Research article

Seed settling and trapping during submerged secondary dispersal: Implications for saltmarsh recruitment and restoration

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ABSTRACT

Given the decline of global salt marshes, there is a pressing need to pinpoint the key processes that limit and facilitate seed-based pioneer recruitment. Secondary seed dispersal, in the form of short-distance submerged movement, is a prerequisite for initiating pioneer establishment in adjacent tidal flats but has not been fully appreciated and understood. In this study, using a settling tube and race-track flume, seeds of four global occurring saltmarsh species were studied in terms of their settlement speed and trapping opportunity to understand how seed traits and physical settings affect submerged dispersal behavior and thus seed-based saltmarsh recruitment. Present study led to the following novel insights: 1) Seeds have density-dependent settling speeds, which are comparable to that of fine sand, but much faster than that of very fine sand and silt. Since the latter is the type of sediment commonly found in many estuaries worldwide (such as the Scheldt), seeds will typically settle faster than local sediments. A sufficiently long hydrodynamic-calm period allows slowly settling sediment to bury settled seeds, otherwise, seeds will remain uncovered if the period is short. 2) Seed trapping ratio increased linearly with surface roughness (a proxy for local topographic complexity), but this effect becomes smaller with increasing hydrodynamic intensity. Seed drag coefficient was identified as the key biotic factor contributing to interspecies variability in trapping ratio. Overall, present results suggest that submerged seed dispersal may form a primary bottleneck for salt marsh recruitment by limiting seed availability via two mechanisms: i) reduced chance of seed burial through asynchronous settling of seeds and sediment particles; ii) reduced probability of seed trapping due to encountering smooth tidal flat surfaces. This study provide mechanistic and data basis for the targeted application of biophysical models in predicting outcomes of saltmarsh recruitment and long-term maintenance, thereby informing seed-based conservation and restoration.

1. Introduction

There is growing interest in integrating salt marshes into "hybrid" engineering designs to mitigate coastal flood risk (Zhu et al., 2020a; van Zelst et al., 2021), due to their superiority in attenuating wave impacts under storm surge conditions while maintaining high stability (Möller et al., 2014; Pannozzo et al., 2021). Combined with the provision of multiple other ecological functions like carbon sequestration (Temmink et al., 2022), salt marshes are also increasingly accepted as a broad nature-based solution contributing to climate stability (Chausson et al.,

2020; Seddon et al., 2021). Under the "multiple whammies" from climate change-related stressors such as rising sea levels and increasing storms (Fagherazzi et al., 2020; Hanley et al., 2020), salt marshes are currently suffering from massive habitat shrinkage, typically by means of erosion-induced lateral retreat at the marsh edge (Leonardi et al., 2016; Murray et al., 2022). Driven by the cyclic alternations inherent in the salt marsh ecosystems, a resilient marsh edge would recover the degraded area by revegetation of pioneer landscape-forming species (van der Wal et al., 2008; Bouma et al., 2016). This can be achieved either by asexual cloning or seed-based recruitment (De Vet et al., 2020;

Cao et al., 2021). The latter is the dominant form of marsh recovery in global regions such as Europe and East Asia, and has significant advantages in enabling rapid vegetation establishment over extensive areas and building population genetic diversity (Larios et al., 2017; Hu et al., 2021; Zhao et al., 2021a). Pinpointing the key processes limiting and facilitating seed-based recruitment is thus integral and of broad importance in assessing the resilience and long-term stability of salt marshes under changing climate scenarios (Zhu et al., 2020b; Hu et al., 2021).

Seed-based salt marsh recruitment is impossible without seed dispersal (Kettenring and Tarsa, 2020). After detaching from a parent plant, seeds of most saltmarsh species would remain drifting with tidal currents due to positive buoyancy (i.e., primary dispersal; cf. Culot et al., 2015), until they are eventually entrapped by vegetation in existing marshes or deposited at the waterline (Shi et al., 2020; Zhao et al., 2021b). Secondary dispersal (i.e., subsequent horizontal or vertical movement of seeds away from their initial deposition site; cf. Culot et al., 2015) of the entrapped seeds from marshes towards tidal flats would contribute to seed availability for seed-based recruitment and has been recognized as the foremost demographic process that kick-start seedling establishment in adjacent tidal flats (van Regteren et al., 2019; Zhao et al., 2021a; Zhu et al., 2020b). Its occurrence first requires the wave-induced bottom shear stress to lift the seeds vertically into the water column, and then the unidirectional tidal current to transport these lifted seeds horizontally (Koch et al., 2010; Kendrick et al., 2012). For buried seeds in particular, entrainment of the entire sediment layer above the seeds, routinely stemming from high-energy hydrodynamic events (e.g., storms), is required to initiate secondary dispersal (Ruiz-Montoya et al., 2012; Zhu et al., 2021). In this case, seeds are predicted to be transported by tidal current as suspended load or bed load mixed with sediment particles (Yoshikawa et al., 2013). The seeds involved in secondary dispersal tend to be negative buoyancy due to saturating with seawater during primary dispersal (Chang et al., 2008), thus are speculated to have a high possibility of settlement after a poorly understood short-distance near-bottom movement (Pereda-Briones et al., 2018). Thereafter, whether the settled seeds can be captured and thus retained depends critically on the local topographic complexity of tidal flats (Pereda-Briones et al., 2018; Qiu et al., 2021). Yet, little is known about the extent to which the submerged secondary dispersal behavior of non-buoyant seeds is affected by physical conditions such as sediment settling, dispersal vectors (i.e., tidal current, waves), and topographic complexity, although it is an indispensable cornerstone toward accurate predictions of the outcomes of seed-based recruitment and comprehensive assessments of long-term salt marsh persistence. Beyond physical conditions, seed traits are highly determinant of their dispersal ability and are widely recognized as a universal unit of comparison to assess and predict the heterogeneity of performance across species in homogeneous environments (Friess et al., 2012; Larson et al., 2015). For example, variation in seed density has been proved to dominate its floating potential (van der Stocken et al., 2019) and may has lingering implications for subsequent seed fates, such as settling speed and dispersal distance, particularly during secondary dispersal (Ruiz-Montoya et al., 2012; Zhao et al., 2021a). A recent flume study focusing on seagrass seeds showed that secondary dispersal is closely relevant to the seed's drag coefficient, with a higher value resulting in a lower lift-off velocity threshold for the seeds (Pereda-Briones et al., 2018). Additionally, species-specific seed traits can influence dispersal patterns by interacting with capture structures (Nilsson et al., 2002; Chang et al., 2008). For example, seed characteristics such as high density, sticky seed coat, and collapsed pappi may increase capture success (Chambers and MacMahon, 1994; Chang et al., 2008). Towards a general trait-based framework/model for evaluating interspecific variations in recruitment outcomes and long-term persistence, there is a need to delineate which seed traits are ultimately responsible for particular processes such as seed settlement and seed trapping during the submerged secondary dispersal.

In this study, we intend to broaden our understanding of the opportunities and limitations of seed-based salt marsh recruitment in tidal flats through the lens of submerged secondary dispersal. Specifically, we hypothesize that such dispersal behavior can diminish salt marsh recruitment by affecting seed availability, contingent upon the chance of seed burial through synchronous settling with sediment particles, as well as the probability of seed trapping due to encountering topographic complexity. To establish generalized response mechanisms, we focused on four global occurring landscape-forming pioneer species with contrasting seed traits that likely affect their interaction with dispersal vectors and topographic complexity: *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, and *Spartina anglica*. Firstly, we quantified the settling speed of negative buoyancy seeds during secondary dispersal using a settling tube filled with seawater, and compared it with that of sediment particles with different grain sizes to explore the possibility of seed accumulation in tidal flats by coincident settlement with sediment particles. Secondly, we established the functional relationships between dispersal vectors, topographic complexity, seed traits, and seed trapping through a flume study, in which we deployed sediment blocks with varied topographic complexity, as collected from eight salt marshes in the Scheldt estuary in NW Europe. The resulting information serves as a "stepping-stone" allowing biogeomorphic modelers to more accurately predict the spatiotemporal dynamics of saltmarsh recruitment and has implications for the optimization of seed-based saltmarsh restoration.

2. Materials and methods

2.1. Seed collection and pre-treatment

Mature seeds of *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, and *Spartina anglica* were collected in the Westerschelde estuary (southwestern Netherlands; Fig. 1, Table 1) where the corresponding species was local dominant pattern-forming species. The seeds whose parent plants were withered and can be readily shed by shaking were regarded as mature seeds. Upon arrival at the laboratory, seeds of the four species were inactivated by repeated freezing and thawing to prevent germination during the experiments. The seeds were then soaked in seawater and placed in a freezer at 4 °C until the start of the experiments. This treatment reproduced the primary dispersal process that seeds experienced after detachment from their parent plant, during which the seeds lost buoyancy and settled due to prolonged water immersion (Zhao et al., 2021b). Only seeds that settled to the bottom were used for the subsequent experiments.

Physical traits of the seeds of the four species were measured prior to the experiments, in order to establish the functional relationships between seed traits and submerged seed dispersal potential. Seed length (mm) and width (mm) were measured using a vernier caliper; seed weight (g) after blotting dry was measured using an electronic balance; seed volume (cm^3) was determined adopting the water displacement method (cf. Ruiz-Montoya et al., 2012); seed density (g cm^{-3}) was calculated by dividing the seed mass by the seed volume; seed frontal area (cm^2) was retrieved using ImageJ software after taking the orthophoto; seed drag coefficient (C_d) was calculated by applying the below empirical formula from Dean and Dalrymple (2004).

$$C_d = 2\left(\frac{\rho_{se} - \rho}{\rho}\right) \frac{gV_{se}}{\omega_{se}^2 A_f}$$

Where ρ_{se} is seed density, ρ is water density, g is gravitational acceleration, V_{se} is seed volume, A_f is seed frontal area, and ω_{se} is seed settlement speed quantified in section 2.2.

2.2. Quantification of seed settlement speed

A transparent PVC tube (1.5 m in height and 0.3 m in diameter; sealed at the bottom) filled with seawater (salinity of 33, water
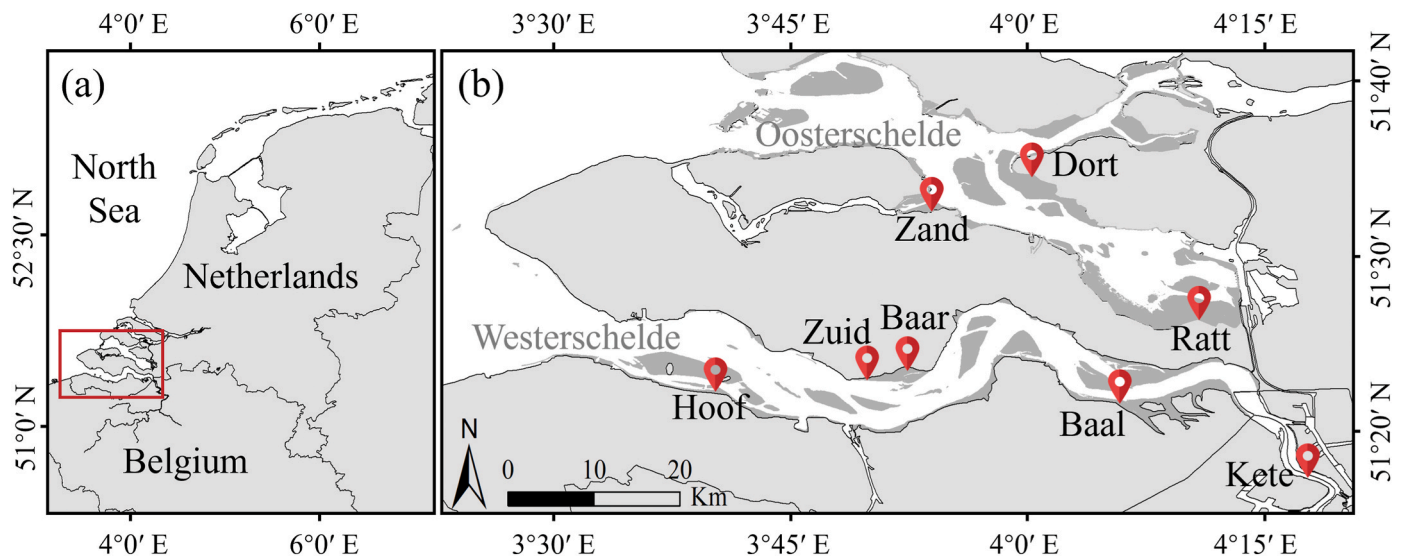
Fig. 1. (a) Locations of the Scheldt estuary. (b) Geographic distribution of selected salt marshes. At the pioneer areas of these marshes, sediment samples and sediment blocks of varying surface complexity were collected for identifying particle settling speed (see section 2.2) and conducting flume experiments (see section 2.3), respectively. The full names of these marshes abbreviated here are shown in Table 1.

Table 1
An overview of the characteristics of selected salt marshes.

Region	Location	Abbreviation	Coordinates	Elevation (m NAP)	Water depth (max, m)	Grain size (D50, μm)	Surface roughness
Oosterschelde	Dortsman	Dort	51.5731 N, 4.009 E	1.14	1.13	126.16	0.016 ± 0.004
	Rattekaai	Ratt	51.4389 N, 4.1669 E	1.10	1.18	108.03	0.018 ± 0.002
	Zandkreek	Zand	51.5414 N, 3.8972 E	0.74	1.93	68.54	0.026 ± 0.006
Westerschelde	Baarland	Baar	51.3914 N, 3.8721 E	1.95	0.70	45.51	0.023 ± 0.003
	Zuidgors	Zuid	51.3906 N, 3.8512 E	2.30	0.34	22.24	0.027 ± 0.005
	Hoofdplaat	Hoof	51.3719 N, 3.6817 E	1.38	1.49	47.06	0.021 ± 0.005
	Baalhoek	Baal	51.3569 N, 4.1042 E	1.92	1.27	58.05	0.017 ± 0.003
	Ketenisse	Kete	51.2848 N, 4.3132 E	2.94	0.19	52.55	0.024 ± 0.002

temperature of 20 °C) was used to quantify the settlement speed of seeds. A seed was slowly lowered into the water column using a tweezer and released at ca. 5 cm below the water surface. A distance of the top 0.5 m was used to stabilize the settlement speed of the seed. The time (t) it took for the seed to travel from the position 0.5 m below the water surface to the bottom, i.e., a distance (d) of 1 m, was recorded using a stopwatch. Seed settlement speed (ω_{se}) was calculated as $\omega_{se} = d/t$. Duplicated tests with the same protocol were conducted using 50 seeds for each of the four species, and the obtained data were averaged as the settlement speed for the species.

To compare the settlement speed of seeds with that of sediment particles, the below theoretical formula developed by Wu and Wang (2006) was adopted to calculate the settling velocity of sediment particles (ω_{sed}). This formula considered the particle shape factor explicitly and was shown to perform better in accurately predicting the settling velocity of sediment particles in a recent study comparing many existing formulas (Shankar et al., 2021). To broadly cover the spectrum of sediment particle sizes for salt marsh habitats, we calculated the settlement speed of border sediment particles based on the Wentworth classification system (Wentworth, 1922, Table 3). Furthermore, surface sediments (ca. 1 cm in depth) were collected at 8 field sites (Fig. 1; Table 1) where sediment blocks of varying surface complexity were collected for flume experiments (see section 2.3). The particle size of surface sediments was analyzed using a laser particle sizer (Malvern Master Sizer-2000) after arrival at the laboratory. Their settlement speeds were then calculated to explore the possibility of coincident settlement of seed and sediment particles in natural tidal flats.

$$\omega_{sed} = \frac{M\vartheta}{Nd}\left[\sqrt{\frac{1}{4} + \left(\frac{4N}{3M^2}D_*^3\right)^{\frac{1}{n}}} - \frac{1}{2}\right]^{n}$$

$$D_* = d\left[\left(\frac{\rho_{sed}}{\rho} - 1\right)\frac{g}{\vartheta^2}\right]^{\frac{1}{3}}$$

where M, N, and n are calibration coefficients with values of 33.9, 0.98, and 1.33, respectively, ϑ is the kinematic viscosity of water (at 20 °C), d is the diameter of sediment particles, ρ_{sed} is sediment density having an empirical value of 2.65×10^3 kg m^{-3}, ρ is water density, g is gravitational acceleration.

2.3. Identification of seed trapping variability

To accurately study how seed-trapping may be affected by surface complexity, we collected sediment blocks (l × w × h = 0.57 × 0.57 × 0.05 m) with varied surface complexities from the pioneer mudflat of eight salt marshes in the Scheldt estuary in NW Europe (Fig. 1; Table 1). At each site, four sediment blocks with bare mud were taken. After the range of a block was delineated, we divided it into 9 equal portions to facilitate excavation with minimal disturbance to the sediment surface. A prefab frame (l × w × h = 0.19 × 0.19 × 0.06 m; made of thin metal sheets) was positioned over a portion of the sediment block, and was carefully pushed into the sediment until its top edge remains ca.1 cm above the sediment surface. The sediment outside the frame was gently peeled off from one side, after which a thin metal plate was slid underneath to enable lifting the frame with the sediment contained

therein. The 9 portions were excavated in turn and reassembled in situ in a metal tray (l × w × h = 0.57 × 0.57 × 0.05 m) to regain their original arrangement. Upon arrival at the laboratory, the sediment blocks were soaked in seawater for at least 24 h to avoid desiccation while allowing reconsolidation. We recognized that this sampling method would affect the original surface structure of the sediment blocks to a certain extent, but its overall surface complexities and the difference between sites were still preserved. This was sufficient to allow us to gauge the role of tidal flat topographic complexity in trapping seeds.

All tests were performed in a racetrack flume at the Royal Netherlands Institute for Sea Research (NIOZ). The flume is 17.55 m long, 0.6 m wide, 0.45 m deep, and equipped with a conveyor belt and adjustable wave paddle (Fig. 2a), allowing repeated tests under specific flow velocities and wave magnitudes. The test section at the straight channel of the flume has a double bottom that allows three identical metal trays to be placed side by side with their upper edge flush with the flume bed (Fig. 2b). The tray containing a sediment block collected in the field was placed in the middle of the test section, and the trays in front and behind it were filled with homogeneous sandy sediment and manipulated to a smooth surface. The trays were put in place with the flume emptied, after which the flume was slowly filled with seawater to a water level of 0.3 m (Fig. 2c). Prior to each test, the flume was run at a high flow velocity of 0.4 m s^{-1} for 20 min to stabilize the surface structure of the sediment block and minimize erosion in subsequent tests. Thereafter, a digital elevation map of the sediment blocks was drawn via the distance scan mode of the Acoustic Doppler Velocimeters (ADV, Nortek). The spatial grid had a resolution of 1 cm in the longitudinal (parallel to the flow) and transverse (across the flow) directions, with a sub-mm resolution in the vertical direction. To make all sediment blocks directly comparable, their surface complexity was parameterized as surface roughness following the method described in Poate et al. (2018), namely four times the standard deviation of elevation associated within the sediment block.

Based on published data on the typical hydrodynamic properties of the Scheldt estuary (Callaghan et al., 2010), a total of three hydrodynamic scenarios were applied in flume tests for simplicity, including (i) low-current of 0.2 m s^{-1}; (ii) low-current of 0.2 m s^{-1} plus wave with height of 8 cm; and (iii) high-current of 0.4 m s^{-1}. Seeds of each of the four species were tested independently and given five replicates under each scenario with one sediment block, leading to a total of 1920 tests (32 sediment blocks × 3 scenarios × 4 species × 5 replicates). For each test, a new set of seeds (n = 15) were deposited in the middle of the first tray with tweezers and equally spaced along the transverse (across the flow) direction (Fig. 2b). The smooth surface of the first tray enabled seeds to easily move to the second tray with current or wave and encounter the exposed surface structures of the sediment block. Each test lasted 10 min, after which the number of seeds trapped within the sediment block was recorded. The seed trapping ratio (R_{trap}) was then calculated as the proportion of deployed seeds resulting in trapped seeds: $R_{trap} = \frac{15-N}{15} \times 100$ % (where N is the number of trapped seeds). Tests in which sheet erosion occurred on the sediment block were not used. Of particular note, *S. europaea* seeds (Φ < 1 mm) were dyed red using Rose Bengal prior to the test to increase their recognition on the sediment surface. After testing, an underwater magnifying glass was used to search for the captured *S. europaea* seeds.

2.4. Statistical analysis

One-way analysis of variance (ANOVA) with the least significant difference (LSD) post-hoc test was used to test the differences in seed physical traits among species. The same method was also adopted to assess the variability in seed settlement speed between species. Regarding the flume study, the effects of surface roughness, scenarios, and species on seed trapping ratio were analyzed by using a generalized linear model (GLM) with "binomial" family for the proportion data (Bolker, 2007), followed by multiple comparison assessments among scenarios and species using the "multcomp" package (Hothorn et al., 2008). The GLM with "binomial" family was also adopted to determine the effects of the drag coefficient on seed trapping ratio. All statistical analyses were performed using R v.4.1.0 (https://www.r-project.org) and a significance level of 0.05.

3. Results

3.1. Seed settlement speed and its correspondence with that of sediment particles

The settlement speed of seeds was shown to have a significant interspecies variability (*P* < 0.001; Fig. 3a). Among the four species, *S. maritimus* settled the fastest with an average speed of 2.53 ± 0.97 cm s^{-1}, *S. europaea* settled the slowest with an average speed of 1.35 ± 0.28 cm s^{-1}, while *A. tripolium* and *S. anglica* settled at a similar average speed of 2.02 ± 0.45 cm s^{-1} and 1.97 ± 0.57 cm s^{-1}, respectively (Table 2; Fig. 3a). Overall, seed settling velocity varied significantly with seed density, showing a linear positive correlation (Table 2, Table 3).

When the settlement speed of seeds was compared with that of border sediment particles identified in the Wentworth classification system, it was found that seeds of the four species had settlement speed comparable to those of fine sand (Φ = 0.062–0.250 mm; Fig. 3a; Table 4). The sediments collected at all field sites were classified as very fine sand or silt (Table 1; Table 4), which were estimated to have a much slower settlement speed than seeds of all the four species (Fig. 3b).

3.2. Variability in seed trapping

A significant positive correlation was detected between seed trapping ratio and surface roughness (a proxy for local topographic complexity), regardless of species and test scenarios (Fig. 4; Table 5). Seed trapping ratio differed across species (*P* < 0.001; Table 5) with a clear trend under all scenarios; that is, *S. europaea* > *S. anglica* > *A. tripolium* > *S. maritimus* (Fig. 4; Table 5). The results of the GLM revealed that changes in drag coefficient across species significantly
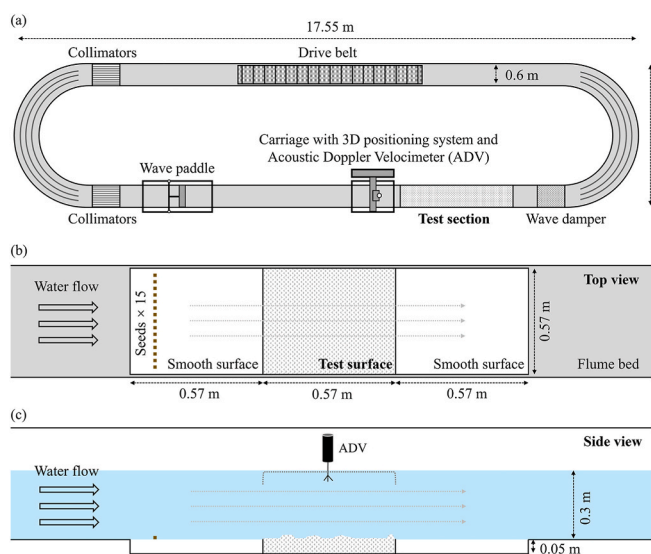

Fig. 2. (a) Schematic representation of the racetrack flume used to quantify seed trapping ratio under varied sediment surface complexities. (b) Top view of the test section in the straight portion of the flume. Three trays with sediment were placed side by side. The tray on the left had a smooth surface allowing the released seeds to travel with water flow and encounter the surface structure contained in the middle tray. The tray on the right side with a smooth surface enables seeds not trapped by the surface structure to move out of the test section. (c) Side view of the test section.
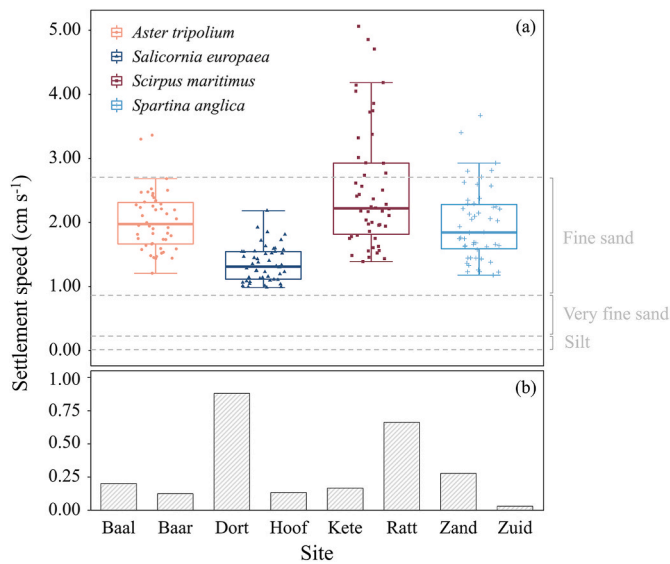
Fig. 3. (a) Seed settlement speed of the four species, i.e., *Aster tripolium, Salicornia europaea, Scirpus maritimus*, and *Spartina anglica*. The gray dashed lines represent the settlement speeds of border sediment particles of the mentioned categories (displayed in gray font) and their comparability with seed settlement speeds of the four species. The settlement speeds of more border sediment particles are shown in Table 4. (b) Estimated settlement speed of sediment particles that were collected from field sites. Full names of the sites on the X-axis are shown in Table 1.

Table 2
Seed traits of the four species, i.e., *Aster tripolium, Salicornia europaea, Scirpus maritimus*, and *Spartina anglica*. All parameters, except the drag coefficient, are displayed as the mean ± standard deviation. Different lowercase letters denote significant differences between species.

Seed traits	*A. tripolium*	*S. europaea*	*S. maritimus*	*S. anglica*
Length (cm)	0.664 ± 0.061 b	0.123 ± 0.020 d	0.344 ± 0.023c	1.667 ± 0.126a
Width (cm)	0.137 ± 0.020c	0.055 ± 0.012 d	0.255 ± 0.025a	0.204 ± 0.029 b
Weight (g)	0.006 ± 0.002c	0.0003 ± 0.000 d	0.008 ± 0.001 b	0.018 ± 0.003a
Volume (cm³)	0.005 ± 0.001c	0.0003 ± 0.000 d	0.007 ± 0.001 b	0.016 ± 0.002a
Density (g cm⁻³)	1.196 ± 0.304 ab	1.053 ± 0.024 b	1.259 ± 0.178a	1.133 ± 0.183 b
Frontal area (cm²)	0.082 ± 0.014 b	0.008 ± 0.002 d	0.065 ± 0.008c	0.257 ± 0.039a
Settlement speed (cm s⁻¹)	2.020 ± 0.453 b	1.354 ± 0.277c	2.527 ± 0.965a	1.970 ± 0.572 b
Drag coefficient	4.984	1.102	7.528	3.214

Table 3
Results of the generalized linear models testing the effects of density on seed settlement speed and the effects of drag coefficient on seed trapping ratio.

Models	Estimate	Std. error	t-value	p-value
Effects on seed settlement speed				
Intercept	−7.180	0.692	−10.376	0.009**
Density	2.801	0.588	4.768	0.041*
Effects on seed trapping ratio				
Intercept	0.616	0.062	9.861	<0.001***
Drag coefficient	−0.645	0.021	−30.819	<0.001***

Significance level: *** 0.001, **0.01, *0.05.

Table 4
Estimated settlement speed of sediment particles. The size and associated category of the border sediment particles are based on Wentworth classification system.

Particle size (mm)	Settlement speed (cm s⁻¹)	Wentworth size class	
2.00	18.5378		Sand
		Very coarse sand	
1.00	11.6035		
		Coarse sand	
0.50	6.3334		
		Medium sand	
0.25	2.7050		
		Fine sand	
0.125	0.8652		
		Very fine sand	
0.0625	0.2327		
		Coarse silt	Silt
0.031	0.0582		
		Medium silt	
0.0156	0.0148		
		Fine silt	
0.0078	0.0037		
		Very fine silt	
0.0039	0.0009		
		Clay	Mud
0.00006	0.0000002		

affected the trapping ratio of seeds in a non-linear pattern (Fig. 5; Table 3). Overall, the larger the drag coefficient, the lower the probability of the seed being trapped by surface structure (Fig. 5).

Seed trapping ratio was maximum under the scenario of low current, with an average value of 75.83 ± 19.19%, 33.04 ± 18.74%, 23.75 ± 17.51%, 3.42 ± 6.43% for *S. europaea*, *S. anglica*, *A. tripolium*, *S. maritimus*, respectively (Fig. 4). With the presence of waves and the increase in current velocity (i.e., the scenario of low current + wave and high current), the trapping ratio of seeds decreased significantly ($P <$ 0.001; Table 5). Under both scenarios, seeds of *S. anglica*, *A. tripolium*, and *S. maritimus* still resulted in a very low trapping ratio, ranging from 0% to 20%, after going through the sediment surface with the highest surface roughness, while the trapping ratio of *S. europaea* seeds was higher than 60% (Fig. 4).

4. Discussion

4.1. Linking submerged dispersal behavior to seed availability

The bare tidal flats in front of salt marshes are often identified as hotspots for lateral marsh expansion due to the provision of suitable conditions for seedling growth and survival (van Regteren et al., 2020; Zhu et al., 2020b). Recent studies underscore that the occurrence of seedling establishment on tidal flats is premised on seed availability (Erfanzadeh et al., 2010; van Regteren et al., 2019; Lõhmus et al., 2020), which requires negatively buoyant seeds captured within adjacent marsh to be able to settle and retain in the tidal flats after undergoing short-distance secondary dispersal (Chang et al., 2008; Zhao et al., 2021a). One of the key mechanisms to promote seed retention in microsites and form seed banks is seed burial, which can originate from the simultaneous settling of seeds and sediment particles or the bioturbation of benthic animals (Yoshikawa et al., 2013; Zhu et al., 2016; Marion et al., 2021). In this study, we reveal that seeds of four globally widespread salt marsh species had settlement speeds comparable to those of fine sand sediments. This suggests that seeds of these species may deposit together with fine sandy as tidal current velocity declines and thus leading to the burial of seeds. However, this case does not apply to most salt marshes in the Scheldt estuary in NW Europe, because sediments collected at all our field sites were classified as very fine sand or silt and were estimated to have a much slower settlement speed than seeds of the four species. Therefore, in order for seeds to be buried, a
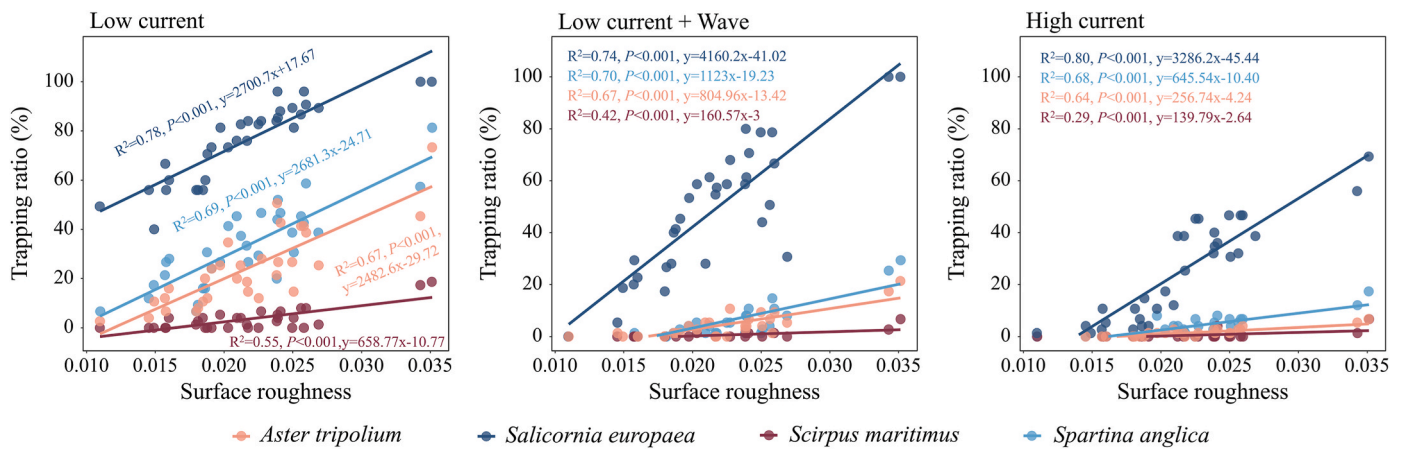
Fig. 4. Response of seed trapping ratio to surface roughness for the four species, i.e., *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, and *Spartina anglica* under different hydrodynamic settings, namely low current, low current + wave, and high current.

Table 5
Results of the generalized linear models testing effects of surface roughness, hydrodynamic scenarios, and species on seed trapping ratio and the multiple comparison assessments among scenarios and species.

Models	Estimate	Std. error	t-value	p-value
Main effect				
Intercept	−3.218	0.452	−7.123	<0.001***
Surface roughness	107.622	15.811	6.807	<0.001***
Scenarios	−0.721	0.108	−6.693	<0.001***
Species	0.264	0.075	3.512	<0.001***
Multiple comparisons among scenarios				
Low current: High current	−1.850	0.081	−22.720	<0.001***
Low current: Low current + Wave	−2.858	0.097	−29.550	<0.001***
High current: Low current + Wave	1.008	0.094	10.700	<0.001***
Multiple comparisons among species				
A. tripolium: *S. europaea*	−3.061	0.096	−31.870	<0.001***
A. tripolium: *S. maritimus*	2.278	0.185	12.291	<0.001***
A. tripolium: *S. anglica*	−0.512	0.097	−5.273	<0.001***
S. europaea: *S. maritimus*	5.339	0.185	28.815	<0.001***
S. europaea: *S. anglica*	2.549	0.087	29.340	<0.001***
S. maritimus: *S. anglica*	−2.789	0.183	−15.283	<0.001***

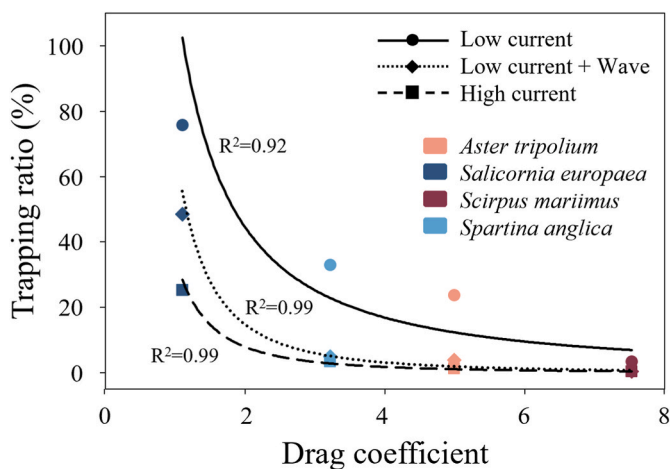Significance level: *** 0.001, **0.01, *0.05.

Fig. 5. Nonlinear relationship between seed trapping ratio and seed drag coefficient. Data are presented as species averages and fitted based on power functions.

longer calm period is required that allows sediment to settle on top of the seeds long after they have initially settled. The discrepancy in settling speeds of seeds and sediment particles may provide an explanation for the lack of seedling establishment on tidal flats at such muddy sites (cf. Hu et al., 2015; van Regteren et al., 2019); that is, in case the hydrodynamic calm period is short, seeds can barely be buried after settlement and, in turn, may dispersal again on a larger spatial scale. This mechanistic understanding also magnifies the sharp contrast between coastal salt marsh ecosystems and river ecosystems. In river ecosystems, the similarity in settlement speed of seeds and sediment particles was documented to be the main driver of vegetation recruitment (Yoshikawa et al., 2013).

In addition to seed burial, increasing studies suggest that seed trapping induced by the topographic complexity of tidal flats may contribute to seed availability at microsites (Chang et al., 2008; Xie et al., 2019). Here, the surface structures such as micro-topography and benthic algae would directly block the bed-load transport of seeds by acting as obstacles/traps (Qiu et al., 2021) or indirectly inhibit the bed-load transport of seeds by attenuating near-bottom flow velocity (Pereda-Briones et al., 2018). Our flume study provided solid evidence for this point and revealed that the probability of seed trapping was jointly regulated by the surface roughness of tidal flats and the drag coefficient of seeds; namely, the smaller the seed drag coefficient is, the rougher the tidal flat surface is, and the easier the seeds are to be trapped. This result echoes the research by Pereda-Briones et al. (2018), in which the seed lift-off threshold of seagrass species was shown to be negatively correlated with the seed drag coefficient. Once seeds being trapped, the attenuated flow velocity by topographic complexity would result in weakened near-bottom shear stress that promotes seed retention and opens a window of opportunity (WoO; i.e., disturbance low/absent periods; Balke et al., 2011). The WoO has been proven to be indispensable for subsequent germination and rooting of the seeds after being trapped/retained (van Belzen et al., 2022; Zhao et al., 2022). Furthermore, topographic complexity would facilitate seedling growth and survival by improving microhabitat conditions such as oxygen content and soil strength (Fivash et al., 2020; Cao et al., 2022). All these findings underscore an underappreciated fact that topographic complexity is critical for saltmarsh recruitment while opening new avenues for seed-based salt marsh creation and restoration (see suggestions in section 4.3).

4.2. Towards a holistic understanding of saltmarsh recruitment bottlenecks

Saltmarsh recruitment involves a sequence of transitions through the seed and seedling stages, during which underlying variations in

demographic proportions induced by bottleneck effects would significantly modulate the trajectories and outcomes of recruitment (Larson et al., 2015; Kettenring and Tarsa, 2020). Previous studies concentrated mainly on WoO associated with seedling establishment on tidal flats, with three consecutive bottlenecks revealed: *i)* seed rooting failure due to inundation, *ii)* seed/seedling dislodgement induced by high hydrodynamic forcing, *iii)* seedling uprooting triggered by sediment erosion (Balke et al., 2011; Zhao et al., 2022). Based on the WoO theory and model studies, the success and failure of seedlings to establish specific sites can be explained ex post or assessed a priori. (see Hu et al., 2015, 2021 for examples). Recently, growing studies pointed to the difficulties of seed retention on tidal flats as a major bottleneck for saltmarsh recruitment (van Regteren et al., 2019; Wang et al., 2018; Zhu et al., 2021). For example, several manipulative field experiments have shown that high-energy hydrodynamic events such as storms tend to dislodge seeds from tidal flat surfaces and even erode buried seeds (Zhu et al., 2014, 2020a). This limits saltmarsh recruitment on tidal flats by reducing seed availability, although there were suitable WoO for seedling establishment (van Regteren et al., 2019). Our study focused on demographic processes prior to seed retention and suggested that submerged seed dispersal from donor areas (e.g., vegetated areas) to tidal flats may be a primary bottleneck limiting saltmarsh recruitment. Seeds of most saltmarsh species can settle on adjacent tidal flats due to their rapid settling speeds, but the surfaces of tidal flats are often too smooth to trap the seeds. In this case, the seeds may be re-transported during subsequent tidal motion, either being redistributed to relatively sheltered sites such as adjacent vegetated area (Chang et al., 2008), or drifting away from the donor population on a larger spatial scale (Zhao et al., 2021b). This finding supports earlier arguments that demographic loss later in life may be trivial in determining population abundance when demographic loss early in life is also taken into account (James et al., 2011; Larson et al., 2015). Here we emphasize that saltmarsh recruitment faces more uncertainty due to submerged seed dispersal behavior and its failure should be attributed to multiple bottlenecks, which arise from different life-stage transitions and are site/species-dependent.

4.3. Implications for salt marsh conservation and restoration

Saltmarsh conservation and restoration become even more ecologically significant when it is targeted for nature-based applications such as coastal defense, climate stability, or carbon sequestration (Bouma et al., 2014; Macreadie et al., 2021; Temmink et al., 2022). Seed availability is a condition precedent and also a major bottleneck for (re)covering vegetation in degraded or new habitats due to the complex submerged seed dispersal behavior (van Regteren et al., 2019; Lõhmus et al., 2020). This is particularly true for tidal flats enriched with very fine sand and/or silty sediments, such as the sites where sediments were collected in this study, where seeds may be difficult to be buried due to their asynchronous settling with sediment particles. Additionally, high bed mobility at these sites may further prohibit seedling establishment via frequent sediment resuspension and low sediment anchoring capacity (Cao et al., 2018; Zhao et al., 2022). Our study demonstrated that the seeds of common saltmarsh species tend to settle in synchrony with fine sand particles. This result supports the potential of sand-capping technology (cf. Flindt et al., 2022) in seed-based restoration practices, namely seeds are mixed with sand when sowing or covered with a layer of sand after sowing. Sand-capping associated with dredging activities is considered a cost-effective approach for coastal ecosystem restoration, however, so far this approach has only been preliminary attempted in seagrass ecosystems (Flindt et al., 2022; Oncken et al., 2022). Sand-capping could promote seed retention by reducing seed exposure, while significantly increasing the threshold for sediment erosion (Flindt et al., 2022; Oncken et al., 2022). The latter is critical for promoting successful seedling establishment (Bouma et al., 2016; Hu et al., 2021). However, sand-capping may initiate a regime shift in local sedimentary

environments, with unknown consequences for benthic communities (Näslund et al., 2012; Samuelsson et al., 2017). Therefore, relevant experimental studies are needed to verify the applicability of this approach in saltmarsh ecosystems and to assess any possible side effects.

In addition, our flume study suggested that increasing the topographic complexity of tidal flats could open "windows of opportunity" for vegetation recruitment by trapping and retaining seeds. The increased topographic complexity has been verified to provide better habitat conditions (e.g., improved drainage and soil oxygen content) for subsequent seedling establishment (Fivash et al., 2020; Cao et al., 2022). Recent field surveys have also indicated that locations with higher topographic complexity had higher seedling establishment densities (Qiu et al., 2021). However, natural tidal flats, especially in relatively young realigned marsh landscapes, have smooth surfaces due to high sedimentation rates (Garbutt et al., 2006; Mazik et al., 2010). In this case, manual assistance measures are recommended to increase the topographic complexity at target restoration sites. For example, Qiu et al. (2021) manipulated hummock micro-topography on tidal flats through ploughing and successfully promoted seed retention and seedling establishment at a large scale. Installing biodegradable temporary materials on tidal flats would also provide a promising solution for restoration practices aimed at facilitating seed trapping and seedling establishment by increasing topographic complexity (see examples in Temmink et al., 2020; Fivash et al., 2021).

5. Conclusion

There is currently relatively limited knowledge concerning the submerged secondary dispersal of saltmarsh seeds. This study contributes first-hand data on seed settlement speeds and seed trapping opportunities closely relevant to such dispersal behavior, providing a mechanistic and data basis for the targeted application of biophysical models in saltmarsh movement ecology. Such models will help to estimate the proportion of demographic loss during secondary seed dispersal processes and disentangle major seedling establishment bottlenecks, thereby making seed-based saltmarsh recruitment more predictive (see one example in Hu et al., 2021). Our results revealed species variability in submerged seed dispersal behavior and underscored the importance of physical settings such as sediment traits and topographic complexity in seed availability for successful saltmarsh recruitment. This information is vital for protecting and restoring salt marshes. By implementing manual assistance measures such as sand-capping and micro-topography creation at target sites, it is possible to maximize the potential windows of opportunity for seedling establishment with limited seed supply and thereby amplifying conservation and restoration output.

Author Contributions

Zhiyuan Zhao: Conceptualization, Investigation, Methodology, Data curation, Visualization, Software, Writing - original draft. **Liquan Zhang:** Conceptualization, Methodology, Writing - review & editing. **Lin Yuan:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition, Project administration, Supervision. **Tjeerd J. Bouma:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition, Project administration, Supervision.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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