

The onset of secondary seed dispersal is controlled by germination-features: A neglected process in sudden saltmarsh establishment

Zhiyuan Zhao^{1,2,3}, Liquan Zhang,¹ Xiuzhen Li,^{1,5} Lin Yuan,^{1,5*} Tjeerd J. Bouma^{2,3,4*}

¹State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai, China

²Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute for Sea Research, Yerseke, The Netherlands

³Faculty of Geosciences, Department of Physical Geography, Utrecht University, Utrecht, The Netherlands

⁴HZ University of Applied Sciences, Building with Nature Group, Vlissingen, The Netherlands

⁵Yangtze Delta Estuarine Wetland Ecosystem Observation and Research Station, Ministry of Education & Shanghai Science and Technology Committee, Shanghai, China

Abstract

Effective seed dispersal is critical for enabling rapid state shift from a bare tidal flat to a vegetated marsh. While tidal currents are the main dispersal vector in coastal environments, biological characteristics that keep seeds afloat have been shown to influence primary seed dispersal, i.e., seed departure from the parent plant. In contrast, secondary seed dispersal processes that move (germinated) seeds trapped within microsites have been largely neglected. Here, we explore the extent to which the coupling between biotic traits and abiotic factors affects secondary seed dispersal, and whether secondary seed dispersal may explain sudden saltmarsh establishment (i.e., rapid colonization of bare tidal flat by large numbers of seedlings in spring). We used two widely spread pioneer species: *Scripus mariqueter* and *Spartina alterniflora*. Combined flume and field results demonstrated that: (1) germination stage, current velocity, and sedimentary regime have a marked effect on the probability of secondary seed dispersal by influencing the threshold lift-off velocity of (germinated) seeds within microsites; (2) density and bud length are critical biotic traits that best predict the potential of secondary-dispersal onset after seed germination; (3) *S. alterniflora* possess a stronger secondary dispersal ability compared to *S. mariqueter*; and (4) secondary dispersal of germinated seeds in spring may explain observed sudden marsh establishment on bare tidal flats. Our findings provide novel insight relevant to understanding the drivers of seed dispersal and thereby sudden saltmarsh establishment events, with important implications for understanding the effects of climate change on critical state transitions and enabling human-aided restoration.

Saltmarshes occur in near-shore coastal environments around the world (Barbier et al. 2011; Mcowen et al. 2017), and provide a multitude of valuable ecosystem services, such as habitat provisioning to unique species (Barbier et al. 2011), wave attenuation (Shepard et al. 2011; Möller et al. 2014), and shoreline stabilization (Temmerman et al. 2013; Bouma et al. 2014). State shifts in this valuable ecosystem between

low-lying bare mudflats and high-elevation vegetated marshes follow alternative stable state dynamics (Van Wesenbeeck et al. 2008; Marani et al. 2013; Wang and Temmerman 2013). Large-scale marsh collapse (i.e., the transition from vegetated marshes to mudflats) caused by ongoing anthropogenic and climatological disturbance has garnered widespread attention (Couvillion and Beck 2013; Kirwan et al. 2016; Hinshaw et al. 2017). In contrast, our understanding of the processes involving the transition from mudflats to vegetated marshes remains limited, despite its importance for the effective management and restoration of saltmarshes (Bouma et al. 2016; Cao et al. 2018, 2020).

Saltmarsh plants can colonize large bare areas slowly by clonal expansion or quickly by establishing seedling cohorts (Zhu et al. 2020a). While clonal expansion is considered to be the main mechanism of marsh expansion in some global regions, such as Georgia, USA (Angelini and Silliman 2012), seedling establishment is the crucial mechanism in other

*Correspondence: lyuan@sklec.ecnu.edu.cn and tjeerd.bouma@nioz.nl

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Author Contribution Statement: Z.Z., L.Z., X.L., L.Y., and T.J.B. conceived various ideas shaping the paper and designed various parts of the methodology; Z.Z. performed field measurements, conducted flume experiments, and collected the data; Z.Z., L.Y., and T.J.B. led the writing of the manuscript and the data analyses. All authors contributed critically to the manuscript and gave final approval for publication.

regions, such as Western Europe and Asia (Zhu et al. 2012; Cao et al. 2018; Zhu et al. 2020a). Seedling establishment involves a multi-stage process of plant regeneration, including seed release, seed dispersal by various vectors, seed arrival and retention in a favorable microhabitat, seed germination, and successful establishment of new seedling cohorts (Schupp et al. 2010; Culot et al. 2015). Among these components, the anchorage/establishment of seedlings following a dispersal event has been increasingly recognized as a dominant stage to promote a positive regime shift (Wang and Temmerman 2013; Balke et al. 2014; Bouma et al. 2016). However, studies on saltmarsh establishment tend to focus on the process of final seedling establishment (Hu et al. 2015b; Cao et al. 2018; Poppema et al. 2019), ignoring the important mechanistic processes involved in seed dispersal. These serve as condition precedents and determine the amount and spatial pattern of the final seedling output (Friess et al. 2012; Van der Stocken et al. 2019; Wang et al. 2019).

Seed dispersal can be divided into primary dispersal, which involves the movement of seeds away from the parent plant, and secondary dispersal, in which these displaced (and sometimes germinated) seeds are moved to another location (Culot et al. 2015; Van der Stocken et al. 2019). Seeds of saltmarsh species lose their ability to float as they become saturated during primary dispersal (Chang et al. 2008). These wet seeds tend to end up at a microsite based on plant interception, sediment burial, or benthic animal capture (Chang et al. 2008; Zhu et al. 2014, 2016). In the presence of waves (Chang et al. 2008), some seeds can move toward more suitable microhabitats for establishment (Zhu et al. 2014, 2016, 2020a). For saltmarsh species, such secondary seed dispersal might be mechanistically similar to sediment entrainment, transport, and deposition, in which the size, shape, weight, and density of sediment grains are key factors determining the critical flow velocity thresholds required to induce transport (i.e., threshold lift-off velocity) (Bull 1979; Carthey et al. 2016; Dorrell et al. 2018). We lack however knowledge on how seed traits affect secondary hydrodynamic transport, and to what extent this may be altered by seeds being partly buried or germinated, thereby altering their size, shape, and buoyancy.

Saltmarsh establishment on bare tidal flats has been related to stochastically determined windows of opportunity, when dispersal events are followed by hydrodynamically calm conditions below a critical disturbance threshold (Balke et al. 2011, 2014; Hu et al. 2015b). As seedlings cannot establish without seed dispersal, we hypothesize that synchronization of secondary dispersal events, and the windows of opportunity for seedling establishment in spring, provide optimal situations for successful saltmarsh establishment. This hypothesis is supported by field observations and remote sensing analysis in the Yangtze Estuary, China (Fig. 1), where there was rapid colonization of large bare areas by single cohorts of seedlings when local seed banks were largely absent and primary seed-fall had already occurred (Yuan et al. 2020 for *Scirpus mariqueter*; Zhao et al. 2020a for *Spartina alterniflora*). This indicates that massive

secondary seed dispersal and seedling establishment occur together over a short but specific period. Given that the dispersal properties of seeds may change due to germination, we speculate that wet seeds are first retained near the parent plants in the mature marsh, and undergo secondary dispersal and subsequent establishment after germination.

The objectives of the present study were to elucidate how changes in seed morphological characteristics during germination affect the potential of secondary hydrophily transport and successful establishment of saltmarsh species. We specifically addressed whether: (1) the threshold lift-off velocity of seed secondary hydrochory onset is affected by seed germination status and partial seed burial; (2) there are key morphological factors that can be used to characterize the potential of wet seed lift-off; and (3) if we can explain observed rapid colonization based on the changing physical factors or seed dispersal behavior, using the Yangtze Estuary in China as example. We address these questions via flume studies and field measurements, using two pioneer saltmarsh species as a model: *S. mariqueter* and *S. alterniflora*. We aim to provide novel insights into seed secondary dispersal and the sudden establishment of saltmarsh species, thereby aiming to aid future restoration schemes.

Materials and methods

Model pioneer species and determination of seed characteristics

S. alterniflora is an invasive pioneer marsh species on a global scale, noted for its capacity to act as an environmental engineer (Liu et al. 2019; Zhao et al. 2020a,b). *S. mariqueter* is the most widely spread native pioneer species in the Yangtze Estuary (Fig. 1a) and is regarded as a favorable habitat for local biodiversity and hence an important species for local ecological conservation and restoration in the Yangtze Estuary (Hu et al. 2015a; Yuan et al. 2020).

In November 2018, the seeds of both species were collected from Chongming Dongtan Nature Reserve (CDNR, Fig. 1b) and then cooled, and wet-stored for vernalization in a fridge at 4°C until the following April. Due to prolonged soaking during vernalization, the seeds used in the study were wet and had lost buoyancy. Seeds were germinated in a climate chamber maintained at 25°C during the day (550 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetic active radiation; 12 h) and 20°C during the night (12 h). To compare seeds at different germination stages, multiple batches of seeds were germinated and divided into six categories based on the germination day and uniform morphological characteristics (Table 1).

Before proceeding to the next step, morphological traits of all seed categories were measured and calculated, including mass after blotting dry (mg; using electronic balance), volume (mm^3), density (g cm^{-3}), superficial area (mm^2), and length of buds (i.e., embryo shoot, which develops into a leaf) and roots (mm; using Vernier caliper). These factors were all considered key physical attributes that affect the potential of seed

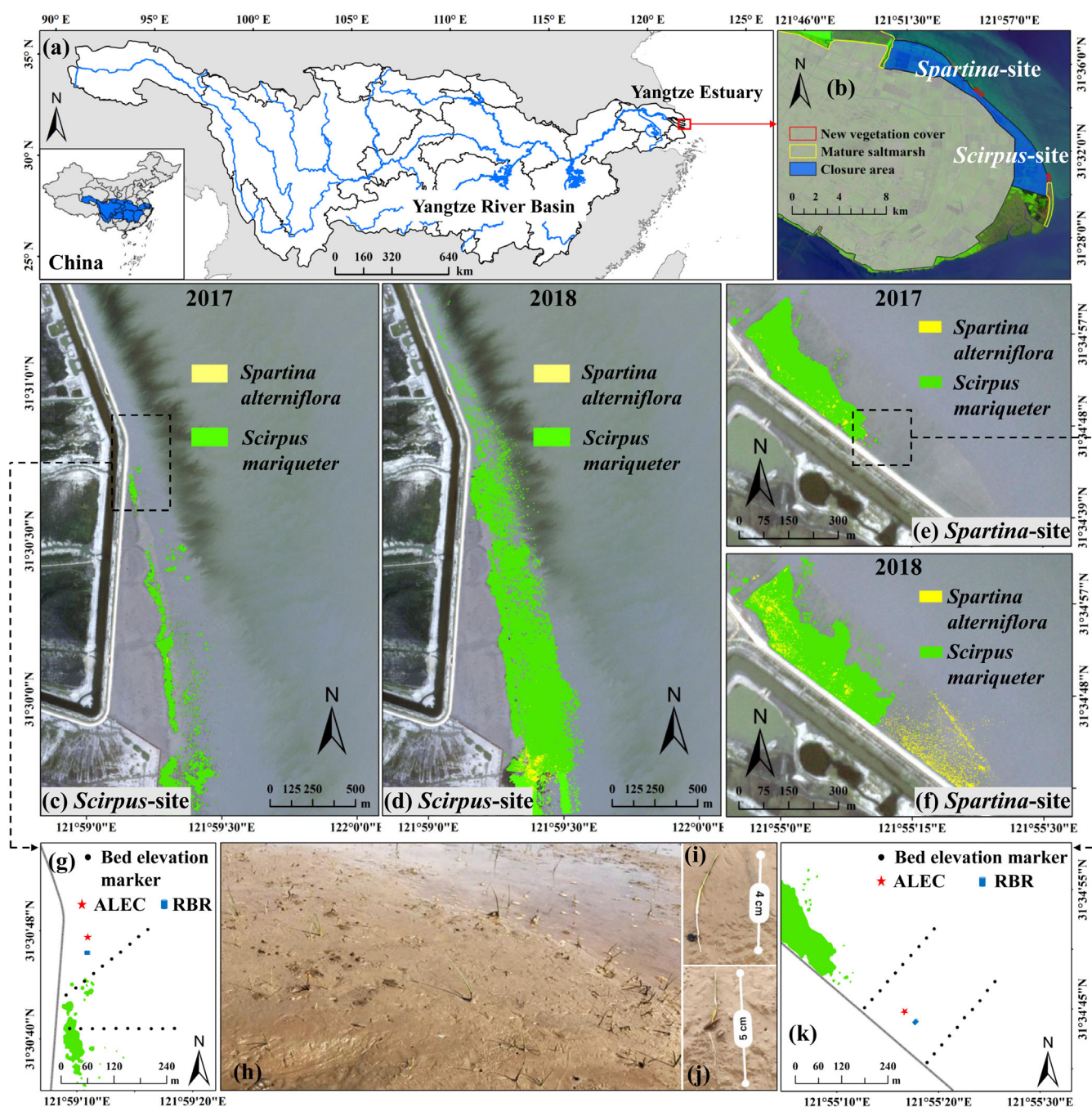




Fig. 1. (a) Yangtze River basin and the Yangtze estuary. (b) Location of the Chongming Dongtan Nature Reserve (CDNR), where there was rapid colonization by saltmarsh pioneers on the tidal flat. (c, d) Rapid colonization of *Scirpus mariqueter* occurred at the *Scirpus*-site from 2017 to 2018. (e, f) Rapid colonization of *Spartina alterniflora* occurred at the *Spartina*-site from 2017 to 2018. Within a growing season, the dispersal distance seaward and parallel to the dike of these saltmarsh pioneers both greatly exceed the distance that can be colonized by “diffusion” based on their asexual reproduction (no more than 5 m per year, Zhu et al. 2012; Ge et al. 2015). At both sites, *S. alterniflora* was chemically removed before flowering in 2017, and the regeneration in 2018 as a consequence of re-invasion from potential sources (Zhao et al. 2020b). The vegetation cover at both sites in 2017 and 2018 was extracted from a Pleiades satellite remote sensing image for July 24, 2017, and an aerial image taken by drones on July 19, 2018, respectively. Images were processed and vegetation was classified as described by Yuan et al. (2020). (g) Schematic distribution of the locations for hydrodynamic (ALEC was used to measure current velocity and direction; RBR was used to record water depth) and bed elevation changes measurement at the *Scirpus*-site. (h) Seedling established in the mudflat at the CDNR. (i) Seedling of *S. mariqueter*. (j) Seedling of *S. alterniflora*. (k) Schematic distribution of the locations for hydrodynamic and bed elevation changes measurements at the *Spartina*-site.

Table 1. Seed characteristics of the two saltmarsh species at different germination stages used in the flume experiment. All morphological parameters are displayed as the mean \pm standard deviation (SD). Different lowercase letters denote significant differences between stages.

	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
						
<i>Scirpus marigueter</i>						
Germination time (d)	0	5	10	15	20	25
Mass (mg)	11.20 \pm 0.55 d	11.71 \pm 1.56 d	12.02 \pm 0.40 d	14.30 \pm 1.56 c	16.30 \pm 0.79 b	22.80 \pm 1.15 a
Volume (mm ³)	10.07 \pm 1.19 d	11.27 \pm 0.68 d	16.67 \pm 1.18 c	20.00 \pm 1.18 b	20.33 \pm 1.39 b	34.20 \pm 1.10 a
Density (g cm ⁻³)	1.13 \pm 0.17 a	1.04 \pm 0.17 a	0.72 \pm 0.05 b	0.72 \pm 0.11 b	0.80 \pm 0.06 b	0.67 \pm 0.04 b
Surface area (mm ²)	6.21 \pm 0.63 d	6.82 \pm 0.26 cd	7.55 \pm 0.57 c	7.86 \pm 0.97 c	10.33 \pm 0.29 b	15.35 \pm 1.40 a
Bud length (mm)		1.29 \pm 0.25 d	7.57 \pm 1.59 c	21.23 \pm 1.47 b	22.20 \pm 3.27 b	29.26 \pm 0.82 a
Root length (mm)						15.35 \pm 1.40
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
						
<i>Spartina alterniflora</i>						
Germination time (d)	0	5	10	15	20	25
Mass (mg)	14.40 \pm 0.14 e	14.90 \pm 0.99 e	16.70 \pm 0.51 d	18.00 \pm 0.75 c	21.10 \pm 0.58 b	26.90 \pm 1.15 a
Volume (mm ³)	12.27 \pm 0.28 f	15.20 \pm 0.30 e	20.60 \pm 0.95 d	26.59 \pm 0.15 c	32.33 \pm 0.75 b	37.67 \pm 2.79 a
Density (g cm ⁻³)	1.17 \pm 0.02 a	0.98 \pm 0.06 b	0.81 \pm 0.04 c	0.68 \pm 0.03 d	0.65 \pm 0.02 e	0.72 \pm 0.06 d
Surface area (mm ²)	8.94 \pm 0.61 e	10.20 \pm 0.53 d	10.97 \pm 0.67 d	12.30 \pm 0.66 c	13.68 \pm 0.84 b	18.55 \pm 0.94 a
Bud length (mm)		3.87 \pm 0.43 e	8.61 \pm 0.88 d	15.89 \pm 1.26 c	25.51 \pm 1.08 b	30.89 \pm 1.07 a
Root length (mm)						13.55 \pm 0.74

dispersal (Ruiz-Montoya et al. 2012; Darnell et al. 2015; Carthey et al. 2016). Volume was determined using the water displacement method (Ruiz-Montoya et al. 2012). Density was calculated by dividing mass by volume. Superficial area was retrieved using Vistar Image 4.0 after obtaining the top and frontal images using a stereomicroscope with a digital camera.

Flume experiments investigating the secondary dispersal of surficial and sedimentary seeds

Hydrodynamic for seeds initiate secondary dispersal were simulated in a 20 m-long and 2 m-wide flume facility, which was filled with saline water (salinity of 10) pumped directly from the adjacent artificial tidal creek (Fig. 2). The inundation depth in the flume was kept constant at 0.3 m, allowing uniform and controllable flow conditions and ensuring the highest flow velocity. Following the protocols of most empirical studies on seed dispersal in coastal systems (Van der Stocken et al. 2015; Meysick et al. 2019), only current was applied in the flume experiments, representing a simplified approach, which did not consider the wave action that would cause erosion of the sediment used. This allows us to distinguish the seed lift-off behavior controlled by germination

features from that controlled by sediment erosion. The maximum streamwise velocity that could technically be achieved was 0.5 m s⁻¹ without waves, consistent with the peak near-bed flow velocity during spring tide at the front of the saltmarsh edge in the CDNR (Shi et al. 2012). The experiments were performed on sediment-filled steel discs with diameter of 0.6 m (i.e., surface area of 0.28 m²) and depth of 0.2 m. The sediment used (with a D50 of 27.62 μ m), was collected from a natural tidal flat of the CDNR, without visible biofilm coverage, and was defaunated by inducing anoxia under airtight tanks for 4 weeks, to eliminate the potential impact of macrobenthos. These experimental discs can be accurately placed into the reserved space at the tail of the flume, thus making the sediment surface flush with the flume bed (Fig. 2).

Prior to the experiment, 50 seeds of one species at one of the six stages were randomly placed on the sediment surface (hereafter, the surficial seeds), to simulate the seeds retained on the tidal flat surface after primary dispersal. At each flume run, the experimental disc with the 50 seeds was slowly submerged, after which the flow velocity was increased in a stepwise manner. The flow speed started at 0 m s⁻¹ and the velocity was increased in steps of 0.1 m s⁻¹ (i.e., 0, 0.1, 0.2, 0.3, 0.4, and 0.5 m s⁻¹). Constant

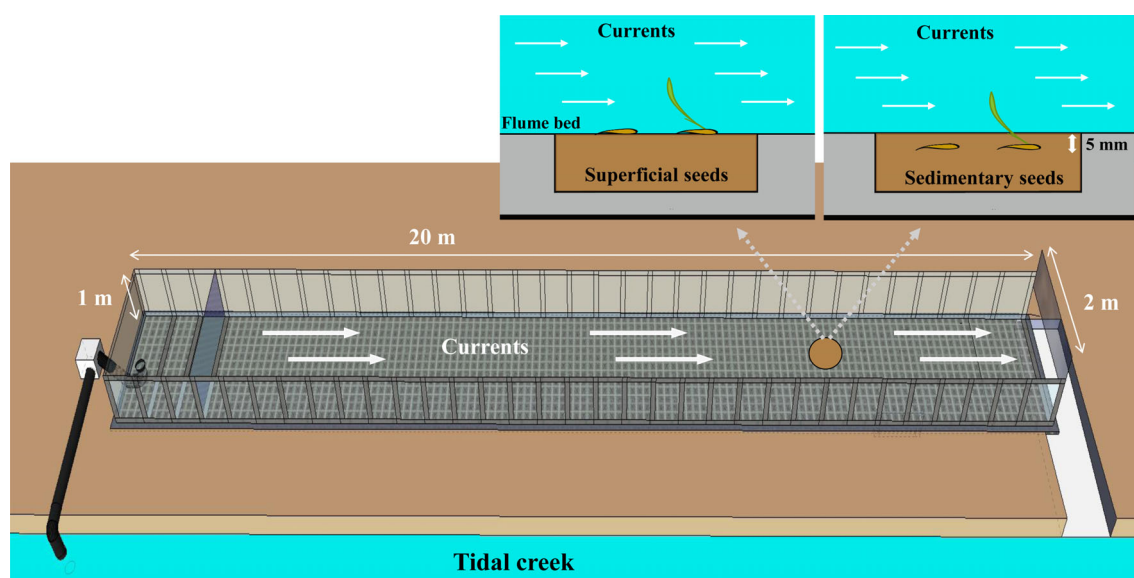


Fig. 2. Schematic representation of the flume used to study variation in the seed lift-off ratio with current velocities and seed germination stages. The reserved space at the tail of the flume served as the experimental area filled with sediment, and seeds were randomly placed at the sediment surface (i.e., superficial seeds, to simulate seeds retained on the tidal flat surface after the primary dispersal) or buried at a depth of 5 mm (i.e., sedimentary seeds, to simulate seeds stored in the local soil bank after the primary dispersal).

flow was held for 5 min, so that each flume run lasted for 30 min. Current speeds were measured using an acoustic Doppler velocimeter (Vectrino Profiler, Nortek, Norway). The lift-off ratio $[R_{LO} = (50 - N)/50 \times 100\%$, where N is the number of remaining seeds] of seeds was recorded following the application of each velocity. Each of the six seed stages was tested five times, giving 60 (= two species \times six seed stages \times five replicates) flume runs in total.

To verify whether seeds stored in the local soil bank will disperse due to changes in germination state, a second flume experiment was performed, in which the seeds were lightly pressed into the sediment (ca. 5 mm), while the bud remained exposed (hereafter, the sedimentary seeds). For simplification, only one burial scenario was considered. All flume settings were consistent with the previous round of experiments. Similarly, the seed lift-off ratio was recorded during five replicate runs for each of the six seed-stages per species.

Abiotic parameters in the rapid colonization area

To verify whether changing physical factors between the primary seed dispersal period (October) and the seedling establishment period (April) relate secondary dispersal to the moment of observed rapid colonization in the CDNR, hydrodynamic forces from current as well as bed elevation changes (i.e., accretion/erosion) were measured in situ at both the *Scirpus*- and *Spartina*-sites (Fig. 1b). Tidal current velocity and direction were measured using an Electromagnetic Current Meter (ALEC AEM-USB, JFE Shoji Trade Corporation, Japan) in eight consecutive tidal cycles during the spring tide in October 2017 and April 2018. At the same time, a Tide Logger (RBR, RBR Ltd., Canada) was deployed

to measure water depth (Fig. 1g,k). All instruments were mounted 5 cm above the mudflat surface and programmed to record measurements every 5 min (sample counter = 30, interval = 1 s). Bed elevation changes were determined monthly from October 2017 to July 2018 using the markers established in the mudflat. Twenty wooden poles (1.5 m long), configured in 10 rows and two columns, were inserted into the sediment at 30 m intervals at each site (Fig. 1g,k). Each pole was exposed about 0.4 m from the sediment surface. The initial elevations of the mudflat surface were set to zero as a reference elevation and the bed elevation changes were measured as the relative positive or negative changes from the initial elevations (Zhu et al. 2012). Data collected from all markers were averaged to evaluate local bed elevation changes.

The water level and temperature were also considered the key physical factors affecting seed germination and establishment (Schwarz et al. 2011; Liu et al. 2016; Zhu et al. 2020a). Daily tide and meteorological data for CDNR were obtained for the period from October 2017 to July 2018. The highest monthly water level and the monthly average temperature were also determined. Tide information was collected at Sheshan station and obtained from the tide tables published by the National Marine Data and Information Service (<http://www.nmdis.gov.cn>). Temperature data was collected from the meteorological observatory at CDNR and provided by the local management office.

Statistical analysis

Two-way ANOVAs with LSD post hoc test was used to assess differences in seed morphological parameters among

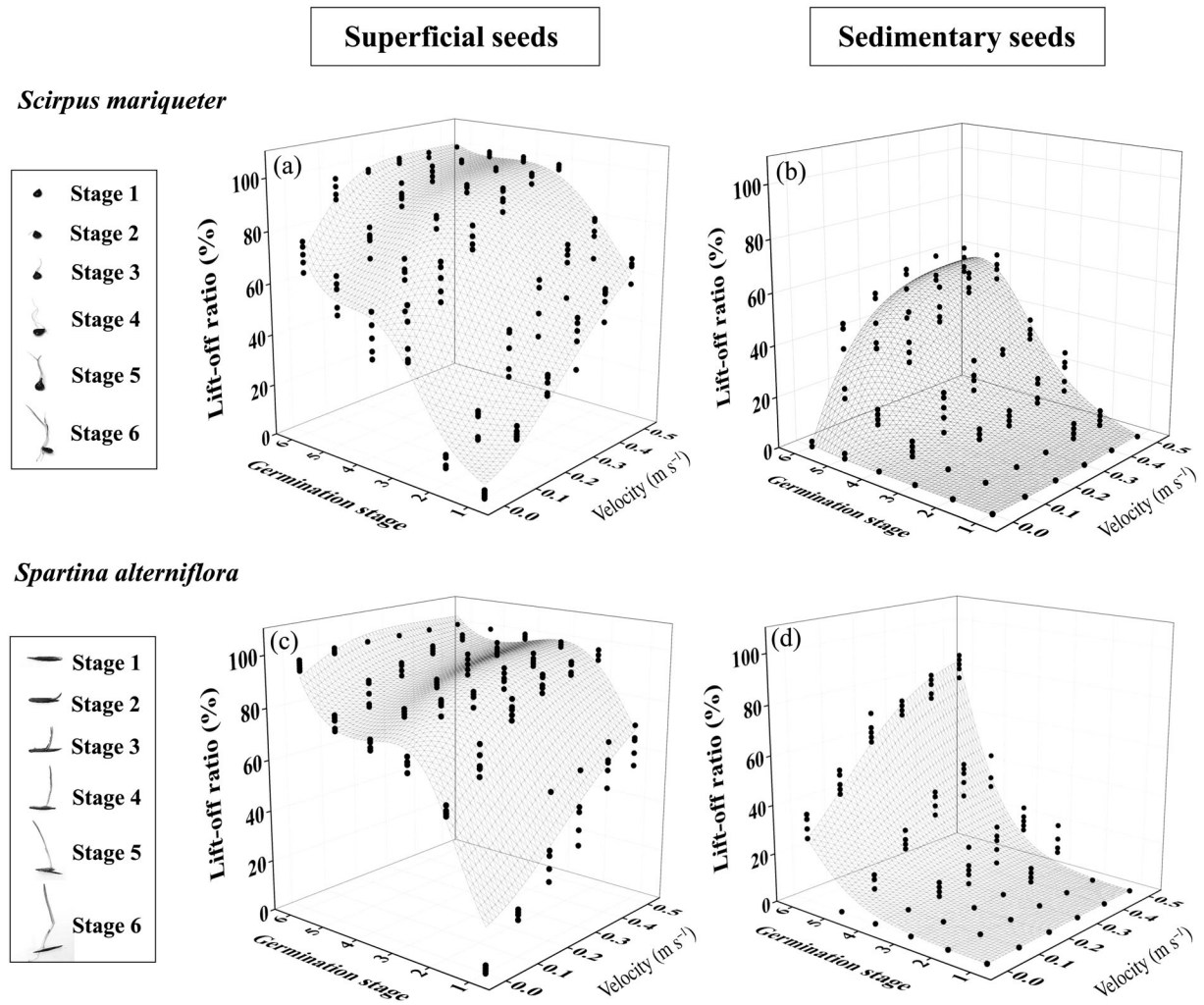


Fig. 3. Lift-off ratio (i.e., secondary dispersal onset) of superficial seeds at the six germination stages of *Scirpus mariqueter* (a) and *Spartina alterniflora* (c) under different current velocities in flume experiments; and lift-off ratio of sedimentary seeds at the six germination stages of *S. mariqueter* (b) and *S. alterniflora* (d) under different current velocities in flume experiments. (Superficial seeds are those that were placed on the sediment surface, to simulate seeds retained on the tidal flat surface after primary dispersal; sedimentary seeds were buried at a depth of 0.5 cm, to simulate those stored in the local soil bank after the primary dispersal).

different germination stages and species. Three-way ANOVAs was adopted to test the effect of germination stages, current velocities, and species on the seed lift-off ratio. The LSD test was used to assess multiple comparisons between germination stages and current velocities. The effect of morphological traits on seed lift-off ratio was analyzed by specifying a generalized linear model (GLM) with “family” = “quasipoisson” because of overdispersion (cf. Zhu et al. 2014; Lai et al. 2020). All statistical analyses were performed in R (<https://www.r-project.org>), applying a significance level of $\alpha = 0.05$.

Results

Variation in seed morphological characteristics during germination

For seeds of both species, there was a significant increase in mass, volume, surface area, and bud length during germination

($P < 0.001$, Table 1). It took 0–5 d for wet seeds that had undergone vernalization to form a bud (see pictures in the heading rows of Table 1), and about 20 d for the first root to grow. With

Table 2. Results of generalized linear models testing the effects of morphological factors on the potential of seeds secondary dispersal onset.

Model	Estimate	Standard error	t-Value	p-Value
Intercept	4.159	0.355	11.701	<0.001***
Mass	0.038	0.12	0.314	0.754
Volume	3.687	8.061	0.457	0.648
Density	−0.933	0.330	−2.828	0.005**
Surface area	0.169	0.102	1.655	0.098
Bud length	0.021	0.007	2.868	0.004**

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

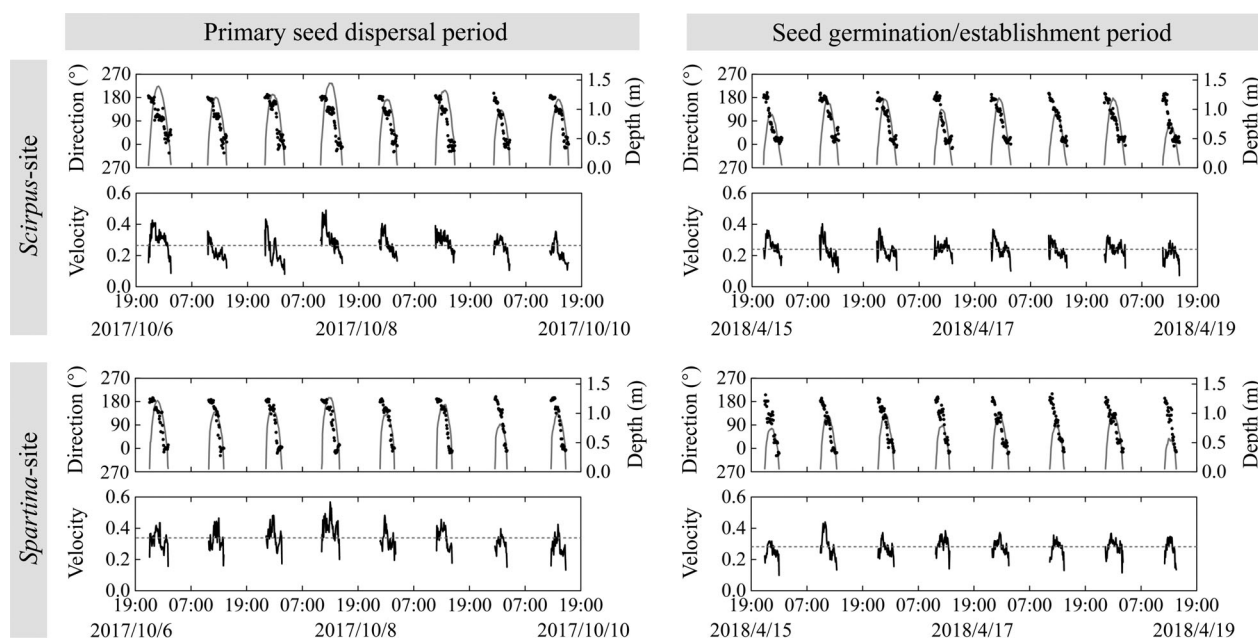


Fig. 4. Comparison of current conditions during the primary seed dispersal period (i.e., October 2017) and the seed germination/establishment period (i.e., April 2018) at two case sites (i.e., *Scirpus*-site and *Spartina*-site). For each section (i.e., one site and one period), the solid gray line on the upper facet represents the water depth; the black solid point on the upper facet represents the current direction (0° indicates east; 180° indicates west); the black solid line on the lower facet represents the current velocity; the gray dashed line on the lower facet indicates the average current velocity during the overall measurement period. At both sites, there was a rapid colonization of seedlings when local seed banks were largely absent, suggesting the co-occurrence of massive seed dispersal and seedling establishment in spring. Comparing the hydrodynamics of these two key periods can verify the relative importance of the hydrodynamic environment in spring to this process.

the extension of buds after germination, the change in seed volume was greater than the change in seed mass, resulting in a significant decrease in seed density with a species-specific pattern (Table 1). For *S. maritima*, seed density was markedly reduced from stage 2 to stage 3, whereafter seed density was lower than that of seawater ($1.02\text{--}1.09\text{ g cm}^{-3}$), implying that the wet seeds would regain buoyancy. In *S. alterniflora*, this change in seed density occurred from stage 1 to stage 2 (Table 1). The seed density of both species increased slightly in the late germination stage (from stage 4 to stage 5 for *S. maritima*, and from stage 5 to stage 6 for *S. alterniflora*), because the seeds invested more in the increase in mass rather than the extension of buds (Table 1). When comparing *S. maritima* with *S. alterniflora*, there were significant differences in mass, volume, and surface area ($P < 0.001$), but no significant difference in density and bud length ($P > 0.05$).

Secondary dispersal onset of surficial seeds

Germination stages and current velocity had significant effects on the onset of seed hydrochory ($P < 0.001$), regardless of species. Overall, increasing germination stage and increasing current velocity caused a non-linear acceleration in the lift-off ratio of wet seeds placed on top of the sediment surface (Fig. 3a,c). Considering the effects of germination, there was a significant difference in lift-off ratio between stages ($P < 0.001$), with a rapid increase observed from stage 2 to stage 3 for *S. maritima* and from stage 1 to stage 2 for

S. alterniflora (Fig. 3a,c). This discrepancy in sensitivity to germination stage may be attributed to differences in seed morphological traits between those two species among germination stages (see Table 1 and the section “Effects of morphological factors on the secondary dispersal of germinated seeds”). Additionally, the sensitivity of the surficial seed lift-off ratio to the germination stages increased with increasing current velocity (Fig. 3a,c). A significant difference in the lift-off ratio was also observed between species ($P < 0.001$). The superficial seeds of *S. alterniflora* would begin to disperse easier than those of *S. maritima* would, because the latter require growth to an older stage (meaning longer in-situ germination time) before being lifted under the same hydrodynamic disturbance.

Secondary dispersal onset of sedimentary seeds

Under the scenario where seeds were buried with an exposed bud, germination stage and current velocity had significant effects on the onset of seed hydrochory ($P < 0.001$), regardless of species. No significant difference in the lift-off ratio was observed between stages 1 and 2 ($P > 0.05$), while the lift-off ratio of sedimentary seeds among the last four stages (i.e., stage 3–6) was significantly higher than that of sedimentary seeds among the first two stages (i.e., stage 1–2) ($P < 0.001$, Fig. 3b,d). In the treatment where seeds were placed under still water (0 m s^{-1}), there was limited dispersal initiation in sedimentary seeds in the first four stages (i.e., 0% lift-off ratio) (Fig. 3b,d), while the lift-off ratio of

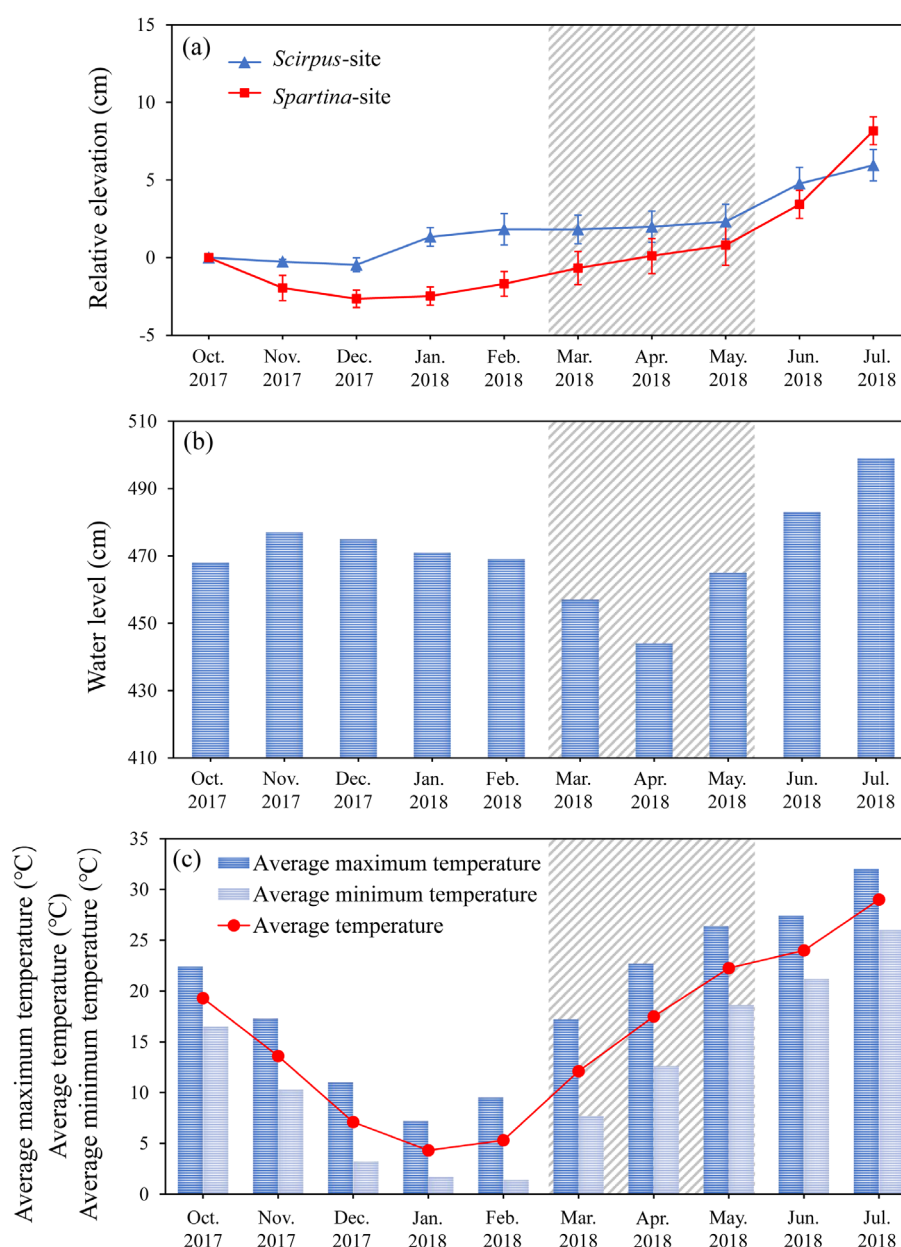


Fig. 5. (a) Net bed elevation changes in terms of the relative elevation change at the two case sites (i.e., *Scirpus*-site and *Spartina*-site, where rapid colonization occurred) between October 2017 and July 2018. (b) Tide regimes in the CDNR in terms of the highest monthly water level from October 2017 to July 2018. Tide information was collected at the Sheshan station close to the two case sites. (c) Monthly temperature dynamics in the CDNR between October 2017 and July 2018. Temperature data were collected from the meteorological observatory within the CDNR. The gray twill belt indicates the key months covering the period of seed germination and seedling establishment.

sedimentary seeds increased significantly from stage 5 to 6. ($P < 0.05$); however, this was only 0.8% for *S. maritima* compared to 31.2% for *S. alterniflora* (Fig. 3b,d). Under flowing water (even at a velocity of 0.1 m s^{-1}), the lift-off ratio of sedimentary seeds became more sensitive to germination stage, and this sensitivity accelerated with increasing velocity (Fig. 3b,d). Additionally, there was a significant difference in lift-off ratio between species ($P < 0.001$).

Effects of morphological factors on the secondary dispersal of germinated seeds

There was a strong correlation between changes in physical seed traits during germination and the potential of seed secondary dispersal onset (Table 2). The results of the GLM revealed that changes in density and bud length during germination significantly affected the lift-off rate of seeds (Table 2). The reduced density enabled the negatively buoyant wet seeds to float, while

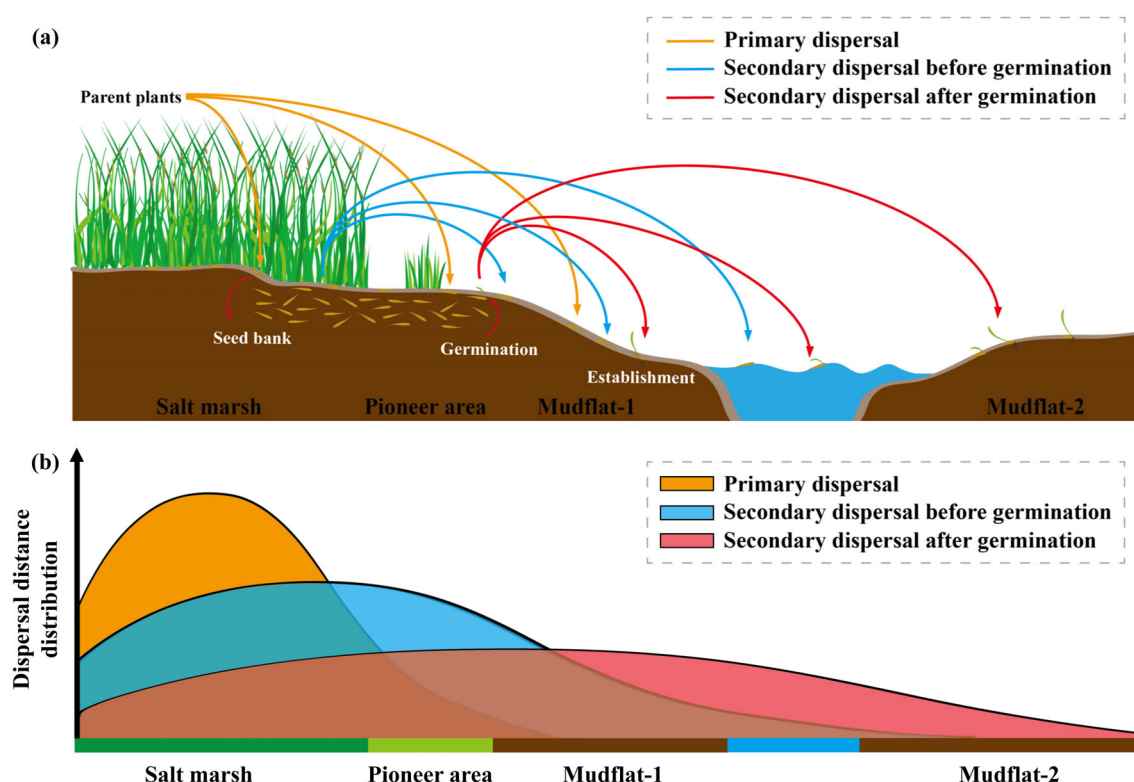


Fig. 6. (a) Schematized seed dispersal processes of saltmarsh species. *Primary dispersal*: Seed departure from the parent plant to the sediment surface or added to the seed bank (from autumn to early winter). *Secondary dispersal before germination*: Additional movement of seeds following primary dispersal, eventually remaining at the seed bank for establishment (from late autumn to early spring). *Secondary dispersal after germination*: Seeds trapped within microsites regain their floating ability after germination and drift with the current, leading to a direct connection with establishment (during spring). Mudflat-1 refers to the bare area adjacent to the vegetation area, while Mudflat-2 refers to the bare area distant to the vegetation area, both assumed suitable for establishment. (b) Schematized dispersal distance distribution of saltmarsh species under different dispersal processes.

the extended bud played the role of a “sail” making the wet seeds more susceptible to hydraulic drag. The coupling effect of these two morphological factors greatly reduced the lift-off velocity of seeds, allowing wet seeds trapped in micro-sites to initiate secondary dispersal even in calm tidal environments.

Abiotic parameters in the rapid colonization area

In-situ hydrodynamic measurements found similar current conditions for both sites: (1) the flood current velocity was higher than the ebb current velocity, (2) the current direction rotated clockwise, tending to be westward (onshore) during the early flood, alongshore during high tide, and eastward or southeastward (offshore) during late ebb (Fig. 4). Specifically, the current velocity at spring tide ranged from 0.08 to 0.49 m s⁻¹ (average, 0.26 m s⁻¹) in October, 2017 and from 0.07 to 0.40 m s⁻¹ (average, 0.24 m s⁻¹) in April, 2018 at the *Scirpus*-site, but ranged from 0.13 to 0.57 m s⁻¹ (average, 0.34 m s⁻¹) in October, 2017 and from 0.09 to 0.44 m s⁻¹ (average, 0.28 m s⁻¹) in April, 2018 at the *Spartina*-site (Fig. 4). These results showed that the hydrodynamic force from the current in the period of seed germination and establishment (i.e., April) was lower than that in the period of primary seed dispersal (i.e., October), regardless of site.

Considering the tide environment on a larger scale, the highest monthly water level at the CDNR between March and May (covering the period of seed germination and establishment) was markedly lower than that in other months (Fig. 5b). This also indicates relatively weak tidal currents, as these are locally proportional to tidal amplitude. This relatively weak hydrodynamic environment meant that wet seeds captured during the primary dispersal in October were likely to withstand the hydrodynamic disturbance in April and remain in their microsites. This is supported by the results of flume experiments (Fig. 3), showing that the relatively weak hydrodynamic force in April (with mean current velocity no more than 0.30 m s⁻¹) did not perform well in moving wet seeds (i.e., stage 1; with lift-off ratio no more than 50% for surficial wet seeds and 0% for sedimentary wet seeds). However, the flume experiments also showed that the April tides are strong enough to trigger re-displacement of most germinated seeds (e.g., the lift-off ratio was no less than 90% and 50% for surficial seeds and sedimentary seeds in stage 6, respectively), thereby initiating secondary dispersal toward the tidal flat.

Based on the local average minimum temperature, from March onwards the threshold temperature at which seeds break dormancy (i.e., above 4°C) was surpassed (Fig. 5c). The

average temperatures in April and May were sufficient to meet the needs of seed germination and seedling growth (Fig. 5c). Changes in the bed elevation on the tidal flat revealed that erosion occurred mainly in autumn and winter (i.e., from October to January), while accretion occurring in spring and summer (i.e., from February to July, Fig. 5a). Particularly, in the months covering the period of seed germination and establishment (i.e., from March to May), the tidal flat at the *Scirpus*-site was in a stable state (compared with other months), while that at *Spartina*-site was in a slight accretion (Fig. 5a). This indicates that the local bed elevation changes enabled any germinated seeds that would arrive at the tidal flat to be trapped and buried, as the result from secondary dispersal.

Discussion

An in-depth understanding of dispersal and establishment processes is essential when using natural processes for the creation or restoration of saltmarsh ecosystems. To our knowledge, the present study is the first to determine how germination features kick-start secondary seed dispersal, serving as a starting point for more extensively dissecting the mechanism of sudden saltmarsh establishment. We found that during germination, *S. mariqueter* and *S. alterniflora* seeds adjust their specific lift-off, thereby greatly increasing the probability of seed re-dispersal during gentle upcoming tides. Combining these findings with in-situ measurements in the field, we revealed that the local tidal currents, the sedimentary regime, and the temperature regime, increased the proportion of seeds available to sudden establishment due to secondary-dispersal, and may therefore be one explanation for the observed sudden saltmarsh establishment.

Extension of saltmarsh dispersal processes

Previous studies have shown that the departure of propagules from parent plants (i.e., primary dispersal) and the movement of propagules between sites (i.e., secondary dispersal) are standard processes through which species colonize new habitats (Chang et al. 2008; Friess et al. 2012; Van der Stocken et al. 2019). We observed an extension of secondary dispersal controlled by germination feature (Fig. 6a). This process begins after bud emergence, driven by regaining buoyancy (i.e., reduced density) and increasing the surface-drag forces (i.e., extended bud), leading to a direct connection with post-dispersal establishment. Unlike the passive re-movement of wet seeds triggered by strong wave-driven hydrodynamics (Chang et al. 2008), such secondary dispersal after germination can occur during calm tidal environments. This process is particularly important for seeds covered by a thin layer of sediment. After germination, the buds that break out of the sediment are directly exposed to the tidal component, resulting in seed entrainment under the coupling of drag force and buoyancy, without requiring the shift of critical currents

and waves from those that transport seeds to those that erode sediments (Koch et al. 2010). Our results imply that the movement of saltmarsh seeds may be more frequent in spring than previously anticipated.

Similar to the general mechanisms of primary and secondary seed dispersal before germination (Koch et al. 2010; Van der Stocken et al. 2015; Cummings et al. 2016), the current velocity, as shown in this study, also played an additive role in seed dispersal after germination, which greatly amplified the sensitivity of seed lift-off to germination stages. For example, the rate of *S. alterniflora* seed lift-off in stage 2 increased by 40% compared to that in stage 1 under still water, while the application of 0.1 m s^{-1} current increased the rate of seed lift-off by a further 20%. Although not tested in this study, secondary seed dispersal after germination would also benefit from wave action, as orbital water movements linked to wave action can more effectively dislodge seeds (also sediments) vertically, considering the increased surface-drag forces (Chang et al. 2008; Koch et al. 2010; Zhu et al. 2020a). However, wave action may also play an antagonistic role in the dispersal process, because the dislodged seeds orbit (oscillate) around their position while the wave propagates, thereby slowing down relative to the prevailing current component (Lai et al. 2020).

Compared with primary and secondary dispersal before germination, seed re-dispersal after germination would benefit from a longer floating period to enable a larger dispersal distance (Fig. 6b). This is because after germination, seed density decreases while surface area increases, making them more buoyant and susceptible to hydrodynamic drag (Darnell et al. 2015). An extended dispersal ability of seeds after seedling development has been reported in previous studies for submersed angiosperm species (including *Ruppia maritima* L., *Potamogeton perfoliatus* L., and *Stuckenia pectinata* L., Koch et al. 2010). The germinated seeds have an increased probability of dispersing to distant populations and new locations that lack an adjacent saltmarsh (Fig. 6). However, the exact or approximate dispersal distance for saltmarsh species during each dispersal stage remains unclear, since the dispersal distance of (germinated) seeds would not be determined solely by the theoretical buoyance-dependent potential, but also by various abiotic conditions, such as tidal rhythm, current velocity, and nearshore structure (Ruiz-Montoya et al. 2012; Wang et al. 2018; Van der Stocken et al. 2019). Here, we conceptually compared the dispersal potential of saltmarsh seeds at different dispersal stages based on existing information (Fig. 6b), aiming to provide a theoretical framework for future in-depth quantitative research.

Can we explain observed rapid colonization in the field?

Considering the CDNR in the Yangtze Estuary, many cohorts of *S. mariqueter* and *S. alterniflora* seedlings suddenly appeared at the mudflat during spring (Fig. 1), despite earlier measurements showing that local seed banks were largely absent (Yuan et al. 2020; Zhao et al. 2020a). This indicates the

massive dispersal of seeds and/or seedlings during spring, which is consistent with findings from a field survey revealing a strong reduction in seed reserves within nearby saltmarshes during spring (Yuan et al. 2020). Seeds trapped within the saltmarsh after local primary dispersal will most likely be waterlogged and lose buoyancy from late autumn to early spring. Moreover, they may be covered by plants or slightly buried with some sediment. Re-displacement of such wet seeds will therefore require high-energy hydrodynamics (Chang et al. 2008; Zhu et al. 2014). This is consistent with the results of our flume experiment regarding partial seed burial, in which sedimentary seeds (i.e., stage 1) remained in place without displacement even under the maximum velocity (i.e., 0.5 m s^{-1}). Although monitoring was not performed in this study, the local hydrodynamic force in winter (after the primary dispersal) was clearly not strong enough to displace the wet seeds further, because the seed bank reserves in the mudflat and adjacent saltmarsh remained stable until spring (Yuan et al. 2020; Zhao et al. 2020a). Surprisingly, in-situ measurements during autumn and spring revealed that local hydrodynamics and associated erosion at both sites did not increase sharply when the sudden colonization event happened (i.e., spring). We explain this discrepancy using the effect of germination, which greatly reduces the required lift-off velocity, enhancing the probability of leaving the local habitat even during a gentle upcoming tide. Additionally, the mild hydrodynamics combined with the slight sediment accretion at the mudflats in the CDNR, provided an opportunity for seedling establishment (Balke et al. 2014; Hu et al. 2015b; Poppema et al. 2019).

The tidal current in the CDNR study area was mainly rotational, and the flood current velocity was higher than that of the ebb current (Ge et al. 2012; Shi et al. 2012; Hu et al. 2015a). At the *Scirpus*-site, the current direction tended to be onshore during the early flood; alongshore at high tide; and offshore during the late ebb, while the vegetation mainly expanded alongshore (from the southeast to the northwest, Fig. 1). We speculate that seeds from nearby sources were more likely to lift-off during the early flood and started to disperse toward the shore, before following the tide to be transported alongshore. Seeds were subsequently able to settle alongshore or offshore during the late ebb. The direction of the high tide determined the main direction of seed dispersal, while the long period and low-flow velocity of the ebb benefited the settlement of negatively buoyant seeds and the interception of positively buoyant (germinated) seeds. However, the situation at the *Spartina*-site was more complicated; the emergence of vegetation (*S. alterniflora*) was the result of re-invasion, which had no nearby source, but multiple distant sources in multiple directions (Zhao et al. 2020a,b). Further research is needed to determine whether the long-distance vegetation invasion is consistent with the tidal current pattern.

Unlike negatively buoyant wet seeds, whose dispersal distances are highly related to their settling velocity in seawater

(Koch et al. 2010; Pereda-Briones et al. 2018), the variation in spatial deposition of positively buoyant seeds following secondary dispersal was mostly related to landscape elements (e.g., plants, topography), which trap/retain seeds, than to the theoretical buoyance-dependent probability of dispersal distance traveled from the seed source (Levine and Murrell 2003). The tidal flat of the CDNR in spring is usually characterized by highly heterogeneous micro-topographic structures, such as hummocks and hollows, as well as caves dug by benthos (e.g., crabs, mudskippers). These structures act as “barriers” or “shelters,” which can effectively trap and retain (positively buoyant) seeds when they periodically contact with the substrate during the semi-diurnal tidal cycle (Wang et al. 2018; Xie et al. 2019; Qiu et al. 2021). Interestingly, recent studies have reported that seedling establishment at new sites tends to occur on raised micro-topography covered by biostabilizers (such as diatom biofilms and fibrous algae *Vaucheria*; Fivash et al. 2020; Van de Vijssel et al. 2020), implying that biostabilizers may also provide a viable conduit for trapping and retaining the dispersed (germinated) seeds. Moreover, these biostabilizers can shape the local microhabitat by affecting sediment erodibility (Van de Vijssel et al. 2020), water content, and dissolved oxygen content (Fivash et al. 2020), and may therefore regulate the rooting rate of seeds, affecting their anchoring ability.

The mechanisms through which the seeds become established in the tidal flat are not yet fully clear. Balke et al. (2011) emphasized that fast root growth after reaching a new location is particularly important for anchoring mangrove propagules sufficiently in order to withstand drag force from the current and wave during establishment. However, a low germination rate is a general characteristic of saltmarsh species (Xiao et al. 2009, 2016; Balke et al. 2014). Under the culture conditions used in this study, it took about 20 d after vernalization for *S. mariqueter* and *S. alterniflora* to grow their first roots; this speed means that a short inundation-free period is not suitable for establishment. Seed burial may overcome this problem (Zhu et al. 2020a). Alternatively, roots that have grown before the secondary dispersal will enable the germinated seed to stick more easily to sediment particles (Koch et al. 2010), thereby accelerating the anchorage and reducing the length of the required windows of opportunity. A similar mechanism has been observed for several riparian invasive species and mangrove species (Rouified et al. 2011; Lamberti-Raverot et al. 2019; Wang et al. 2019), which would benefit from dispersal after germination, in terms of increased dispersal distance and enhanced early survival of seedlings.

Implications for ecological restoration under climate change

Recently, the importance of dispersal processes on the restoration success of ecosystems has been emphasized in a number of studies (Prach et al. 2015; Crouzeilles and Curran 2016; Aavik and Helm 2018), which suggest managing the

connectivity between populations to maintain the long-term success of restoration measures (Bommarco et al. 2013; Kovács-Hostyánszki et al. 2017). The findings of this study contribute critical data on the poorly documented germination-features related to secondary dispersal mechanism of wet seeds of pioneer saltmarsh species. This insight is highly relevant, especially for seeds with limited floating ability (e.g., *Salicornia europaea*, which can only float for a few hours. Huiskes et al. 1995), since our results underscore the extended dispersal ability (in terms of both period and distance) of seeds after germination. Dispersal of germinated seeds increases the likelihood of connectivity between populations. In addition, human-aided dispersal of germinated halophyte seeds just before a window of opportunity (i.e., a hydrodynamically calm period allowing dispersed seeds/seedlings to settle and grow; Balke et al. 2011) in spring, may be an option for large-scale restoration in areas without a nearby natural seed source. The latter may become increasingly important if marshes are targeted for coastal defense (e.g., see suggestion in Zhu et al. 2020b).

Conversely, the present results on the secondary-dispersal of germinated seeds may also represent an unrecognized bottleneck for widely promoted seed-based restoration strategies (e.g., Yuan et al. 2020). This may be counterbalanced by maintaining a suitable sedimentary rate to facilitate seed retention and subsequent successful establishment. In general, seeds and seedlings do better under accreting than eroding conditions (Bouma et al. 2016; Cao et al. 2018). Hence, seed-based revegetation policies should preclude the risk of sowed seed displacement after germination that allows for higher restoration yields, especially for coastal systems with a low sediment supply. This may be achieved by the supply of dredging materials (Mendelssohn and Kuhn 2003; Temmerman et al. 2013) specifically during the crucial period of seed germination and establishment, or by using biodegradable auxiliary structures (e.g., Temmink et al. 2020) that locally suppress physical stress. The present findings on secondary dispersal provide important insights to further optimize restoration strategies.

Data availability statement

The data that support the findings of this study are openly available in 4TU.Research Data at <https://doi.org/10.4121/14479548>

References

- Aavik, T., and A. Helm. 2018. Restoration of plant species and genetic diversity depends on landscape-scale dispersal. *Restor. Ecol.* **26**: S92–S102. doi:[10.1111/rec.12634](https://doi.org/10.1111/rec.12634)
- Angelini, C., and B. R. Silliman. 2012. Patch size-dependent community recovery after massive disturbance. *Ecology* **93**: 101–110. doi:[10.1890/11-0557.1](https://doi.org/10.1890/11-0557.1)
- Balke, T., T. J. Bouma, E. M. Horstman, E. L. Webb, P. L. A. Erftemeijer, and P. M. J. Herman. 2011. Windows of opportunity: Thresholds to mangrove seedling establishment on tidal flats. *Mar. Ecol. Prog. Ser.* **440**: 1–9. doi:[10.3354/meps09364](https://doi.org/10.3354/meps09364)
- Balke, T., P. M. J. Herman, and T. J. Bouma. 2014. Critical transitions in disturbance-driven ecosystems: Identifying windows of opportunity for recovery. *J. Ecol.* **102**: 700–708. doi:[10.1111/1365-2745.12241](https://doi.org/10.1111/1365-2745.12241)
- Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* **81**: 169–193. doi:[10.1890/10-1510.1](https://doi.org/10.1890/10-1510.1)
- Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: Harnessing ecosystem services for food security. *Trends Ecol. Evol.* **28**: 230–238. doi:[10.1016/j.tree.2012.10.012](https://doi.org/10.1016/j.tree.2012.10.012)
- Bouma, T. J., and others. 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities and steps to take. *Coast. Eng.* **87**: 147–157. doi:[10.1016/j.coastaleng.2013.11.014](https://doi.org/10.1016/j.coastaleng.2013.11.014)
- Bouma, T. J., and others. 2016. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics. *Limnol. Oceanogr.* **61**: 2261–2275. doi:[10.1002/lno.10374](https://doi.org/10.1002/lno.10374)
- Bull, W. B. 1979. Threshold of critical power in streams. *Geol. Soc. Am. Bull.* **90**: 453–464. doi:[10.1130/0016-7606\(1979\)90<453:TOCPIS>2.0.CO;2](https://doi.org/10.1130/0016-7606(1979)90<453:TOCPIS>2.0.CO;2)
- Cao, H. B., Z. C. Zhu, T. Balke, L. Q. Zhang, and T. J. Bouma. 2018. Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration. *Limnol. Oceanogr.* **63**: 647–659. doi:[10.1002/lno.10657](https://doi.org/10.1002/lno.10657)
- Cao, H. B., Z. C. Zhu, R. James, P. M. J. Herman, L. Q. Zhang, L. Yuan, and T. J. Bouma. 2020. Wave effects on seedling establishment of three pioneer marsh species: Survival, morphology and biomechanics. *Ann. Bot.* **125**: 345–352. doi:[10.1093/aob/mcz136](https://doi.org/10.1093/aob/mcz136)
- Carthey, A. J., K. A. Fryirs, T. J. Ralph, H. Bu, and M. R. Leishman. 2016. How seed traits predict floating times: A biophysical process model for hydrochorous seed transport behaviour in fluvial systems. *Freshw. Biol.* **61**: 19–31. doi:[10.1111/fwb.12672](https://doi.org/10.1111/fwb.12672)
- Chang, E. R., R. M. Veeneklaas, R. Buitenwerf, J. P. Bakker, and T. J. Bouma. 2008. To move or not to move: Determinants of seed retention in a tidal marsh. *Funct. Ecol.* **22**: 720–727. doi:[10.1111/j.1365-2435.2008.01434.x](https://doi.org/10.1111/j.1365-2435.2008.01434.x)
- Couvillion, B. R., and H. Beck. 2013. Marsh collapse thresholds for coastal Louisiana estimated using elevation and vegetation index data. *J. Coast. Res.* **63**: 58–67. doi:[10.2112/SI63-006.1](https://doi.org/10.2112/SI63-006.1)
- Crouzeilles, R., and M. Curran. 2016. Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *J. Appl. Ecol.* **53**: 440–448. doi:[10.1111/1365-2664.12590](https://doi.org/10.1111/1365-2664.12590)
- Culot, L., M. C. Huynen, and E. W. Heymann. 2015. Partitioning the relative contribution of one-phase and two-

- phase seed dispersal when evaluating seed dispersal effectiveness. *Methods Ecol. Evol.* **6**: 178–186. doi:[10.1111/2041-210X.12317](https://doi.org/10.1111/2041-210X.12317)
- Cunnings, A., E. Johnson, and Y. Martin. 2016. Fluvial seed dispersal of riparian trees: Transport and depositional processes. *Earth Surf. Process. Landf.* **41**: 615–625. doi:[10.1002/esp.3850](https://doi.org/10.1002/esp.3850)
- Darnell, K. M., D. M. Booth, E. W. Koch, and K. H. Dunton. 2015. The interactive effects of water flow and reproductive strategies on seed and seedling dispersal along the substrate in two sub-tropical seagrass species. *J. Exp. Mar. Biol. Ecol.* **471**: 30–40. doi:[10.1016/j.jembe.2015.05.006](https://doi.org/10.1016/j.jembe.2015.05.006)
- Dorrell, R. M., L. A. Amy, J. Peakall, and W. D. McCaffrey. 2018. Particle size distribution controls the threshold between net sediment erosion and deposition in suspended load dominated flows. *Geophys. Res. Lett.* **45**: 1443–1452. doi:[10.1002/2017GL076489](https://doi.org/10.1002/2017GL076489)
- Fivash, G. S., J. Van Belzen, R. J. M. Temmink, K. Didderen, W. Lengkeek, T. Van der Heide, and T. J. Bouma. 2020. Elevated micro-topography boosts growth rates in *Salicornia procumbens* by amplifying a tidally driven oxygen pump: Implications for natural recruitment and restoration. *Ann. Bot.* **125**: 353–364. doi:[10.1093/aob/mcz137](https://doi.org/10.1093/aob/mcz137)
- Friess, D. A., K. W. Krauss, E. M. Horstman, T. Balke, T. J. Bouma, D. Galli, and E. L. Webb. 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biol. Rev.* **87**: 346–366. doi:[10.1111/j.1469-185X.2011.00198.x](https://doi.org/10.1111/j.1469-185X.2011.00198.x)
- Ge, J. Z., C. S. Chen, J. H. Qi, P. X. Ding, and R. C. Beardsley. 2012. A dike-groyne algorithm in a terrain-following coordinate ocean model (FVCOM): Development, validation and application. *Ocean Model.* **47**: 26–40. doi:[10.1016/j.ocemod.2012.01.006](https://doi.org/10.1016/j.ocemod.2012.01.006)
- Ge, Z. M., L. Q. Zhang, and L. Yuan. 2015. Spatiotemporal dynamics of salt marsh vegetation regulated by plant invasion and abiotic processes in the Yangtze estuary: Observations with a modeling approach. *Estuaries Coasts* **38**: 310–324. doi:[10.1007/s12237-014-9804-7](https://doi.org/10.1007/s12237-014-9804-7)
- Hinshaw, S. E., C. Tatariw, N. Flournoy, A. Kleinhuizen, C. Taylor, P. A. Sobczyk, and B. Mortazavi. 2017. Vegetation loss decreases salt marsh denitrification capacity: Implications for marsh erosion. *Environ. Sci. Technol.* **51**: 8245–8253. doi:[10.1021/acs.est.7b00618](https://doi.org/10.1021/acs.est.7b00618)
- Hu, Z. J., and others. 2015a. Revegetation of a native species in a newly formed tidal marsh under varying hydrological conditions and planting densities in the Yangtze estuary. *Ecol. Eng.* **83**: 354–363. doi:[10.1016/j.ecoleng.2015.07.005](https://doi.org/10.1016/j.ecoleng.2015.07.005)
- Hu, Z., J. van Belzen, D. van der Wal, T. Balke, Z. B. Wang, M. Stive, and T. J. Bouma. 2015b. Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. *Eur. J. Vasc. Endovasc. Surg.* **120**: 1450–1469. doi:[10.1002/2014JG002870](https://doi.org/10.1002/2014JG002870)
- Huiskes, A. H. L., B. P. Koutstaal, P. M. J. Herman, W. G. Beeftink, M. M. Markusse, and W. De Munck. 1995. Seed dispersal of halophytes in tidal salt marshes. *J. Ecol.* **83**: 559–567. doi:[10.2307/2261624](https://doi.org/10.2307/2261624)
- Kirwan, M. L., S. Temmerman, E. E. Skeehean, G. R. Guntenspergen, and S. Fagherazzi. 2016. Overestimation of marsh vulnerability to sea level rise. *Nat. Clim. Change* **6**: 253–260. doi:[10.1038/nclimate2909](https://doi.org/10.1038/nclimate2909)
- Koch, E. W., M. S. Ailstock, D. M. Booth, D. J. Shafer, and A. D. Magoun. 2010. The role of currents and waves in the dispersal of submersed angiosperm seeds and seedlings. *Restor. Ecol.* **18**: 584–595. doi:[10.1111/j.1526-100X.2010.00698.x](https://doi.org/10.1111/j.1526-100X.2010.00698.x)
- Kovács-Hostyánszki, A., A. Espíndola, A. J. Vanbergen, J. Settele, C. Kremen, and L. V. Dicks. 2017. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecol. Lett.* **20**: 673–689. doi:[10.1111/ele.12762](https://doi.org/10.1111/ele.12762)
- Lai, S., Z. Y. Cheok, T. J. Bouma, S. M. Yaakub, and P. A. Todd. 2020. The relative importance of light and hydrodynamics in the decay and transport of vegetative seagrass fragments. *Estuar. Coast. Shelf Sci.* **232**: 106430. doi:[10.1016/j.ecss.2019.106430](https://doi.org/10.1016/j.ecss.2019.106430)
- Lamberti-Raverot, B., F. Piola, F. Vallier, V. Gardette, and S. Puijalon. 2019. Achene traits involved in the water dispersal of the invasive *Fallopia × bohemica* complex: Variability and dispersal strategies. *Flora* **251**: 88–94. doi:[10.1016/j.flora.2019.01.002](https://doi.org/10.1016/j.flora.2019.01.002)
- Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annu. Rev. Ecol. Syst.* **34**: 549–574. doi:[10.1146/annurev.ecolsys.34.011802.132400](https://doi.org/10.1146/annurev.ecolsys.34.011802.132400)
- Liu, W. W., K. Maung-Douglass, D. R. Strong, S. C. Pennings, and Y. H. Zhang. 2016. Geographical variation in vegetative growth and sexual reproduction of the invasive *Spartina alterniflora* in China. *J. Ecol.* **104**: 173–181. doi:[10.1111/1365-2745.12487](https://doi.org/10.1111/1365-2745.12487)
- Liu, H. Y., X. Z. Qi, H. B. Gong, L. H. Li, M. Y. Zhang, Y. F. Li, and Z. S. Lin. 2019. Combined effects of global climate suitability and regional environmental variables on the distribution of an invasive marsh species *Spartina alterniflora*. *Estuaries Coasts* **42**: 99–111. doi:[10.1007/s12237-018-0447-y](https://doi.org/10.1007/s12237-018-0447-y)
- Marani, M., C. Da Lio, and A. D'Alpaos. 2013. Vegetation engineers marsh morphology through multiple competing stable states. *Proc. Natl. Acad. Sci. USA* **110**: 3259–3263. doi:[10.1073/pnas.1218327110](https://doi.org/10.1073/pnas.1218327110)
- Mcowen, C. J., and others. 2017. A global map of saltmarshes. *Biodivers. Data J.* **5**: e11764. doi:[10.3897/BDJ.5.e11764](https://doi.org/10.3897/BDJ.5.e11764)
- Mendelssohn, I. A., and N. L. Kuhn. 2003. Sediment subsidy: Effects on soil–plant responses in a rapidly submerging coastal salt marsh. *Ecol. Eng.* **21**: 115–128. doi:<https://doi.org/10.1016/j.ecoleng.2003.09.006>
- Meysick, L., E. Infantes, and C. Boström. 2019. The influence of hydrodynamics and ecosystem engineers on eelgrass

- seed trapping. PLoS One **14**: e0222020. doi:[10.1371/journal.pone.0222020](https://doi.org/10.1371/journal.pone.0222020)
- Möller, I., and others. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. Nat. Geosci. **7**: 727–731. doi:[10.1038/ngeo2251](https://doi.org/10.1038/ngeo2251)
- Pereda-Briones, L., E. Infantes, A. Orfila, F. Tomas, and J. Terrados. 2018. Dispersal of seagrass propagules: Interaction between hydrodynamics and substratum type. Mar. Ecol. Prog. Ser. **593**: 47–59. doi:[10.3354/meps12518](https://doi.org/10.3354/meps12518)
- Poppema, D. W., P. W. Willemsen, M. B. de Vries, Z. C. Zhu, B. W. Borsje, and S. J. Hulscher. 2019. Experiment-supported modelling of salt marsh establishment. Ocean Coast. Manag. **168**: 238–250. doi:[10.1016/j.ocecoaman.2018.10.039](https://doi.org/10.1016/j.ocecoaman.2018.10.039)
- Prach, K., K. Fajmon, I. Jongepierová, and K. Šehounková. 2015. Landscape context in colonization of restored dry grasslands by target species. Appl. Veg. Sci. **18**: 181–189. doi:[10.1111/avsc.12140](https://doi.org/10.1111/avsc.12140)
- Qiu, D. D., X. Ma, J. G. Yan, D. D. Shao, J. H. Bai, and B. S. Cui. 2021. Biogeomorphological processes and structures facilitate seedling establishment and distribution of annual plants: Implications for coastal restoration. Sci. Total Environ. **756**: 143842. doi:[10.1016/j.scitotenv.2020.143842](https://doi.org/10.1016/j.scitotenv.2020.143842)
- Rouified, S., S. Puijalon, M. R. Viricel, and F. Piola. 2011. Achene buoyancy and germinability of the terrestrial invasive *Fallopia × bohemica* in aquatic environment: A new vector of dispersion? Ecoscience **18**: 79–84. doi:[10.2980/18-1-3397](https://doi.org/10.2980/18-1-3397)
- Ruiz-Montoya, L., R. J. Lowe, K. P. Van Niel, and G. A. Kendrick. 2012. The role of hydrodynamics on seed dispersal in seagrasses. Limnol. Oceanogr. **57**: 1257–1265. doi:[10.4319/lo.2012.57.5.1257](https://doi.org/10.4319/lo.2012.57.5.1257)
- Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: A conceptual review. New Phytol. **188**: 333–353. doi:[10.1111/j.1469-8137.2010.03402.x](https://doi.org/10.1111/j.1469-8137.2010.03402.x)
- Schwarz, C., T. Ysebaert, Z. C. Zhu, L. Q. Zhang, T. J. Bouma, and P. M. J. Herman. 2011. Abiotic factors governing the establishment and expansion of two salt marsh plants in the Yangtze estuary, China. Wetlands **31**: 1011–1021. doi:[10.1007/s13157-011-0212-5](https://doi.org/10.1007/s13157-011-0212-5)
- Shepard, C. C., C. M. Crain, and M. W. Beck. 2011. The protective role of coastal marshes: A systematic review and meta-analysis. PLoS One **6**: e27374. doi:[10.1371/journal.pone.0027374](https://doi.org/10.1371/journal.pone.0027374)
- Shi, B. W., S. L. Yang, Y. P. Wang, T. J. Bouma, and Q. Zhu. 2012. Relating accretion and erosion at an exposed tidal wetland to the bottom shear stress of combined current-wave action. Geomorphology **138**: 380–389. doi:[10.1016/j.geomorph.2011.10.004](https://doi.org/10.1016/j.geomorph.2011.10.004)
- Temmerman, S., P. Meire, T. J. Bouma, P. M. J. Herman, T. Ysebaert, and H. J. De Vriend. 2013. Ecosystem-based coastal defence in the face of global change. Nature **504**: 79–83. doi:[10.1038/nature12859](https://doi.org/10.1038/nature12859)
- Temmink, R. J., and others. 2020. Mimicry of emergent traits amplifies coastal restoration success. Nat. Commun. **11**: 3668. doi:[10.1038/s41467-020-17438-4](https://doi.org/10.1038/s41467-020-17438-4)
- Van de Vijssel, R. C., J. Van Belzen, T. J. Bouma, D. Van der Wal, V. Cussedu, S. J. Purkis, M. Rietkerk, and J. Van de Koppel. 2020. Estuarine biofilm patterns: Modern analogues for Precambrian self-organization. Earth Surf. Process. Landf. **45**: 1141–1154. doi:[10.1002/esp.4783](https://doi.org/10.1002/esp.4783)
- Van der Stocken, T., B. Vanschoenwinkel, D. J. De Ryck, T. J. Bouma, F. Dahdouh-Guebas, and N. Koedam. 2015. Interaction between water and wind as a driver of passive dispersal in mangroves. PLoS One **10**: e0121593. doi:[10.1371/journal.pone.0121593](https://doi.org/10.1371/journal.pone.0121593)
- Van der Stocken, T., and others. 2019. A general framework for propagule dispersal in mangroves. Biol. Rev. **94**: 1547–1575. doi:[10.1111/brv.12514](https://doi.org/10.1111/brv.12514)
- Van Wesenbeeck, B. K., J. Van De Koppel, P. M. Herman, M. D. Bertness, D. Van Der Wal, J. P. Bakker, and T. J. Bouma. 2008. Potential for sudden shifts in transient systems: Distinguishing between local and landscape-scale processes. Ecosystems **11**: 1133–1141. doi:[10.1007/s10021-008-9184-6](https://doi.org/10.1007/s10021-008-9184-6)
- Wang, C., and S. Temmerman. 2013. Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states? An empirical study on intertidal flats and marshes. J. Geophys. Res. Earth. Surf. **118**: 229–240. doi:[10.1029/2012JF002474](https://doi.org/10.1029/2012JF002474)
- Wang, Q., B. S. Cui, M. Luo, and W. Shi. 2018. Designing microtopographic structures to facilitate seedling recruitment in degraded salt marshes. Ecol. Eng. **120**: 266–273. doi:[10.1016/j.ecoleng.2018.06.012](https://doi.org/10.1016/j.ecoleng.2018.06.012)
- Wang, W. Q., X. F. Li, and M. Wang. 2019. Propagule dispersal determines mangrove zonation at intertidal and estuarine scales. Forests **10**: 245. doi:[10.3390/f10030245](https://doi.org/10.3390/f10030245)
- Xiao, D. R., L. Q. Zhang, and Z. C. Zhu. 2009. A study on seed characteristics and seed bank of *Spartina alterniflora* at saltmarshes in the Yangtze estuary, China. Estuar. Coast. Shelf Sci. **83**: 105–110. doi:[10.1016/j.ecss.2009.03.024](https://doi.org/10.1016/j.ecss.2009.03.024)
- Xiao, D. R., C. Zhang, L. Q. Zhang, Z. C. Zhu, K. Tian, and W. Gao. 2016. Seed dispersal capacity and post-dispersal fate of the invasive *Spartina alterniflora* in saltmarshes of the Yangtze estuary. Estuar. Coast. Shelf Sci. **169**: 158–163. doi:[10.1016/j.ecss.2015.11.032](https://doi.org/10.1016/j.ecss.2015.11.032)
- Xie, T., B. S. Cui, S. Z. Li, and J. H. Bai. 2019. Topography regulates edaphic suitability for seedling establishment associated with tidal elevation in coastal salt marshes. Geoderma **337**: 1258–1266. doi:[10.1016/j.geoderma.2018.07.053](https://doi.org/10.1016/j.geoderma.2018.07.053)
- Yuan, L., Y. H. Chen, H. Wang, H. B. Cao, Z. Y. Zhao, C. D. Tang, and L. Q. Zhang. 2020. Windows of opportunity for salt marsh establishment: The importance for salt marsh restoration in the Yangtze estuary. Ecosphere **11**: e03180. doi:[10.1002/ecs2.3180](https://doi.org/10.1002/ecs2.3180)

- Zhao, Z. Y., L. Yuan, W. Li, B. Tian, and L. Q. Zhang. 2020a. Re-invasion of *Spartina alterniflora* in restored saltmarshes: Seed arrival, retention, germination, and establishment. *J. Environ. Manage.* **266**: 110631. doi:[10.1016/j.jenvman.2020.110631](https://doi.org/10.1016/j.jenvman.2020.110631)
- Zhao, Z. Y., Y. Xu, W. Li, X. J. Zhu, L. Q. Zhang, and L. Yuan. 2020b. Emergency control of *Spartina alterniflora* re-invasion by a chemical method in the Chongming Dongtan, China. *Water Sci. Eng.* **13**: 24–33. doi:[10.1016/j.wse.2020.03.001](https://doi.org/10.1016/j.wse.2020.03.001)
- Zhu, Z. C., L. Q. Zhang, N. Wang, C. Schwarz, and T. Ysebaert. 2012. Interactions between the range expansion of saltmarsh vegetation and hydrodynamic regimes in the Yangtze estuary, China. *Estuar. Coast. Shelf Sci.* **96**: 273–279. doi:[10.1016/j.ecss.2011.11.027](https://doi.org/10.1016/j.ecss.2011.11.027)
- Zhu, Z. C., T. J. Bouma, T. Ysebaert, L. Q. Zhang, and P. M. J. Herman. 2014. Seed arrival and persistence at the tidal mudflat: Identifying key processes for pioneer seedling establishment in salt marshes. *Mar. Ecol. Prog. Ser.* **513**: 97–109. doi:[10.3354/meps10920](https://doi.org/10.3354/meps10920)
- Zhu, Z. C., J. van Belzen, T. Hong, T. Kunihiro, T. Ysebaert, P. M. J. Herman, and T. J. Bouma. 2016. Sprouting as a gardening strategy to obtain superior supplementary food: Evidence from a seed-caching marine worm. *Ecology* **97**: 3278–3284. doi:[10.1002/ecy.1613](https://doi.org/10.1002/ecy.1613)
- Zhu, Z. C., J. van Belzen, Q. Zhu, J. van de Koppel, and T. J. Bouma. 2020a. Vegetation recovery on neighboring tidal flats forms an Achilles' heel of saltmarsh resilience to sea level rise. *Limnol. Oceanogr.* **65**: 51–62. doi:[10.1002/lno.11249](https://doi.org/10.1002/lno.11249)
- Zhu, Z. C., and others. 2020b. Historic storms and the hidden value of coastal wetlands for nature-based flood defence. *Nat. Sustain.* **3**: 853–862. doi:[10.1038/s41893-020-0556-z](https://doi.org/10.1038/s41893-020-0556-z)

Acknowledgments

The authors would like to acknowledge the Chongming Dongtan Nature Reserve and Yangtze Delta Estuarine Wetland Ecosystem Observation and Research Station for providing the necessary support when conducting this study. We give our heartfelt thanks to Jianwei Sun, Jinlei Zhang, Jialin Pan, Xianye Wang, and Yang Li for their help preparing and establishing the flume experiments. Special thanks are given to Haobing Cao and Jim van Belzen for their constructive comments on an earlier version of the manuscript. T.J.B. acknowledges the RWS-funded Perkpolder project and the Zuidgors project, which was funded by the Province of Zeeland; both aim to obtain a better understanding of salt-marsh establishment. .L.Y. and L.Z. were supported by the National Natural Science Foundation of China (41876093) and the National Key R&D Program of China (2016YFE0133700). Z.Z. also acknowledges financial support from the China Scholarship Council.

Conflict of Interest

None declared.

Submitted 05 November 2020

Revised 18 April 2021

Accepted 20 May 2021

Deputy editor: Julia Mullarney