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Research article

Co-occurring intertidal ecosystem engineers with opposing growth strategies show opposite responses to environmental gradients during establishment

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Coastal vegetated ecosystems including mangroves, seagrasses, and salt marshes are often shaped by positive plant–environment feedbacks. Plants improve their own living conditions with increasing patch size and density by attenuating hydrodynamics and stabilizing sediments. As these habitat modifications are critical for survival and growth, the positive density-dependent nature of these feedbacks can lead to establishment thresholds for young plants in absence of mature conspecifics. Although feedback strength is known to depend on hydrodynamic exposure and plant traits (e.g. stiff versus flexible stems), it remains unclear how 1) opposing morphological plant traits affect establishment in contrasting environments, and 2) whether trait plasticity influences establishment success. Here, we investigate this by transplanting two tidal species with opposing growing strategies – *Spartina anglica* forms tussocks of stiff stems while *Zostera noltii* forms patches of stress-avoiding flexible shoots – from two different donor sites in eight experimental locations. Results show that the survival and growth of both species was most successful at field locations with diverging environmental characteristics, while overall survival was highest for *Z. noltii*. Mainly, *S. anglica* survival was highest at locations with high organic matter and silt content and higher elevation relative to the tidal amplitude. In contrast, *Z. noltii* survival was highest at locations with larger grainsize and lower relative elevations. Furthermore, despite initial differences in plant traits between the two donor sites of *Z. noltii*, we found no effects of donor origin. Contrastingly, we found a significant effect of donor origin on *S. anglica* growth, even though transplants from the two donor sites showed no initial trait differences. Collectively, these results suggest that the stress-tolerance strategy of *S. anglica* hampers establishment in exposed conditions, whereas the stress-avoiding *Z. noltii* appears to be more susceptible to stress from desiccation and silty sediments.

Key words: ecosystem engineers, establishment, intertidal wetlands, *Spartina anglica*, stress avoidance, stress tolerance, *Zostera noltii*

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Introduction

Coastal vegetated wetlands such as mangrove forests, salt marshes and seagrass meadows are important ecological and economic components of coastal zones worldwide supporting valuable ecosystem services (Martínez et al. 2007, Barbier et al. 2011). Main services that these wetlands provide include coastal protection (Barbier et al. 2011, Zhu et al. 2020) and carbon storage (Temmink et al. 2022), as well as providing habitat heterogeneity in which associated species can feed and find nursery habitats (Lefcheck et al. 2019). Through their dense aboveground structures and belowground root mats, the plants forming these ecosystems attenuate currents and waves, trap and accumulate suspended particles, and provide a structurally complex habitat that would not exist in their absence (Hemminga et al. 1998, Corenblit et al. 2011). Although the importance of their functions and services are increasing due to climate change and sea level rise, the cover of vegetated coastal wetlands is still decreasing due to habitat modification and other anthropogenic stressors and only partly offset by area gains (Gedan et al. 2009, Waycott et al. 2009, Murray et al. 2022).

Coastal vegetated wetlands are often shaped by ecosystem engineering plants that improve their own growing conditions by modifying their environment (Jones et al. 1994). By attenuating flow with their canopies and stabilizing sediment with their root mat, coastal plants reduce hydrodynamic stress, while trapping nutrient-rich organic matter from the water column (Hemminga et al. 1998, Bouma et al. 2005a, Peralta et al. 2008). However, this self-facilitation is driven by positive plant–environment feedback which is typically patch size- and density-dependent (Bouma et al. 2007, 2009a). For example, small and sparse vegetation patches often insufficiently attenuate flow to allow sediment deposition and stabilization. Particularly in stressful environments this mechanism can result in a situation where growth and survival of the vegetation is only possible when the plant is sufficiently large and dense, yielding thresholds that hamper plant establishment (Van Der Heide et al. 2007, Maxwell et al. 2016, Silinski et al. 2016). The existence of such thresholds pose questions about the required conditions for natural establishment along the mudflat–salt marsh border and presents challenges to restoration practitioners.

The strength of plant–environment feedback is also influenced by plant traits (Bouma et al. 2005b, 2013). For example, plants with stiff versus flexible shoots represent opposing strategies that can either result in stress avoidance (i.e. reduce physical force exerted on plant) or stress tolerance (i.e. resistance to breakage) (Bouma et al. 2005b, Puijalon et al. 2011). Typically, stress avoidance is associated with enhanced flexibility, allowing plants to bend or flex under physical stress and thus avoid drag (Schoelynck et al. 2013, Silinski et al. 2018). Stress tolerance on the other hand is associated with plants that have higher mechanical resistance to breaking, often with rigid structures (Coops and Van Der Velde 1996, Puijalon et al. 2011). Vegetation with stiff shoot biomass tends to be highly effective in flow attenuation, yet also causes additional flow divergence and scouring around patch edges (Peralta et al. 2008, Van Wesenbeeck et al. 2008, Schwarz et al. 2015, Duggan-Edwards et al. 2019). Consequently, compared to the stress avoidance strategy of flexible plants, stiff stress-tolerant species can induce additional feedback processes that have a negative effect on plant growth and increase the establishment threshold. The effects of vegetation on landscape formation is therefore species-specific and contrasting plant traits can lead to different landscape outcomes such as the formation of hummocks or gullies (Temmerman 2007, Van Hulzen et al. 2007, Bouma et al. 2013, Schwarz et al. 2018).

As positive feedbacks are important in more stressful environments, establishment thresholds for young plants typically occur in hydrodynamically exposed conditions with higher risk of dislodgement and erosion (Bouma et al. 2009b, 2016, Friess et al. 2012). This environmental variation may favor species with different strategies (i.e. avoidance versus tolerance) leading to vegetation zonation, with lower elevated areas dominated by flexible species and stiffer vegetation growing more landwards (Schoutens et al. 2020). Additionally, environmental variation may also drive trait plasticity within single species (Puijalon et al. 2008, Cabaço et al. 2009, Silinski et al. 2018). For instance, differences along hydrodynamic gradients can induce morphological changes that increase resistance to breakage, such as shorter shoots and higher stem flexibility (Silinski et al. 2018), wider leaf cross sections (Peralta et al. 2006) as well as lower shoot densities (Schanz and Asmus 2003, Van Hulzen et al. 2007) and increased root anchorage (Peralta et al. 2006, Cao et al. 2020) in hydrodynamically exposed conditions. In addition, recent studies on dune grasses highlight that shoot organisation (i.e. the distribution of shoots within a patch) of clonal plants affect feedback strength (sediment capture) and can be optimized to local sand availability (Reijers et al. 2020). Such plasticity in traits that drive engineering strength and stress avoidance or tolerance may allow establishing plants to adapt to locally prevailing environmental conditions. However, other traits can be fixed such as shoot organization in establishing cordgrasses, which we recently found to be highly similar across a range of environmental conditions (van de Ven et al. 2023). For this 'stiff' species a clustered shoot organization minimizes erosion around the patch edges and therefore even stiff engineers can balance stress avoidance with tolerance during establishment (van de Ven et al. 2023). Ultimately plant survival and growth depend on environmental conditions and corresponding trait expression. However, it is still unknown if species can adapt their strategy to overcome environment-specific establishment thresholds and if trait expression and plastic responses are affected by prevailing environmental conditions of donor populations. Furthermore, it is unclear how species with opposing morphological strategies are affected by establishment thresholds in contrasting environments.

Here, we investigate 1) how environmental conditions within a single delta affect establishment and growth of co-occurring tidal engineering species with opposing

morphological strategies and 2) if prevailing environmental conditions of donor populations affect plant establishment and growth response. In temperate tidal systems dwarf eelgrass *Zostera noltii* and common cordgrass *Spartina anglica* co-occur along the mudflat–salt marsh boundary. Dwarf eelgrass is a truly marine plant that can photosynthesize and take up nutrients during inundation and the upper boundary of its distribution is restricted by desiccation (Koch 2001). Contrastingly, cordgrasses are terrestrial plants that evolved to withstand regular flooding (Bouma et al. 2002). Whereas *S. anglica* and *Z. noltii* have partly overlapping intertidal habitats, flexible shoots of *Z. noltii* are associated with stress avoidance, and stiff shoots of *S. anglica* with stress tolerance (Bouma et al. 2005b, Peralta et al. 2008). The stiff shoots of *S. anglica* are more effective in attenuating flow, but also receive more drag compared to the flexible shoots of *Z. noltii*. We transplanted both *S. anglica*, with a stiff morphology, and *Z. noltii*, with a flexible morphology, from either end of their hydrodynamic exposure gradient (protected versus exposed) and with contrasting sediment conditions (sandy versus silty) across a range of tidal flats. We hypothesize that stiff engineers suffer stronger establishment thresholds and are more vulnerable to hydrodynamic stress during initial establishment than flexible engineers. We further hypothesize that plants from donor locations that have similar environmental conditions compared to the new planting locations will have higher establishment success. This study paves the way towards understanding how species expansion strategy and morphological plasticity affect density-dependent feedbacks, and how these relationships are modified under differing environmental contexts.

Material and methods

Field locations and species description

We conducted our research at eight different field locations distributed along the southern Dutch Delta. Locations naturally varied in sediment composition, porewater nutrients and hydrodynamic conditions (Eastern Scheldt, Western Scheldt, Fig. 1a–b, Supporting information). The Eastern Scheldt is a heavily modified tidal basin (Smaal and Nienhuis 1992, de Jong et al. 1994). Storm surge barriers close during

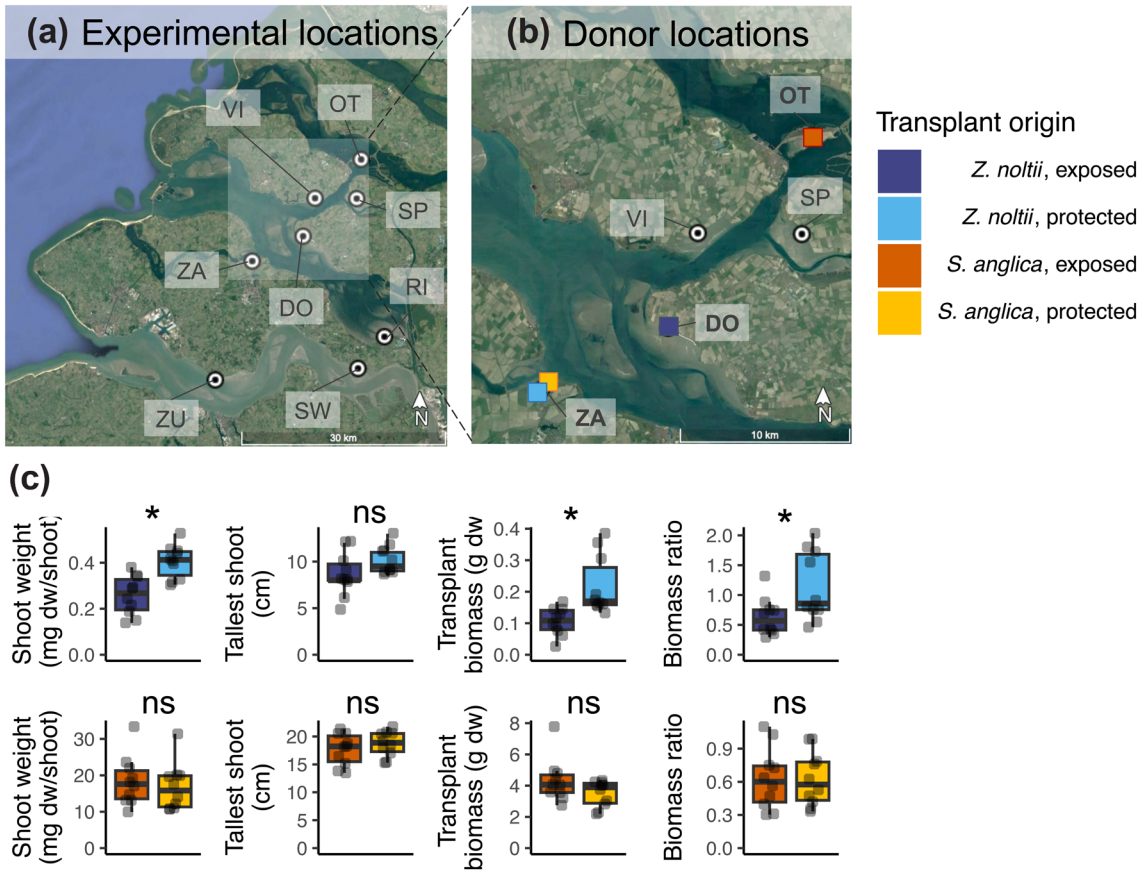

Figure 1. Field map and transplant traits. Maps show (a) the experimental locations and (b) a zoom panel specifying the donor sites (in bold) where transplants from protected or exposed donor origin were collected. (c) shows traits of transplants from exposed and sheltered donor origin at time of collection. Biomass ratio represents the above- to belowground ratio of transplant biomass. OT, Oude Tonge; VI, Viane; SP, Sint Philipsland; DO, Dortsman; ZA, Zandkreek; RI, Rattekaai; SW, Schor van Waarde; ZU, Zuidgors; *, p-value t-test < 0.05 (significant); ns, p-value t-test > 0.05 (not significant). Coordinates of the locations are shown in the Supporting information.

storm conditions but otherwise allow tidal exchange, while freshwater input is largely regulated with sluices. Under these influences the former estuary transitioned to a largely tide-flushed marine system with reduced sediment availability (Eelkema et al. 2012, Ysebaert et al. 2016). The Western Scheldt is a natural funnel shaped estuary with a longitudinal salinity gradient (Soetaert et al. 2006). Dredging activities in this important shipping channel have further amplified the tidal range (Winterwerp and Wang 2013). The common cordgrass *S. anglica* widely occurs on the intertidal areas of this estuary (de Jong et al. 1994, Van der Wal et al. 2008, Balke et al. 2016) and was naturally present at all locations. Contrastingly, cover of dwarf eelgrass *Z. noltii* is restricted and the species mainly occurs on specific tidal flats in the Eastern Scheldt (Suykerbuyk et al. 2012). Natural populations of *Z. noltii* were present at most Eastern Scheldt locations (except OT) but absent from all Western Scheldt locations (ZU, SW) (Fig. 1).

Experimental set-up

To investigate the establishment success of tidal species with opposing strategies under a range of environmental conditions, and to study the influence of environmental adaptation of donor material on establishment success, we transplanted *S. anglica* and *Z. noltii* from two different donor sites across eight experimental field locations (hereafter: location). At each location, the transplants were planted at a similar elevation and in parallel to the marsh edge to cover the pioneer zone. A total of 40 transplants were planted per site following a randomized block design with 10 replicates for each combination of species × donor origin. These treatments lead to a total of 320 plots (10 replicates × 2 species × 2 donor origins × 8 locations).

We harvested *S. anglica* and *Z. noltii* transplants from donor populations in the Eastern Scheldt basin: Zandkreek (ZA, 51°32′30.5″N, 03°53′47.5″E; protected donor site for both species), Dortsman (DO, 51°34′28.1″N, 04°00′13.6″E; exposed donor site for *Z. noltii*) and Oude Tonge (OT, 51°40′30.6″N, 04°07′36.9″E; exposed donor site for *S. anglica*) (Fig. 1a–b). While fetch at OT is limited in this sidearm of the Eastern Scheldt, the orientation of the marsh makes it exposed to dominant southwestern wind and waves (Callaghan et al. 2010). Differences in hydrodynamic exposure are typically reflected in the sediment composition, with coarser grain sizes at more exposed locations. Median grainsize and organic matter were 41 ± 1 µm and 9 ± 0% at ZA, versus 137 ± 1 µm and 1 ± 0% at DO and 226 ± 2 µm and 1 ± 0% at OT (Supporting information).

At each donor site transplants were collected from 10 isolated different source patches (donor patch 1–10) and from each donor patch eight transplants were collected to plant at the eight experimental locations, and a 9th to measure differences in initial plant traits. This way we ensured that the 10 replicates per treatment that were planted at the field locations corresponded to the donor patches, such that transplant 1 at location *x* and transplant 1 at location *y* both came from donor patch 1. Transplants for both species were collected from edges of large expanding patches. *S. anglica* transplants were collected by hand and gently rinsed in the field to verify clonal connections between shoots. Larger transplants were trimmed down to approximately eight shoots. *Zostera noltii* transplants of 10 cm depth and 9 cm diameter were collected with cores. Cores were taken at the edge of patches to increase the probability of active meristems in the transplant and thus increasing chance of new outgrowth success (Peralta et al. 2006). The *Z. noltii* transplants were planted with their original sediment core because they were too fragile to rinse without damaging the plants. At the time of collection, the *Z. noltii* transplants varied based on their origin, while *S. anglica* transplants had comparable traits (Fig. 1c). *Zostera noltii* transplants from the protected donor site (ZA) were overall larger with more biomass, heavier shoots, and higher relative shoot biomass allocation compared to transplants from the exposed donor site (DO), whereas length of the tallest shoot was comparable. All transplants were planted back in the field within 24 h after collection. The experiment ran for four months during the growing season, from the end of May until the end of September 2020.

Data collection

After four months we determined survival (yes/no), number of shoots (count), and transplant circumference (cm) of individual transplants in the field. The shoot number increase was calculated as percent new shoots based on the change in shoot number throughout the experiment, and relative to number of shoots at the start. In addition to the binary survival count, we calculated percent survival in each treatment (species × donor origin × location). Next, we ended the experiment by harvesting entire plants and separating above- and below-ground parts (shoots versus roots + rhizomes, respectively). Those were oven dried (60°C, 48 h) to determine their dry weight (g_{dw}) and calculate the above- to belowground biomass ratio (hereafter, biomass ratio). To assess the environmental variation across our eight field locations we used 10 different environmental variables regarding sediment structure (grainsize, percent silt, percent organic matter), relative hydrodynamic exposure (inundation frequency, elevation, maximum fetch and modified fetch), nutrient availability (porewater concentration of phosphate and nitrogen) and salinity. Specifically, we collected sediment and porewater from the center of our experimental blocks (n = 10 per location). Sediment samples were taken at 2–8 cm depth from which organic matter (%) was estimated as loss on ignition by burning dry homogenized sediment samples at 560° for 4 h. Median grainsize (µm) and percent silt (V% of particles < 0.63 µm) were determined on freeze-dried homogenized material with Polarized Intensity Differential Scattering (Beckman Coulter LS 13 320). We sampled porewater using 5 cm rhizons (Eijkelkamp) connected to vacuumized syringes and samples were frozen until analysis. Porewater concentrations (µmol l^{-1}) of phosphate (PO_4^-) and total nitrogen (NO_2^-, NO_3^{2-}, NH_4^+)

were colorimetrically measured (TrAAcs 800 autoanalyzer, Bran en Luebbe). Plot elevation (mNAP) was measured in the field using an RTK-GPS system (Topcon). Tidal amplitudes differ with geographical position and plot positions within the tidal landscape were determined with an inverse metric of inundation frequency: the so-called Tide skipping frequency. Inundation frequency indicates the relative occurrence of inundation events over a period of tidal cycles and is a better predictor for presence of vegetation than the often-used emergence time (Balke et al. 2016, Fivash et al. 2023). The inverse, i.e. the frequency of skipped tidal inundations (TideSkip), ranks locations on a slope from 0% tides skipped (lower mudflat) to 100% of tides skipped (high marsh). Finally, fetch-length is a major determinant of the occurrence of wind-waves and bed shear stress in intertidal basins (Fagherazzi and Wiberg 2009, Callaghan et al. 2010). We used satellite images to calculate the 'maximum fetch' (Fmax, km) and the 'modified effective fetch' (Fmod, i.e. the average of fetches in km at 45, 90 and 135 degrees from the coastline) as a metric of hydrodynamic exposure at the experimental locations (Howes et al. 1999).

Statistical analysis

We analysed the effect of our treatments on transplant survival and three growth traits: shoot number increase, circumference and the above- to belowground biomass ratio. We analysed treatment effects on our response variables *y* with two-way ANOVA of a linear fixed effect model (y ~ location × donor origin). To assess whether experimental block affected our results we compared the fixed effect model to a mixed effect model with block as random factor (y ~ location × donor origin + (1|block)). The best model was chosen based on the Akaike information criterion (AIC). Survival of individual transplants was fitted with a generalized linear model (glm () or glmer () in lme4, family = 'binomial', Supporting information) (Bates et al. 2015). Growth traits were analysed with a linear model and only data of living plants were included (lm () or lmer () in lmerTest, family = "gaussian", Supporting information (Kuznetsova et al. 2017). Shoot number increase contained negative values (i.e. when transplants at the end of the experiment had lost shoots relative to the start of the experiment) which created difficulty for transformations during the statistical analysis. Shoot number increase was therefore normalized between 0 and 1 using the formula $Z = X - \min(X) / (\max(X) - \min(X))$. We report original shoot number increase in the results text and in the figures. For both species we transformed the response y with log (y + c) and sqrt (y) for shoot number increase and circumference, respectively, to meet the normality assumption of the residuals. The biomass ratio was sqrt-transformed for *S. anglica*. Residuals in the biomass ratio model of *Z. noltii* did not meet normality assumptions after transformation, and were therefore analysed with a Kruskal–Wallis test. Overall, there was no effect of experimental block (random factor) or the interaction between location and donor origin. These were omitted in the next steps of our analysis.

We used principal component analysis (PCA) to reduce the dimensionality of environmental variables into a few main environmental axes that describe the between-site environmental variation. These axes were then used as explanatory variables for transplant survival, shoot number increase, and circumference. Here we analysed the two species separately and calculated survival as percentage in the different treatments (species × donor origin × location). Percent survival and plant traits (shoot number increase, circumference) were analysed with a linear additive model in which the three main PCA axes and donor origin were included as fixed factors (y ~ PC1 + PC2 + PC3 + plant origin). We used AIC-based stepwise backward model regression to find the best and most parsimonious model for our data. Residuals of were checked for normality with qqplots and Shapiro–Wilk tests and shoot number increase and circumference were log- and sqrt-transformed, respectively, for both species. The transformation, regressed best-fit models and model output are included in the results text and Table 1. For interpretation of PC-axes we considered variables with more than 10% contribution to the respective component as the most important. This 10% threshold is derived from the number of included variables (10 in our case), and the expected contribution per variable assuming a uniform contribution (i.e. 1/10 = 10%) (Abdi and Williams 2010).

All analyses were conducted in R ver. 4.2.3 (www.r-project.org) using the Rstudio interface (ver. 2023.6.0.421). Mixed effect models were analysed with the function *glmer()* and *lmer()* in the 'lme4' and 'lmerTest' R packages (Bates et al. 2015, Kuznetsova et al. 2017). PCA-axes were calculated with prcomp() (base R) and visualized using the 'factoextra' package (Kassambara and Mundt 2020). Other figures were made with the packages 'ggplot2' (Wickham 2016) and 'ggpubr' (Kassambara 2023).

Results

Transplant survival depends on field conditions, while donor selection can determine growth

After four months, *Z. noltii* had higher overall transplant survival than *S. anglica* varying from 61 ± 8% to 43 ± 7%, respectively (Fig. 2; χ^2 (1) = 9.8, $p < 0.01$, n = 160 per species). Within species, survival of *Z. noltii* was affected by location and plant origin (location: χ^2 (7) = 78.9, $p < 0.01$; plant: χ^2 (1) = 4.5, $p < 0.05$), while *S. anglica* survival was only affected by location (location: χ^2 (7) = 53.9, $p < 0.01$). We found no interaction of donor origin and location for either species. In general, location also influenced growth traits of both species (Fig. 3a–c), except patch circumference and biomass ratio of *S. anglica* (Fig. 3d, Supporting information). For example, irrespective of donor origin, the average number of shoots of *Z. noltii* transplants at the end of the experiment ranged between 7 ± 2 at SW and 65 ± 27 at VI. This corresponded to a shoot number increase of -67 ± 8% at SW and 252 ± 162 at VI. In contrast, donor origin only

Table 1. Statistical output of regression analysis and variable transformations. The start model was an additive model with PC1, PC2, PC3 and donor origin as fixed factors. The regressed and most parsimonious model for each response variable was obtained through Akaike information criterion (AIC)-based backward stepwise regression of the start model (y ~ PC1 + PC2 + PC3 + donor origin). Adj. R^2, Adjusted R^2; df, degrees of freedom; D, Donor origin.

Response variable (y)	Trans-formation	Regressed model	Adj. R^2	F	df	p model	Factor	p value
Spartina anglica								
Survival (%)	Na	y ~ **PC1 + PC3**	0.54	9.66	2/13	0.003	**PC1**	**0.04**
							PC3	**0.00**
Shoot number increase (scaled 0–1)	log (y + 0.01)	y ~ **PC1** + PC3 + **D**	0.24	8.06	3/65	0.000	**PC1**	**0.00**
							PC3	0.06
							D	**0.00**
Circumference (cm)	Sqrt (y)	y ~ **PC1** + PC3 + **D**	0.24	7.97	3/65	0.000	**PC1**	**0.01**
							PC3	0.10
							D	**0.00**
Zostera noltii								
Survival (%)	Na	y ~ **PC1** + PC2 + D	0.86	32.61	3/12	0.000	**PC1**	**0.00**
							PC2	0.05
							D	0.06
Shoot number increase (scaled 0–1)	log (y + 0.001)	y ~ **PC1 + PC3** + D	0.17	7.57	3/94	0.000	**PC1**	**0.03**
							PC3	**0.00**
							D	0.14
Circumference (cm)	sqrt (y)	y ~ **PC1 + PC2 + PC3**	0.15	6.57	3/94	0.000	**PC1**	**0.00**
							PC2	**0.01**
							PC3	**0.00**

affected growth traits of *S. anglica* (Fig. 3b–d). In general, *S. anglica* transplants from protected donor origin had higher shoot number increase, larger circumference and relatively more above-ground biomass (Fig. 3b–d, Supporting information), compared to plants from exposed donor origin. For example, at SW the shoot number increase of *S. anglica* transplants was 232 ± 101% compared to 8 ± 18% for transplants with protected donor origin versus exposed donor origin. Specifically, for *S. anglica* we found a significant effect of location and donor origin on the shoot number increase (lm: location $F(6) = 2.6$, $p < 0.05$), donor origin $F(1) = 13.4$, $p < 0.01$). The circumference and biomass ratio were only affected by donor origin (circumference: lmer: $\chi^2(1) = 14.9$, $p < 0.01$; biomass ratio: lm: $F(1) = 4.0$, $p < 0.05$). For *Z. noltii* traits, location had a significant effect on the shoot number increase (lm: $F(6) = 5.9$, $p < 0.01$), circumference (lmer: $\chi^2(6) = 43.8$, $p < 0.01$) and biomass ratio (Kruskal–Wallis: $\chi^2(6) = 26.7$, $p < 0.01$). Despite initial size differences (Fig. 1d) there was no effect of donor origin or the interaction of donor origin and location on *Z. noltii* traits (Fig. 3a, c, Supporting information).

Field locations vary in sediment composition, hydrodynamic exposure and nutrient availability

The first three principal components described 38.3, 27.2 and 18.3% of the environmental variation at the experimental locations, respectively. The variables with strongest contribution to PC1 (with > 10% contribution, Supporting information) were sediment parameters: percent silt and

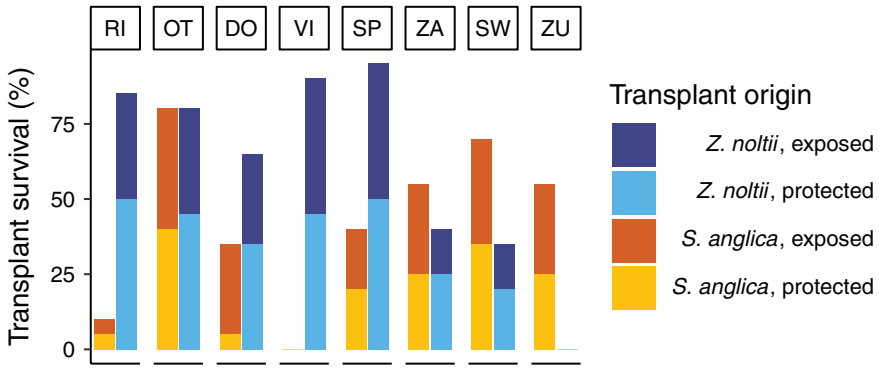

Figure 2. Species survival across experimental locations in the Dutch delta. Transplant survival was higher for *Z. noltii* compared to *S. anglica* (overall mean survival was 61 versus 43%, respectively). OT, Oude Tonge; VI, Viane; SP, Sint Philipsland; DO, Dortsman; ZA, Zandkreek; RI, Rattekaai; SW, Schor van Waarde; ZU, Zuidgors. Locations are ordered by the first axis of our principle component analysis with environmental variables (Fig. 4d, Supporting information).

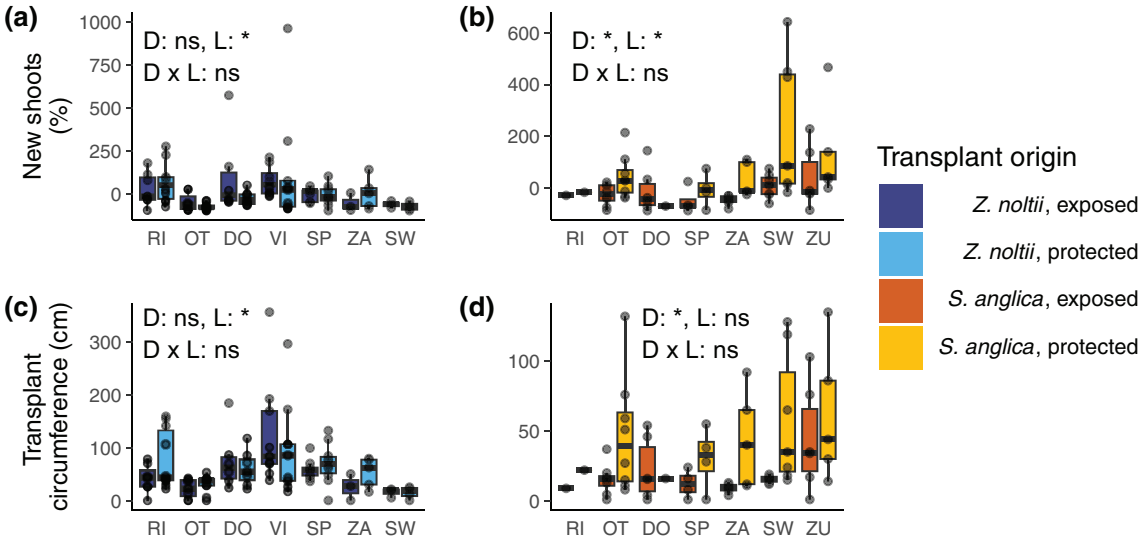

Figure 3. Transplant traits depend on location *Z. noltii* and origin of the donor material *S. anglica*. (a–b) show the shoot number increase for *Z. noltii* and *S. anglica*, respectively. In (a) one *Z. noltii* transplant at VI with exposed donor origin falls out of y-axis range (shoot number increase = 2833%). (c–d) show the circumference of *Z. noltii* and *S. anglica*, respectively. New shoots (%), shoot number increase; D, Donor origin; L, Location; *, p-value < 0.05; ns, p-value > 0.05 (not significant). Locations are ordered by the first axis of our principle component analysis (Fig. 4d, Supporting information).

percent organic matter, followed by maximum fetch (Fmax), inundation frequency (TideSkip) and median grainsize. The variables with strongest contribution to PC2 were exposure indicators: modified effective fetch (Fmod), inundation frequency (TideSkip), maximum fetch (Fmax), and elevation. Porewater nutrient concentration (phosphate and total nitrogen) and median grainsize were the main parameters driving PC3 (Supporting information).

Field conditions have opposite effects on *Z. noltii* and *S. anglica*

We found diverging effects of PC-axes and plant origin on species survival (Fig. 4a, Table 1). The survival of *S. anglica* transplants correlated positively with PC1 and PC3, while survival of *Z. noltii* correlated negatively with PC1 (Fig. 4a). For *S. anglica*, the regressed best-fit survival model included PC1 and PC3 and both were significant ($F(2/13) = 9.7$, $p < 0.01$, adj. $R^2 = 0.54$; PC1: $p < 0.05$, PC3: $p < 0.01$). For *Z. noltii*, the regressed best-fit model included PC1, PC2 and plant origin and PC1 was the only significant factor in this model ($F(3/12) = 32.6$, $p<0.01$, adj. $R^2 = 0.86$; PC1: $p < 0.01$, PC2: $p = 0.05$, plant origin: $p = 0.06$).

To analyse transplant traits (Fig. 4b–c) we used the same backward stepwise model selection procedure to survival. We found that donor origin had a significant effect on shoot number increase and circumference of *S. anglica*, while the effect of PC-axes differed per trait. Specifically, we found that the shoot number increase of *S. anglica* was best described by the model with PC1, PC3 and plant origin as fixed factors of which PC1 and plant origin were significant (model fit: $F(3/65) = 8.06$, $p <. 0.01$, adj. $R^2 = 0.24$; PC1: $p < 0.01$, plant origin: $p < 0.01$, PC3: $p = 0.06$). The circumference of *S. anglica* transplants was best described by the model with PC1, PC3 and plant origin as fixed factors (model fit: $F(3/65) = 7.97$, $p < 0.01$, adj. R^2 0.24). Here, plant origin and PC1 were the only significant factors (PC1: $p < 0.05$, plant origin $p < 0.01$, PC3: $p = 0.1$).

We found that PC-axes had low albeit significant explanatory value for *Z. noltii* traits, with a negative correlation between the PC-axes and transplant traits and no effects of donor origin. Specifically, the shoot number increase of *Z. noltii* was best explained by the regressed model with PC1, PC3 and plant origin as fixed factors (model fit: $F(3/94) = 7.57$, $p < 0.01$, adj. $R^2 = 0.17$) Here, only PC1 and PC3 were significant (PC1: $p < 0.05$, PC3: $p < 0.01$, plant origin: $p = 0.14$). Patch circumference of *Z. noltii* was best explained by a regressed model with PC1, PC2 and PC3 as fixed factors (model fit: $F(3/94) = 6.57$, $p < 0.01$, adj. $R^2 = 0.15$). Here, all PC-axes were significant despite the low overall explained variation (PC1: $p < 0.01$, PC2: $p < 0.01$, PC3: $p < 0.01$).

Discussion

Our results show that survival and growth of two co-occurring intertidal engineering species was most successful at field sites with opposite environmental characteristics. Mainly, *S. anglica* survival was highest at nutrient-poor but muddy sites that are still relatively exposed (> 50% survival at OT, ZA, SW, ZU), while *Z. noltii* survival was highest at nutrient-rich but sandy sites that are frequently inundated and relatively sheltered (> 50% survival at RI, OT, DO, VI, SP). This indicates that, as we expected, the plants showed opposite responses to environmental conditions, with the combined

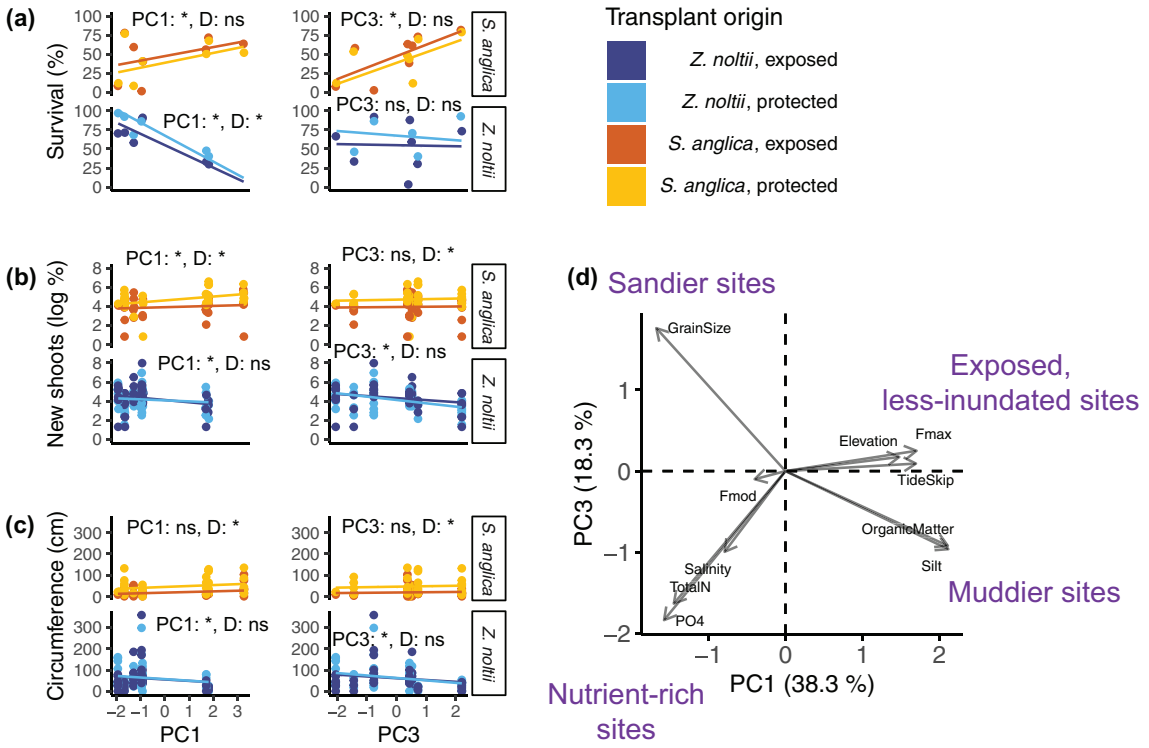

Figure 4. Transplant traits of *Z. noltii* and *S. anglica* show opposite response to environmental variation and depend on donor origin. (a–c) Correlation between transplant trait (y-axis) and the two most important PC-axes for plant survival and growth based on our analysis (x-axis, left panel: PC1, right panel: PC3). Multiple linear regression results are shown in Table 1. (d) PCA results of field locations and environmental variables along PC1 and PC3. For PCA results annotated with the experimental locations see the Supporting information. PC, Principal component; D, Donor origin; *, $p < 0.05$; ns, $p > 0.05$; Fmax, maximum fetch; Fmod, modified effective fetch; TideSkip, Skipped tidal inundations; TotalN, total nitrogen.

effects of sediment type, hydrodynamic exposure and nutrients explaining most variation in survival.

In addition, the overall survival of the flexible seagrass species *Z. noltii* was higher compared to the stiff salt-marsh building plant *S. anglica*. These differences occurred irrespective of donor origin and reflect opposite species response to transplantation at contrasting field locations. We found that transplant survival at the various locations ranged from 0–95% for *Z. noltii* and from 0–80% for *S. anglica*. Based on these results we conclude that both species had potential high survival rates following transplantation and that prevailing environmental conditions were the main driver of differences in survival across our field locations. Possibly our seagrass transplants with flexible shoot morphology, which favours stress avoidance, were less vulnerable to stress during establishment. Our results also show that despite initial differences in transplant traits between the two donor sites of *Z. noltii*, we found no effect of donor origin on neither survival nor growth. Contrastingly, we found an effect of donor origin on the growth of *S. anglica* transplants, with transplants from the protected site having relatively more shoots and higher expansion rates, even though transplant traits were initially similar. Collectively, these results suggest that the stress-tolerance strategy of *S. anglica* leads to stronger establishment thresholds especially in frequently inundated sandy sites, whereas the stress-avoiding *Z. noltii* demonstrated to be less susceptible to hydrodynamic exposure and more to desiccation stress and silty sediments.

Stiff versus flexible morphology can explain transplant survival differences

Although both species need to deal with establishment thresholds, environmental conditions affect them differently. Stiff plants like *S. anglica* attenuate more energy and generate stronger scouring effects, and suffer high risk of dislodgement especially in sandy environments (Van Hulzen et al. 2007) that are generally less cohesive (Defew et al. 2002). Flexible leaves of *Z. noltii* on the other hand avoid stress by bending, thereby avoiding drag (Peralta et al. 2008). In line with the hypothesis that stiff establishing plants are more vulnerable to hydrodynamic stress compared to flexible plants, our results show that *Z. noltii* survival is overall higher than *S. anglica*. This seems to contrast recent findings that establishing *S. anglica* patches can avoid or minimize stress from flow attenuation through a clustered shoot pattern (van de Ven et al. 2023). However, our small transplants (maximum eight shoots at start) still lacked such a clustered network to withstand adverse conditions and we expect this stress-avoidance expansion strategy to occur during later stages

of establishment when the plants have expanded beyond 40 shoots (i.e. minimum size of plants in aforementioned study). Additionally, by transplanting excavated clonal fragments of *S. anglica* we ensured that all shoots were clonally connected, but we disrupted the original spatial organization of the transplants and reduced soil anchorage by roots. In contrast, the *Z. noltii* plants were too fragile to be excavated and we therefore transplanted the plants in an intact core, maintaining its spatial organization and root structure, which could potentially affect transplant survival. Overall, we conclude that our stiff, stress tolerant species *S. anglica* was relatively more vulnerable to early establishment thresholds than the flexible *Z. noltii*.

Site characteristics determine transplantation success of both species

We found that transplant survival could be well explained by environmental conditions. Locations with contrasting environmental characteristics had opposite effects on survival of *S. anglica* and *Z. noltii*. Our PCA results showed that PC1 correlated positively with *S. anglica* and negatively with *Z. noltii* survival. As this axis is predominately shaped by percent silt, percent organic matter and also maximum fetch, inundation frequency and median grainsize, these findings suggest that *S. anglica* survival was generally higher at locations with lower inundation frequency, high organic matter and silt content, that are still relatively exposed. By contrast, *Z. noltii* survival was higher at locations with higher inundation frequency and lower organic matter and silt content. Survival of *S. anglica* further positively correlated with PC3, which was mostly driven by porewater nutrients (phosphate and total nitrogen) and median grainsize. The fine sediment conditions in some locations seemed to contrast the relative high hydrodynamic exposure as indicated by maximum fetch on PC1 (Fig. 2, e.g. locations ZU, SW). Yet, sediment supply and hydrodynamic exposure in marsh vegetation depend strongly on sediment availability on adjacent tidal flats (de Jong et al. 1994), its inundation frequency (Fivash et al. 2023) and tidal flat morphology (Marin-Diaz et al. 2023). This is a natural relationship observed in the Western Scheldt, where tidal flats may have relatively fine sediments even in exposed conditions (van der Wal and Herman 2007, Callaghan et al. 2010) that can be transported to adjacent marshes. Marshes with lower inundation frequency and adjacent tidal flats may therefore be fairly protected from hydrodynamic exposure (Supporting information). This relationship is disturbed in the Eastern Scheldt where fine sediment is generally deficit due to lack of supply (Eelkema et al. 2012). Using modified fetch, which is a weighted fetch-length in multiple offshore angles and multiple indicators, may be a good way to incorporate the non-linear and multidimensional aspect of environmental conditions. Our results therefore show that rather than focusing on one environmental variable (e.g. hydrodynamic exposure, sediment composition) it is the combination of all conditions that determines plant response.

Interestingly, environmental conditions only had a limited effect on growth of *S. anglica* and explained a small percentage of the variation in growth of *Z. noltii*. Shoot number increase and patch circumference of *Z. noltii* were negatively linked to PC1 and PC3, showing a slightly better growth at locations with higher porewater nutrient concentrations. These results correspond to the literature, as *Z. noltii* can respond to nutrient availability with rapid growth (Cabaço et al. 2013). However, despite being significant, PC1 and PC3 together only explained 16 and 10% of the variation in shoot number increase and transplant circumference of *Z. noltii*, respectively. Possibly, unknown factors such as local (sub-site) variation in sediment, or differences between transplant quality could influence transplant growth, explaining the unexplained variation in growth of *S. anglica* and *Z. noltii*.

Donor material only affects the growth of *S. anglica*

Trait differences between populations may result from adaptive responses to site-specific environmental conditions (Silinski et al. 2018). While we found initial differences in plant traits of *Z. noltii* between donor sites (Fig. 1), we observed no differences in survival nor growth between donor origins for this species (Fig. 3–4). In contrast, transplants from either donor sources of *S. anglica* showed initially no morphological differences in plant traits, but at the end of growing season the plants from the protected site grew relatively larger (Fig. 3). Despite some ambiguity regarding trait plasticity and seemingly small effect sizes after one season, donor origin may be important for the persistence of vegetation by influencing the growth of establishing plants. The absolute differences in final *S. anglica* transplant size were small, yet it is unknown how those differences would extrapolate to long term success. Differences in transplant size after one season can influence winter survival as plant size and morphology can increase transplantation success for both seagrass (Govers et al. 2015, van Katwijk et al. 2016, Suykerbuyk et al. 2018) and cordgrass (Schwarz et al. 2011, Silliman et al. 2015).

Implications

Our results show that the main ecosystem engineers in intertidal pioneer zone, *Z. noltii* and *S. anglica*, are affected differently, but predictably, by environmental conditions in their establishment phase. Indeed, whereas niches partly overlap, these species have different physiological limits and where they co-occur both exist at the upper and lower limit of their respective distributions in relation to tidal inundation (Hemminga et al. 1998, Koch 2001). Nevertheless, we found clear support for both species that other environmental characteristics such as sediment structure and nutrient concentrations were also important for successful establishment. It is well accepted that stiffness and flexibility represent opposing strategies to deal with hydrodynamic stress (Bouma et al. 2005b, Friess et al. 2012). The morphological differences between the two species and how those interact

with hydrodynamic exposure are likely drivers of the diverging response to site-specific establishment thresholds next to differences in inundation duration and their physiological tolerance to flooding and desiccation, respectively.

Contrasting vulnerability to hydrodynamic intertidal gradients may result in zonation of species with opposite strategies and ecosystem engineering capacities. For example, species with a high capacity to avoid hydrodynamic drag due to their simple, single stem geometry *Schoenoplectus tabernaemontani* were found to colonize exposed tidal areas, while stiffer plants, exhibiting more complex geometries with multiple leaves *Bolboschoenus maritimus* and with a high attenuation capacity, establish in their wake (Schoutens et al. 2020). Authors thereby highlight that, while highest attenuation capacity may be theoretically beneficial at exposed sites, establishment thresholds are too fierce for successful establishment of the relatively stiffer species, stressing the importance of tolerance–avoidance trade-offs. While differences in growth strategy may lead to zonation, *S. anglica* and *Z. noltii* typically co-occur on tidal flats, suggesting that conditions are such that opposite strategies can both be successful in this zone. Where they co-occur, inter- and intraspecific interactions may also influence the establishment of either species. For example, weak flow attenuation by mature *Z. noltii* patches may promote establishment success of both species (Carr et al. 2018). In contrast, the strong engineering capacity of mature *S. anglica* patches, which promotes sediment accretion, might facilitate the establishment of conspecifics, but will likely inhibit the establishment of *Z. noltii*. Indeed, our results also show that fine sediments and higher elevations relative to the tidal frame have a negative effect on establishing *Z. noltii* plants, a change that may be caused by accretion of fine sediments by expanding *S. anglica* tussocks (Van Hulzen et al. 2007).

Our finding that species with opposing morphological strategies are affected differently but predictably by environmental conditions may have implications for wetland restoration. First, by considering a range of natural field conditions our results may increase our understanding of potential suitable sites for establishment of either species. Despite numerous studies assessing environmental requirements of target species, it remains difficult to predict habitat suitability for successful establishment (Suykerbuyk et al. 2016). In addition, recent work showed that self-facilitative feedbacks are highly context dependent (van der Heide et al. 2021). Selection of a suitable pioneer species to establish on bare tidal flats is an important step in context-dependent restoration (Zhao et al. 2023), yet restoration often focuses on specific target species of the desired end stage, potentially skipping important steps in landscape development by ignoring interspecific interactions or facilitation cascades (Van De Koppel et al. 2015). However, it remains to be tested whether differences in establishment thresholds are linked to species morphology of other ecosystem engineers.

Second, our findings highlight that transplant size of the targeted species is an important factor to consider under exposed conditions for stiff vegetation. Specifically, we found that *S. anglica* transplants were vulnerable to dislodgement, most likely because 1) these transplants do not follow the clustered stress avoiding strategy of naturally establishing plants, while 2) their patch size was too small to mitigate hydrodynamic stress. Our small but flexible *Z. noltii* transplants, on the other hand, were less susceptive to dislodgement. However, these small transplants may have been more vulnerable to desiccation at higher elevations (such as ZA, SW and ZU; Fig. 2, 4) as their limited patch size is not able to trap water during low tide (Hemminga and Duarte 2000, Cabaço et al. 2009). Within the spatial scale of our experiment, differences in donor origin appeared more important for the survival and growth of *S. anglica*. Therefore, for transplant-based restoration with *S. anglica*, we recommend selecting transplants from more sheltered donor sites. If donor material is limiting here, mixing donor material from exposed and sheltered sites might be an alternative approach to enhance success.

Overall, our finding that establishment thresholds affect species differently adds to a growing body of work demonstrating that facilitation through organism–environment feedback is highly context dependent yet relevant for inclusion in restoration designs. Recent work has shown that targeted stress mitigating measures that mimic these facilitative interactions are effective to bridge establishment thresholds for coastal engineering species (Temmink et al. 2021). For example, physical structures mimicking plant biomass around transplants benefitted eelgrass *Zostera marina* through sediment stabilization, whereas cordgrass benefitted from above ground physical structures reducing stem movement (Temmink et al. 2020). Hence, we conclude that understanding species' strategies and plasticity to changes in environmental conditions can help identify bottlenecks that result from plant–environment feedbacks and may be driving site-specific establishment thresholds. This knowledge can be applied to design appropriate restoration strategies to either mimic, strengthen or avoid these plant–environment feedbacks.

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Heide: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Tjeerd J. Bouma:** Conceptualization (supporting); Methodology (supporting); Writing – review and editing (equal). **Lennart van Ijzerloo:** Conceptualization (supporting); Methodology (equal); Writing – review and editing (supporting). **Djeli D. Lindhout:** Methodology (supporting); Writing – review and editing (equal). **Valérie C. Reijers:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from: https://doi.org/10.25850/nioz/7b.b.9g (van de Ven et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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