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RESEARCH ARTICLE

Establishing cordgrass plants cluster their shoots to avoid ecosystem engineering

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Abstract

1. Vegetated coastal ecosystems such as salt marshes, dunes and seagrass meadows occur at the land–sea interface—a dynamic environment typified by harsh growing conditions. These ecosystems are known as biogeomorphic landscapes because their functioning depends on biophysical interactions by which organisms engineer landforms to their own benefit. The strength of such biogeomorphic feedbacks depends on plant traits, such as stem flexibility and shoot density.
2. Recent work demonstrated that dune grasses with similar morphological traits can build contrasting landscapes due to differences in their spatial shoot organization. However, in contrast to dune grasses that trap and stabilize sand particles in aeolian landscapes, flow attenuation in aquatic environments can generate scouring around plant stems and cause uprooting, leading to establishment thresholds for young plants.
3. Yet, it remains unknown how findings from aeolian landscapes translate to aquatic systems and how young clonally expanding plants in hydrodynamically exposed conditions overcome these establishment thresholds by optimizing shoot placement.
4. Here, we measured shoot patterns of 90 establishing cordgrass patches *Spartina anglica* at 18 European field sites that cover a broad range of hydrodynamic conditions. Next, we carried out a field experiment to investigate how observed spatial shoot patterns affect plant–sediment feedbacks.
5. Surprisingly, field survey analyses reveal highly consistent clustered shoot patterns, regardless of environmental conditions. Experimental results demonstrate that this clustered pattern minimizes scouring compared to densely clumped organizations typically observed in established patches.
6. *Synthesis*. In contrast to earlier findings highlighting that establishing dune grasses optimize their landscape engineering capacity via a flexible shoot placement strategy, we find that cordgrass instead follows a fixed strategy that minimizes engineering effects in its early life stages. We suggest that marsh grasses avoid physical stress and associated establishment thresholds in their early life stage,

and switch to an ecosystem engineering strategy once established. These findings shed new light on how plant traits interact with their environment to shape the landscape and pave the way for improved restoration designs by mimicking the natural shoot organization of establishing vegetation.

KEYWORDS
biogeomorphic feedbacks, clonal expansion strategy, ecosystem engineering, establishment thresholds, plant development and life-history traits, salt marshes, shoot organization, vegetated coastal ecosystems.

1 | INTRODUCTION

Vegetated coastal ecosystems such as salt marshes, dunes and seagrass meadows occur at the land–sea interface—a dynamic environment typified by harsh growing conditions—where they provide vital ecosystem services, including coastal protection, water and carbon storage, and biodiversity enhancement (Barbier et al., 2011; Temmink et al., 2022). These ecosystems are known as biogeomorphic landscapes because their formation and functioning critically depend on so-called biogeomorphic feedbacks (Corenblit et al., 2011, 2015). Biogeomorphic feedbacks entail self-reinforcing interactions between biota and geomorphic processes by which organisms engineer landforms to their own benefit. For instance, vegetation increasingly stimulates sedimentation of airborne and water-suspended particles with increasing patch size and shoot density, thereby reducing physical stress (e.g. drag, salinity, elevation) and enhancing resource availability (e.g. nutrients, underwater light) (Bouma, De Vries, Low, Kusters, et al., 2005; Van Hulzen et al., 2007).

The strength of these biogeomorphic feedbacks depends on the traits of the ecosystem engineering species involved (Corenblit et al., 2015; Friess et al., 2012; Jones et al., 1994). Differences between species in morphological (e.g. height, leaf size, shoot flexibility, rooting depth) and life-history (e.g. mode of reproduction, number of seeds) traits can have major consequences for their engineering capacity at both the local patch scale and the emerging coastal landscape. At the patch scale, stiff stems of cordgrasses effectively attenuate flow, leading to within-patch particle trapping, while accelerated flow induces scouring around the edges (Bouma, De Vries, Low, Peralta, et al., 2005; Bouma, Friedrichs, Klaassen, et al., 2009). Contrastingly, the flexible shoots of seagrasses typically bend with the flow, leading to weaker local flow attenuation and sedimentation effects, but also less erosion around patch edges (Bouma et al., 2010; Bouma, De Vries, Low, Peralta, et al., 2005; Bouma, Friedrichs, Klaassen, et al., 2009). At the landscape scale, differences in longevity and dispersal mode between two salt marsh species drive the emergence of distinct landscapes features. Salt marshes formed by clonally propagating perennial cordgrass exhibit complex channel systems, whereas the seed-dispersal strategy of annual glasswort consolidates existing landscape topography without causing further channelization (Schwarz et al., 2018).

Recent work in coastal dunes highlights that, apart from shoot-specific traits, spatial shoot organization can also affect the strength of biogeomorphic feedbacks. Specifically, these studies demonstrated that even species with similar morphological and life-history traits can build contrasting coastal landscapes due to seemingly small differences in their shoot organization (Reijers et al., 2019). The observed heavy-tailed distribution of shoot placement by marram grass, approximating a power law, was found to yield a patchy shoot organization that promotes high local sediment deposition with minimum investment in tissue development. By contrast, the congeneric American beachgrass exhibits a more dispersed strategy, generally placing shoots further apart, that promotes faster colonization but results in a wider and lower dune profile. Follow-up work even revealed that marram grass can shift its shoot placement strategy from densely clumped (i.e. exponentially distributed) in low sediment environments to patchy (i.e. long-tailed approximating a power law) when ample sediment is available. These findings highlight that coastal plants may gear clonal growth towards optimal shoot placement for maximum sedimentation under varying local environmental conditions (Reijers et al., 2020).

In contrast to coastal dune grasses that trap and stabilize sand particles in aeolian landscapes, clonally expanding seagrasses and salt marsh grasses modify physical conditions in aquatic environments, potentially driving the formation of different spatial shoot organization patterns. Compared to wind, forces exerted by water are much larger, while water-suspended particles can also be much smaller and lighter. Consequently, more flow energy needs to be dissipated by submerged plants to attenuate water flow sufficiently to allow particle settlement and sediment stabilization. While flow and sedimentation feedbacks benefit the plant in large, established patches, flow modifications may in fact hamper plant establishment in hydrodynamically exposed environments. In such cases, flow is accelerated around establishing vegetation patches to the degree that sediment erodes, potentially causing vegetation uprooting (Bouma, Friedrichs, Klaassen, et al., 2009; Bouma, Friedrichs, Van Wesenbeeck, et al., 2009; Koch et al., 2006; Van Der Heide et al., 2010). Hence, under exposed conditions, negative plant–environment feedbacks may result in establishment thresholds that can seriously inhibit vegetation establishment and landscape-forming processes (Balke et al., 2012; Maxwell et al., 2016; Van Wesenbeeck, Van De Koppel, Herman, Bertness, et al., 2008). Recent work suggests that established marsh grasses may be plastic in their response to local conditions in the sense that they exhibit distinct morphological traits depending on wave exposure and sediment conditions (Silinski et al., 2018). Yet, it remains unknown whether young clonally expanding marsh plants can overcome establishment thresholds in exposed conditions by minimizing flow acceleration around individual shoots by optimizing shoot placement.

Cordgrasses (genus *Spartina*) are globally important salt marsh-building species. Outside their native region, *Spartina* spp. (i.e. smooth and common cordgrass) were introduced in Eastern Asia and Europe for erosion control and are now established invasive species with profound effect on salt marsh ecosystem functioning (Borges et al., 2021; Hacker et al., 2001). Cordgrass occurs from the lower pioneer zone, where it shares its habitat with only few other species, to more elevated, older succession stages where it is gradually outcompeted by other species (Balke et al., 2012; Proffitt et al., 2005). Cordgrass can colonize new areas through both seed dispersal and clonal expansion. Whereas seed dispersal can lead to rapid colonization of bare areas in benign conditions, seedlings are very sensitive to disturbance (Balke et al., 2014; Hu et al., 2015). Clonal expansion of patches yields slower but steady colonization, leading to larger patches that become increasingly more stress tolerant (Balke et al., 2012; Van Wesenbeeck, Van De Koppel, Herman, Bertness, et al., 2008).

In this study, we investigate the spatial shoot organization of the salt marsh grass *Spartina anglica* (common cordgrass) in small (0.5–1.5 m), establishing patches across a wide range of wave exposure and sediment conditions along the European coast. *S. anglica* is a key species in European marshes and its dense canopy is well known to influence sedimentation and erosion patterns (Bouma et al., 2007; Bouma, Friedrichs, Klaassen, et al., 2009; Bouma, Friedrichs, Van Wesenbeeck, et al., 2009; Van de Koppel et al., 2005; Van Hulzen et al., 2007). We hypothesize that the shoot organization of *S. anglica* modulates sedimentation feedbacks and varies across exposure conditions. Specifically, we expect shoot organization to become less densely packed with increasing hydrodynamic exposure to reduce generation of turbulence and scouring. To explore how shoot placement strategies of establishing *S. anglica* may depend on environmental conditions, we first determined above-ground shoot patterns of 90 clonally connected tussocks at 18 sites, covering a wide range of environmental conditions, along the Northwestern European coast. Second, to test the effect of contrasting shoot patterns on sedimentation feedbacks, we constructed a field experiment with various arrangements of shoot mimics in both exposed and sheltered hydrodynamic conditions.

2 | MATERIALS AND METHODS

2.1 | Field survey

We studied the natural variation in shoot organization patterns of establishing *S. anglica* across 18 Northwestern European salt marshes that vary in their hydrodynamic exposure and related environmental conditions (Figure 1; Table S1). Locations were visited during the growing season between 11 April and 11 September 2019. Per location, we selected five isolated plants at the pioneer zone on the mudflat with a maximum patch diameter of 150 cm. For each plant ($N = 90$, 18 locations × 5 replicates), we determined shoot organization using still images following the methods described in Reijers and Hoeks (2019). We first clipped all above-ground biomass and marked the shoot bases with coloured glass pins (Figure S1). The plant was then photographed within a 150 cm graduated square frame as scale reference. Plants were excavated to verify clonal rhizomal connections between all shoots. For three plants, rhizomal connections were missing between parts of the plant, these shoots were considered unconnected and excluded from further analyses. Each photograph was individually checked to mark all coloured pins, and shoot coordinates were extracted using Matlab (Reijers et al., 2019). No permits were required due to the non-invasive and small-scale nature of the measurements.

To investigate the potential relation between spatial shoot organization and their surroundings, we sampled multiple variables as proxies of the general environmental setting. Per plant, we collected sediment from 2 to 8 cm depth from the centre of the tussock, from which organic matter was estimated as loss on ignition by burning dry homogenized sediment samples at 560° for 4 h. Median grain-size and percent silt (particles <0.63 μm) were determined on freeze-dried homogenized material with polarized intensity differential scattering (Beckman Coulter LS 13320; NIOZ, Texel). We sampled porewater using 5 cm rhizons (Eijkelkamp) connected to vacuum syringes after which porewater samples were frozen for later analysis. In the laboratory, porewater phosphate (PO_4^-) and total nitrogen (NO_2^-, NO_3^{2-}, NH_4^+) were colorimeterically measured (TrAAcs 800 autoanalyzer; Bran en Luebbe). Finally, as a metric of hydrodynamics exposure, we used satellite images to calculate the *maximum fetch* and the *modified effective fetch* (i.e. the average of fetches at 45, 90 and 135 degrees from the coastline) (Howes et al., 1999). These estimates were used to categorize locations from very protected (exposure index 0) to exposed (exposure index 4) (Figure 1).

2.2 | Quantification of shoot organization

2.2.1 | Distribution of step lengths

As a proxy of spatial shoot organization, we assessed the distribution of step lengths (inter-shoot distances) of each individual plant ($N = 90$). This method assumes that shoot organization of clonal plants is the outcome of a movement strategy driven by rhizomal expansion, where the distances between shoots are interpreted as step lengths. Step lengths were estimated using a nearest neighbour algorithm that selects the shortest path out of n possible paths and starting points, with n being the number of shoots in an individual plant (Reijers et al., 2019). These step lengths were used to approximate above-ground distances between shoots and provide an estimate of the emergent spatial shoot pattern, but do not necessarily represent the below-ground rhizomal network. The extracted step

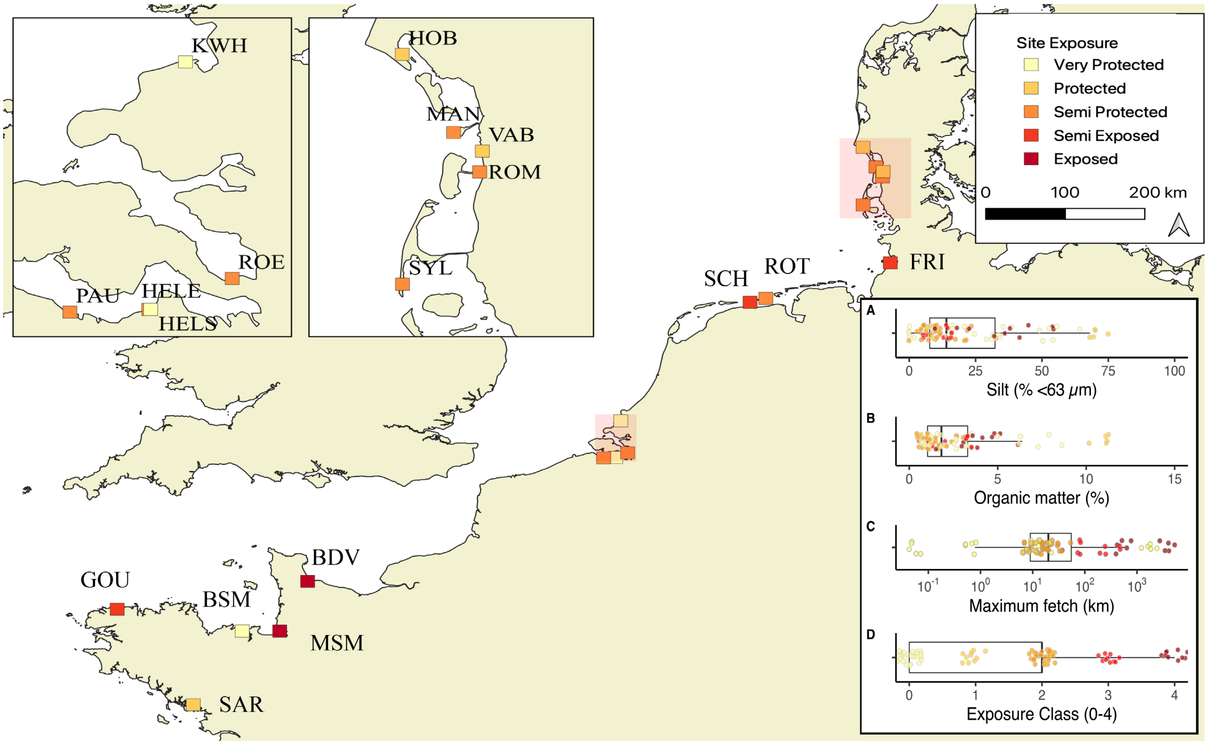

FIGURE 1 Map with survey locations. Locations are classified based on Exposure Index (Howes et al., 1999, also see methods) and range between Very Protected (0) and Exposed (4). Panels (a)–(d) show the range of environmental conditions that occurred over all 18 sites ($n = 5$ per location, except for fetch and Exposure Class where $n = 1$ per location). Detailed information per location is included in Table S1.

length distribution of individual plants was compared to four previously used candidate distributions models, representing an exponential, single-scale, distribution and more heavy-tailed models that can represent both single-scale (i.e. lognormal) and multi-scale (i.e. double exponential and exponentially bounded power law) distributions (a description of the different models is included in Appendix S1). Model parameter values were estimated using maximum likelihood methods based on the measured step length data, with minimum and maximum step lengths set to the largest and smallest step identified in our dataset (0.4 and 77.3 cm for the assembled step length data of all plants) (Edwards et al., 2012).

2.2.2 | Clustering analysis

We further analysed the spatial shoot organization pattern through Ripley's K statistics and k-means clustering analyses. First, we used Ripley's K to investigate whether point patterns of individual plants deviated from complete spatial randomness (Ripley, 1977). Second, we used clustering analyses (K-means) to describe and compare the shoot organization of individual plants. Based on the 'gap' statistics, that compare the change in within-cluster dispersion, we determined the optimal number of clusters (K), the position of the cluster centroid and number of shoots belonging to a cluster (Reijers et al., 2020; Tibshirani et al., 2001). We then calculated the distance between the centroids of clusters (cluster spacing) and the distance between the shoots within every cluster (shoot spacing), to compare the clustering patterns of all 90 individual plants (Figure 2). Cluster spacing was calculated by taking the distance from the centroid of K clusters to every other cluster in the plant. Per cluster, the distance to the nearest cluster was selected to obtain an estimate for the closeness of clusters, thus obtaining $K-1$ number of distances to the number of clusters. Similarly, to estimate the closeness of shoots within a cluster, shoot spacing was calculated between shoots by taking the distance from each shoot within the cluster to its nearest neighbour. This approach provided an estimate for cluster and shoot spacing that is independent of the number of shoots within the cluster or plant, in contrast to the mean cluster and shoot spacing which is influenced by plant and cluster size. Because clustering output was heavily right skewed by some plants with exceptionally large clusters, we selected the median and interquartile range (IQR) to best describe plant clustering.

2.2.3 | Mimic experiment

To study the effect of plant shoot organization on sedimentation, we compared bed-level changes around *S. anglica* shoot mimics representing different possible shoot patterns (i.e. dense, clustered and sparse) at two field locations that differed in hydrodynamic exposure. We selected two locations in the Mok Bay, Texel, with similar elevation but varying fetch and distance to the channel (Figure S2). The hydrodynamically most exposed location was close to the opening of the bay at ~30 m from the channel

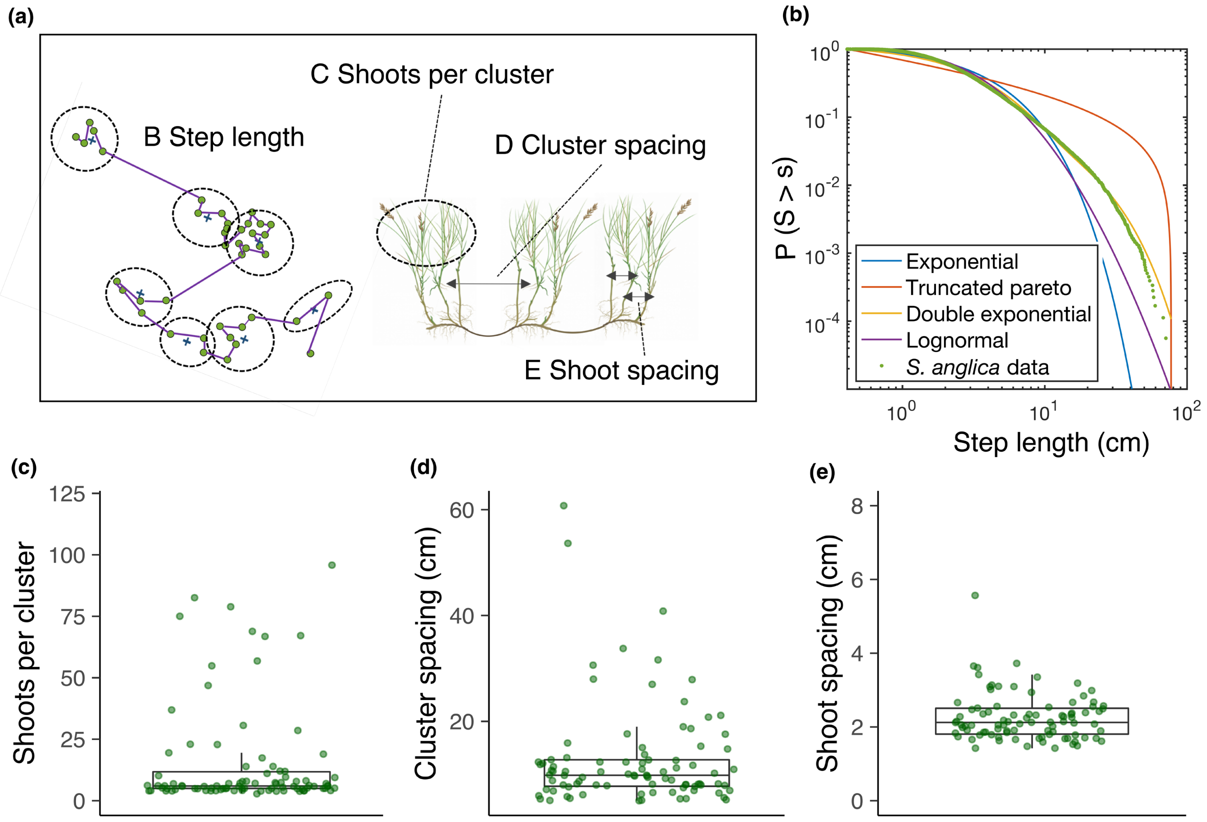

FIGURE 2 Field data on the spatial organization of establishing *Spartina anglica* plants. (a) Schematic representation of different parameters describing shoot organization. Step lengths (derived by following the shortest path connecting all shoots), shoots per cluster, cluster spacing and shoot spacing. (b) Inverse cumulative frequency distribution of the pooled step length data ($n = 90$ plants with 17,825 steps). (c) median shoots per cluster, (d) cluster spacing and (e) shoot spacing per plant. Horizontal line indicates the median, box height depicts the first and third quartiles. One outlier with 190 shoots per cluster lies outside of the y-axes range.

(31U 617716 5874777, UTM). The more sheltered location was located further inside the bay at 900 m from the channel (31U 619199 5874051, UTM). The Exposure Class (ranging from 0—very protected to 4—exposed) was 0 for the sheltered and 2 for the more exposed site. Prior to the experiment, 24 × 1 m^2 plots were covered with dark plastic for 1 week to remove benthic bioturbating, sediment-destabilizing fauna, after which they were left to recover for 48 h prior to the start of the experiment. Shoot organization treatments (dense, clustered and sparse) were assigned following a three-replicate randomized block design that also included control plots. As shoot mimics, we used 40-cm long glass fibre rods pushed halfway into the sediment. No permit was required due to the temporary and non-invasive nature of this experiment. The experiment ran between October and December 2021.

Shoots number (i.e. 168 mimics per plot) and spatial organization were determined using our dataset comprising 90 *S. anglica* plants. The *dense* treatment imitated a dense homogeneous pattern with all shoots spaced at 2 cm distance, which represents the median shoot spacing in the survey and resembles the mean step length in the full step length dataset (~2.5 cm). The *clustered* treatment consisted of 28 clusters with 6 shoots per cluster (median observed shoot count per cluster survey), with a similar shoot spacing inside clusters of 2 cm with clusters spaced 10 cm apart (median inter-cluster distance survey). The sparse pattern was created by spreading shoots homogenously over a similar area as the clustered arrangement, resulting in 4 cm distance between shoots, which corresponded to the median step length in the field data (~4 cm). Changes in sediment level in plots were determined relative to 16 marked mimics per plot by measuring the distance from the top of the mimic to the sediment on six occasions over the course of 8 weeks. Sediment height was carefully measured with a ruler while avoiding sediment and mimic disturbance.

2.2.4 | Statistical analyses

For the step length distributions, we compared the relative performance of candidate models on assembled step length data with the differences in the Akaike information criteria between each candidate model and the best fitting model (ΔAIC) (Wagenmakers & Farrell, 2004). For step length distributions of individual plants, we selected the best fitting model with the weighted AIC (wAIC) (Johnson & Omland, 2004; Wagenmakers & Farrell, 2004). The goodness of fit of candidate models was assessed using a one-sample Kolmogorov–Smirnov test (hereafter KS test), with rejection or acceptance of a fitted model based on $p < 0.1$ as a criterium (Clauset et al., 2009).

We used linear models with Bonferroni-corrected post hoc tests to explore potential differences in clustering between the 18 sampling locations. Next, we used single linear regression models to explore the relation between observed shoot pattern and measured environmental variables from the field survey. Normality of residuals was checked and data was log transformed if needed.

For the mimic experiment, we first standardized sediment height to values measured in the paired control plots per measured time point to account for local and weather-related differences in sedimentation. Next, we constructed a generalized linear model which included different measurement days (six instances) and replicate measurements (16 per plot) as random factors nested within the plots. Treatment differences within locations were assessed with planned Bonferroni-adjusted post hoc comparisons. All statistical analyses were performed with R version 4.0.4 (R Core Team, 2021).

3 | RESULTS

3.1 | Field survey

3.1.1 | *S. anglica* step length distribution is heavy tailed

Frequency distribution analysis of step lengths demonstrated that the shoot organization of *S. anglica* clearly deviated from a simple exponential strategy. Instead, heavy-tailed models (i.e. with a higher occurrence of large steps)—either lognormal or double exponential—proved the best fit when all step length data are combined (Figure 2b, ΔAIC scores: lognormal = 0, double exponential = 1667, exponential = 2893, truncated pareto = 13,233). Specifically, although the double exponential model demonstrates a better fit on the larger step sizes of the distribution, lognormal provides a better overall fit because it better describes the smaller step sizes that comprise the majority of the data. The overall results are consistent with the analyses of individual plants where 73 out of 90 plants fitted best to lognormal or double exponential distributions (Table 1). Moreover, the KS test showed that the double exponential model fitted acceptably to 83% of the plants, while the lognormal distribution fitted well to 88% of the plants.

TABLE 1 Model selection based on weighed Akaike information criteria (wAIC) and Kolmogorov–Smirnov (KS) test. Note that only one model has the *best fit* to the data based on the wAIC, while more than one model can have an *acceptable fit* to the data based on the KS test.

Candidate model	Best fitting model Number of plants, highest wAIC	Acceptable fit Number of plants, KS test $p > 0.1$
Double exponential	36	75
Lognormal	37	79
Truncated pareto	4	17
Exponential	13	57

3.1.2 | *S. anglica* shoots are clustered

We found that establishing *S. anglica* plants showed a consistent clustered shoot pattern. First, Ripley's *K* analysis on the point patterns of shoots showed that patterns deviated from complete spatial randomness and dispersed patterns, that is all points lie above the confidence interval of the Poisson distribution (Ripley, 1977; Van Wesenbeeck, Van De Koppel, Herman, & Bouma, 2008). Next, clustering analysis revealed that all 90 plants across 18 different locations exhibit highly similar clustering characteristics with a median and IQR of 6 (5–12) shoots per cluster, a median distance of 2.1 (1.8–2.5) cm between shoots in a cluster and median distance of 9.8 (7.7–12.7) cm between clusters (Figure 2, see Table S2 for plant summary per location). Cluster spacing and shoot spacing were not related to the number of shoots (linear regression, $p > 0.05$).

3.1.3 | Environmental variation does not influence shoot pattern

We found a large variation in environmental conditions across the sampled locations with ranges in silt, organic matter and grainsize that represent both sheltered and exposed marshes (Figure 1, Table S1 for values per location). Location was a significant factor for cluster spacing (F[17, 72] = 2.31, $p < 0.05$), but post hoc analysis showed that only two pairs of locations differed significantly from each other. Location also proved significant for shoot spacing despite the low observed variation (F[17, 72] = 5.22, $p < 0.005$). From comparing all 18 locations, only 14% of post hoc comparisons were significant (21 out of 153 post hoc comparisons). Despite the environmental variability across the sampled marshes, variation in clustering parameters (cluster spacing, shoot spacing, shoots per cluster) was low (Figure 2) and showed no relation to any of the included environmental parameters (i.e. median grainsize, organic matter, silt content, plant available nutrients, fetch and exposure class; Figure S3).

3.1.4 | Mimic experiment

Our field experiment showed that shoot organization significantly affected bed level around the mimics, but that this effect depended on the level of hydrodynamics exposure (Figure 3; Figure S4). At the exposed site, average sediment height of the dense shoot pattern was three times lower compared to the clustered treatment (−0.3 (dense) vs. +0.7 cm (clustered)). By contrast, treatments did not differ from each other at the sheltered site. In fact, the dense treatment

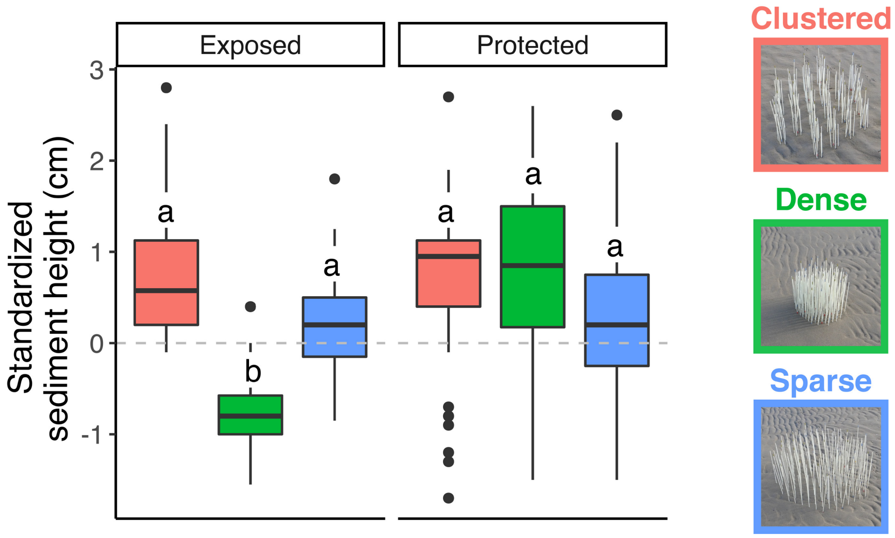

FIGURE 3 Effect of shoot organization on standardized sediment height at the end of experiment (day = 50). Values were standardized to sediment level in control plots ($n = 16$ sediment height measurements per plot and $n = 3$ plots per treatment). Letters depict post hoc grouping ($p < 0.05$) on full data (6 measurement time points), which shows similar trends as individual time points.

at the exposed site turned out to be the only treatment to significantly deviate from the others.

4 | DISCUSSION

Contrary to our expectations, the results from our European survey show that clustering of shoots by establishing *S. anglica* patches was universally observed across sites, despite widely varying environmental conditions. Specifically, we found that the step length distribution was heavy tailed and best described by either double exponential or lognormal distribution models. These models suggest that a two-mode movement drives the shoot patterning, resulting in the formation of small clusters alternated with longer steps between clusters. This suggestion was supported by point pattern analysis which revealed that shoot patterns deviated from spatial randomness and generally formed a consistent clustered pattern with 5–12 shoots per cluster, 1.8–2.5 cm between shoots and clusters typically spaced 8–13 cm apart. Results from our shoot mimic experiment demonstrate that this observed clustering strategy benefits plants during early establishment under exposed conditions as it avoids sediment erosion around the shoots, and therefore prevents uprooting. Under sheltered conditions, no clear optimal strategy was found, presumably because lower flow velocities did not generate sufficient turbulence and thus erosion around individual shoots in any of the treatments. Combined with earlier studies which show that sediment erosion hampers lateral *S. anglica* expansion (Duggan-Edwards et al., 2020; Van Wesenbeeck, Van De Koppel, Herman, Bertness, et al., 2008; Van Wesenbeeck, Van De Koppel, Herman, & Bouma, 2008), our findings suggest that the spatial distribution of establishing *S. anglica* shoots represents a stress avoidance strategy to overcome erosion-related establishment thresholds in exposed tidal environments.

4.1 | *S. anglica* has a heavy-tailed expansion strategy

Similar to earlier findings for dune grasses, we demonstrate that *S. anglica* expansion patterns can be described by random walk models that are typically used to study movement of mobile organisms. These findings suggest that such models might be able to approximate shoot organization patterns of clonal coastal ecosystem engineering plants in general as the outcome of rhizomal 'steps' and highlight that the identified patterns are vital for the engineering strength of the species. In contrast to many mobile species, the step length distribution of the emergent shoot pattern does not follow the simplest 'Brownian' distribution. Random walk models are typically used to approximate step length distributions in search strategies employed by mobile organisms such as bacteria, mussels, birds and fish (Codling et al., 2008; De Jager et al., 2012; Edwards et al., 2012; Reynolds et al., 2016). The simplest form, the Brownian walk, follows an exponential distribution of step lengths and yields a single densely spaced cluster, whereas others include relatively more larger steps, yielding heavy-tailed step length distributions. Indeed, earlier work by Reijers et al. (2019, 2020) highlighted that the shoot organization of two species of establishing dune grasses can also be well described by this class of models. Specifically, these studies found that dune grasses do not follow a Brownian walk, but instead adopt a scale-invariant and heavy-tailed Levy-like shoot organization pattern that was found to optimize sand trapping efficiency (Reijers et al., 2019). We find that, similar to dune grasses, *S. anglica* does not follow a Brownian step length distribution in its establishment phase. However, it also clearly deviates from the scale-invariant levy-type distributions, and instead seems to take an 'in-between-strategy' that was best approximated by lognormal and double exponential distributions. In contrast to dune grasses, that optimize engineering strength by employing patchy shoot placement strategies, our field experiment demonstrates that establishing *S. anglica* instead adopt a clustered strategy that avoids physical stress by minimizing engineering rather than mitigating it.

4.2 | Engineering and avoidance strategies in coastal vegetation

Especially in dynamic coastal areas, clonally growing plants are most vulnerable during their establishment phase. Extreme events such as storms cause sediment instability around the roots and intense drag on plant stems of individual small patches (Koch et al., 2006; Van Der Heide et al., 2010), resulting in high losses, which, in turn, complicates the expansion and recolonization of salt marshes (Bouma, Friedrichs, Van Wesenbeeck, et al., 2009). By contrast, large, established patches are able to mitigate such physical stress by stabilizing the sediment with their root mat and attenuating flow with their dense canopy (Van Hulzen et al., 2007). This illustrates that establishing plants suffer from establishment thresholds as below a certain critical patch size and stem density, they are unable to sufficiently dissipate flow and stabilize sediment. They lack the beneficial effects of engineering occurring at larger tussock scales, while turbulence around individual stems in fact increases the risk of uprooting (Koch et al., 2006; Van Der Heide et al., 2010). Our survey results combined with a manipulative experiment demonstrate that the clustered growth pattern observed in establishing *S. anglica* plants can circumvent such negative effects.

In contrast to marram grass, that was found to modify its shoot placement strategy depending on sand availability (Reijers et al., 2020), the observed organization patterns in establishing *S. anglica* patches were remarkably similar regardless of environmental conditions. This is surprising as physical stress at various locations can clearly differ depending on hydrodynamic exposure (Bouma et al., 2016; Callaghan et al., 2010; Cao et al., 2018; Schoutens et al., 2020). Nevertheless, if establishing *S. anglica* indeed employs its distinct strategy to avoid erosion and uprooting, it may also benefit from this strategy in sheltered conditions as storms may also cause these issues here, particularly when sediments are muddy and incohesive (Hu et al., 2020; Ma et al., 2018). Next to the clustered strategy, the sparse arrangement also caused no negative effects in our experiment. However, earlier work from dunes highlights that such a dispersed shoot pattern is associated with higher costs as the rhizomal distances that need to be covered are longer (Reijers et al., 2019). Hence, and in contrast to dune grasses, we suggest that even in sheltered conditions there may be some risk and no benefit in altering shoot placement strategy during early establishment for *S. anglica*. As such, establishing cordgrass plants seem to have adopted a safe and relatively cost-efficient strategy regardless of conditions.

As many earlier studies have highlighted the strong positive effects of engineering by *S. anglica* on its own growth (Balke et al., 2012; Van der Wal et al., 2008), our findings raise the question of how and when establishing plants may switch their behaviour from stress avoidance to beneficial habitat engineering. Contrary to our expectations, prevailing environmental conditions did not induce a shift from a sparse organization in exposed environments, to dense clumped organization in sheltered conditions. Therefore, we hypothesize that larger and older plants may instead alter their shoot organization pattern by filling in space between clusters once the plants reach a certain minimum patch size-dependent tolerance threshold (Van Belzen et al., 2022). In other words, we expect that lateral expansion is initiated with clustered growth, after which shoot density increases by filling open spaces. This would explain the much higher densities observed in mature patches the field (3000 shoots m^{-2}, own data) and literature (1600 m^{-2}, Van Wesenbeeck, Van De Koppel, Herman, & Bouma, 2008) compared to the small establishing patches in our survey (median 373 shoots m^{-2}).

To date, it is unknown which spatiotemporal factors trigger such ‘space filling’. We theorize that *S. anglica* changes its strategy from ‘stress avoidance’ to ‘habitat engineering’ once the patch size is large enough to generate self-facilitation via engineering. Earlier work has demonstrated that this minimum required patch size depends on the prevailing environmental conditions (Silliman et al., 2015). If this is indeed the case, it would mean that the growth strategy of *S. anglica* is dictated by a patch-size-dependent trade-off between safety and engineering (Figure 4). However, whether *S. anglica* indeed changes its strategy from ‘stress avoidance’ to ‘habitat engineering’ beyond a certain patch size, and whether this patch size depends on environmental conditions, remains to be investigated.

4.3 | Implications for conservation and restoration

Recent work from salt marshes and seagrasses has highlighted the importance of including facilitation into restoration designs. In seagrasses for instance, it was found that large-scale approaches favour facilitative interactions and are therefore typically more successful (Van Katwijk et al., 2016). Moreover, experimental work revealed that facilitation can be harnessed at smaller scales by planting transplants grouped in clumps rather than applying plantation-style dispersed designs, leading to double restoration yields in salt marshes (Silliman et al., 2015). The same result was achieved in follow-up work where individual small seagrass or marsh grass plants were transplanted within biodegradable structures that temporarily mimic facilitating effects of larger patches (Temmink et al., 2020). Yet, although facilitation is clearly important in many coastal systems, other work has shown that clumped strategies or mimicry of such effects are not always favourable, and that their success depends on local environmental conditions (Renzi et al., 2019; Van der Heide et al., 2021), specific plant traits (Huang et al., 2022) and plant plasticity (Reijers et al., 2020). Our results add to this body of work by showing that establishing *S. anglica* organizes themselves, independent of prevailing environmental conditions, in clustered patterns that prevent sediment erosion and shoot dislodgment.

At first sight, our finding seems contradictory to earlier work highlighting beneficial effects of clumped planting in transplantation

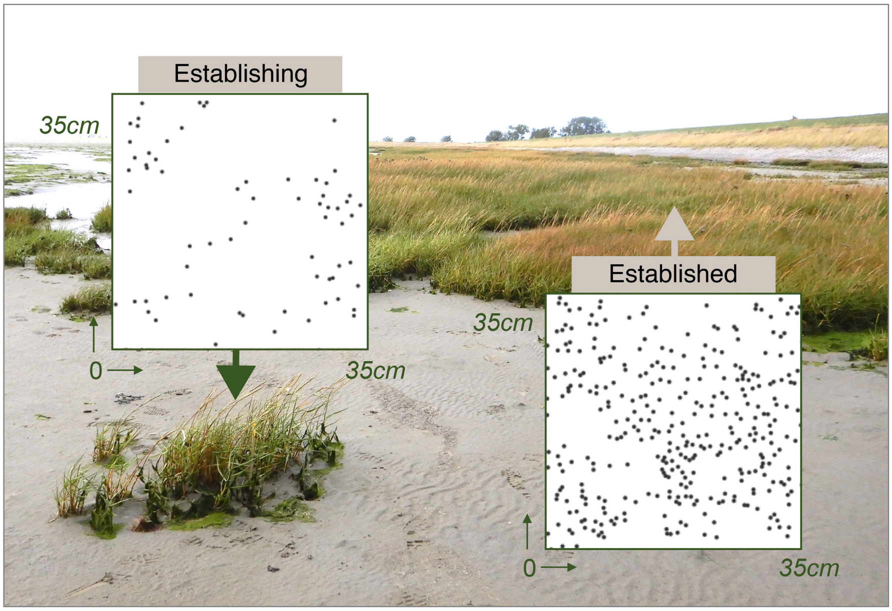

FIGURE 4 Different shoot patterns in establishing and established patches possibly indicate a size-dependent shift in strategy. Establishing plants on salt marshes favour a clustered strategy that avoids local inhibition, independent of environment. As patch size increases, we observe higher shoot densities (e.g. Van Wesenbeeck, Van De Koppel, Herman, & Bouma, 2008) with less clustering (personal observations). We hypothesize that plants shift (through a process called space filling) from stress avoidance to engineering after reaching size-dependent tolerance thresholds (Van Belzen et al., 2022). Possibly the timing of switches differs depending on the environment and exposure at different salt marshes.

experiments (Silliman et al., 2015), as our results suggest that restoration designs may increase plant vulnerability during establishment by enhancing erosion. However, it is possible that, depending on the severity of hydrodynamic exposure, clumping marsh transplants in large enough patches could by-pass the stress avoidance phase, thus increasing their chances of survival. However, in doing so, this approach also by-passes a more dispersed expansion phase that at least in theory allows for more rapid colonization. To date, there have been no experiments that have tested mimicking natural shoot organization patterns for restoration purposes, whereas our results and previous work (Reijers et al., 2019, 2020) suggest that such an approach could increase efficiency. Perhaps, temporary mimicry of patches by artificial structures might be a solution that combines the best of both clumped and dispersed planting. However, at present, it remains unknown whether and how transplants of coastal vegetation alter their expansion behaviour when protected by such solutions and how this affects their long-term survival once they expand outside of these temporary structures.

AUTHOR CONTRIBUTIONS

Valérie C. Reijers, Jim van Belzen and Tjisse van der Heide conceptualized the field survey. Clea N. van de Ven, Carlijn Lammers and Valérie C. Reijers designed the survey and collected field data and Clea N. van de Ven and Valérie C. Reijers did the analysis. Clea N. van de Ven, Valérie C. Reijers, Tjisse van der Heide and Tjeerd J. Bouma conceptualized the experiment which Clea N. van de Ven and Yeyeong Chung designed and analysed. Clea N. van de Ven wrote the first version of the manuscript and all authors contributed substantially to revisions.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data for this publication are available from the NIOZ Dataverse repository https://doi.org/10.25850/nioz/7b.b.2d (van de Ven, 2023).

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SUPPORTING INFORMATION

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

Figure S1: Picture overview showing field method for deriving shoot coordinates and above-ground distances (step lengths) between shoots.

Figure S2: Schematic treatments and map of mimic experiment.

Figure S3: Environmental variability does not explain clustering ($n = 90$ plants).

Figure S4: Standardized sediment height in mimic experiment (cm) per measuring day.

Table S1: Environmental characteristics per site.

Table S2: Plant data summarized per site.

Appendix S1: Distribution fitting.

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