3.5 Creek edge proximity does not (consistently) affect sediment properties and nutrient content

The measured sediment properties did not show clear patterns or trends in relation to distance from the creek edge in transects 1 to 5 (Figure 1b, box 2022 & Figure 6). Linear mixed-effects models

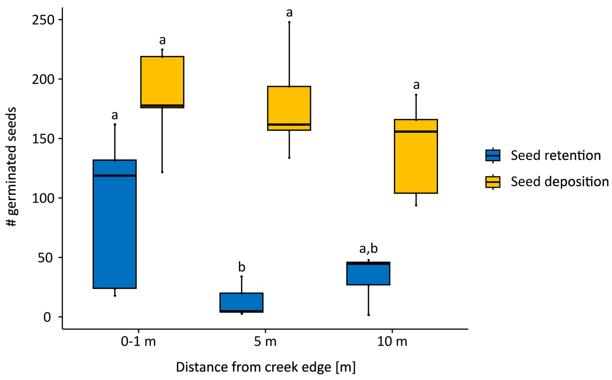

FIGURE 4
The number of germinated seeds found at varying distances from the creek edge based on five transects (T1 - T5 in box 2022). Seed deposition relates to the seeds collected during the seed rain period using seed traps, while seed retention refers to seeds collected at the end of the seed rain period by scraping the top 1 cm of the sediment surface. Box plots show the median, the lower and upper quartiles, and outliers outside the interquartile range. Labels with different letters indicate a significant difference.

with transect as a random effect confirmed that none of the sediment properties varied significantly with distance: organic matter content (β = −0.037 ± 0.059%, p = 0.53), median grain size (β = 0.076 ± 0.095 μm, p = 0.43), fraction below 63 μm (β = −0.002 ± 0.096%, p = 0.98), and dry bulk density (β = 0.000002 ± 0.000002 g/cm^3, p = 0.20). The distance effect differed among the transects.

The sediment water content (Supplementary Figure 6a) and dry bulk density (Supplementary Figure 6b) measured in transects 6 to 9 (Figure 1b, box 2023) showed only slight spatial variation. We found lower sediment water content and higher dry bulk density values near the creek edge. These trends were particularly pronounced for transects 8 and 9, while transect 6 showed a

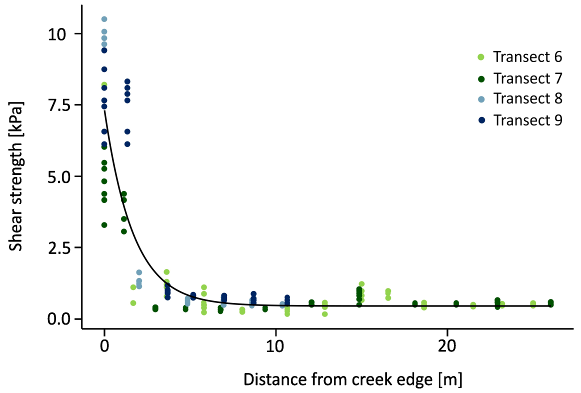

FIGURE 5
Relationship between sediment shear strength (kPa) and distance from the creek edge based on four transects (T6 - T9 in box 2023). The solid black line shows the fitted exponential decay function: $y(x) = a(e^{-bx}) + c$. The model captures a significant decline in shear strength with increasing distance from the creek edge.

less distinct pattern. Transect 7, however, appeared to follow a completely different trend.

Bulk density did not vary significantly with distance from the creek edge (β = −0.0048 ± 0.0040 g/cm^3, p = 0.236), nor did sediment water content (β = 0.29 ± 0.24%, p = 0.228). Although no consistent distance-related patterns were detected, substantial variability was observed among transects.

Furthermore, our results did not show spatial variation in total nitrogen and phosphorus content along varying distances from the creek edge (Supplementary Figure 7), which is also confirmed by the generalized linear model. We did not find significant differences between the varying distances for total phosphorus (likelihood-ratio χ^2 (2) = 0.380, p = 0.827) and nitrogen (likelihood-ratio χ^2 (2) = 1.736, p = 0.420).

4 Discussion

Pioneer vegetation often establishes preferentially along tidal creek edges, but the underlying mechanisms causing this spatial pattern to remain poorly understood. Our study aimed to identify the mechanisms that promote early vegetation establishment near creeks during the transition from mudflat to marsh. Our findings confirmed that proximity to tidal creeks significantly enhances the establishment success of both pioneer algae (*Vaucheria* sp.) and plants (*Aster tripolium*). Creek edges showed higher *Aster* seed retention and greater seedling survival compared to the interior tidal flat, which indicates that creek edges provide favorable conditions for early colonization. This was associated with higher sediment shear strength at the creek edges, implying that higher sediment erosion resistance along creek edges may promote enhanced seed retention and seedling survival. In contrast, these patterns were not consistently associated with spatial variations in other sediment properties, including grain size distribution, water content, dry bulk density and nutrient contents, indicating that these sediment properties had a negligible influence. Our results suggest that pioneer vegetation establishment is governed by multiple interacting constraints. Tidal creek edges appear to provide conditions that help overcome several of these constraints (i.e. inundation stress, erosion-related loss of seeds and seedlings, and seedling mortality). In contrast, these conditions are largely absent from the interior tidal flat. Below we discuss the potential mechanisms underlying the higher seed retention and seedling survival near tidal creek edges.

4.1 Enhanced drainage near creek edges facilitates pioneer colonization

While inundation frequency typically poses a strong constraint on seedling survival (Balke et al., 2014; Friess et al., 2012; Hu et al., 2021), our findings indicate that proximity to tidal creeks enable pioneer establishment outside commonly tolerable inundation thresholds (Figure 2; Supplementary Figures 4, 5). This suggests that creek proximity effects mitigate the physiological stress typically associated with frequent inundation. This effect is likely caused by the enhanced drainage of the sediment surface layer that reduces

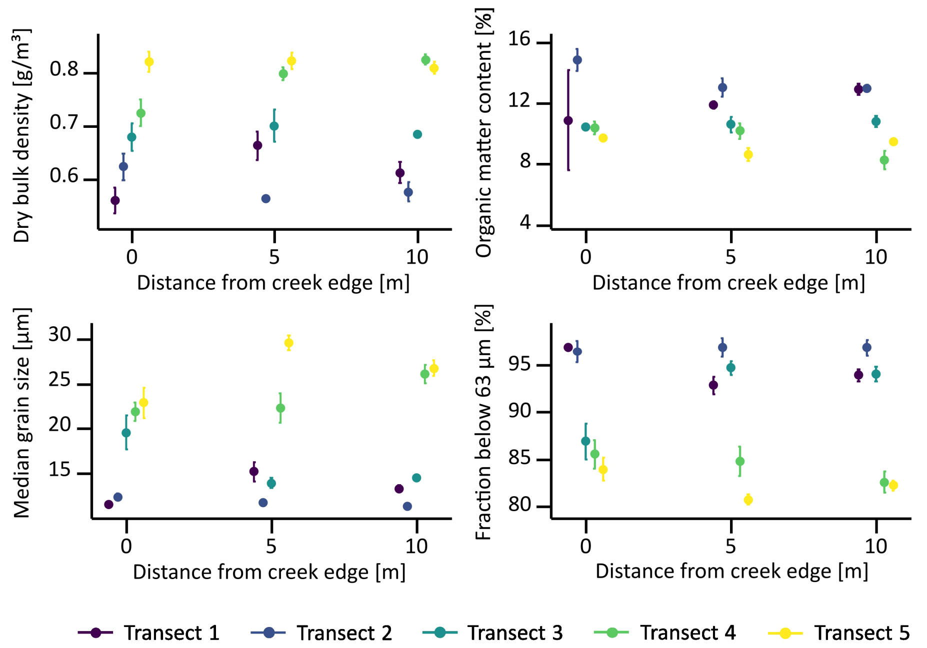

FIGURE 6
Sediment properties (i.e. dry bulk density, organic matter content, median grain size and fraction below 63 µm) at varying distances from the creek edge (0 m, 5 m and 10 m) across five transects within box 2022 (n = 3). Error bars represent standard errors of the mean. Points indicate mean values.

waterlogging and improves sediment aeration (Ursino et al., 2004; Van Putte et al., 2022; Xin et al., 2022).

Support for this drainage hypothesis comes from the 2023 transects (Figure 1b, box 2023), where we observed reduced sediment water content near creeks (Supplementary Figure 6), which is a pattern often associated with better-drained sediments (Cao et al., 2022; Stoorvogel et al., 2024). Furthermore, improved drainage conditions may enhance plant growth by reducing anoxic stress during early seedling development (Cao et al., 2012), which potentially explains the higher survival observed in the transplantation experiment (Figure 3). However, dry bulk density (Figure 6, Supplementary Figure 6), also often used as a proxy for drainage, did not show similar spatial patterns, which does not support the hypothesis.

4.2 Drivers of sediment erosion resistance near tidal creeks

Creek proximity was also strongly associated with increased sediment shear strength (Figure 5), a key factor in sediment erosion resistance. This increase in sediment erosion resistance was most pronounced within the first few meters from the creek edge coinciding with zones of algae and pioneer plant establishment (Figure 2; Supplementary Figures 4, 5). These patterns agree with previous studies showing that higher sediment shear strength facilitates early-stage marsh plant establishment by enhancing seedling anchorage and resistance to uprooting under the influence of tidal currents, waves and erosion (Cao et al., 2018, 2022).

Notably, the measured shear strength values reflect the superficial sediment layer (0–1 cm depth), where we observed a clear spatial variation. In contrast, sediment properties measured over a greater depth (0–5 cm), such as grain size distribution, organic matter content, nutrient contents and dry bulk density, did not show consistent spatial patterns (Figure 6). We did not find trends typically associated with increased erosion resistance (i.e. higher dry bulk density and lower sediment water content values), apart from lower sediment water content near creeks in the 2023 transects. This contrasts with previous studies showing that sediment consolidation, which could be higher near creeks due to higher sediment deposition rates (Hill et al., 2013; Temmerman et al., 2003, 2004), is often accompanied by increased dry bulk density and organic matter content (Grabowski et al., 2011; Stoorvogel et al., 2025). In our study, however, we found neither consistent sediment property trends nor distinct elevated levees indicative of enhanced sediment deposition along creek edges. The absence of these indicators therefore suggests that other processes, such as surface drainage and evaporation of the thin upper sediment layer, may be more important drivers of sediment shear strength in dynamic, early-successional intertidal environments. This interpretation aligns with other recent findings that demonstrated that lateral porewater drainage and surface evaporation during low tide, and amplified by wind, can rapidly increase sediment shear strength of cohesive sediment beds, on the timescale of just a few hours (Colosimo et al., 2023; Fivash et al., 2024; van Rees et al., 2024).

Evaporation-induced sediment strengthening is especially pronounced in the upper few millimeters to centimeters of the sediment bed, where drying quickly increases shear strength (van Rees et al., 2024). This thin erosion-resistant surface layer appears to be a primary contributor to sediment shear strength on cohesive intertidal flats (Fivash et al., 2024). This process depends on the capacity for residual surface water to drain away, and for the sediment surface to dry between tidal cycles -conditions that appear more favorable near tidal creeks (Fagherazzi et al., 2017). Drone imagery of our study site, taken in 2020 during ebb (see Supplementary Figure 2), revealed visibly drier sediment along creek edges compared to the waterlogged tidal flat interior, which indicates that surface drainage is improved near tidal creeks. By enhancing sediment surface drying, added to the effect of evaporation, tidal creek proximity may create erosion resistant sediment zones, thereby improving (1) seed retention and (2) reducing seedling loss due to uprooting, ultimately supporting pioneer vegetation establishment.

In addition to these abiotic mechanisms, pioneer species themselves contribute to sediment erosion resistance. Vegetation growth enhances shear strength both indirectly, by trapping cohesive sediment particles (Feagin et al., 2015), and directly, through the binding effects of root biomass, which increases aggregation and sediment cohesion (Brooks et al., 2021; Gyssels et al., 2005; Lo et al., 2017). Filamentous benthic algae, particularly *Vaucheria*, also play a critical role in creating erosion resistant sediment beds. *Vaucheria* mats trap sediment, build elevated hummocks, and increase surface roughness, all of which effectively enhance the probability of seed trapping and local sediment erosion resistance (van de Vijsel et al., 2021; Zhao et al., 2023). This could improve conditions for seed retention and seedling survival. As such, *Vaucheria* not only benefits from erosion resistant, well-drained conditions near creeks but may actively contribute to their formation, acting as an ecosystem engineering species during the critical early phases of tidal marsh development (in agreement with van de Vijsel et al., 2020, 2021). Together, these biostabilization processes likely increase sediment strength in zones near creek edges where algae and pioneer plants are most abundant, potentially creating a positive feedback that increases erosion resistance and promotes further colonization by other species.

4.3 Implications for restoration practices

This study confirms and explains the importance of creek edges as key zones for pioneer vegetation establishment. The improved seed retention and seedling survival is likely attributed to increased sediment erosion resistance by faster drainage and drying of the sediment surface near creek edges. These insights may help to improve restoration of tidal marshes. Specifically, the insights suggest that an appropriate platform elevation (potentially through raising the landscape) and an efficiently draining creek network, which could be created by excavating creeks, may accelerate vegetation establishment, which aligns with earlier work (Liu et al., 2020; Van Putte et al., 2022). This is particularly relevant in low-elevation or frequently inundated restoration sites where poorly drained fluid sediment would otherwise delay or prevent colonization (Oosterlee et al., 2020).

Data availability statement

All data are available at https://doi.org/10.5281/zenodo.16962480.

Author contributions

SH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. GF: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. LVN: Formal analysis, Investigation, Methodology, Writing – review & editing. KS: Conceptualization, Investigation, Methodology, Writing – review & editing. JvB: Conceptualization, Writing – review & editing. OG: Data curation, Writing – review & editing. WM: Data curation, Writing – review & editing. BV: Data curation, Writing – review & editing. MK: Supervision, Writing – review & editing. ST: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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