Adventures of salt marsh recruits

Mechanistically understanding the journey to dispersal and establishment

Zhiyuan Zhao

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2022

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Adventures of salt marsh recruits

Mechanistically understanding the journey to dispersal and establishment

Avonturen van kwelder rekruten

Het mechanisme van zaadverspreiding en zaailingen vestiging

(met een samenvatting in het Nederlands)

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1

General introduction

1 General introduction

1.1 Salt marshes – valuable and vulnerable ecosystem

Salt marshes (Fig. 1.1) are a blend of terrestrial, aquatic, and marine communities that thrive along coastlines, particularly in mid-to-high latitudes (Mcowen et al., 2017). Their formation begins as tidal flats elevate relative to sea level due to sediment accretion, with a corresponding decrease in the frequency and period of tidal flooding, which subsequently allows pioneer vegetation to colonize on bare surfaces (Balke et al., 2012; Fagherazzi et al., 2013). The pioneer vegetation typically consists of herbaceous plants that exhibit morphological and physiological adaptations (e.g., leaf salt glands, anaerobic root respiration) to salinity and flooding regimes in intertidal habitats (Richards et al., 2005; Colmer et al., 2008). Although salt marshes are “small potatoes” to the ocean’s surface (occupies less than 0.2%; Duarte et al., 2013), they have long been considered one of the most ***valuable*** but also most ***vulnerable*** ecosystems around the world.

Valuable *because of the multitude of critical ecosystem functions they provided*. Salt marshes represent areas of high biological productivity (Alongi, 2020) and can sequester large amounts of blue carbon in soils (Santos et al., 2019; Xiao et al., 2021), contributing to regional and global carbon budgets that affect climate stability (Macreadie et al., 2021; Temmink et al., 2022). They also serve as rare and unique habitats which support both nursery grounds for marine invertebrates (e.g., crabs, oysters, and mussels; Baumann et al., 2020), and breeding/feeding grounds for shorebirds (e.g., gulls, terns, and passerine; Smith et al., 2020). More notably, salt marshes have functional capacities to stabilize shorelines through stabilizing sediment (Silliman et al., 2019) and dissipating wave impacts (Möller et al., 2014), especially during extreme events (e.g., storms; Pannozzo et al., 2021). Meanwhile, they possess the adaptive ecosystem engineering ability to maintain high stability and persistence under changing environmental conditions (Spencer et al., 2016;

Crotty et al., 2018). Together these build on the great potential of salt marshes to reduce coastal flood risk, thus supporting the paradigm shift from conventional hard-engineering flood defenses towards nature-based solutions (Bouma et al., 2014; Zhu et al., 2020b; Gijsman et al., 2021). Other benefits of salt marshes include pollutant removal and detoxification (Sruthi et al., 2017), fisheries production (Jinks et al., 2020), and supporting eco-tourism that can fuel local economies (Saunders et al., 2020).

Fig. 1.1 Salt marshes at the Westerschelde estuary, the Netherlands (a) and the Yangtze estuary, China (b). Photos were taken by Zhiyuan Zhao.

Vulnerable *because of their low-lying position at the land-sea interface.* Rising sea levels pose a serious threat of "ecological drowning" in salt marshes, by increasing the frequency and duration of inundation above a threshold of species-specific vegetation tolerance (Friess et al., 2012; Fagherazzi et al., 2020). Global-scale projections suggest that sea-level rise would lead to a 20% – 90% reduction in the current extent of salt marshes by 2100 (Kirwan et al., 2016; Schuerch et al., 2018; Thorne et al., 2018). This number is particularly high for salt marshes that cannot migrate landward due to coastal defense structures, and for which suffer reduced accretion due to sediment starvation (Crosby et al., 2016; Peteet et al., 2018). Salt marshes also need to resist the lateral erosion at the seaward edge induced by tidal currents and waves (Bouma et al., 2016; Fagherazzi et al., 2020). Once a pronounced cliff has initiated at the mudflat/vegetation boundary, the discontinuity in topographic and vegetation appear to accelerate the loss and/or collapse of salt marshes (van der Wal et al., 2008; Wang et al., 2017). Given ongoing climate change, especially the increasingly severe storms, erosion-driven salt marshes losses may be expected to increase in both magnitude and frequency (Bouma et al., 2016; Leonardi et al., 2018). Additionally, salt marshes are under immense pressure from human activities and coastal development, such as the immediate loss of habitat during the construction of hard structures (e.g., dykes, weirs, docks) and the excavation of canals and ditches (Ma et al., 2014; Gu et al., 2018).

Under the “multiple whammies”, salt marshes around the world have undergone massive shrinkage over the last decades, accompanied by the disintegration of their critical functions and services (Schuerch et al., 2018; Fagherazzi et al., 2020). Underpinned by the United Nations’ call to action in “The UN Decade on Ecosystem Restoration” (cf. Waltham et al., 2020), restoration is gaining traction as a vital tool to reverse the degradation of salt marshes (Suding et al., 2015; Waltham et al. 2020; Adams et al., 2021). Significant global efforts are urgently required to pin-point and generalize the mechanisms behind the dispersal, establishment, and persistence of salt marshes (Friess et al., 2012; Bouma et al., 2014; Temmink et al., 2020). These insights are needed to inspire creative and transformative ideas, that advance existing conservation and/or restoration strategies or identify novel ones (e.g., Temmink et al., 2020; Fivash et al., 2021) and may ultimately achieve the intended effects of restoration.

1.2 Recruitment processes of salt marshes

Recruitment processes are critical components of a plant's life cycle (Larson et al., 2015), and play an important role in the long-term stability and resilience of ecosystems, particularly in dynamic environments such as coastal areas (Zhu et al., 2020a; Hu et al., 2021). Although the recruitment of salt marshes in some areas is predominantly accomplished by asexual reproduction through tillering and cloning (e.g., Angelini and Silliman, 2012), seed-based recruitment (Fig. 1.2) appears to be important in meso- and macrotidal marsh ecosystems around the world (Bouma et al., 2016; Redelstein et al., 2018; Cao et al., 2018), especially in areas where bare tidal flats are disconnected from existing vegetation (e.g., due to the presence of high cliffs; Zhu et al., 2020a; Cao et al., 2021). Compared with asexual reproduction, seed-based recruitment has the significant benefit of rapidly establishing vegetation (Fig. 1.2; Balke et al., 2014; Zhu et al., 2020a) and increasing genetic diversity (van der Stocken et al., 2019a) on tidal flats over vast areas.

Successful recruitment from seeds (Fig. 1.2 and 1.3) broadly requires seed availability and subsequent seedling persistence (Balke et al., 2011; Friess et al., 2012; Statton et al., 2017), involving multiple life-stage transitions subject to abiotic factors and biotic interactions (Friess et al., 2012; van der Stocken et al., 2019a). Key life stages related to seed-based recruitment in salt marshes include:

- **Primary dispersal**: The initial movement of seeds away from an existing marsh following detachment from the parent plant (cf. Culot et al., 2015).
- **Secondary dispersal**: The additional horizontal or vertical movement of seeds after the initial deposition (cf. Culot et al., 2015).
- **Retention**: The seeds remain at a micro-site post dispersal (cf. Chang et al., 2008).
- **Emergence**: The retained seeds germinate and grow out of the soil surface (cf. Finch-Savage and Leubner-Metzger, 2006).
- **Rooting**: The newly germinated/emerged seedlings remain standing and

take root (cf. Balke et al., 2011).

- **Survival**: The persistence of established seedlings through the growing season (cf. Larson et al., 2015).

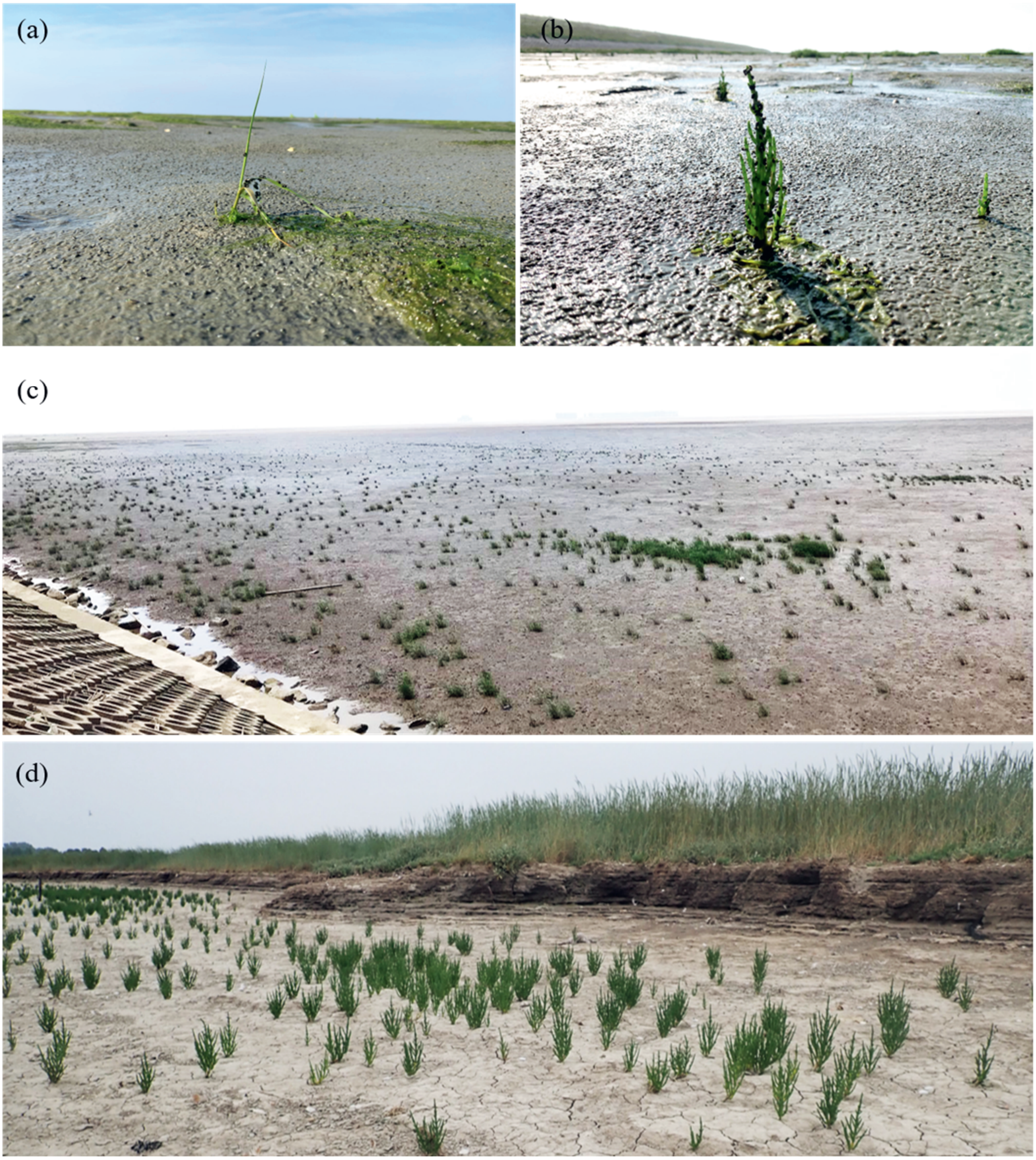


Fig. 1.2 Seedling of *Spartina anglica* (a) and *Salicornia europaea* (b) in the

Westerschelde estuary, the Netherlands. (c) Rapid vegetation (*Spartina alterniflora*) establishment on bare mudflats through seed-based recruitment in Chongming Dongtan, the Yangtze estuary, China. (d) Rapid vegetation (*Salicornia europaea*) recovery in front of the erosive salt marsh cliff through seed-based recruitment in Zuidgors, the Westerschelde estuary, the Netherlands. Photos (a, b, and c) were taken by Zhiyuan Zhao. Photo (d) was adopted from De Vet et al. (2020).

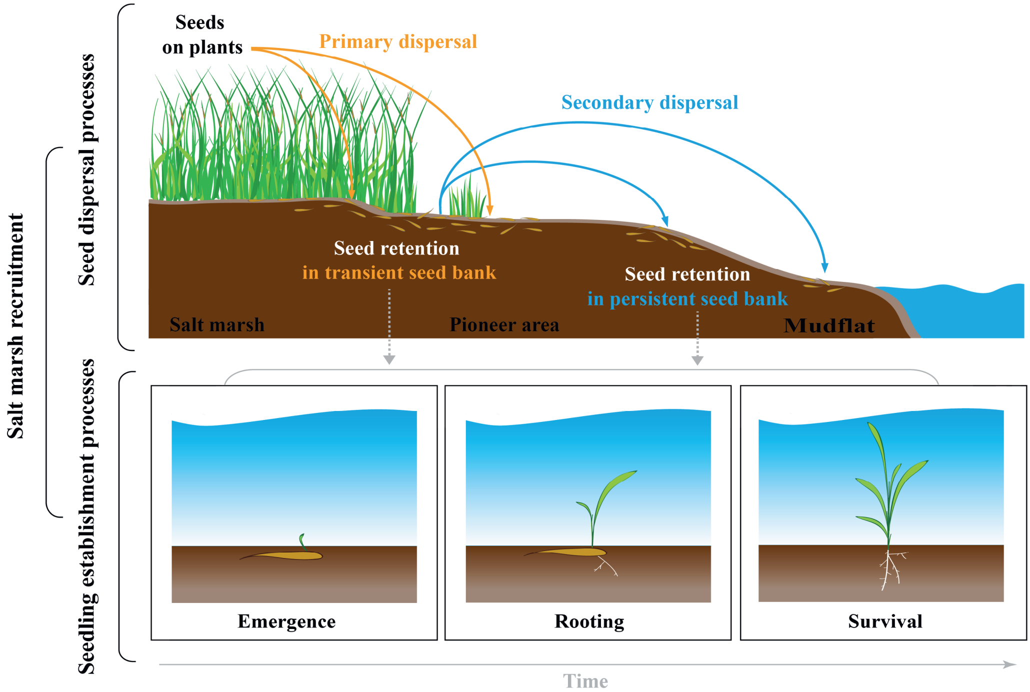


Fig. 1.3 Schematic diagram of the processes of seed-based recruitment in salt marshes. The recruitment processes are composed of key transitions in several seed and seedling stages, including primary seed dispersal, secondary seed dispersal, seed retention, seedling emergence, seedling rooting, and seedling survival.

Among them, *i*) primary dispersal, *ii*) secondary dispersal, and *iii*) retention constitute the **seed dispersal processes** (Fig. 1.3), which control the migratory capacity of seeds and set the latent spatial template for salt marsh recruitment (Nathan and Muller-Landau, 2000; van der Stocken et al., 2019a). While *iv*) emergence, *v*) rooting, and *vi*) survival constitute the **seedling establishment processes** (Fig. 1.3), which regulate the effectiveness of dispersal events and the eventual recruitment outcome (Balke et al., 2011; Fraaije et al., 2015). Therefore, the inherently causative factors, thresholds, and bottlenecks that govern the seed dispersal processes and seedling establishment processes need to be discerned and quantified (Friess et al., 2012; Bouma et al., 2014, 2016). Such information is imperative for a holistic understanding of salt marsh recruitment mechanisms and has implications for optimizing the designs of seed/seedling-based salt marsh restoration.

1.3 Seed dispersal in salt marshes

1.3.1 Importance of seed dispersal

After detachment from the parent plant, salt marsh seeds will drift with the tidal currents to replenish existing marshes and colonize new suitable habitats (Rand, 2000; Friess et al., 2012). Where a seed ends up post dispersal determines the physical and biological conditions, such as sedimentary regime, hydrodynamic intensity, competition degree, and predator abundance, that influence all later stages of salt marsh recruitment (Rey and Alcántara, 2000; Wolters et al., 2005). Therefore, seed dispersal has long-term implications on population persistence (Wolters et al., 2005; Beckman et al., 2018). The spatial pattern resulting from dispersal plays an important role in population structure and metapopulation connectivity (Rand, 2000; Bullock et al., 2012). Seed dispersal is also central for maintaining and enriching the genetic complexity of salt marsh habitats at local, landscape, and even global scales (Levin et al., 2003; van der Stocken et al., 2019b). Over time, salt marsh communities with genetic diversity are better able to resist climate change-related stressors (Bernhardt and Leslie, 2013). More importantly, seed dispersal, especially over long distances, may allow salt marsh species to keep pace with climate change-driven habitat loss (Travis et al., 2013; Kottler and Gedan, 2020). In view of the above, elucidating the dispersal mechanism of salt marshes is crucial for the management, conservation, and restoration of salt marsh ecosystems (Friess et al., 2012; Shi et al., 2020).

1.3.2 Knowledge gaps related to seed dispersal processes

Primary seed dispersal in salt marshes is mainly accomplished through hydraulic transport by tidal currents, with dispersal trajectories thus being modulated by the magnitude of tidal flow (Huiskes et al., 1995; Rand, 2000). This is why previous quantification and modeling studies on salt marsh dispersal behavior have prioritized flow velocity as the dominant control factor (Friess et al., 2012; van der Stocken et al., 2015; Shi et al., 2020). However, current-only scenarios are uncommon in salt marsh habitats, and seeds are documented to be transported at the same velocity as prevailing currents in the absence of wind or waves (van der Stocken et al., 2015). Instead, the effect of wave action on salt marsh dispersal behavior may not be linear and much more intricate (Lai et al., 2020). Under wave action with larger amplitude, seeds are expected to be drifted at the free surface of water waves with a larger longitudinal component of their circular orbits and a greater Stokes drift velocity (Holthuijsen, 2007). Wind and its coupling to currents and waves may be equally important in influencing the probability and trajectory of primary seed dispersal in salt marshes (van der Stocken et al., 2013, 2015). However, little is currently known about the primary dispersal potential of salt marsh seeds under varying wave and wind scenarios, although this represents the dominant dispersal mechanism in wind- and wave-dominated salt marsh habitats.

Salt marsh seeds do not disperse uniformly because their dispersal potential typically comes from the interaction between physical settings and seed traits (Friess et al., 2012; Shi et al., 2020). Biological traits that determine the spatiotemporal patterns of primary seed dispersal include mass, shape, density, buoyancy, and longevity (Clarke et al., 2001; De Ryck et al., 2012; van der Stocken et al., 2019a). In addition, seeds may remain in positively buoyant plant structures such as spikelets (Bockelmann et al., 2003), inflorescences (Strong and Ayres, 2013), or plant fragments (Dethier and Hacker, 2004). All of these structures are realistically available during disturbance events and can act as dispersal units that drift with the tidal current to transport seeds (Ingrouille and Pearson, 1987; Minchinton, 2006). These seed-containing dispersal units are speculated to have greater potential for long-distance dispersal than individual seeds, due to their larger interaction surface with the tidal current component (Lai et al., 2020). Nonetheless, the dispersal units that contribute to seed dispersal have traditionally been excluded from assessments of salt marsh dispersal ability in existing studies. In summary, to more completely understand and predict the behavioral dynamics of salt marsh seeds, it is indispensable to answer the *Question: How does the primary dispersal process of salt marsh seeds respond to changing conditions in wind- and wave-dominated environments? And what is the relative importance of biotic dispersal units in primary seed dispersal?*

Regarding secondary seed dispersal, especially for the seeds that settled due to losing buoyancy, its occurrence first requires the hydrodynamic processes occurring in the bottom boundary layer to lift the seeds vertically into the water column, and then the unidirectional tidal current transports the lifted seeds further horizontally (Koch et al., 2010; Kendrick et al., 2012). In coastal areas like salt marsh habitats, the bed shear stress caused by wave action is usually much stronger than that caused by unidirectional current (Callaghan et al., 2010), and thus as the primary mechanism for lifting off the settled seeds and triggering secondary dispersal (Koch et al., 2010; Ruiz-

Montoya et al., 2012; Zhu et al., 2020a). Since the negatively buoyant seeds typically require significant energy to initiate near-surface transport, secondary dispersal events of salt marsh seeds may mainly occur during extreme wave events (Chang et al., 2008; Zhu et al., 2020a) and are difficult to reproduce the longer dispersal distances achieved during the primary dispersal (Culot et al., 2015; Xiao et al., 2016). From the mechanistic perspective, the secondary dispersal process of salt marsh seeds is similar to the process of sediment entrainment, transport, and deposition, where sediment properties, such as size and density, dominate the critical hydrodynamic conditions required to induce transport (Carthey et al., 2016; Dorrell et al., 2018). In contrast, the extent to which seed traits affect the secondary dispersal process remains to be determined. Particularly in spring, seed germination would induce significant changes in seed size, shape, and buoyancy (Koch et al., 2010; Rouifed et al., 2011; Lamberti-Raverot et al., 2019), which may amplify the likelihood of secondary seed dispersal during mild tides. Hence, it is necessary to understand the *Question: How do seed traits affect key hydrodynamic thresholds that kick-start secondary seed dispersal, and to what extent this may be altered by seed germination?*

Another question encountered when studying the dispersal process is “how many viable seeds will be retained at a suitable site for establishment?” During dispersal (both primary and secondary dispersal), a certain number of seeds may naturally lose their vitality before reaching a microsite (Statton et al., 2017; van der Stocken et al., 2019a). Once arrived, seed retention on the ground is first related to landscape elements that capture seeds, such as vegetation and microtopography (Levine and Murrell, 2003; Xie et al., 2019). Dense flexible plants were documented to retain greater numbers of seeds than discrete rigid plants (Chang et al., 2008). Depressed micro-topographic structures, such as crab holes, also show great potential for trapping deposited seeds (Qiu et al., 2021). Additionally, species-specific seed traits can influence dispersal patterns not only by affecting dispersal processes but also by interacting with trapping structures (Nilsson et al., 2002; Chang et al., 2008). For example, seed traits such as high density, sticky seed coat, and collapsed pappi may enhance seed retention (Chambers and MacMahon, 1994; Chang et al., 2008). Seed retention can be facilitated through seed burial induced by sediment accretion (Zhu et al., 2014) and/or ecosystem engineering of bioturbation infauna (Zhu et al., 2016b). Subsequently, the persistence of retained seeds fluctuates with changes in environmental factors at the local microsite level (Friess et al., 2012; Cunnings et al., 2016). The potential factors regulating seed retention may include elevation, flow velocity, wave energy, bed-level change, grain size, etc. (Koch et al., 2010; Zhu et al., 2014, 2020a, 2021). These process-based understandings, while long recognized, have not been studied in sufficient detail for most salt marsh species to establish generalized response mechanisms. Therefore, it is necessary to investigate the *Question: What are the key physical factors that inhibit seed retention at the microsite level? Are there species-specific tipping points below or above which durable seed retention can be expected?*

1.4 Seedling establishment in salt marshes

1.4.1 Importance of seedling establishment

Seed-based salt marsh recruitment is impossible without seed dispersal, which sets the potential spatial template for subsequent vegetation development (Nathan and Muller-Landau, 2000; van der Stocken et al., 2019a). However, seedling establishment, the principal demographic process post dispersal, has the potential to significantly alter the recruitment patterns set by seed dispersal (Friess et al., 2012; Fraaije et al., 2015). The strong temporal heterogeneity of biotic and abiotic conditions in the microsites where seeds reside may form an important filter for seedling establishment (Noe and Zedler, 2001; Bouma et al., 2016; Redelstein et al., 2018). In particular, the dynamic nature of currents, waves, and bed-level in salt marsh habitats would restrict seedling establishment in a variety of ways (Balke et al., 2013; Cao et al., 2018, 2020; Fivash et al., 2020). This leads to a sporadic and event-driven pattern of seedling establishment behavior and makes its success elusive and unpredictable (Balke et al., 2014; Hu et al., 2015a). Therefore, seedling establishment is unanimously recognized as a critical bottleneck that needs to be overcome to initiate the rapid transition from bare mudflats to vegetated states in potential salt marsh habitats (Wang and Temmerman, 2013; Yuan et al., 2020; Fivash et al., 2021). Once seedlings managed to be established, the effectiveness of recruitment may be further amplified by lateral clonal growth (Vandenbruwaene et al., 2011; Angelini and Silliman, 2012). Taken together, pinpointing the key mechanisms limiting and facilitating seedling establishment is integral and of broad importance in assessing the recruitment potential of salt marshes in changing climate (Bouma et al., 2016; Zhu et al., 2020a; Hu et al., 2021).

1.4.2 Knowledge gaps related to seedling establishment processes

Successful transition from stranded or buried seeds to emerged seedlings is the first and foremost demographic process that kick-start seedling establishment (James et al., 2011; Larson et al., 2015; Statton et al., 2017). In salt marsh habitats, inundation and high salinity can reduce oxygen content (Titus and Hoover, 1991) and water potential (Facelli, 2008) in sediments, respectively, thereby impeding seed germination. Both factors were thus identified in earlier studies as major physical stressors regulating seedling emergence (Coops and van der Velde, 1995; Noe and Zedler, 2001; Engels et al., 2011). Several emerging studies devoted to quantifying the recruitment potential of salt marshes have revealed a significant, species-specific negative correlation between seedling emergence and sedimentary regime (Bouma et al., 2016; Abbas et al., 2020). Especially for pioneer species, sediment burial of a few centimeters or even a few millimeters can completely hamper seedling emergence (Langlois et al., 2001; Zhao et al., 2020a; Abbas et al., 2020). Due to limited seed reserve, the capability of germinated seeds to grow out of the surface may also rely on nutrient availability in the sediment (Lamichhane et al., 2018). In addition, other physical properties of the sediment, such as grain size and compactness, may exacerbate the difficulty of penetrating the soil to further impede seedling emergence (Cambi et al., 2018). To drastically enhance our understanding of how seedling emergence and its effects on salt marsh recruitment vary as a function of environmental settings, it is fundamental to investigate the *Question: Which environmental factors have overriding influences on seedling emergence? Are there species-specific environmental thresholds that can be adopted to predict emergence probability?*

After emergence, dislodgement is recognized as the biggest challenge for seedling establishment and survival (Bywater-Reyes et al., 2015; Schoutens et al., 2021). During the early development stage, seedlings tend to be dislodged in form of slipping out of the substrate or cutting off roots when the drag force from hydraulic disturbance exceeds the anchoring force of seedlings (Fig. 1.4a; Balke et al., 2011; Hu et al., 2015a). As roots elongate, seedling dislodgement requires the shift of critical hydraulic disturbance from those that drag seedlings to those that erode sediments (Fig. 1.4a; Bouma et al., 2016; Cao et al., 2018; Hu et al., 2021). To resist and survive the dislodgement events at different stages, seedling establishment processes need to be synchronized with the disturbance absent/low periods, which are referred to as Windows of Opportunity (WoO; cf. Balke et al., 2011, 2014). The WoO is framed to include an initial short-term disturbance-absent window (WoO-1) that provokes seedling rooting and subsequent long-term windows (WoO-2 and WoO-3) in which hydrodynamic and associated erosion disturbances remain below the resistance of seedling (Fig. 1.4b; Balke et al., 2011; van Belzen et al., 2022). All windows are stochastic in timing and their effectiveness is highly correlated with the species-specific temporal evolution of seedling resistance against dislodgement (Hu et al., 2021). Although the WoO framework has been widely recognized and applied to the interpretation of salt marsh establishment events (Balke et al., 2014; Hu et al., 2015a; Yuan et al., 2020), we still lack experimental studies to quantify the time-varying entanglement between maximum instantaneous disturbance versus seedling resistance during the establishment process. Therefore, it is imperative to address the *Question: Are there key parameters characterizing seedling's resistance against the dislodgement induced by hydrodynamics and sediment scouring? And how does seedling's resistance change over time and across species?*

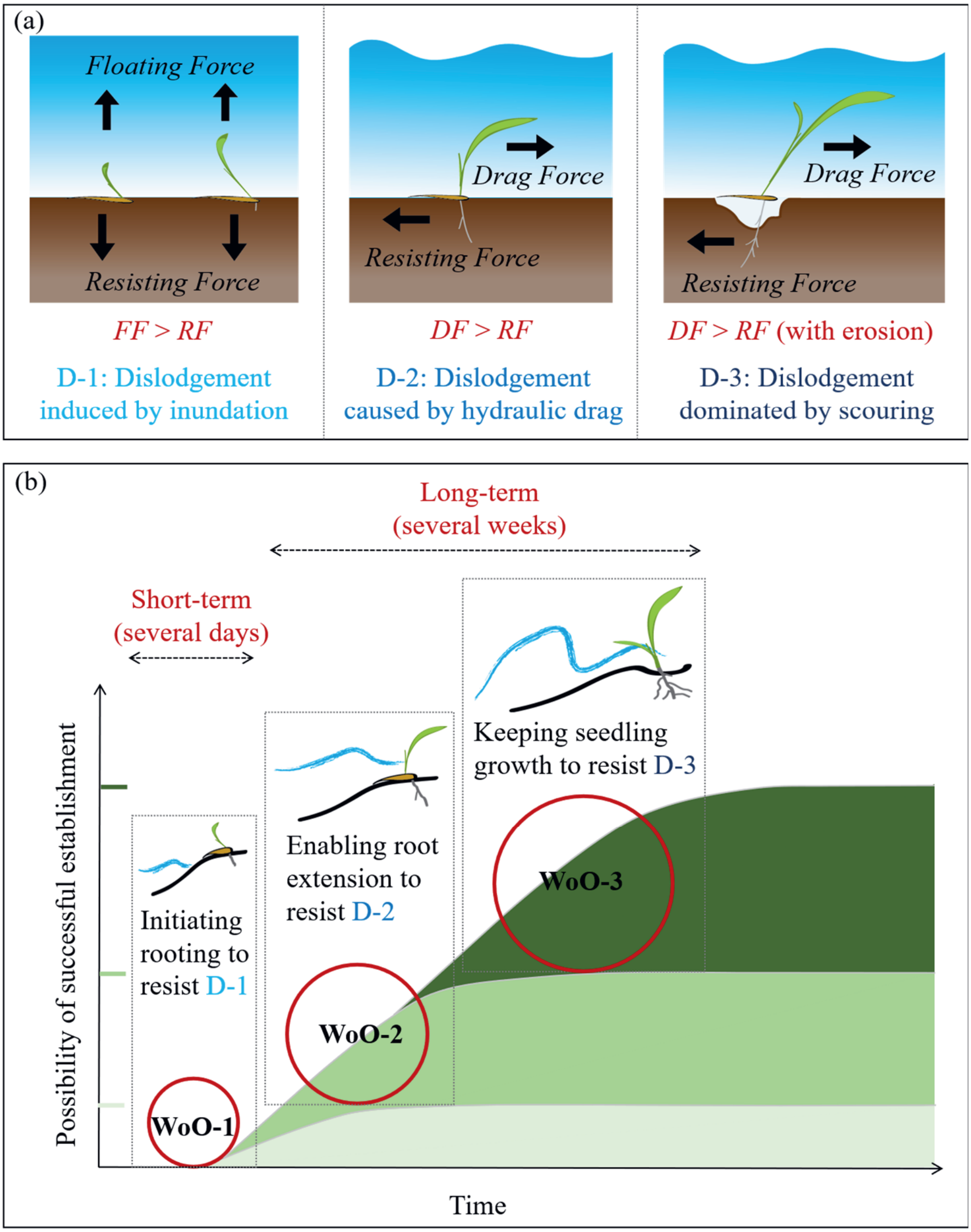


Fig. 1.4 (a) Schematic representation of the mechanism of seedling dislodgement. D-1: Dislodgement induced by the positive buoyancy affiliated to seed and/or shoot when seedlings are under inundation. D-2: Dislodgement

caused by seedling's anchoring capacity inferior to the drag force generated by tidal currents and waves. D-3: Dislodgement dominated by sediment scouring (related to high-energy events), which undermines seedlings' anchoring ability and results in uprooting under the effect of drag forces. (b) A general introduction to the Windows of Opportunity (WoO; cf. Balke et al., 2011) framework. The WoO includes an initial short-term disturbance-free window (i.e., WoO-1) and subsequent long-term disturbance-low windows (i.e., WoO-2 and WoO-3). With WoO-1, seedlings are allowed to root and be exempt from the dislodgement induced by following inundation (i.e., D-1). WoO-2 is a disturbances calm period that enables seedlings to maintain rooting and resist the dislodgement caused by drag force from currents and waves (i.e., D-2). In WoO-3, seedlings are empowered to grow stronger to survive the dislodgement dominated by sediment scouring (i.e., D-3).

1.5 Thesis outline

The main objective of this thesis is to bridge the current knowledge gaps related to salt marsh recruitment mechanisms, as identified in sections 1.3 and 1.4. Through the lens of several globally occurring landscape-forming pioneer species, we seek integrated experimental evidence generalizing the relative importance of biotic and abiotic factors in governing salt marsh recruitment, from *i*) primary seed dispersal, *ii*) secondary seed dispersal, *iii*) seed retention, i*v*) seedling emergence, and *v*) seedling rooting to *vi*) seedling survival. These experiment-based insights will be beneficial in lessening parameter and model uncertainty, thereby supporting more robust evaluations and predictions of recruitment variability and long-term distributional responses of salt marsh species under varied climate scenarios. Additionally, the resulting information is expected to inform the management and restoration of degraded salt marshes or the creation of new ones, which is particularly ecologically significant if the marshes are targeted for nature-based applications such as coastal defense, climate stability, or carbon sequestration.

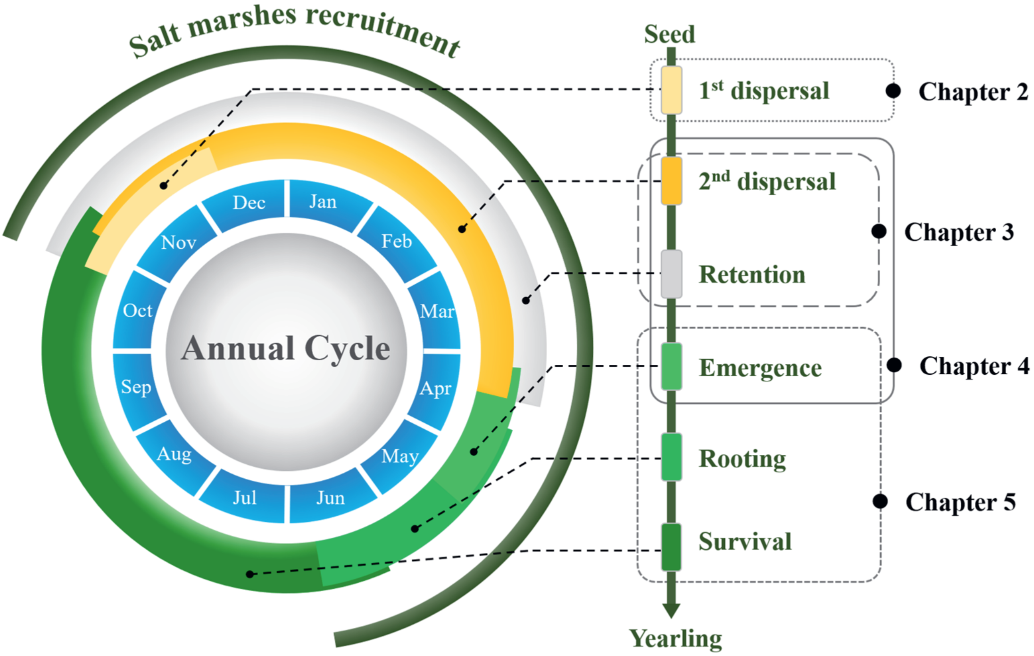


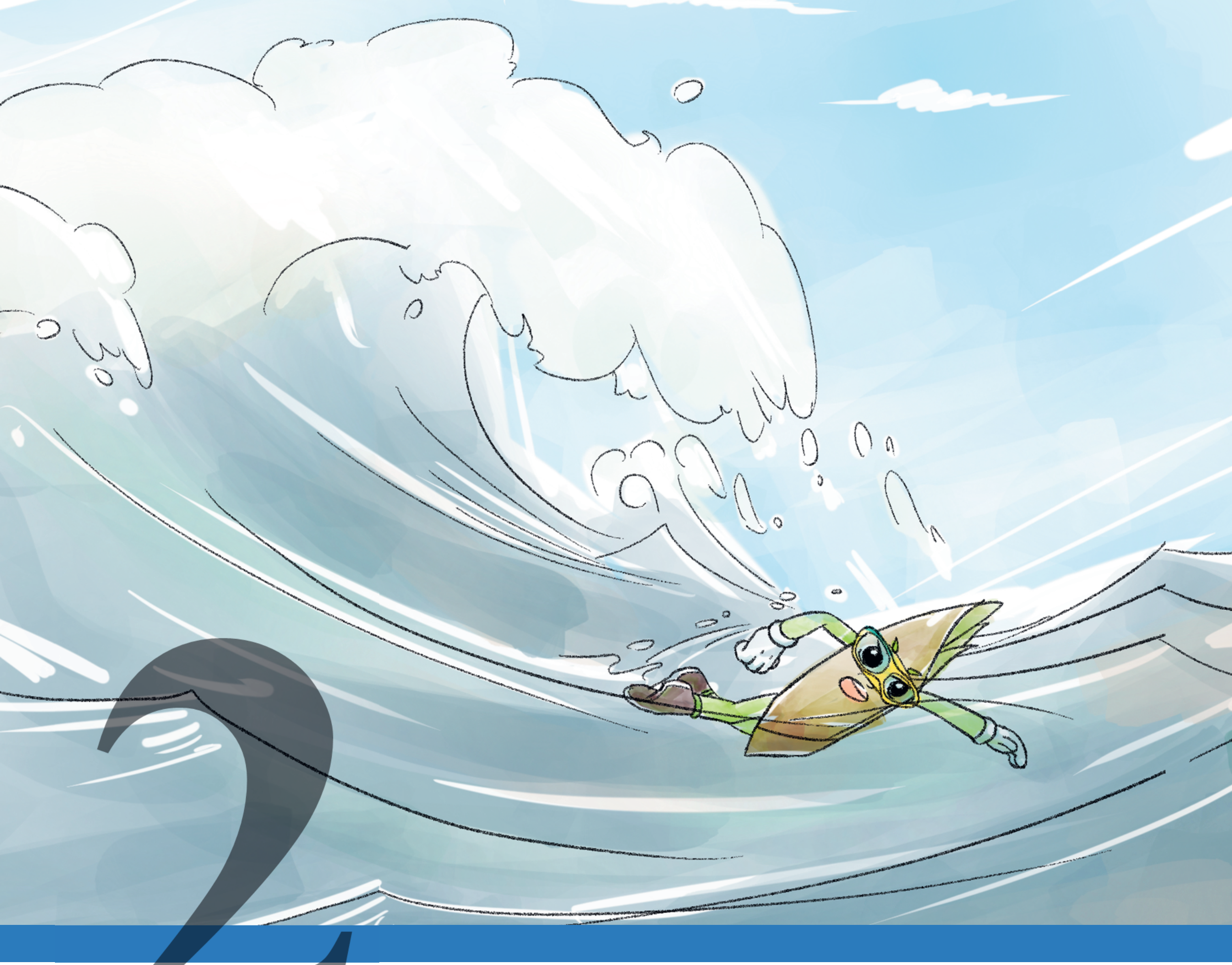
Fig. 1.5 Generalized diagram illustrating the annual life cycle of salt marsh plant starting from a seed and relation with the thesis chapters. The months associated with the annual cycle are exemplified by the approximate timing of salt marsh phenology in the study area (i.e., China and the Netherlands) covered in this thesis.

In **Chapter 2** – *Salt marsh seeds in motion: the relative importance of dispersal units and abiotic conditions* – we answer the **Question: How does the primary dispersal process of salt marsh seeds respond to changing conditions in wind- and wave-dominated environments? And what is the relative importance of biotic dispersal units in primary seed dispersal?** Specifically, we studied the seeds and seed-containing dispersal units of 4 globally distributed salt marsh species (i.e., *Elymus athericus*, *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*). Through mesocosm experiment and flume study, we collected quantitative data on their buoyancy periods under various flooding regimes and their traveling speed under a range of contrasting current, wave, and wind conditions, respectively. The potential influence of morphological characteristics of seeds and seed-containing dispersal units on dispersal processes was also investigated in both experiments.

In **Chapter 3** – *The onset of secondary seed dispersal is controlled by germination-features: A neglected process in sudden salt marsh establishment* – we answer the **Question: How do seed traits affect key hydrodynamic thresholds that kick-start secondary seed dispersal, and to what extent this may be altered by seed germination?** Specifically, 2 model species (i.e., *Scripus mariqueter*, *Spartina alterniflora*) were employed in a flume study to quantify the threshold lift-off velocity required for their seeds to initiate secondary dispersal under different germination stages and being partially buried. Combined with field investigations, we then explored the potential of secondary seed dispersal after germination in explaining rapid salt marsh recruitment events.

In **Chapter 4** – *Retention versus emergence: can we identify which forms the recruitment bottleneck for seed-based wetland restoration?* – we answer the **Question: What are the key physical factors that inhibit seed retention at the microsite level? Are there species-specific tipping points below or above which durable seed retention can be expected?** And the **Question: Which environmental factors have overriding influences on seedling emergence? Are there species-specific environmental thresholds that can be adopted to predict emergence probability?** By means of large-scale field experiments, spanning 100 microhabitats across 10 locations and using four global occurring salt marsh species (i.e., *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*) as models, we identified key factors governing seed retention and seedling emergence and defined the overall response curves for seed retention and seedling emergence to those key factors. Subsequently, using machine learning, we translated the resulted insights and datasets into artificial neural network predictors for targeted application in dissecting stage-specific bottleneck effects.

In **Chapter 5** – *Unraveling the wheel of recruitment for salt-marsh seedlings: resistance to and recovery after dislodgement* – we answer the **Question: Are there key parameters characterizing seedling's resistance against the dislodgement induced by hydrodynamics and sediment erosion? And how does seedling's resistance change over time and across species?** Using race-track flume, we quantified the hydrodynamic thresholds and critical erosion depths that seedlings can resist before being dislodged at different developmental stages, and evaluated how morphological traits affect their dislodgement susceptibility. This was followed by two mesocosm experiments determining the dispersal ability and the re-establishment potential of seedlings dislodged at various ages, respectively.



2

Salt marsh seeds in motion: the relative importance of dispersal units and abiotic conditions

Zhiyuan Zhao, Liquan Zhang, Lin Yuan, Tjeerd J. Bouma

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Abstract

Propagule dispersal is fundamental to the colonization of new habitats, metapopulation connectivity, and gene flow and thus enables salt marsh species to cope with global change. In this study, mesocosm and flume experiments were used to quantify the effects of different dispersal units (i.e., seed, spikelet, inflorescence, and plant fragment-containing seeds) and abiotic conditions on the dispersal processes of four globally distributed salt marsh species: *Salicornia europaea, Scirpus maritimus, Spartina anglica,* and *Elymus athericus*. The results show that: 1) moving seawater has a species-specific effect on buoyancy, leading to prolonged floatability of high tidal-flat species *E. athericus* and reduced floatability of pioneer species; 2) tidal currents increase dispersal speed, whereas wind can have additive or antagonistic effects on current-dominated dispersal speed depending on its direction; 3) wave action reduces dispersal speed, but this effect becomes smaller with increasing wave magnitudes and/or applied co-directional wind; 4) dispersal speed may vary depending on the physical forcing and type and morphology of the dispersal units, but the largest species effect is related to the period in which units remain buoyant; and 5) the dispersal potential of salt marsh species in wind wave-dominated coastal environments can be ordered as follows: *E. athericus* > *S. maritimus* > *S. anglica* > *S. europaea*. This study provides valuable guidance for future numerical hydrodynamic models of salt marsh dispersal and establishment, allowing more accurate prediction of the distributional responses of salt marsh species to climate change, thereby supporting appropriate management and restoration strategies.

2.1 Introduction

Salt marshes are increasingly valued because of their capacity to form elevated biogeomorphic landscapes by attenuating hydrodynamic energy (Bouma et al., 2005, 2007; Temmerman et al., 2007). They contribute to coastal protection (Gedan et al., 2011; Shepard et al., 2011; Bouma et al., 2014), even under extreme storm conditions (Möller et al., 2014; Willemsen et al., 2020; Zhu et al., 2020b), and provide habitat to unique species (Barbier et al., 2011; Duarte et al., 2013). Unfortunately, global coastlines are facing accelerated sea-level rise in combination with more frequent and powerful storms (Kirwan et al., 2016; Hanley et al., 2020), resulting in the geographic shifting of habitat suitable for salt marsh ecosystems (Tonelli et al., 2010; Temmerman et al., 2012). Propagule dispersal, a critical process to track and survive the shift of habitats, plays a key role in population replenishment and recovery after disturbance events and preserves a healthy genetic population structure at the local, landscape, and even global scale (Levin et al., 2003; Travis et al., 2013; van der Stocken et al., 2019a, b). Thus, the nature and extent of the dispersal process must be known to understand the distributional responses of salt marsh species and establish appropriate management and restoration strategies (Dethier and Hacker, 2004; Friess et al., 2012; Shi et al., 2020).

Seed dispersal is a common long-distance dispersal strategy, which is also used by salt marsh species (Rand, 2000; Shi et al., 2020). Salt marsh seed dispersal occurs mainly through abiotic transport by tidal currents, with dispersal trajectories being modulated by the magnitude of tidal currents, wave action, and wind effects (Bonte et al., 2007; Chang et al., 2008; Friess et al., 2012; Zhu et al., 2014, 2020a). In addition, most salt marsh species exhibit a variety of structures, which serve as dispersal units for their seeds, such as spikelets, inflorescence, and fragments (for spikelets see e.g., Ingrouille and Pearson, 1987; Bockelmann et al., 2003; for inflorescence see e.g., Strong et al., 2013; for fragments see e.g., Dethier and Hacker, 2004; Minchinton et al., 2006). These seed-containing units easily detach from the withered parent plant in autumn and winter through disturbance events (e.g., storm). It has been speculated that they have a stronger dispersal ability than seeds due to the larger interaction surface with the tidal current component. Similar to single seeds, the actual dispersal potential of these dispersal units might also be mirrored by their morphological properties such as mass and shape (Chang et al., 2008; Friess et al., 2012). Although these dispersal units have traditionally been excluded from assessments of the salt marsh propagule dispersal ability, evidence suggests that they may be important for dispersal (Ingrouille and Pearson, 1987; Bockelmann et al., 2003; Minchinton et al., 2006; Strong et al., 2013). Therefore, we aim to provide a more complete understanding of salt marsh dispersal strategies by comparing the dispersal behaviors of such dispersal units with those of isolated seeds under abiotic conditions.

Dispersal distance is a useful metric to describe, explore, and predict dispersal processes and patterns and is widely adopted in existing mechanistic or phenomenological dispersal models (Di Nitto et al., 2013; Sinclair et al., 2018; Shi et al., 2020). This metric generally depends on the combination of the buoyancy period of the dispersal units in the water column and the achievable dispersal speed based on the abiotic environmental setting (van der Stocken et al., 2013, 2019a; Xiao et al., 2016; Lai et al., 2020). The buoyancy of dispersal units, such as single seeds, has been widely analyzed in experiments and is readily available (Xiao et al., 2009, 2016; Guja et al., 2010; Stafford-Bell et al., 2015). In these studies, generally still water in containers was employed (Guja et al., 2010; Stafford-Bell et al., 2015) instead of replicating the fluctuating tidal water the dispersal units experience in the natural tidal flat environment. This may cause an overestimation of the long-term buoyancy of the dispersal units because the floating of small units is supported by surface tension. However, the floating period can be much shorter in moving water in which turbulence can break the surface tension (Vogel, 1988; van den Broek et al., 2005). Another flaw in assessing the long-term buoyancy of dispersal units is the use of tap or purified water rather than natural seawater, without assessing the validity of these alternatives (Xiao et al., 2009, 2016). Salt marsh dispersal processes are potentially reflected in long-term floating ability; therefore, it is important to detect the true buoyancy behavior of these dispersal units under different seawater flooding regimes.

Previous studies on hydrochory dispersal processes have focused on quantifying and modeling the dispersal speed and trajectory with tidal current velocities as a dominant control variable (Chambert and James, 2009; van der Stocken et al., 2015, 2017; Cunnings et al., 2016). This focus has recently shifted to wave action because the drifting speed of dispersal units at the top of the water column can be drastically affected by the orbital motion caused by waves (Holthuijsen, 2007; Lai et al., 2020). For example, Lai et al. (2020) reported that the wave magnitude negatively affected the dispersal ability of seagrass fragments, that is, the transport speed was slower under larger waves. In addition, the coupling of wind draft with hydrodynamic conditions has shown to affect the probability of hydrochorous dispersal and the shape of the dispersal trajectories, as documented for seagrass and mangroves (van der Stocken et al., 2013, 2015; Lai et al., 2020). In contrast, surprisingly little is known about the behavior of dispersal units of salt marsh species under changing wave and wind conditions, even though it could represent a dominant dispersal mechanism in wind wave-dominated coastal environments.

In this study, we bridge these knowledge gaps by conducting a series of mesocosm and flume experiments. We used different dispersal units (i.e., seed, spikelet, inflorescence, and plant fragments; see Fig. 2.1) of four globally distributed salt marsh species (*Salicornia europaea, Scirpus maritimus, Spartina anglica, and Elymus athericus*; see Fig. 2.1) and investigated: 1) variation in the buoyancy period under different flooding regimes (i.e., still seawater vs. moving seawater), 2) variation in the dispersal speed under varying wind, current, and wave scenarios, and 3) effects of the morphological characteristics of the dispersal units on the dispersal speed. The results of this study will contribute to the improvement of existing dispersal models and prediction of realistic distributional responses of salt marsh species to global climate change, thereby supporting the establishment of appropriate management and restoration strategies for coastal salt marshes.

2.2 Materials and methods

2.2.1 Plant materials

The salt marsh species *Salicornia europaea* (*Salicornia*)*, Scirpus maritimus* (*Scirpus*)*, Spartina anglica* (*Spartina*)*, and Elymus athericus* (*Elymus*) were selected as representatives of common functional species in salt marshes worldwide (Fig. 2.1; for *Salicornia* see e.g., Ellison, 1987; for *Scirpus* see e.g., Charpentier et al., 2000; for *Spartina* see e.g., Cao et al., 2018; for *Elymus* see e.g., Müller et al., 2013) and of distinctive growth strategies. *Salicornia, Scirpus*, and *Spartina* are typical pioneer species distributed in the low tidal flat, which have a distinctive seed morphology. In contrast, *Elymus* grows in the high tidal flat and has a seed morphology similar to that of *Spartina* (Fig. 2.1). All species can disperse in the form of a single seed or as units containing seeds (Ingrouille and Pearson, 1987; Bockelmann et al., 2003; Minchinton et al., 2006; Strong et al., 2013). To determine how the dispersal units may affect their dispersal capability, seeds, spikelets, inflorescence, and plant fragments of these species were considered as four categories of dispersal units based on the number of seeds and their morphological characteristics (Fig. 2.1; Table 2.1).

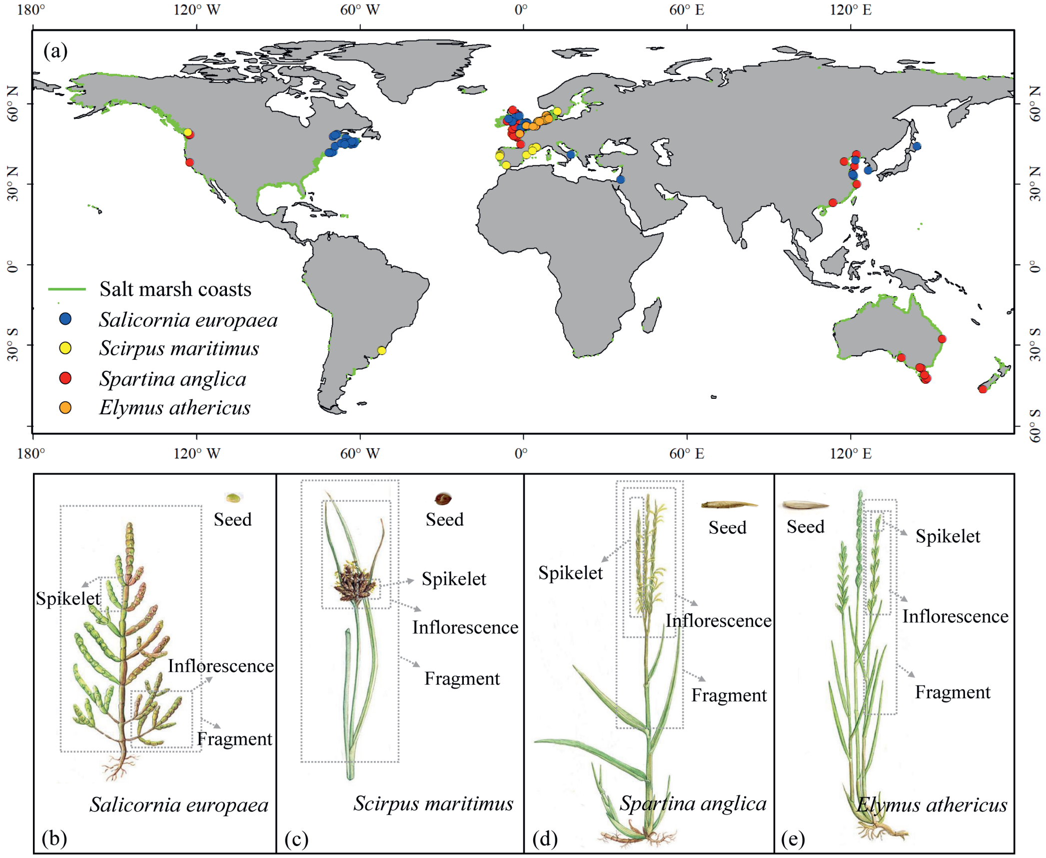


Fig. 2.1 (a) Distribution of *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*, and *Elymus athericus* along global coasts based on literature records (may not show the complete distribution). The global salt marsh coasts shown here as green line are based on the occurrence data (surveys and/or remote sensing), available in the open-access dataset (v6.1; Mcowen et al., 2017; https://doi.org/10.34892/07vk-ws51); (b-e) Schematic diagram of the dispersal units (i.e., seed, spikelet, inflorescence, and fragment) of the four species. See Table 2.1 for the relevant scales and other morphological traits of each unit. These pictures were modified from internet resources (https://www.field-studies-council.org).

Table 2.1. Morphological traits of the dispersal units (i.e., seed, spikelet, inflorescence, and fragment) of the four species used in this study. All morphological parameters were obtained through 100 measurements. The results are displayed in Mean ± SD.

Dispersal unit	Mass (g)	Length (mm)	Width (mm)
Salicornia europaea			
Seed	0.0002 ± 0.00001	1.10 ± 0.09	0.75 ± 0.11
Spikelet	0.16 ± 0.05	61.93 ± 13.79	2.62 ± 0.56
Inflorescence	1.27 ± 0.47	128.45 ± 14.07	12.94 ± 2.81
Fragment	2.36 ± 1.16	259.62 ± 24.11	14.71 ± 6.62
Scirpus maritimus			
Seed	0.005 ± 0.0009	3.35 ± 0.39	2.36 ± 0.28
Spikelet	0.11 ± 0.06	12.64 ± 1.82	7.20 ± 1.76
Inflorescence	0.55 ± 0.29	26.18 ± 5.81	14.91 ± 3.74
Fragment	0.84 ± 0.31	239.46 ± 36.22	15.54 ± 4.01
Spartina anglica			
Seed	0.01 ± 0.003	18.13 ± 1.77	2.10 ± 0.34
Spikelet	0.22 ± 0.07	110.49 ± 17.13	2.91 ± 0.43
Inflorescence	0.79 ± 0.26	182.53 ± 32.24	4.40 ± 0.87
Fragment	1.97 ± 0.62	361.48 ± 34.89	4.12 ± 1.30
Elymus athericus			
Seed	0.006 ± 0.002	10.98 ± 1.12	1.46 ± 0.18
Spikelet	0.02 ± 0.01	17.02 ± 2.03	4.11 ± 0.50
Inflorescence	0.37 ± 0.12	104.41 ± 15.66	5.49 ± 0.85
Fragment	0.55 ± 0.21	308.45 ± 33.35	4.56 ± 0.90

Individual plants containing mature seeds of the four species were collected from the Westerschelde estuary (southwestern Netherlands) in early November (coinciding with the presence of mature seeds and timing of dispersal) and subsequently divided into four dispersal unit categories. Seeds were considered to be mature when (1) the leaves and stems of the parent plant are withered (dark brown for *Salicornia* and *Scirpus*, brown-yellow for *Spartina* and *Elymus*), and (2) the seeds readily shed from the parent plant when shaken. Based on physics and geometry, the larger an entity is the less likely it is that it can be supported by the surface tension of water (Vogel, 1988). Based on this correlation and the capacity limit of our equipment, only seeds and spikelets with smaller shapes and masses were considered for the mesocosm experiments, which were carried out to detect the floating difference in still and moving seawater. All four dispersal units of each species were used in flume experiments to determine the variation in the dispersal speed under varying wind, current, and wave conditions. Prior to proceeding with the flume experiments, the mass and shape (indicated by the ratio of the length to width) of the dispersal units were determined. Width was obtained by measuring in the middle and at both sides of the dispersal unit and averaging the results.

2.2.2 Buoyancy measurement in mesocosm experiments

To estimate the effects of flooding regimes on the buoyancy of the dispersal units, 50 seeds or spikelets per species were placed in a cylindrical container (height: 25 cm, diameter: 28 cm) filled with seawater (salinity of 32) to a depth of 20 cm. A total of 40 containers were randomly placed in seven tanks to simulate the floating process in still seawater (five replications for each dispersal unit per species) and 40 additional containers were randomly placed in seven tanks equipped with oscillatory shakers to simulate the floating process in moving seawater (Fig. 2.2a, b). The oscillatory shaker moved via a pneumatic piston, driving the containers back and forth (30 cm in both directions) over a period of 2.6 s (cf. Cao et al., 2020). This resulted in the movement of water in the containers, with a swing amplitude of ~4 cm. The resulting oscillatory flow regimes do not reflect natural wave action but mimic wave-related hydrodynamic stress based on which the dispersal units are moved back and forth, similar to drifting across a trough from one crest to another. The floating ratio (*R*) of the dispersal units in each container was determined after 5 min and 6 h on Day 1. Subsequently, it was determined once per day for the following 29 d.

$$R = (50 - N)/50 \times 100$$

where N is the number of sunk seeds/spikelets and 50 refers to the total number of seeds/spikelets used. During each monitoring, the containers under the still water treatments were gently stirred to reduce the surface tension (Favre-Bac et al., 2017).

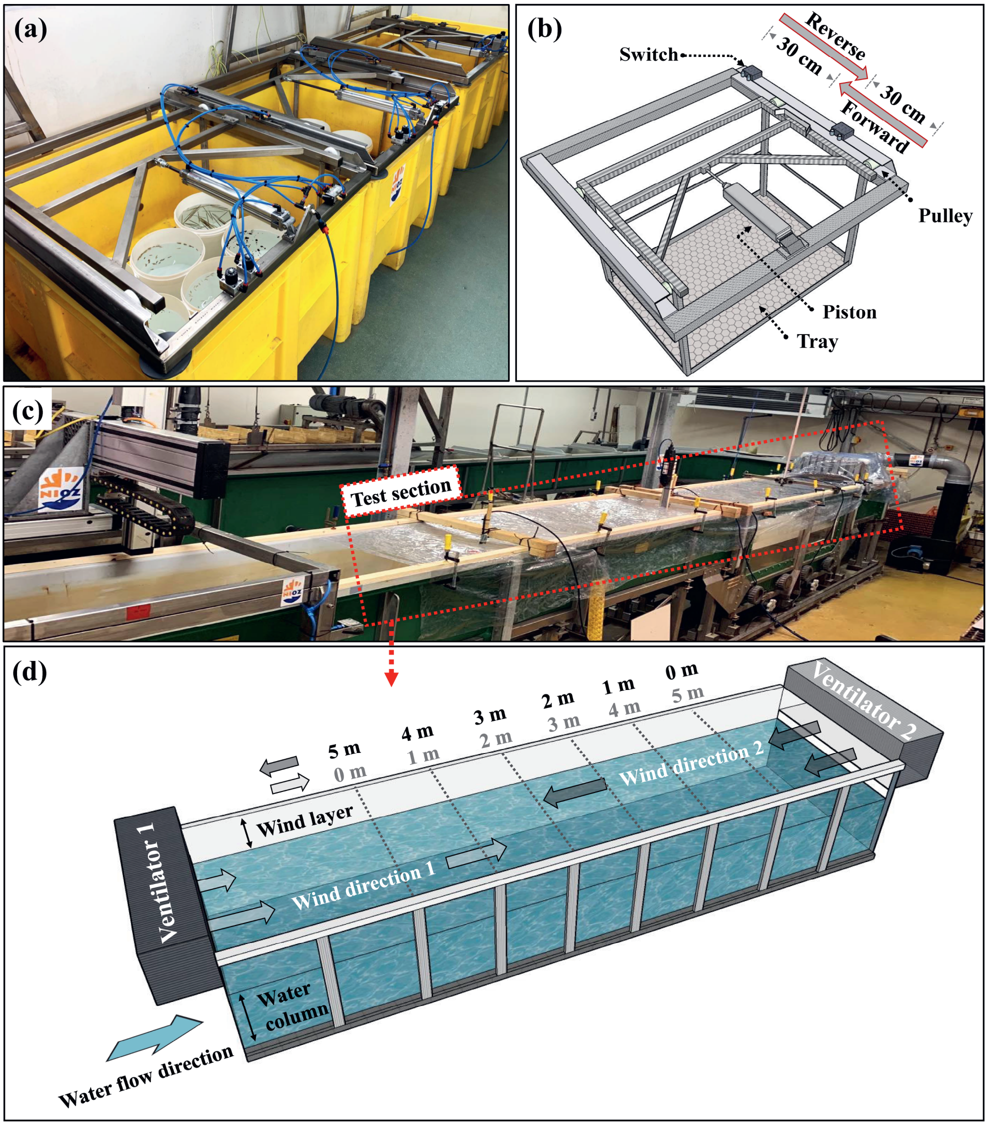


Fig. 2.2 Schematic diagrams and photographs showing the experiment setups

including references for more complete descriptions of the systems. (a) Photograph of the mesocosm setup, which was designed to simulate the floating process of the dispersal units in moving seawater; (b) diagram of the oscillatory shaker that was used to create moving seawater. The shaker was stroked via a pneumatic piston, moving the containers on the tray back and forth (30 cm in both directions, controlled by switches) over a period of 2.6 s. This resulted in the movement of water within the containers, with a swing amplitude of ~4 cm, in turn moving the dispersal units back and forth under the mimicked wave-related hydrodynamic stress; (c) photograph of the racetrack flume that was used to quantify the dispersal speeds of the dispersal units containing seeds under varying hydrodynamic and wind conditions. Note that the codirectional wind-generating system was not in place in this picture. In our study, the test section (red box) is a larger area than the 2 m long section, with a deepened bottom. The latter was covered with a hardwood board to obtain an undisturbed long smooth surface at the flume floor; (d) schematic representation of the test section located in the linear portion of the flume. Wind direction 1 (produced by ventilator 1) represents the scenario in which the wind is imposed in the same direction as the water currents and waves, whereas wind direction 2 (produced by ventilator 2) represents the scenario in which the wind is imposed in the opposite direction to the water current. The dispersal time was measured at intervals of one meter (see dotted lines).

2.2.3 Dispersal speed quantification in flume experiments

The racetrack flume facility (17.55 m long, 0.6 m wide, and 0.45 m deep) at the Royal Netherlands Institute for Sea Research (NIOZ) was used for the quantification of the dispersal speed of dispersal units containing seeds under varying hydrodynamic and wind conditions (Fig. 2.2c; Bouma et al., 2005). This flume equipped with a conveyer belt, adjustable wave paddle, and industrial ventilator, allowed for repetitions under controlled unidirectional currents, regular waves, and constant wind (Bouma et al., 2005; Chang et al., 2008; van der Stocken, 2013). The flume was filled with seawater (salinity of 32), which was directly pumped from the adjacent sea outside the NIOZ, and run at a constant water depth of 0.33 m, ensuring uniform and controllable flow conditions and the highest flow velocity and wave magnitude (cf. Lai et al., 2020). Although the generated waves will be somewhat distorted by the interaction with the flume floor, our setup mimics relevant conditions because a similar process occurs in shallow coastal areas in which marshes are typically located (Bouma et al., 2014). The experimental section, spanning 5 m, was located in the linear portion of the flume and covered with a transparent plastic ceiling to homogenize the internal wind speed (Fig. 2.2c, d). In the middle and at 1 m from both sides of the experimental section, the current velocities, wave heights, wave frequency, and wind speeds were measured using acoustic doppler velocimeters (Nortek AS, Oslo, Norway), pressure sensors (Druck PTX 1830, GE, USA), and anemometers (AN100 CFM, Extech, USA), respectively. The values recorded by these sensors were used to calibrate and define the various conditions in the flume. As a technical characteristic of the NIOZ flume, the wave frequency differs depending on the wave height; hence, we used the wave magnitude (indicated by the wave height and frequency) to define the various wave conditions (cf. Lai et al., 2020).

The dispersal units were released in sequence at the beginning of the experimental section and were subjected to one of the following 18 combinations of wind and hydrodynamic conditions (categorized into four scenarios):

1) *Current and wind from the same direction*: current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the same direction as the water current;
2) *Current and wind from the opposite direction*: current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the opposite direction of the water current;
3) *Waves without wind*: waves of four magnitudes (**i**: wave height [h] = 4 cm,

frequency [*f*] = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed without wind and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction;

4) *Waves and wind from the same direction*: waves of four magnitudes (**i**: *h* = 4 cm, *f* = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed with constant wind (3.0 m s^{-1}) in the same direction and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction. Any effects of wind-driven surface ripples on the wave height were considered negligible due to its millimeter-level amplitude.

These experimental settings were selected to reflect the typical conditions of natural salt marshes based on the measurement of Bouma et al. (2005) in the Westerschelde estuary. The current-only scenario was not considered because dispersal units are transported at the same speed as the prevailing current in the absence of wind or waves (van der Stocken et al., 2015; Lai et al., 2020). Wave-only (no-wind) scenarios may not be common for salt marshes in estuaries in which waves are typically wind-generated. These scenarios were added to isolate the relative effect of the wave action from the intermixing effect with other physical disturbances such as wind, thereby providing insights into the effects of various factors on the dispersal speed of various dispersal units.

Each dispersal unit per species was tested 20 times, leading to a total of 5,760 runs (4 species × 4 dispersal units × 18 treatments × 20 replicates). For each run, the dispersal time per meter under the set scenarios was recorded using a stopwatch. Following similar flume studies in other coastal systems (e.g., van der Stocken et al., 2013; Lai et al., 2020) and our preliminary tests, a distance of 3 m is long enough to enable an equilibrium dispersal speed of the dispersal units. Hence, to avoid possible instabilities (e.g., turbulent wind flow near the ventilator), only the data obtained over the middle 3 m of the experimental section were averaged to calculate the dispersal speed. Runs in which the dispersal units touched the wall or bottom of the flume were not used.

2.2.4 Statistical analysis

For the data obtained from mesocosm experiments, the effects of flooding regimes and dispersal units on the floating ratio were analyzed by specifying a generalized linear model (GLM) with “family” = “binomial” for the proportion data (Bolker et al., 2007; Zhu et al., 2014). The Pairwise Wilcoxon rank-sum test was adopted to test the difference in the floating ratio between species. For the data obtained from flume experiments, the effects of dispersal units, current velocities, and wave magnitudes on the dispersal speed were analyzed by specifying a GLM with “family” = “Gamma” for the non-negative data (Bolker et al., 2007; Lai et al., 2020). For variables with significant effects, a post hoc multiple comparison analysis among the variables was run using the “glht” function in “multcomp” CRAN (Hothorn et al. 2008; http://multcomp.R-forge.R-project.org). The pairwise Wilcoxon rank-sum test was also adopted to test the difference in the dispersal speed between species under the same treatment. In addition, the GLM with “family” = “Gamma” was also adopted to determine the effects of morphological factors on the dispersal speed (Bolker et al., 2007, Lai et al., 2020). All statistical analyses were performed using R v3.6.1 (https:// www.r-project.org) and a significance level of 0.05.

2.3 Results

2.3.1 Effects of flooding regimes on the buoyancy period

As expected, flooding regimes have a species-specific effect on the buoyancy of the dispersal units over time (Fig. 2.3). Overall, for the three pioneer species (i.e., *Salicornia*, *Scirpus*, and *Spartina*), both seeds and spikelets tend to lose buoyancy more rapidly under moving seawater compared with still seawater (Fig. 2.3), although this difference was only significant for the seeds of *Salicornia* ($P < 0.05$) and spikelets of *Scirpus* ($P < 0.01$). Surprisingly, an opposite trend was observed for the high tidal flat species *Elymus*; that is, the buoyancy of the seeds and spikelets increases under moving seawater (Fig. 2.3), with significant differences only observed for the spikelets ($P < 0.01$).

When focusing on the effects of dispersal units, the buoyancy of seeds and spikelets did not differ significantly under moving seawater regardless of the species ($P > 0.05$; Fig. 2.3). During the treatment with still seawater, the seeds of *Scirpus* lost its buoyancy significantly faster than the spikelets ($P < 0.05$), whereas the buoyancy of seeds and spikelets for other species was similar ($P > 0.05$; Fig. 2.3).

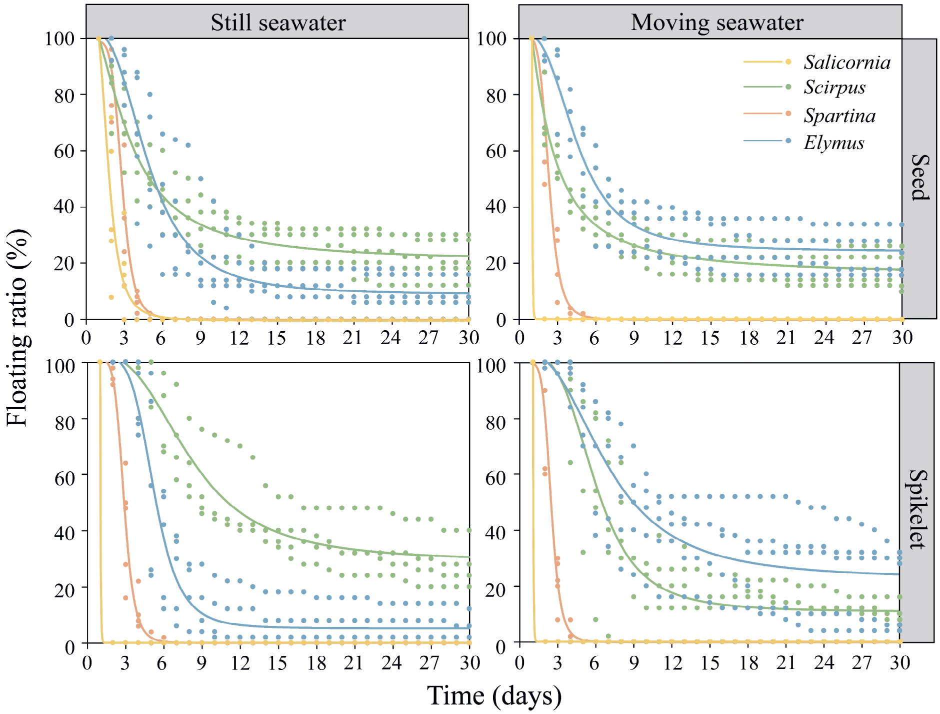


Fig. 2.3 Floating ratio of the seeds and spikelets of each species under different flooding regimes (i.e., still seawater vs. moving seawater) as a function of time.

Solid circles: measured data; solid lines: the fitting curves based on the logistic function.

The buoyancy differed significantly among different species ($P < 0.01$) regardless of the use of still or moving seawater. Under still seawater, *Scirpus* exhibited the strongest floating capacity and highest floating rate after 30 d, whereas *Salicornia* had the weakest floating capacity and zero floating after 30 d. However, a different trend was observed during the treatment with moving seawater; that is, *Elymus* > *Scirpus* > *Spartina* > *Salicornia* ($P < 0.01$).

2.3.2 Effects of currents and wind on the dispersal speed of different dispersal units

Currents have significant effects on the dispersal speed regardless of the dispersal units, species, or wind directions. Dispersal speed linearly increased with increasing current velocity ($P < 0.001$; Fig. 2.4; Table S2.1). In the scenario in which the current and wind come from the same direction, wind had a positive effect on dispersal speed. Under lower current velocities (i.e., 0.1, 0.2, and 0.3 m s^{-1}), the dispersal units of all species were the most sensitive to wind action, causing the dispersal speeds to exceed prevailing current velocities (Fig. 2.4a). In addition, the dispersal speeds of the dispersal units for *Salicornia* were significantly different ($P < 0.05$; Table S2.1). The fastest dispersal speed was observed for a single seed; however, such a trend was not observed for other species ($P > 0.05$; Table S2.1). The dispersal speeds of different species were quasi-identical ($P > 0.05$; Fig. 2.4a).

When wind was imposed in the opposite direction to the water current, the dispersal speeds of the dispersal units of all species decelerated compared with the prevailing current velocities (Fig. 2.4b). The dispersal velocities of the dispersal units of all species were quasi-identical ($P > 0.05$; Table S2.2).

Interestingly, the dispersal velocities varied significantly among species. The high tidal flat species (i.e., *Elymus*) exhibited the lowest dispersal speeds among the three pioneer species ($P < 0.05$), whereas *Salicornia* showed the fastest dispersal speed ($P < 0.05$; Fig. 2.4b).

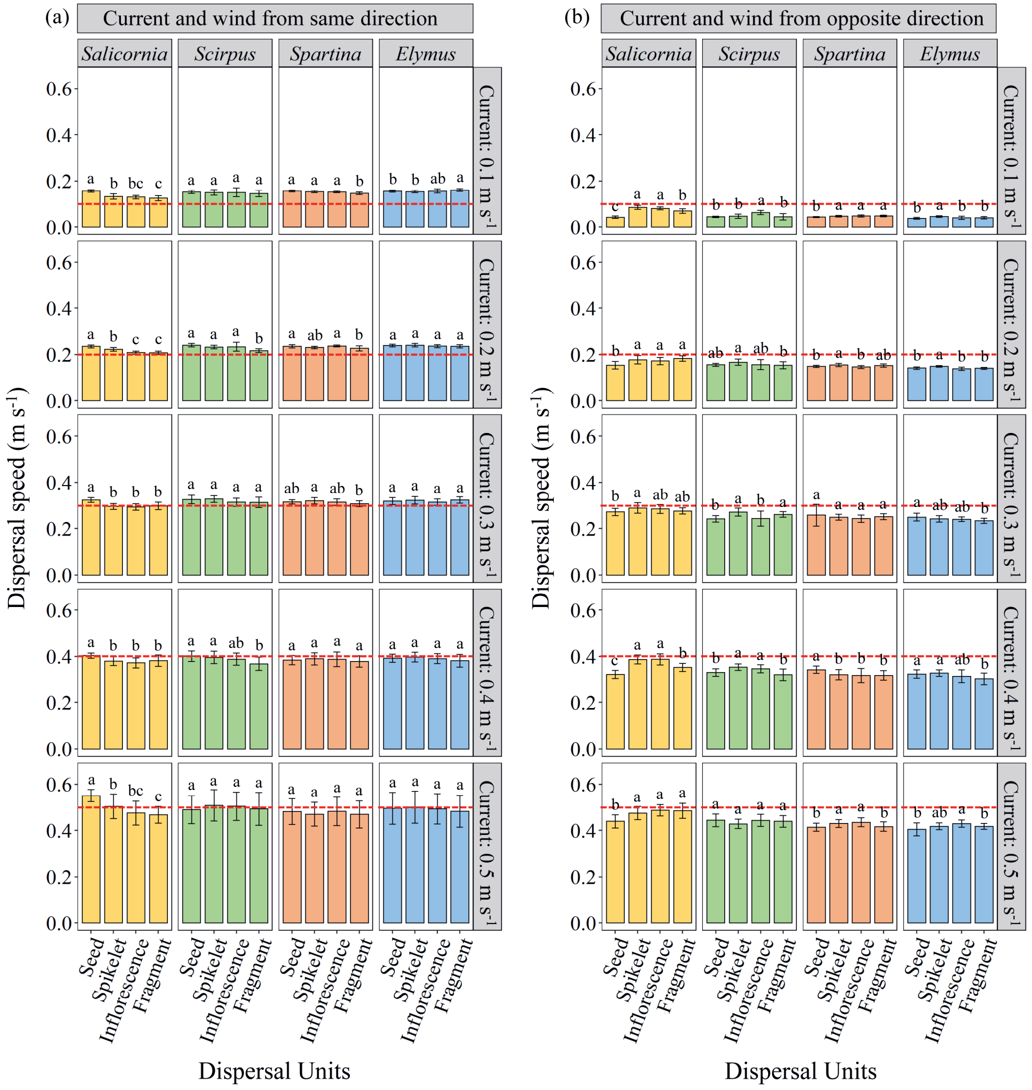


Fig. 2.4 Mean (± SD) dispersal speeds of four dispersal units (i.e., seed, spikelet, inflorescence, and fragment) per species under different current velocities and wind conditions. (a) Current velocities of 0.1, 0.2, 0.3, 0.4, and

0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the same direction. (b) Current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the opposite direction. Different lowercase letters denote significant differences in the dispersal speed among different dispersal units. The red dotted line represents the water current speed of each treatment, which serves as a reference to reflect the additive or antagonistic effects of the treatments on the dispersal speeds of the dispersal units.

2.3.3 Effects of waves and wind on the low-flow dispersal speed of different dispersal units

In the absence of wind, the waves had an overall decelerating effect on the dispersal process ($P < 0.001$; Table S2.3), causing the transport of the dispersal units of all species to become notably slower than the speed of the prevailing current (Fig. 2.5a). As the wave magnitude increased, the overall deceleration effect of the waves on the dispersal speed was alleviated, but this mitigation effect was not linear and varied among species (Fig. 2.5a, S2.1). Dispersal speeds of the dispersal units of each species also significantly differed ($P < 0.001$), except for the high tidal flat species *Elymus* (Fig. 2.5a; Table S2.3). However, variability among the dispersal units was species-specific and does not follow a common pattern or trend (Fig. 2.5a). For instance, the single seed of *Spartina* had a drastically lower average dispersal speed than other dispersal units ($P < 0.05$), whereas that of *Salicornia* exhibited a significantly faster average dispersal speed ($P < 0.05$; Fig. 2.5a). The across-species comparison showed quasi-identical dispersal velocities without significant differences, although *Spartina* and *Elymus* moved at a slightly higher average speed than *Scirpus* and *Salicornia* ($P > 0.05$; Fig. 2.5a).

The treatment with wind in the same direction as the waves resulted in an acceleration in dispersal speed regardless of the dispersal units, species, or wave magnitudes (Fig. 2.5b). The dispersal speeds differed significantly among dispersal units ($P < 0.001$), with the morphologically largest unit (i.e., fragment) always exhibiting the lowest dispersal speed ($P < 0.001$; Fig. 2.5b; Table S2.4). Similarly, the dispersal speeds varied significantly depending on the wave magnitude ($P < 0.001$), except for *Scirpus*, but the variability was not linear and differed among species (Fig. 2.5b; Table S2.4). In addition, the dispersal speeds of the four species differed significantly ($P < 0.001$; Fig. 2.5b). The high tidal flat species *Elymus* had the fastest dispersal speed, and the dispersal speeds of *Spartina* and *Scirpus* were significantly higher than that of *Salicornia* ($P < 0.001$; Fig. 2.5b).

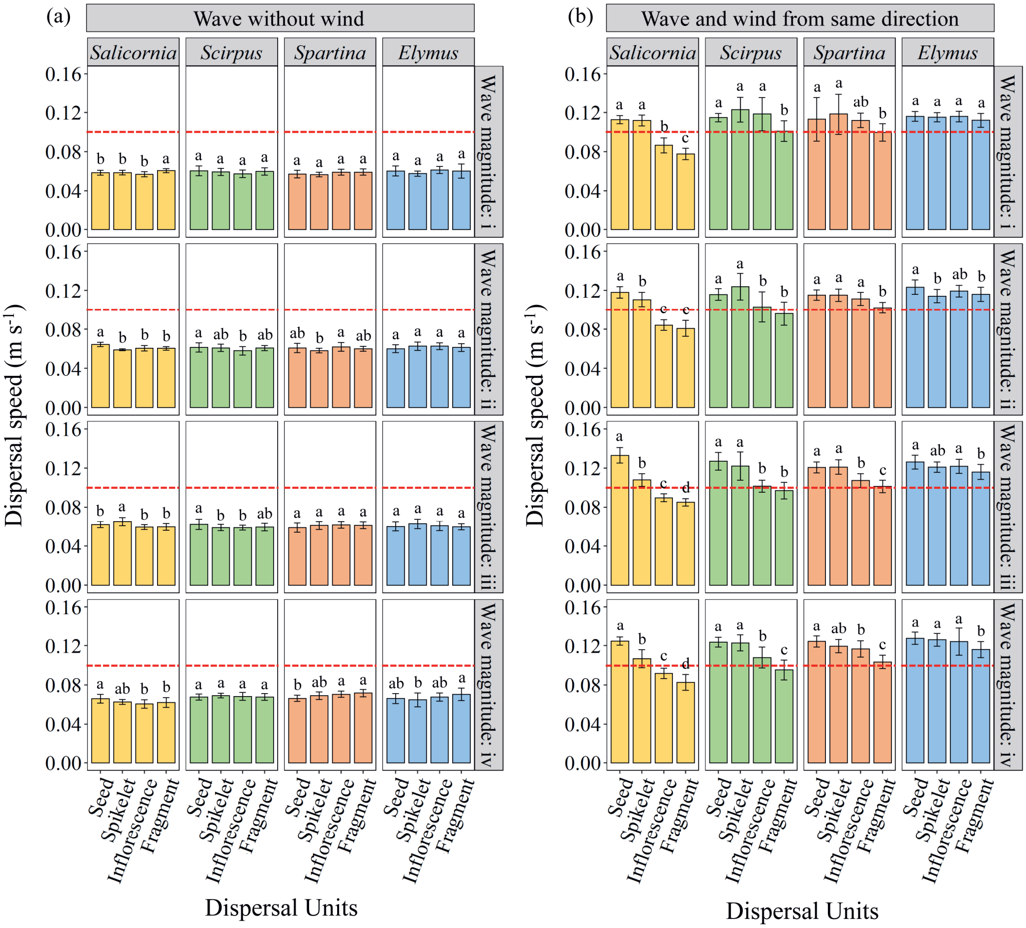


Fig. 2.5 Mean (± SD) dispersal speeds of four dispersal units (i.e., seed,

spikelet, inflorescence, and fragment) per species under different wave magnitudes and wind conditions. (a) Waves of four magnitudes (**i**: wave height [*h*] = 4 cm, frequency [*f*] = 0.45 Hz; **ii**: $h = 6$ cm, $f = 0.50$ Hz; **iii**: $h = 8$ cm, $f = 0.56$ Hz; **iv**: $h = 10$ cm, $f = 0.67$ Hz) were imposed without wind and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction. (b) Waves of four magnitudes (**i**: $h = 4$ cm, $f = 0.45$ Hz; **ii**: $h = 6$ cm, $f = 0.50$ Hz; **iii**: $h = 8$ cm, $f = 0.56$ Hz; **iv**: $h = 10$ cm, $f = 0.67$ Hz) were imposed with constant wind (3.0 m s^{-1}) coming from the same direction and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction. Different lowercase letters denote significant differences in the dispersal speeds among different dispersal units. The red dotted line represents the water current speed of each treatment, which serves as a reference to reflect the additive or antagonistic effects of the treatments on the dispersal speeds of the dispersal units.

2.3.4 Effects of the morphological characteristics of dispersal units on the dispersal speed

With respect to the effects of morphological characteristics of dispersal units, the dispersal speeds varied significantly with changing mass at all current velocities regardless of the direction of the wind ($P < 0.01$; Table 2.2 and 2.3). The shapes of the dispersal units also had significant effects on the dispersal speeds, but these effects depended on the wind direction and prevailing current velocities. For example, the dispersal speeds varied significantly with the changing shape of the dispersal unit at lower current velocities (i.e., 0.1, 0.2, and 0.3 m s^{-1}) accompanied by codirectional wind ($P < 0.05$; Table 2.2). However, when the wind was imposed in the opposite direction to the current, the dispersal speeds varied significantly with the changing shape of the dispersal unit at all current velocities, except for the lowest current velocity (i.e., 0.1 m s^{-1}; $P < 0.001$; Table 2.3). Furthermore, a significant effect of the mass on the dispersal speed was also found in the scenario in which waves and wind were imposed from the same direction ($P < 0.001$; Table 2.5), whereas the shape of the dispersal unit only had a significant effect on the dispersal speed at higher wave magnitudes (i.e., **ii**: $h = 6$ cm, $f = 0.50$ Hz; **iii**: $h = 8$ cm, $f = 0.56$ Hz; **iv**: $h = 10$ cm, $f = 0.67$ Hz; $P < 0.05$; Table 2.5). In addition, in the scenario in which only waves were imposed without wind, neither the mass nor the shape of dispersal unit had a significant effect on the dispersal speed under lower wave magnitudes (i.e., **i**: $h = 4$ cm, $f = 0.45$ Hz; **ii**: $h = 6$ cm, $f = 0.50$ Hz; **iii**: $h = 8$ cm, $f = 0.56$ Hz; $P > 0.05$; Table 2.4), but the dispersal speed varied significantly with the changing mass and shape of the dispersal unit at the highest wave magnitude (i.e., **iv**: $h = 10$ cm, $f = 0.67$ Hz ; $P < 0.05$; Table 2.4).

Table 2.2. Results of the generalized linear models testing the effects of the morphological characteristics on the dispersal speeds under scenario-1, i.e., current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the same direction as the water current.

Model	Estimate	Std. error	t-value	p-value
Current (0.1 m s^{-1}) and wind from the same direction				
Intercept	6.5696	0.0511	128.5090	<0.001***
Mass	0.5394	0.0609	8.8570	<0.001***
Shape	-0.0060	0.0012	-4.9480	<0.001***
Current (0.2 m s^{-1}) and wind from the same direction				
Intercept	4.2902	0.0197	217.4290	<0.001***
Mass	0.2345	0.0239	9.8300	<0.001***
Shape	-0.0025	0.0005	-4.8720	<0.001***
Current (0.3 m s^{-1}) and wind from the same direction				
Intercept	3.1658	0.0166	191.0800	<0.001***
Mass	0.1290	0.0186	6.9250	<0.001***
Shape	-0.0013	0.0005	-2.5930	0.0102*
Current (0.4 m s^{-1}) and wind from the same direction				
Intercept	2.5659	0.0162	158.1090	<0.001***
Mass	0.0555	0.0150	3.6970	<0.001***
Shape	0.0005	0.0005	1.1290	0.2602
Current (0.5 m s^{-1}) and wind from the same direction				
Intercept	2.0141	0.0238	84.7690	<0.001***
Mass	0.0565	0.0209	2.7030	0.0075**
Shape	0.0011	0.0007	1.5810	0.1156

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

Table 2.3. Results of the generalized linear models testing the effects of the morphological characteristics on the dispersal speeds under scenario-2, i.e., current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the opposite direction of the water current.

Model	Estimate	Std. error	t-value	p-value
Current (0.1 m s^{-1}) and wind from the opposite direction				
Intercept	19.8265	0.7154	27.7140	<0.001***
Mass	-2.3589	0.4700	-5.019	<0.001***
Shape	0.0355	0.0191	1.8560	0.0655
Current (0.2 m s^{-1}) and wind from the opposite direction				
Intercept	6.4149	0.0824	77.8720	<0.001***
Mass	-0.3555	0.0719	-4.9410	<0.001***
Shape	0.0084	0.0022	3.7220	<0.001***
Current (0.3 m s^{-1}) and wind from the opposite direction				
Intercept	3.8915	0.0330	117.8830	<0.001***
Mass	-0.0860	0.0252	-3.4080	<0.001***
Shape	0.0034	0.0010	3.6080	<0.001***
Current (0.4 m s^{-1}) and wind from the opposite direction				
Intercept	2.9392	0.0270	108.8420	<0.001***
Mass	-0.0688	0.0257	-2.6800	0.0080**
Shape	0.0034	0.0007	4.7360	<0.001***
Current (0.5 m s^{-1}) and wind from the opposite direction				
Intercept	2.3061	0.0147	156.4340	<0.001***
Mass	-0.0903	0.0155	-5.8090	<0.001***
Shape	0.0019	0.0004	4.6680	<0.001***

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

Table 2.4. Results of the generalized linear models testing the effects of the morphological characteristics on the dispersal speeds under scenario-3, i.e., waves of four magnitudes (**i**: wave height [*h*] = 4 cm, frequency [*f*] = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed without wind and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction.

Model	Estimate	Std. error	t-value	p-value
Wave (magnitude **i**) without wind				
Intercept	17.0366	0.1680	101.4210	<0.001***
Mass	-0.1297	0.1331	-0.9740	0.3320
Shape	0.0002	0.0104	0.0230	0.9820
Wave (magnitude **ii**) without wind				
Intercept	16.2921	0.1441	113.0770	<0.001***
Mass	0.0265	0.1085	0.2450	0.8070
Shape	0.0107	0.0086	1.2490	0.2140
Wave (magnitude **iii**) without wind				
Intercept	16.5845	0.1557	106.4920	<0.001***
Mass	-0.0068	0.0982	-0.0690	0.9450
Shape	-0.0064	0.0096	-0.6740	0.5010
Wave (magnitude **iv**) without wind				
Intercept	14.9524	0.1209	123.6260	<0.001***
Mass	0.2872	0.1281	2.2410	0.0265*
Shape	-0.0132	0.0028	-4.6560	<0.001***

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

Table 2.5. Results of the generalized linear models testing the effects of the morphological characteristics on the dispersal speeds under scenario-4, i.e., waves of four magnitudes (**i**: *h* = 4 cm, *f* = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed with constant wind (3.0 m s^{-1}) in the same direction and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction.

Model	Estimate	Std. error	t-value	p-value
Wave (magnitude **i**) and wind from the same direction				
Intercept	8.6116	0.1221	70.5080	<0.001***
Mass	1.2237	0.1242	9.8500	<0.001***
Shape	-0.0064	0.0036	-1.7590	0.0802
Wave (magnitude **ii**) and wind from the same direction				
Intercept	8.6294	0.0908	95.0660	<0.001***
Mass	1.3566	0.1134	11.9680	<0.001***
Shape	-0.0042	0.0015	-2.8680	0.0046**
Wave (magnitude **iii**) and wind from the same direction				
Intercept	8.5366	0.0846	100.8690	<0.001***
Mass	1.1995	0.0869	13.8040	<0.001***
Shape	-0.0056	0.0025	-2.2570	0.025*
Wave (magnitude **iv**) and wind from the same direction				
Intercept	8.2481	0.0877	94.0460	<0.001***
Mass	1.5863	0.1189	13.3380	<0.001***
Shape	-0.0056	0.0022	-2.5310	0.0121*

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

2.4 Discussion

Insights into the behavioral dynamics of dispersal units are indispensable for understanding and predicting the connectivity and persistence of salt marshes. Our mesocosm experiments provide the first numbers foe the floatability variation of seeds and spikelets of salt marsh species in seawater with oscillatory flow regimes. The results show that moving seawater has a species-specific effect on the buoyancy. It reduces the floatability of pioneer species but prolongs that of high tidal flat species. The flume experiments provide valuable first-hand data regarding the traveling speed of salt marsh dispersal units under a range of hydrodynamic and wind conditions. The results clearly demonstrate the positive effects of currents; that is, the linear acceleration of dispersal speed with increasing current velocity. Wave action negatively affects the dispersal process, but the deceleration decreases nonlinearly with increasing wave magnitude. Wind has an additive or antagonistic effect on dispersal speed depending on its direction relative to the direction of the ambient water currents. Most importantly, the results show that the dispersal speed of dispersal units can vary significantly, especially under wave action. The results of this study provide guidance for future efforts to model salt marsh seed motion and evaluate its potential dispersal distance or range and thus contribute to the prediction of realistic distributional responses of salt marsh species to a wide range of disturbance scenarios.

2.4.1 Floatability in still seawater vs. moving seawater

Floating time is a critical factor affecting the potential dispersal distances of water-dispersed propagules (Carthey et al., 2016; van der Stocken et al., 2019a, b). Moving seawater, which was created by an oscillatory shaker in this study, provides more realistic estimates of the buoyancy period of dispersal units that are subjected to currents and wave action in natural salt marshes. As expected, both the seeds and spikelets of the three pioneer species lose their buoyancy more rapidly in moving seawater than in still seawater. These results are consistent with those of a previous study by McDonald (2014), who reported a reduced buoyancy period for *Spartina densiflora* seeds based on an agitated treatment. Surprisingly, the opposite trend was observed for the high tidal flat *Elymus* species. The floatability of both seeds and spikelets was prolonged by at least 20 d in moving seawater. The longer buoyancy period of *Elymus* seeds in moving water may be due to its unique physical traits and the orbital motion of moving water. The seed coat of *Elymus* is thicker and covered with a waxy layer, making it relatively impermeable to water and air. Under moving water, the lighter mass and larger shape of *Elymus* seeds may allow them to move with a relatively larger amplitude, resulting in a relatively reduced contact time with the water. Furthermore, the effect of moving water on a single seed is superimposed and amplified in the case of a spikelet because it contains multiple seeds. Therefore, we assume that it takes longer for *Elymus* seeds and spikelets to soak up water in moving water than in still water. This discrepancy in sensitivity to the flooding regime further indicates that current assessments of the dispersal capacity of the salt marsh propagules may be rather imprecise because even a floating time difference of one day has a significant effect on dispersal distance, resulting in a significant shift of the magnitude and direction of the potential connectivity between habitats (van der Stocken et al., 2019b). The results of current studies also reveal that the high tidal flat species have a longer buoyancy period than the pioneer species despite similar seed shapes (e.g., *Elymus* vs. *Spartina*). This may underpin the importance of widely recognized research reveling that the environment of the mother plant serves as a regulator of the offspring's traits (so-called "maternal effect," Wolf and Wade, 2009). Species in high tidal flat salt marshes are typically exposed to much fewer inundations than the pioneer species in low tidal flats. Hence, high-marsh species may have evolved traits that amplify their dispersal ability, thereby seizing rare opportunities to explore and colonize new habitats. For example, compared with *Spartina* (with seed shapes similar to those of *Elymus*), seeds of *Elymus* have a harder seed coat and an additional waxy layer, which makes them relatively impermeable to water, leading to a longer floating time.

2.4.2 Relative role of dispersal units and abiotic conditions on dispersal speed

Salt marsh species are hydrochorous (i.e., they have seeds that are dispersed by water), which means that the hydrodynamics of tidal currents are the dominant abiotic drivers underlying dispersal dynamics (Chang et al., 2008; Friess et al., 2012; Shi et al., 2020). In addition to the widely recognized positive effect of the current velocity (Chambert and James, 2009; van der Stocken et al., 2015, 2017; Cunnings et al., 2016), our flume experiments revealed the potential decelerating effect of wave action on the seed dispersal process. Compared with current-only scenarios (where the dispersal units are transported at the same speed as the prevailing current), it took the dispersal units longer to travel the same distance under all tested wave magnitudes. This might be attributed to the orbital movement of the dispersal units around their position, which slows them down relative to the prevailing current component (Holthuijsen, 2007). Lai et al. (2020) described a reduced dispersal speed for seagrass fragments under growing waves (i.e., wave height of 4 cm and frequency of 0.40 vs. wave height of 6 cm and frequency of 0.56). However, this deceleration trend is not supported by current findings because the highest wave magnitude (i.e., wave height of 10 cm and frequency of 0.67) corresponds to the highest dispersal speed, although it is slower than the prevailing current velocity. This implies that the effects of waves on the dispersal speed are not linear and much more intricate. The covariation of the wavelength with the imposed wave height in our flume scenarios could be a reason for the complex nonlinear effects of waves. The relatively faster speed of the dispersal unit under waves with larger amplitude might be explained by the larger longitudinal component of the circular orbits described by the dispersal unit and the greater Stokes drift velocity at the free surface of water waves (Holthuijsen, 2007). With rising sea levels and increasing storm frequency and intensity (Silinski et al., 2015; Hanley et al., 2020; Krauss and Ostler, 2020), wave forcing can be expected to become more severe in the near future. Thus, more general mechanisms underlying the effects of waves on the propagule dispersal of coastal salt marsh species, such as the relative contribution of specific wave parameters including the wavelength and wave period to the seed dispersal speed must be considered, particularly in future numerical models, to predict the salt marsh dispersal and distribution under global climate change.

Although it was assumed that the dispersal units would react similarly to wind conditions in previous modeling estimates of the dispersal distance (Di Nitto et al., 2013), the results of our study demonstrate that important differences exist not only among species but also among dispersal units of the same species. Unlike mangroves and seagrass (Ruiz-Montoya et al., 2012; van der Stocken et al., 2019a), the dispersal units of salt marsh plants generally float on top of the water column and do not differ in terms of the floating orientation (i.e., vertically or horizontally). The floating behavior strongly determines how wind can exert a drag force on the dispersal units (van der Stocken et al., 2013), pushing them to disperse faster than the prevailing current velocity. In most coastal areas, historical average wind speeds during seed dispersal are generally faster than those that were imposed in our flume experiment (Archer and Jacobson, 2005; https://globalwindatlas.info), which means that the effect of wind might be more prominent. Furthermore, our results emphasize the importance of the wind direction, which can shift the role of wind during salt marsh dispersal (i.e., additive or antagonistic) but also adjust the sensitivity of dispersal units to the effects of currents and waves. The dominant wind direction does not always align with the prevailing current (see examples in Zhu et al., 2014; Wang et al., 2017), which may result in more complex dispersal pathways of coastal species.

Interestingly, note that the dispersal units containing seeds play additional roles in the dispersal speed under wave action. Once the wind is imposed with waves, the morphologically largest dispersal units (i.e., fragment) exhibit the lowest dispersal speed. This is due to their heavier mass and larger shape, as shown by our GLM results, which leads to greater friction between the dispersal units and the waterbody, thus dissipating more energy to travel over the same distance. Similarly, in mangroves, the travel distance of smaller dispersal units was estimated to be 10–200 times that of larger dispersal units (Sousa et al., 2007). On the other hand, the larger dispersal units appear to be easily intercepted by vegetation or other obstacles, thus resulting in lower long-distance dispersal probability (Chang et al., 2008; De Ryck et al., 2012). However, once settled, many seeds in larger dispersal units can simultaneously germinate, which is expected to lead to a higher probability of successful establishment due to the mutually beneficial effects among multiple individuals and overall larger biomass (Bouma et al., 2009; Silliman et al., 2015). A similar situation has been reported for mangroves, in which the advantage of long-distance dispersal might be offset by reduced establishment potential (Simpson et al., 2017). This trade-off between dispersal and establishment among dispersal units or species would be an evolved life-history but requires further scrutiny (Friess et al., 2012; van der Stocken et al., 2019a).

2.4.3 Species-specific differences in the dispersal strategies

When comparing the dispersal ability among species, we noted that all species were dispersed at a quasi-identical average speed in scenarios in which currents are accompanied by codirectional wind and only waves. This indicates that their ability to disperse in the field is fundamentally constrained by the substantial differences in the buoyancy period. The key role of the propagule's floating ability has been similarly reported in other aquatic systems such as freshwater wetlands, seagrass and mangroves, where higher buoyancy enhances the possibility for long-distance hydrochory and is of great importance for both dispersal efficiency and vegetation dynamics (Nilsson et al., 2010; Friess et al., 2012; Ruiz-Montoya et al., 2012; van der Stocken et al., 2019a). Interestingly, when wind is imposed in the same direction as the water current and waves are applied, a clear trend regarding both buoyancy and dispersal speed can be observed among species: *Elymus* > *Scirpus* > *Spartina* > *Salicornia*. This might reflect potential differences in the dispersal strategies and niche distribution of these species. Based on the longer floating period and faster dispersal speed, *Elymus* dispersal units can attain large dispersal distances, which may enable them to remain drifting with tidal currents until they are eventually entrapped by high tidal flat vegetation or deposited at the waterline. In contrast, the low floatability of *Salicornia* dispersal units coupled with their slower dispersal speed results in a high probability to be deposited near their parent plants in the pioneer area. Such a relation between dispersal ability and niche segregation supports the theory of "directed dispersal" proposed for shoreline wetlands and more terrestrial systems, suggesting that there are adaptations that magnify the potential to disperse to an environment suitable for survival (Howe and Smallwood, 1982; Pufal and Garnock-Jones, 2010; Soons et al., 2017).

2.4.4 Implications for salt marsh restoration

A basic principle for formulating a successful and cost-effective ecological restoration scheme is to understand the natural distribution and establishment patterns of dispersal units at the restoration and/or reference sites (Lewis III, 2005; Bouma et al., 2014). Incorporating hydrology and natural regeneration via propagule establishment has the potential to gain a faster recovery and more spatially extensive effect compared with man-made restoration attempts based on transplanting (Nilsson et al., 2010; Prach et al., 2015; Aavik and Helm, 2018). The lateral expansion of transplants by clonal growth is slow compared with seedling colonization (Zhu et al., 2020a). As a first step to achieve restoration via seedling colonization, hydrologic restrictions or physical blockages that prevent natural waterborne transport of dispersal units to a restoration site must be distinguished (Lewis III, 2005; van Regteren et al., 2019), whereafter windows of opportunity may dominate seedling survival (Balke et al., 2011, 2014).

The present study provides critical information for biophysical models aimed at exploring and predicting the dispersal process of common salt marsh dispersal units. It thereby allows ecologists/engineers to more accurately assess the connectivity and persistence of target communities and prioritize restoration sites. Furthermore, integrating these results into dispersal models could help to identify locations that are likely dispersal sources and those that might be experiencing a high propagule pressure (Weatherall et al., 2016). Such insights are highly relevant for the prevention and control of invasive species (such as *Spartina* and *Elymus*) because eradicating possible dispersal source areas appears to be the most efficient way to contain the invasion (Zhao et al., 2020a, b). Overall, the current study contributes to the quantitative and in-depth understanding of the dispersal processes of salt marsh species by highlighting the relative roles of dispersal units and abiotic conditions. This new information serves as a crucial “stepping stone” for the development of accurate predictive models for salt marsh dispersal and thereby contributes to the design of ecological activities to maintain and restore salt marshes and control invasive species.

2.5 Supporting information

Table S2.1. Results of the generalized linear models testing effects of dispersal units and current velocities on dispersal speeds. In this scenario, current velocities of 0.1, 0.2, 0.3, 0.4 and 0.5 m s^{-1} were imposed with the constant wind (3.0 m s^{-1}) come from the same direction.

Models	Estimate	Std. error	t-value	p-value
Salicornia europaea				
Intercept	6.512	0.093	70.379	< 0.001 ***
Dispersal units	0.111	0.020	5.674	< 0.001 ***
Velocities	-9.901	0.184	-53.877	< 0.001 ***
Scirpus maritimus				
Intercept	6.185	0.088	70.272	< 0.001 ***
Dispersal units	0.041	0.019	2.128	0.054
Velocities	-8.877	0.175	-50.589	< 0.001 ***
Spartina anglica				
Intercept	6.145	0.081	75.504	< 0.001 ***
Dispersal units	0.023	0.018	1.251	0.212
Velocities	-8.545	0.163	-52.551	< 0.001 ***
Elymus athericus				
Intercept	6.050	0.078	77.707	< 0.001 ***
Dispersal units	0.013	0.017	0.778	0.437
Velocities	-8.411	0.155	-54.100	< 0.001 ***

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

Table S2.2. Results of the generalized linear models testing effects of dispersal units and current velocities on dispersal speeds. In this scenario, current velocities of 0.1, 0.2, 0.3, 0.4 and 0.5 m s^{-1} were imposed with the constant wind (3.0 m s^{-1}) come from the opposite direction.

Models	Estimate	Std. error	t-value	p-value
Salicornia europaea				
Intercept	9.437	0.229	41.293	<0.001 ***
Dispersal units	-0.084	0.043	-1.944	0.053
Velocities	-14.838	0.453	-32.741	<0.001 ***
Scirpus maritimus				
Intercept	10.570	0.295	35.783	<0.001 ***
Dispersal units	0.001	0.054	0.027	0.979
Velocities	-17.339	0.584	-29.699	<0.001 ***
Spartina anglica				
Intercept	10.959	0.312	35.166	<0.001 ***
Dispersal units	0.018	0.056	0.319	0.75
Velocities	-18.078	0.616	-29.368	<0.001 ***
Elymus athericus				
Intercept	11.607	0.337	34.437	<0.001 ***
Dispersal units	0.023	0.060	0.387	0.699
Velocities	-19.360	0.666	-29.089	<0.001 ***

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

Table S2.3. Results of the generalized linear models testing effects of dispersal units and wave heights on dispersal speeds under different wave conditions. In this scenario, waves of four magnitudes (**i**: wave height [*h*] = 4 cm, frequency [*f*] = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed without wind, and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction.

Models	Estimate	Std. error	t-value	p-value
Salicornia europaea				
Intercept	17.039	0.210	81.059	< 0.001 ***
Dispersal units	0.212	0.047	4.503	< 0.001 ***
Wave magnitudes	-0.169	0.024	-7.180	< 0.001 ***
Scirpus maritimus				
Intercept	18.304	0.258	70.922	<0.001 ***
Dispersal units	0.112	0.057	1.969	0.044 *
Wave magnitudes	-0.343	0.029	-12.003	<0.001 ***
Spartina anglica				
Intercept	19.847	0.240	82.658	< 0.001 ***
Dispersal units	-0.221	0.052	-4.217	< 0.001 ***
Wave magnitudes	-0.447	0.026	-16.978	< 0.001 ***
Elymus athericus				
Intercept	18.260	0.299	61.046	< 0.001 ***
Dispersal units	-0.126	0.066	-1.900	0.058
Wave magnitudes	-0.271	0.033	-8.191	< 0.001 ***

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

Table S2.4. Results of the generalized linear models testing effects of dispersal units and wave heights on dispersal speeds. In this scenario, waves of four magnitudes (**i**: wave height [*h*] = 4 cm, frequency [*f*] = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *h* = 8 cm, *f* = 0.56 Hz; **iv**: *h* = 10 cm, *f* = 0.67 Hz) were imposed with the constant wind (3.0 m s^{-1}) come from the same direction, and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction.

Models	Estimate	Std. error	t-value	p-value
Salicornia europaea				
Intercept	7.270	0.169	43.126	< 0.001 ***
Dispersal units	1.433	0.040	35.891	< 0.001 ***
Wave magnitudes	-0.089	0.019	-4.596	< 0.001 ***
Scirpus maritimus				
Intercept	7.210	0.217	33.193	<0.001 ***
Dispersal units	0.671	0.050	13.317	<0.001 ***
Wave magnitudes	0.013	0.025	0.521	0.603
Spartina anglica				
Intercept	8.268	0.179	46.117	< 0.001 ***
Dispersal units	0.448	0.041	10.996	< 0.001 ***
Wave magnitudes	-0.069	0.020	-3.388	< 0.001 ***
Elymus athericus				
Intercept	8.681	0.116	74.998	< 0.001 ***
Dispersal units	0.165	0.026	6.378	< 0.001 ***
Wave magnitudes	-0.103	0.013	-7.912	< 0.001 ***

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

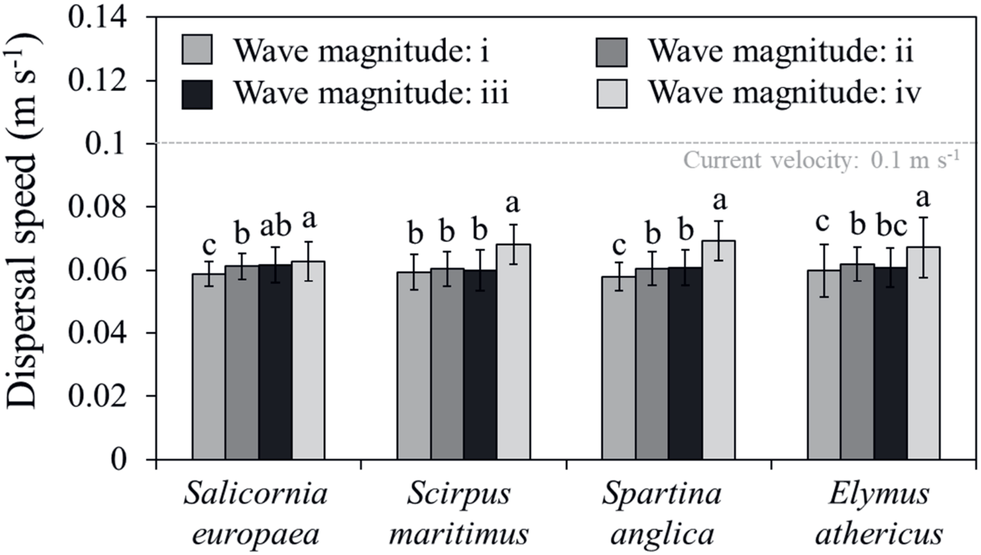
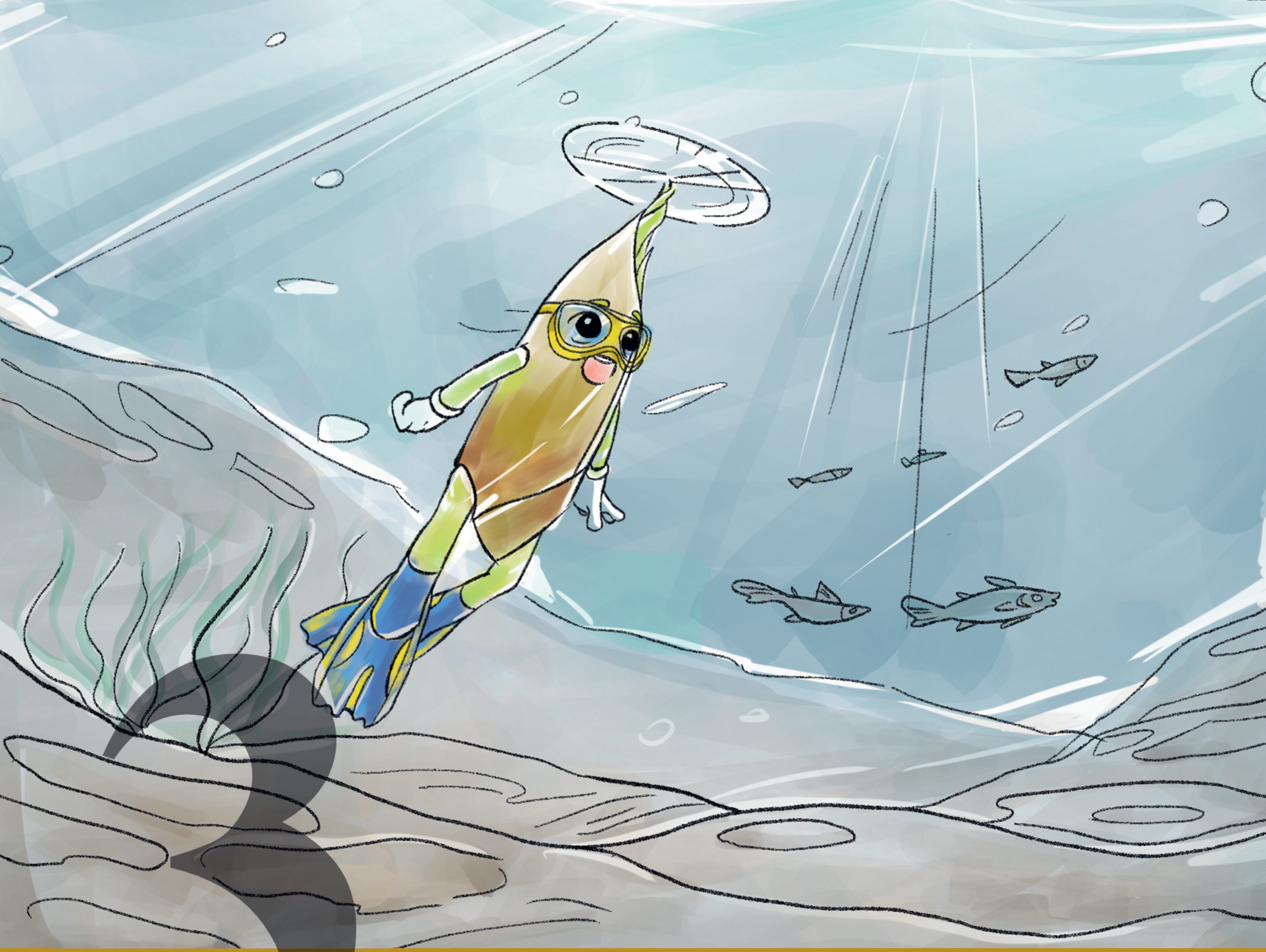


Fig. S2.1 Dispersal speeds (mean ± SD) of four species under different wave magnitudes. In this scenario, waves of four magnitudes (i: wave height [h] = 4 cm, frequency [f] = 0.45 Hz; ii: h = 6 cm, f = 0.50 Hz; iii: h = 8 cm, f = 0.56 Hz; iv: h = 10 cm, f = 0.67 Hz) were imposed without wind, and a slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction. Different lowercase letters denote significant differences in dispersal speed among different wave magnitudes. The gray dotted line shows the water current speed, which serves as a reference to reflect the deceleration effect of waves on the dispersal speed of dispersal units.



3

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

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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 salt marsh 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 salt marsh establishment events, with important implications for understanding the effects of climate change on critical state transitions and enabling human-aided restoration.

3.1 Introduction

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 et al., 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 salt marshes (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 regions, such as Western Europe and Asia (Zhu et al., 2012, 2020a; Cao et al., 2018). 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 salt marsh establishment tend to focus on the process of final seedling establishment (Hu et al., 2015a; 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., 2019a; 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., 2019a). Seeds of salt marsh 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, 2016b). In the presence of waves (Chang et al., 2008), some seeds can move towards more suitable microhabitats for establishment (Zhu et al., 2014, 2016b, 2020a). For salt marsh 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, 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., 2015a). 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 salt marsh establishment. This hypothesis is supported by field observations and remote sensing analysis in the Yangtze Estuary, China (Fig. 3.1), 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 salt marsh 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 salt marsh species as a model: *S. mariqueter* and *S. alterniflora*. We aim to provide novel insights into seed secondary dispersal and the sudden establishment of salt marsh species, thereby aiming to aid future restoration schemes.

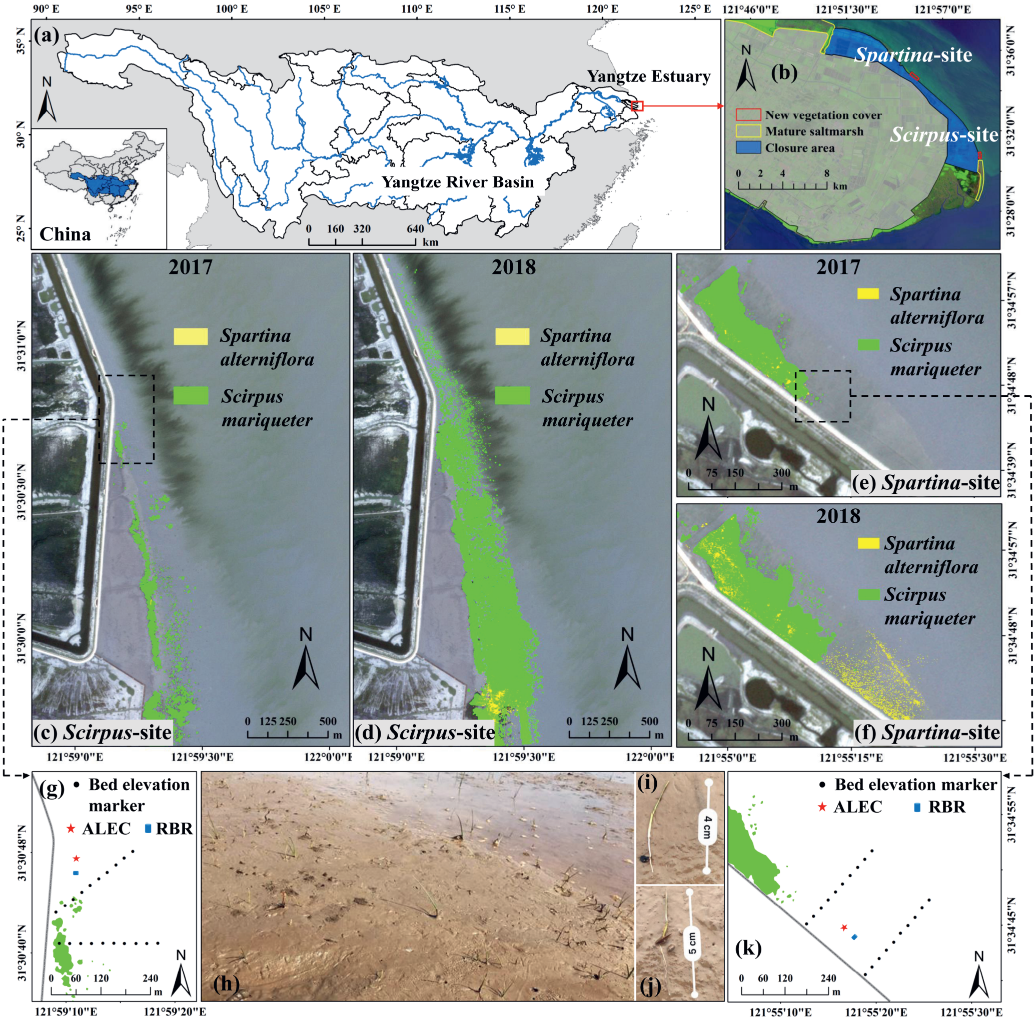

Fig. 3.1 (a) Yangtze River Basin and the Yangtze Estuary. (b) Location of the Chongming Dongtan Nature Reserve (CDNR), where there was rapid colonization by salt marsh pioneers on the tidal flat. (c, d) Rapid colonization of *Scripus mariqueter* occurred at the *Scirpus*-site from 2017 to 2018. (e, f) 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 salt marsh 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). Note: 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.

3.2 Materials and methods

3.2.1 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. 3.1a) 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., 2015; Yuan et al., 2020).

In November 2018, the seeds of both species were collected from Chongming Dongtan Nature Reserve (CDNR, Fig. 3.1b) 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 μmol m^{-2} 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 3.1).

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 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.

Table 3.1. Seed characteristics of the two salt marsh species at different germination stages used in the flume experiment. All morphological parameters are displayed as the mean ± standard deviation (SD). Different lowercase letters denote significant differences between stages.

Scirpus mariqueter	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
Germination time (d)	0	5	10	15	20	25
Mass (mg)	11.20±0.55 d	11.71±1.56 d	12.02±0.40 d	14.30±1.56 c	16.30±0.79 b	22.80±1.15 a
Volume (mm^3)	10.07±1.19 d	11.27±0.68 d	16.67±1.18 c	20.00±1.18 b	20.33±1.39 b	34.20±1.10 a
Density ($g\ cm^{-3}$)	1.13±0.17 a	1.04±0.17 a	0.72±0.05 b	0.72±0.11 b	0.80±0.06 b	0.67±0.04 b
Surface area (mm^2)	6.21±0.63 d	6.82±0.26 cd	7.55±0.57 c	7.86±0.97 c	10.33±0.29 b	15.35±1.40 a
Bud length (mm)		1.29±0.25 d	7.57±1.59 c	21.23±1.47 b	22.20±3.27 b	29.26±0.82 a
Root length (mm)						15.35±1.40

Spartina alterniflora	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6
Germination time (d)	0	5	10	15	20	25
Mass (mg)	14.40±0.14 e	14.90±0.99 e	16.70±0.51 d	18.00±0.75 c	21.10±0.58 b	26.90±1.15 a
Volume (mm^3)	12.27±0.28 f	15.20±0.30 e	20.60±0.95 d	26.59±0.15 c	32.33±0.75 b	37.67±2.79 a
Density ($g\ cm^{-3}$)	1.17±0.02 a	0.98±0.06 b	0.81±0.04 c	0.68±0.03 d	0.65±0.02 e	0.72±0.06 d
Surface area (mm^2)	8.94±0.61 e	10.20±0.53 d	10.97±0.67 d	12.30±0.66 c	13.68±0.84 b	18.55±0.94 a
Bud length (mm)		3.87±0.43 e	8.61±0.88 d	15.89±1.26 c	25.51±1.08 b	30.89±1.07 a
Root length (mm)						13.55±0.74

3.2.2 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. 3.2). 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 salt marsh 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 m^2) and depth of 0.2 m. The sediment used (with a D50 of 27.62 μm), 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. 3.2).

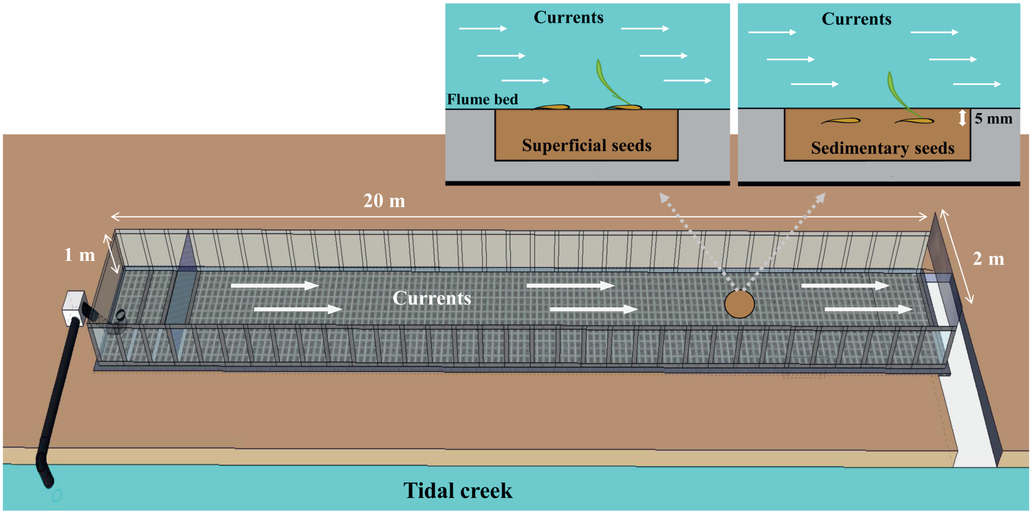

Fig. 3.2 Schematic representation of the flume used to study variation in the seed lift-off ratio with current velocities and seed germination stages. The reserved space at the tail of the flume served as the experimental area filled with sediment, and seeds were randomly placed at the sediment surface (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).

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 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 × six seed stages × 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.

3.2.3 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. 3.1b). 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. 3.1g, 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. 3.1g, 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.

3.2.4 Statistical analysis

Two-way ANOVAs with LSD post-hoc test was used to assess differences in seed morphological parameters among 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 $\alpha = 0.05$.

3.3 Results

3.3.1 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 3.1). It took 0-5 days for wet seeds that had undergone vernalization to form a bud (see pictures in the heading rows of Table 3.1), and about 20 days for the first root to grow. With 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 3.1). For *S. mariqueter*, seed density was markedly reduced from stage 2 to stage 3, whereafter seed density was lower than that of seawater (1.02-1.09 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 3.1). The seed density of both species increased slightly in the late germination stage (from stage 4 to stage 5 for *S. mariqueter*, 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 3.1). When comparing *S. mariqueter* 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 ($P > 0.05$).

3.3.2 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. 3.3a, 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. mariqueter* and from stage 1 to stage 2 for *S. alterniflora* (Fig. 3.3a, 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 3.1 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. 3.3a, 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. mariqueter* would, because the latter require growth to an older stage (meaning longer in-situ germination time) before being lifted under the same hydrodynamic disturbance.

3.3.3 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 life-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. 3.3b, 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. 3.3b, d), while the lift-off ratio of sedimentary seeds increased significantly from stage 5 to 6. (P < 0.05); however, this was only 0.8% for *S. mariqueter* compared to 31.2% for *S. alterniflora* (Fig. 3.3b, 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. 3.3b, d). Additionally, there was a significant difference in lift-off ratio between species (P < 0.001).

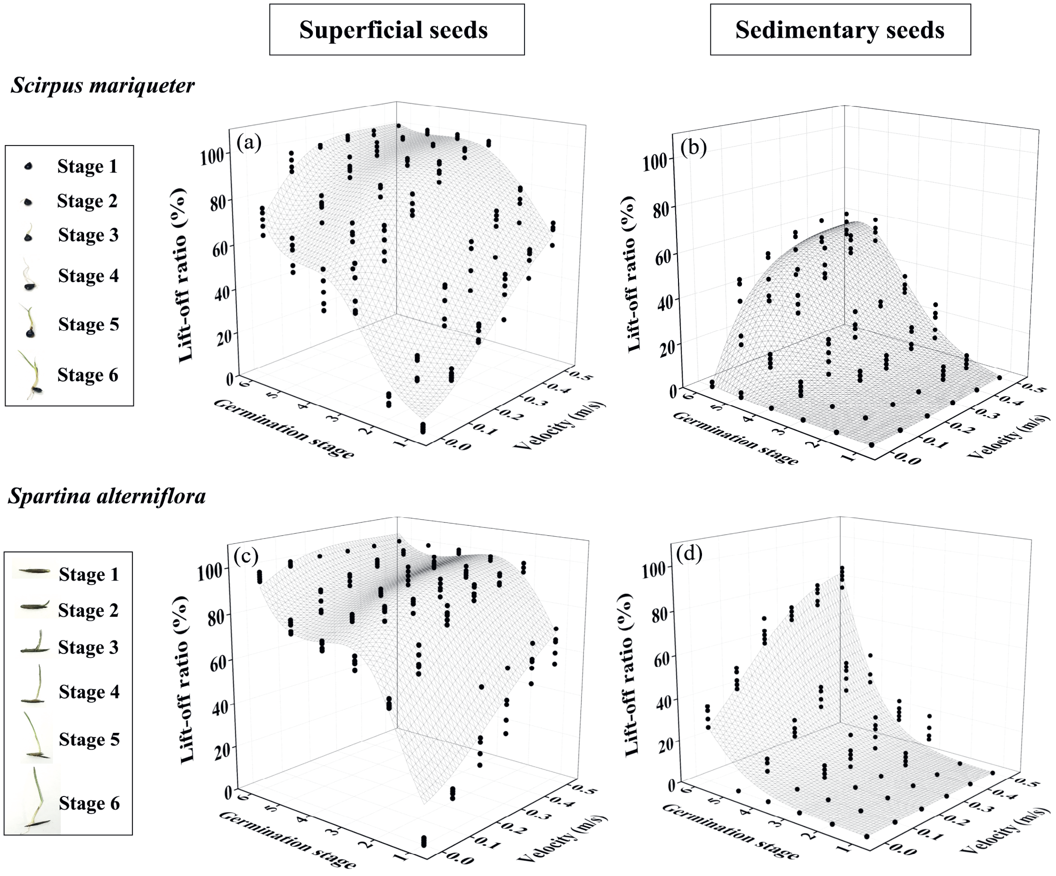

Fig. 3.3 Lift-off ratio (i.e., secondary dispersal onset) of superficial seeds at the six germination stages of *Scripus mariqueter* (a) and *Spartina alterniflora* (c) under different current velocities in flume experiments; and lift-off ratio of sedimentary seeds at the six germination stages of *S. 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).

3.3.4 Effects of morphological factors on 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 3.2). The results of the GLM revealed that changes in density and bud length during germination significantly affected the lift-off rate of seeds (Table 3.2). The reduced density enabled the negatively buoyant wet seeds to float, while 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.

Table 3.2. 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

3.3.5 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. 3.4). 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. 3.4). 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.

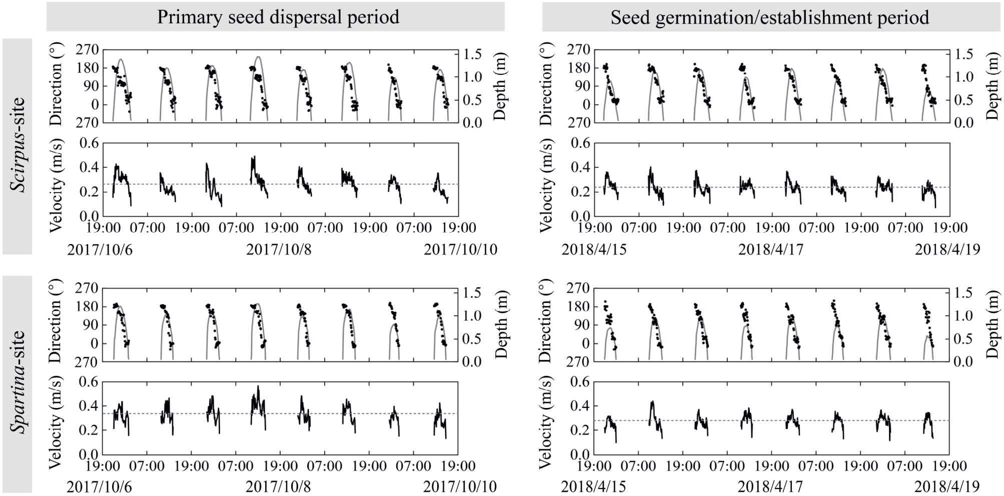

Fig. 3.4 Comparison of current conditions during the primary seed dispersal period (i.e., October 2017) and the seed germination/establishment period (i.e., April 2018) at two case sites (i.e., *Scirpus*-site and *Spartina*-site). For each section (i.e., one site and one period), the solid gray line 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. Note: 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.

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. 3.5b). 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. 3.3), 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 towards 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. 3.5c). The average temperatures in April and May were sufficient to meet the needs of seed germination and seedling growth (Fig. 3.5c). 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. 3.5a). 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. 3.5a). 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.

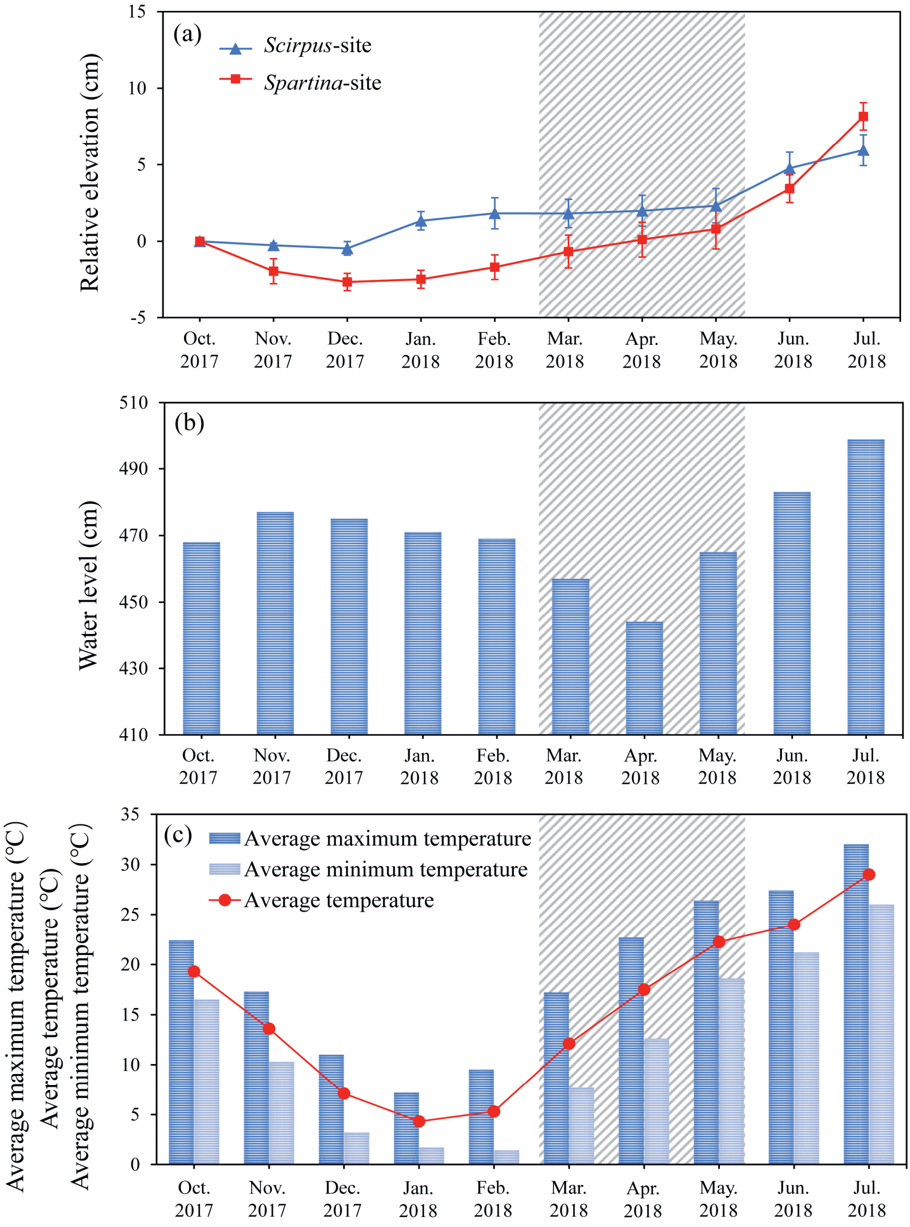

Fig. 3.5 (a) Net bed elevation changes in terms of the relative elevation change at the two case sites (i.e., *Scirpus*-site and *Spartina*-site, where rapid colonization occurred) between October 2017 and July 2018. (b) Tide regimes in the CDNR in terms of the highest monthly water level from October 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 grey twill belt indicates the key months covering the period of seed germination and seedling establishment.

3.4 Discussion

An in-depth understanding of dispersal and establishment processes is essential when using natural processes for the creation or restoration of salt marsh 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 salt marsh 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 salt marsh establishment.

3.4.1 Extension of salt marsh 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., 2019a). We observed an extension of secondary dispersal controlled by germination feature (Fig. 3.6a). 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 salt marsh seeds may be more frequent in spring than previously anticipated.

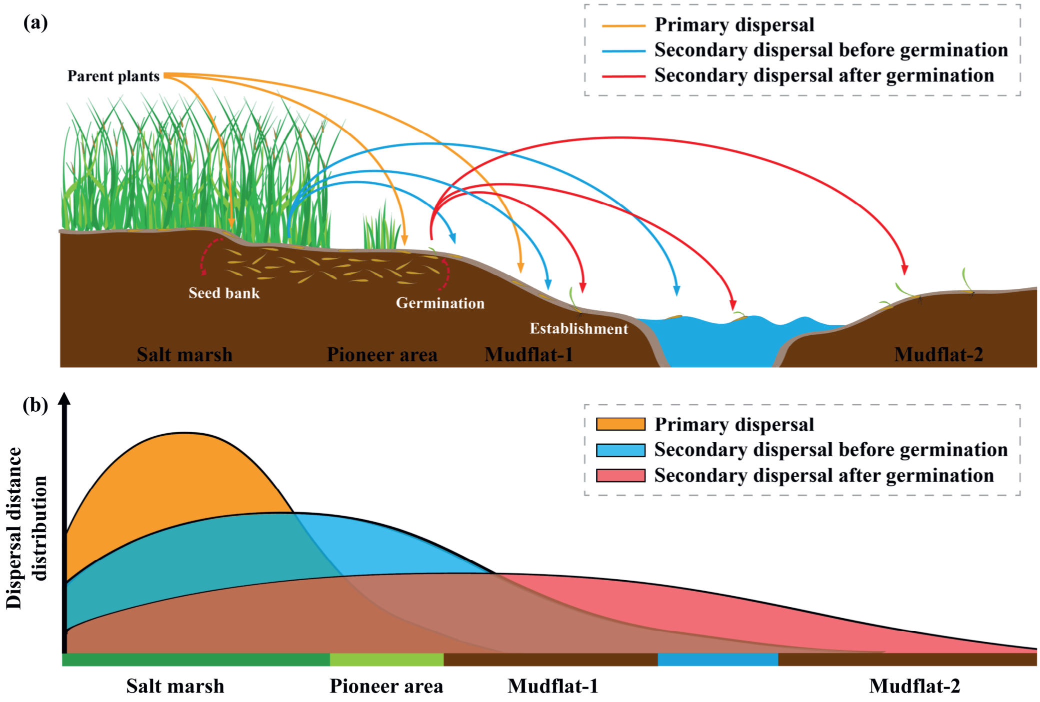

Fig. 3.6 (a) Schematized seed dispersal processes of salt marsh species. *Primary dispersal*: seed departure from the parent plant to the sediment surface

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). Note: 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 salt marsh species under different dispersal processes.

Similar to the general mechanisms of primary and secondary seed dispersal before germination (Koch et al., 2010; van der Stocken et al., 2015; Cunnings 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. 3.6b). 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 salt marsh (Fig. 3.6). However, the exact or approximate dispersal distance for salt marsh 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., 2019a). Here, we conceptually compared the dispersal potential of salt marsh seeds at different dispersal stages based on existing information (Fig. 3.6b), aiming to provide a theoretical framework for future in-depth quantitative research.

3.4.2 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. 3.1), 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 salt marshes during spring (Yuan et al., 2020). Seeds trapped within the salt marsh 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 salt marsh 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., 2015a; 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., 2015). 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. 3.1). We speculate that seeds from nearby sources were more likely to lift-off during the early flood and started to disperse towards 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 Vijsel 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 Vijsel 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 salt marsh species (Xiao et al., 2009, 2016; Balke et al., 2014). Under the culture conditions used in this study, it took about 20 days 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 (Rouifed 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.

3.4.3 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 salt marsh 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.

4

Retention versus emergence: can we identify which forms the recruitment bottleneck for seed-based wetland restoration?

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Submitted

Abstract

1. Attaining the goals of “The UN-Decade on Ecosystem Restoration” requires efficient methods for large-scale restoration of degraded ecosystems. Seed-based approaches may offer opportunities for massive recovery of foundation vegetation, but are prone to failure when applied to highly-valued coastal wetlands such as salt marshes. Pinpointing the impact of early life-stage transitions on recruitment variation across species and contexts is a critical first step toward amplifying seed-based restoration efficiency.
2. Large-scale field experiments were conducted in 100 microhabitats across eight salt marshes for investigating the root-causes of variation in seed retention and seedling emergence, using four globally-occurring salt marsh species as models. Resulted insights and dataset were then translated into predictors using machine learning, for targeted application in disentangling recruitment bottlenecks.
3. Seed retention, regardless of species, was identified as the principal bottleneck to recruitment with hydrodynamic intensity, bed-level dynamics, and burial depth as critical governing factors. Seedling emergence was discerned as the critical bottleneck driving cross-species variability of recruitment and pivotally influenced by soil salinity and burial depth.
4. Model experiments using predictors indicated that simple management, such as seed burial or species selection, can create opportunities to bypass potential recruitment bottlenecks.
5. *Synthesis and applications.* Our results suggest that the failure of seed-based coastal wetland restoration should be attributed to multiple recruitment bottlenecks that arise from different life-stage transitions and are context/species-dependent. In planning future seed-based restoration practices, managers should assess the variability of life stage-specific

dominant factors at target sites for identifying site-specific recruitment bottleneck(s). Our work underscores the need for strategic management that buffers against recruitment bottlenecks to improve restoration efficiency and advances the application of data-driven techniques to make seed-based restoration predictive.

4.1 Introduction

Coastal wetlands such as salt marshes, seagrasses, and mangroves are both ecologically and economically highly valuable given that they sustain many critical ecosystem functions and services, for example, in maintaining biodiversity (Schuerch et al., 2018), sequestering carbon (Temmink et al., 2022), attenuating waves (Gijsman et al., 2021), and stabilizing sediment (Silliman et al., 2019). Consequently, they are incorporated into nature-based solutions to reduce coastal flood risk and contribute to climate stability (Saunders et al., 2020; Gijsman et al., 2021). However, climate-change-related and anthropogenic stressors have, over the last decades, caused a massive shrinkage of coastal wetlands worldwide, accompanied by the disintegration of their key functions and services (Schuerch et al., 2018; Murray et al., 2022). Since natural recovery may take decades or may not even occur at all (O’Brien et al., 2018), significant global efforts are urgently required for the large-scale restoration of these degraded coastal wetlands (Silliman et al., 2019; Saunders et al., 2020), in line with the United Nations’ call to action in ‘The UN Decade on Ecosystem Restoration’ (Waltham et al. 2020).

Significant potential exists to recover foundation vegetation through seed-based restoration approaches (Palma and Laurance, 2015; Kettenring and Tarsa, 2020). Relative to other revegetation strategies such as planting seedlings, transplanting rhizomes, and installing vegetated patches, the seed-based approach is typically less expensive and logistically more feasible to achieve large-scale restoration (van Katwijk et al., 2016; Balestri et al., 2021). Moreover, the use of seeds allows for the inclusion of high levels of genetic diversity, which may have far-reaching implications for enhancing long-term ecosystem resilience under changing climate (Balestri and Lardicci, 2012; Larios et al., 2017). However, demographic losses/mortality during the seed-seedling transition may strongly curtail the effectiveness of this approach (Larson et al., 2015; Kettenring and Tarsa, 2020). Particularly for coastal wetlands, in which the highly dynamic disturbance regimes introduce more uncertainty to seed/seedling persistence (Zhu et al., 2020a; Hu et al., 2021), results with success stories lag far behind those of their terrestrial counterparts (e.g., forests and drylands; Palma and Laurance, 2015; Kildisheva et al., 2016).

Uncovering the recruitment bottlenecks driving demographic plummets represents an important step toward amplifying restoration outcomes (Saunders et al., 2020; Balestri et al., 2021). Compared to terrestrial ecosystems, in coastal wetlands the seed fate post-sowing might be more convoluted due to being subject to strong spatiotemporal heterogeneity of multiple disturbances (e.g., inundation and sheet erosion), with the relative importance of these disturbances varying with time as the seed transitions through its life course (Friess et al., 2012; Statton et al., 2017). Key life-stage transitions include seed retention, seedling emergence, and seedling establishment (Friess et al., 2012). It is well known that seedling establishment in coastal wetlands needs to be synchronized with the disturbance absent/low periods (i.e., windows of opportunity, WoO), which allow seedlings to root and build resistance while growing (Balke et al., 2011). Due to the stochastic nature of the occurrence of WoO, seedling establishment is failure-prone and hence widely recognized as a critical recruitment bottleneck in coastal wetland restoration (Hu et al., 2015a, 2021). Increasing restoration practices have been dedicated to overcoming this bottleneck (e.g., Temmink et al., 2020; Fivash et al., 2021). However, recent evidence suggests that life stages before seedling establishment (i.e., seed retention and seedling emergence) appear to be even more vulnerable to dynamic disturbances (van Regteren et al., 2020; Zhu et al., 2021). Most experimental studies using seed addition have reported massive seed losses, while the remaining seeds may still fail to germinate due to unsuitable habitat conditions (Statton et al., 2017; van Regteren et al., 2019; Zhu et al., 2020a). This suggests that seed-based restoration in coastal wetlands may encounter multiple recruitment bottlenecks nested in different life stages.

Differences in environmental settings may drive recruitment bottlenecks formed at varied life-stage transitions, causing the outcomes of similar restoration approaches to differ among sites (Larson et al., 2015; Statton et al., 2017). Yet, identifying specific bottleneck(s) that may occur at a targeted restoration site remains a formidable challenge (Brudvig et al., 2017), because we have a fragmented understanding of the underlying causes of variation in transitions across stages, particularly for the stages before seedling establishment. Another critical recognition is that the success of life-stage transitions is likely to vary among species even under homogeneous settings, given their contrasting seed and seedling traits or survival strategies (Zirbel et al., 2017; van Regteren et al., 2019). Resolving these context dependencies is integral to guiding restoration ecology toward a more predictive science, enabling restoration practitioners to ameliorate existing restoration strategies and thus overcome possible bottlenecks through forecasting based on site-specific conditions (Brudvig et al., 2017; Barnard et al., 2019). The latter would benefit from applying novel technologies such as machine learning, provided that sufficient large data-sets are available for the application of such techniques (Hu et al., 2021).

In this study, we intended to make seed-based wetland restoration predictive and inform management by (1) seeking integrated experimental evidence generalizing stage-specific causative factors for demographic loss/mortality and (2) developing predictors oriented toward site-specific bottlenecks. Specifically, this study is focused on seed retention and seedling emergence, since they represent the most vulnerable life stages that follow sowing. Firstly, by means of large-scale field experiments, we tested how seed retention and seedling emergence were affected by varied management options (i.e., seed-planting depth and species selection) and a wide range of physical settings (i.e., elevation, hydrodynamic intensity, bed-level dynamics and sediment properties). Variable screening was then implemented to identify stage-specific governing factors. Secondly, the resulting insights and dataset were used to develop stage-specific predictive models using machine learning. Model experiments under various scenarios were then conducted to assess site-specific feasibility of potential seed-based restoration practices. Finally, we discussed the implications of our results in decision-making for restoring coastal wetlands.

4.2 Materials and methods

4.2.1 Experiments: monitoring dynamics of seed retention and seedling emergence

4.2.1.1 Study sites and species

We employed salt marsh as a model ecosystem. Eight salt marshes (Fig. 4.1a, b) in the Scheldt estuary in NW Europe were selected to encompass a spectrum of environmental settings comparable to those of areas that are potentially targeted for marsh restoration (details in Table S4.1 and Appendix S4.1). The pioneer area in two chosen marshes (i.e., Baar and Kete) is characterized by hummocks and hollows (Fig. S4.1), which are two distinct microhabitats and may have a significant impact on seed-seedling transition (Fivash et al., 2020). We conducted experiments at both microhabitats separately to include environmental differences due to micro-topography. A total of 10 locations (i.e., eight sites, with hummocks and hollows sub-habitat at two of these sites) were used in this study (Table S4.1).

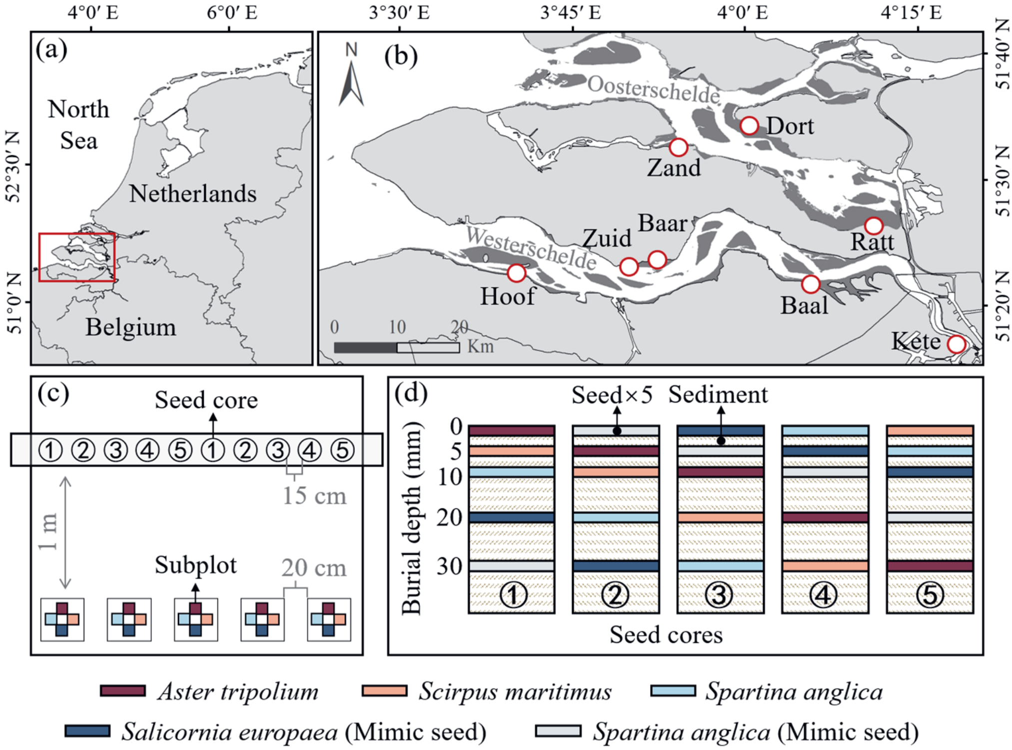

Fig. 4.1 (a) Location of the Scheldt estuary. (b) Geographical distribution of eight chosen salt marshes. See Table S4.1 for complete names of all sites. (c) Setup in each experiment plot. Circles with numbers indicate the order in which seed cores were deployed. Different numbers represent cores assembled with different rules shown in (d). Subplots were setup to conduct seedling emergence experiments and assigned with different sowing depths. (d) Protocol for making the layered seed cores. To avoid confusion when retrieving cores, each core was assembled from different types of seeds buried at specific depths. Different colors in (c) and (d) indicate different species or seed types.

Four dominant landscape-forming pioneer species in NW Europe salt marshes were considered as models: *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, and *Spartina anglica* (see Table S4.2 for traits overview). Mature seeds were collected from field locations where the corresponding species formed monospecific meadows in autumn, 2020. Collected seeds were stored in a controlled environment at 4°C until the commencement of this study.

4.2.1.2 Manipulated experiment concerning seed retention

To establish the response of seed retention to varied environmental settings, a seed addition and recovery experiment was conducted across all locations in 2021. This experiment was repeated twice, before (mid-March to mid-April) and during (mid-April to mid-May) the period of seed germination, to expand the available environmental gradients. Before the experiment, seeds of the four species were repeatedly freeze-thawed until inactive to avoid germination during the experiment. Following this, layered seed/sediment cores were created in transparent PVC pipes (Φ=36 mm, h=50 mm; bottom sealed) with homogenized sediment and the pre-treated seeds. Pre-tests showed that *S. europaea* seeds cannot be discerned from sediment/plant debris due to their small size (Φ<1 mm) and dark color. Considering the contrast of *S. europaea* seeds with other species seeds (Table S4.2) and that seed retention may vary with seed size, we employed *S. europaea* seed mimics as a substitute for using real seeds. The use of seed mimics has been shown to be an effective method to obtain realistic outcomes (Zhu et al., 2021). Furthermore, *S. anglica* seed mimics were used as controls, whose retention dynamics were then compared to those of real *S. anglica* seeds to verify the surrogate effectiveness of mimic seeds relative to real seeds. Mimic seeds are plastic chips with red color and of similar size to the real seeds of *S. europaea* or *S. anglica*. Each core contained five seed addition depths: 0, 5, 10, 20, and 30 mm. Seeds of the five types (i.e., real seeds of *A. tripolium*, *S. maritimus*, and *S. anglica* and seed mimics of *S. europaea*, *S. anglica*) were placed at different depths according to the protocol shown in Fig. 1d. Each depth contained five seeds of the same type.

At each location, 10 fixed 1.5 × 1.5 m plots were established along two parallel transects located 5 m and 35 m from the marsh edge. Each transect consisted of five plots with an interval of 20 m. Within each plot, 10 seed/sediment cores were deployed at 15 cm intervals with their surface flush with the sediment bed, using a prefabricated template (cf. Zhu et al., 2021) and following the protocol shown in Fig. 1c. A total of 2,000 cores were deployed in the two rounds of experiments (n = 200 for each seed type in each round). Each round of experiments lasted four weeks, after which all cores were positioned using the same template and retrieved completely using PVC pipes with a larger size (Φ=100 mm, h=150 mm). Each seed type and their corresponding burial depth was determined using the deployment protocol (Fig. 4.1c, d) and their retrieved location. After sieving through a 1 mm sieve, seed retention rate for each depth in each core was calculated as the proportion of deployed seeds resulting in retrieved seeds.

At each plot during each round of experiments, elevation was determined using the differential-global-positioning-system (DGPS) measuring five scattered points and expressed as an average. A dissolving plaster block wrapped in net pockets was arranged above the sediment bed and was retrieved after two weeks. Relative mass (g; after hot-air drying at 60°C) loss of the plaster block was employed to quantify the integrated hydrodynamic intensity (%) from tidal currents and waves. Bed-level dynamics (i.e., accretion/erosion) were determined using the sediment-erosion-bar (SEB) technique (cf., Hu et al., 2020). The initial height of SEB from the sediment surface was measured at 10 fixed and regularly-spaced spots, and was set to zero as a reference elevation. Bed elevation change was calculated as the relative positive or negative change from the reference elevation. Data collected from the 10 spots were averaged to evaluate bed-level dynamics within the plot.

4.2.1.3 Manipulated experiment concerning seedling emergence

Prior to the experiment, seeds of *S. anglica* and *S. maritimus* were subjected to water immersion treatment in a fridge at 4°C to break dormancy; seeds of *S. europaea* and *A. tripolium* were nondormant but were kept dry in the same fridge. Germination pre-tests for all species showed that at least 80% of the seeds germinated under ideal culture conditions in the laboratory (Fig. S4.2).

Seedling emergence experiments were implemented when seed germination requirements overlapped with field climatic conditions (i.e., from mid-April to mid-May 2021). Within each plot at each location, five subplots (20 × 20 cm) were established at 20 cm intervals (Fig. 4.1c). These subplots were assigned to five different sowing depths: 0, 5, 10, 20, and 30 mm. At each subplot, four mesh bags each containing 20 seeds of one species were deployed in a "cross-shaped" pattern to avoid mutual interference and were fixed on a permanent wooden pole. Such deployment would prevent seeds from being swept away by tidal motion. After six weeks, seedling emergence was determined by counting the shoots emerging from sediment surface. Thereafter, emergence rate was calculated as the proportion of sowed seeds resulting in emerged seedlings.

During the experiment, five replicates of sediment cores (8 cm diameter, 5 cm depth) were collected randomly in each plot within each location. These cores were cut in situ into separate sections: 0–5, 5–10, 10–20, 20–30, and 30–50 mm. One of the sediment core replicates (n=500, covering five depth sections of 10 plots at 10 locations) was used in situ to measure soil salinity using a portable salinometer (EC1200, NIEUWKOOP). In laboratory, the other sediment core replicates were used to *i*) analyze median grain size (D50) using a laser particle sizer (Malvern Master Sizer 2000); *ii*) measure water content by calculating the difference of wet and dry weight (after oven-drying at 105°C for 48 h); *iii*) measure pH using a pH meter (after air-drying; soil: water = 1: 5); *iv*) determine organic content using the loss on ignition method (after burning at 510 °C for 3 h). In addition, elevation is closely related to the inundation period and was considered likely to affect seedling emergence, thus elevation at each plot was measured using the method described in section 4.2.1.2.

4.2.2. Exploration: identifying stage-specific governing factors

Regarding seed retention dataset. In a priori steps, the pairwise Wilcoxon rank sum test was used to determine the difference in retention rate between real and mimic *S. anglica* seeds. The resulting insignificant differences ($P = 0.26$) validate the surrogate effectiveness of mimic seeds relative to real seeds. Therefore, the retention rate of mimic *S. europaea* seeds was regarded as that of the real *S. europaea* seeds and was compared with that of the other three species in subsequent analyses. The same method showed that seed retention rate did differ dramatically between the two rounds of experiments ($P < 0.001$), thus we considered that the seed retention experiment was conducted at 20 contrasting locations. Two-way analysis of variance (ANOVA) was used to test the effect of two fixed variables (i.e., species and burial depth) on retention rate. Since variability in retention rate across species was negligible ($P = 0.96$; Table S4.3), pooled species data were used for subsequent analyses.

As a result, there were one fixed variable (i.e., burial depth) and three random variables (i.e., elevation, hydrodynamic intensity, and bed-level dynamics) that could affect seed retention at the plot level. The following protocol was then implemented to identify the critical factor(s) governing seed retention:

- *Screening random variables for potential associations using pairwise correlation analysis*. The random variables with correlation coefficients $|\rho| > 0.7$ were considered autocorrelated and were filtered to retain one variable. To achieve this, seed retention was modeled with one of the autocorrelated variables using the function lme4::glmer() considering the non-normal distribution of the response variable (Bates et al., 2015). The random variable corresponding to the candidate model with a smaller AIC (Akaike's information criterion) was delivered to the next step.

- *Assessing statistical evidence for the effect of remained variable*. Using the function lme4::glmer() and stats::drop1(), we fitted a full model with all remaining variables and a series of reduced models in which one of the variables was dropped. The likelihood ratio tests were used to compare the full model to each of the reduced models. If the likelihood of a reduced model did not significantly decrease relative to the full model (with $P > 0.05$), its corresponding dropped variable was removed from the final model. To minimize the probability that a significant variable is actually spurious, two corrections to the P values from multiple comparisons during drop-one model selection were applied using the Benjamini and Hochberg method and the Holm method (Tredennick et al., 2021).

Regarding seedling emergence dataset. Two-way ANOVA was used in an a priori step to test the variability in emergence rate among two fixed variables (i.e., species and burial depth). The results indicated that both had a significant effect on emergence rate ($P < 0.001$; Table S4.3). The random variables that may affect emergence rate included soil salinity, pH, water content, organic content, grain size, and elevation. The same protocol as above was applied but with emergence rate as the response variable, to identify the critical factor(s) dominating seedling emergence. All analyses were performed using R (v4.1.0).

4.2.3. Prediction: assessing site-specific bottlenecks to inform restoration

4.2.3.1 Developing machine learning predictors

The machine learning predictors were built based on the artificial neural network (ANN; Greener et al., 2022) using datasets obtained from field experiments. We qualified seed retention and seedling emergence as regression problems since both are continuous variables with a range from 0% to 100%. Retention rate and emergence rate was targeted as output variables of the ANN predictor, while their respective critical dominating factors were used as input variables. All variables were scaled to [−1, 1] in a pre-processing step using min-max normalization. Two-stage calibration was involved in the development of the ANN predictors, enabled by diving the datasets into training, validation, and testing subset. To simplify the ANN structure, we started the training with one hidden layer. The maximum number of neurons in the hidden layer was set to be twice the number of input variables (cf. Oehler et al., 2012). Following this, the number of neurons was increased from one to the maximum to obtain the relative optimal performance of the predictor. Additional hidden layer(s) were added on the condition of drastically improving predictability. Performance of developed predictors was evaluated based on 10-fold cross validation and using the root mean square error (RMSE) criterion. The RMSE from 10 runs of validations were averaged to obtain the final RMSE for the predictor's performance.

4.2.3.2 Identifying site-specific bottlenecks using predictors

To identify potential bottleneck effects at restoration sites with specific environmental settings, the constructed ANN predictors were used to carry out model experiments in which various restoration scenarios were compared. Burial depths and species were regarded as controllable management options and were modeled as grouping factors. To reveal potential bottlenecks that originated from seed retention, in each prediction group, hydrodynamic intensity varied from 0% to 100% and bed-level dynamics varied from −20 mm to 20 mm (see section 4.3.1 for the determination of critical factors). Regarding seedling emergence, the critical physical factor was identified as soil salinity (see section 4.3.2), which was set from 0 to 15. All above environmental setting ranges were chosen to represent the typical marsh habitats in NW Europe. The threshold criterion for identifying bottlenecks was set at 20% (cf. Stagg et al., 2020), i.e., seed retention or seedling emergence tends to irreversibly fail when their probability of success falls below this 20% tipping point, thus forming a bottleneck for potential restoration practice.

4.3 Results

4.3.1 Critical factors governing seed retention

In the variable screening procedure, elevation was excluded due to its significant correlation with hydrodynamic intensity ($|\rho| = 0.73$, Table S4.4) and relatively weak explanatory potential for seed retention variability (Table S4.5). The final model revealed that the critical factors dominating seed retention were burial depth, hydrodynamic intensity, and bed-level dynamics (Table S4.8). Overall, the higher seed retention rates could be predominantly explained by *i*) deeper burial depth (Fig. 4.2a) and/or *ii*) weaker hydrodynamic intensity (Fig. 4.2b) and/or *iii*) stable or accreted sediment regimes (Fig. 4.2c).

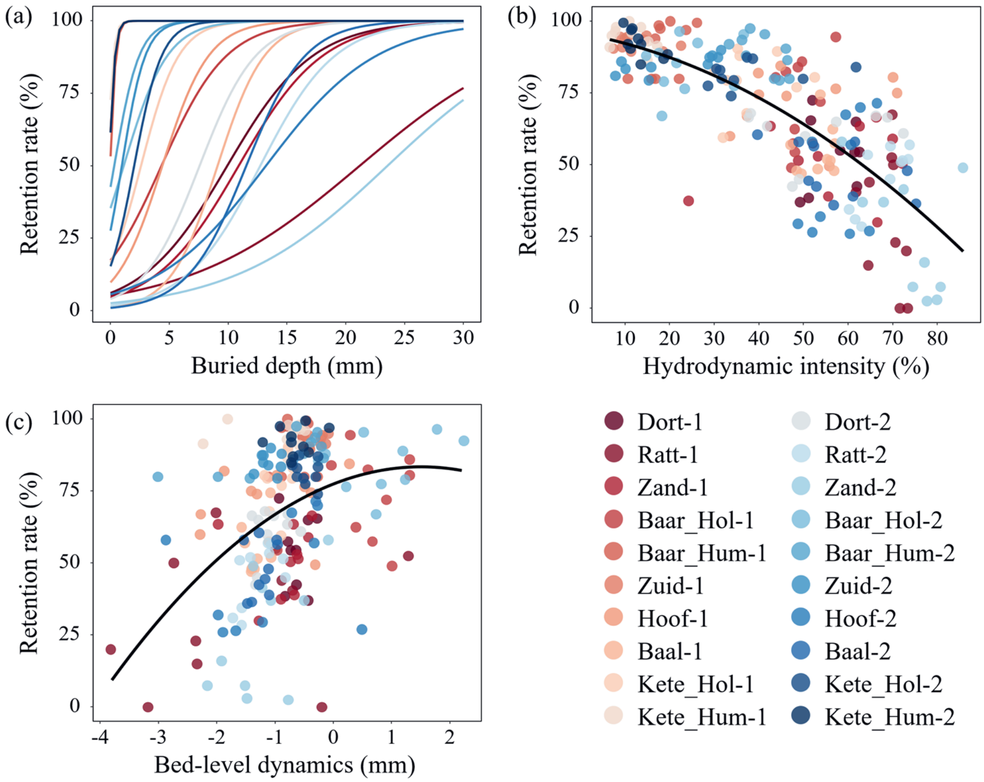

Fig. 4.2 (a) Seed retention rate at varying burial depths. (b) Response of seed retention rate to hydrodynamic intensity. (c) Response of seed retention rate to bed-level dynamics. Positive values on the X-axis indicate accretion while negative values indicate erosion. All figures were made using the pooled species data. In the legend, abbreviations indicate field locations while numbers represent experimental rounds at different periods. See Table S4.1 for complete names of all locations.

4.3.2 Critical factors dominating seedling emergence

Regarding factors affecting seedling emergence, the grain size was excluded firstly due to its significant correlation with organic content (|ρ| = 0.77; Table S4.6) and relatively weak explanatory potential for seedling emergence variability (Table S4.7). The likelihood ratio tests showed that dropping pH, water content, organic content, and elevation individually from the full model did not significantly degrade the model performance, they were thus excluded during the drop-one model selection (Table S4.9). The final model revealed that the variability in seedling emergence can only be accurately accounted for when species, burial depth, and soil salinity were considered. Overall, seedlings of all species were more likely to emerge in microsites with a relatively lower soil salinity (Fig. 4.4). Their emergence possibility would be further inhibited by increasing burial depth, while the response curve varied among species (Fig. 4.3).

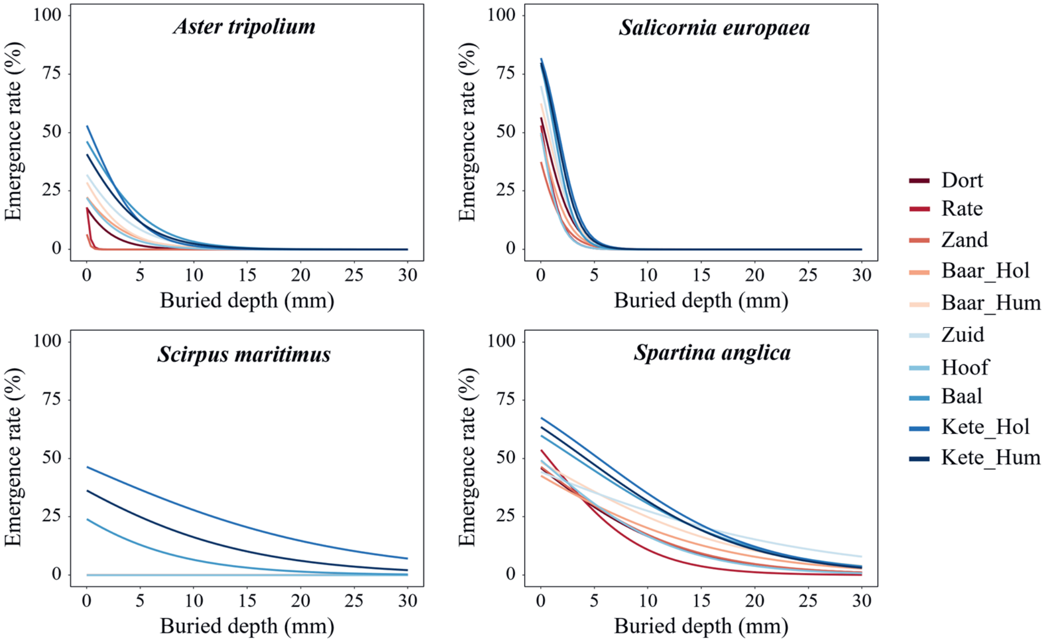

Fig. 4.3 Seedling emergence rate at varying burial depths. The curves are the fitted response from logistic regression based on 10 replicate measurements for each species at each burial depth at each location. See Table S4.1 for complete names of all locations.

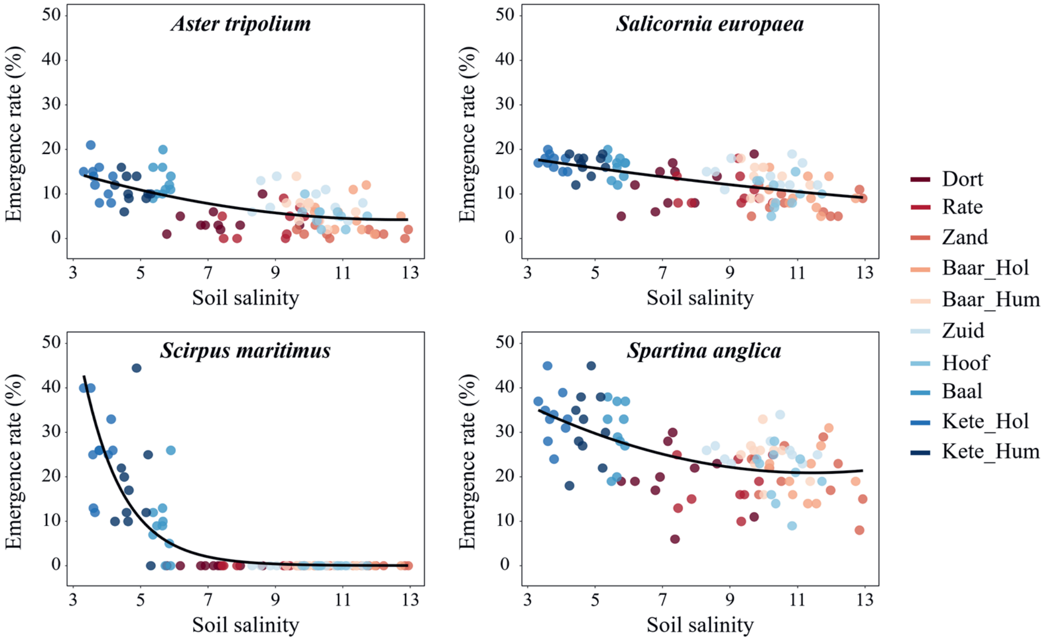

Fig. 4.4 Response of seedling emergence to soil salinity. Emergence rate is the average of different depths at each plot. See Table S4.1 for complete names of all locations.

4.3.3 Application of ANN predictors on seed retention

Burial depth, hydrodynamic intensity, and bed-level dynamics were included as inputs to develop the ANN predictor for predicting seed retention dynamics, based on the results described in section 4.3.1. The best predictor was obtained with a topology of two hidden layers, with 4 and 1 neurons, respectively (Table S4.10; Appendix S4.2). This predictor showed a good capability to reproduce the retention of deployed seeds observed at field locations, with average RMSE of 0.22±0.03 and 0.23±0.04 for the validation and testing subset, respectively (Table S4.10).

When the predictor was applied to assess seed retention variability in potential restoration practices, it turned out that the retention of seeds sown on the sediment surface (hereafter, surficial seeds) would invariably form a bottleneck effect (i.e., a seed retention rate below the tipping point of 20%) in erosion-prone sites (Fig. 4.5). In sites with stable or accretion-prone sediment regimes, surficial seeds would successfully remain in place while the possibilities (ranged from 20% to 100%) were negatively correlated by local hydrodynamic intensity (Fig. 4.5). Increasing sowing depth was shown to alleviate the emergence of the bottleneck effect, i.e., the deeper the seeds were buried, the wider the rang of habitats that will enable the seeds to persist (Fig. 4.5).

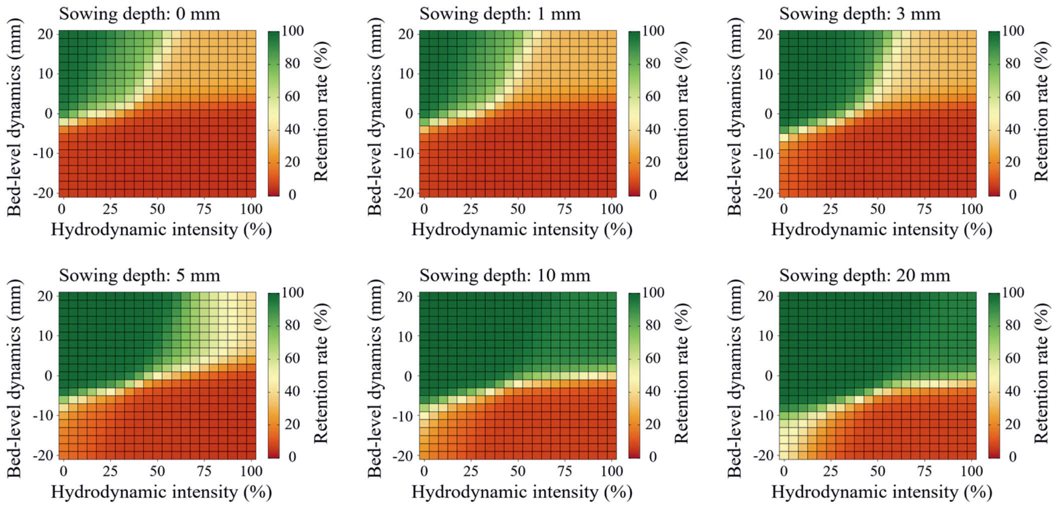

Fig. 4.5 Modeling results of the developed machine learning predictors on retention variability for seeds buried at different depths, when placed in contrasting restoration scenarios. These scenarios were parametrically characterized with broad variation in critical site-level factors, i.e., hydrodynamic intensities and bed-level dynamics.

4.3.4 Application of ANN predictors on seedling emergence

Driven by the results described in section 4.3.2, we developed four ANN predictors of seedling emergence for the four species using burial depth and soil salinity as input variables. The final predictors consist of one hidden layer, embedded with 3, 5, 3, and 3 neurons for *A. tripolium*, *S. europaea*, *S. maritimus*, and *S. anglica*, respectively (Table S4.10; Appendix S4.3). The average RMSE of these predictors ranged from 0.08 to 0.12 both for the validation and testing subsets (detailed in Table S4.10), suggesting their consistent performance in reproducing seedling emergence dynamics for all of the species observed at field locations.

Species-specific bottleneck effects formed by seedling emergence were detected while applicating predictors under a wide range of key physical settings (Fig. 4.6). *S. anglica* was proven to have the widest habitat range suitable for seedling emergence. Only when *S. anglica* seeds were buried deeper than 10 mm in areas with higher soil salinity did their emergence rate fall below 20%. For *S. europaea*, emergence of surficial seeds did not form bottleneck, while seeds failed to emerge once buried deeper than 5 mm. For *S. maritimus*, the emergence bottleneck always existed in areas with higher soil salinity. With increasing burial depth, the narrowness of the salinity range in which *S. maritimus* could emerge increased. *A. tripolium* showed the narrowest habitat range suitable for seedling emergence; their seeds hardly emerged once buried below 5 mm or deployed in areas with higher soil salinity.

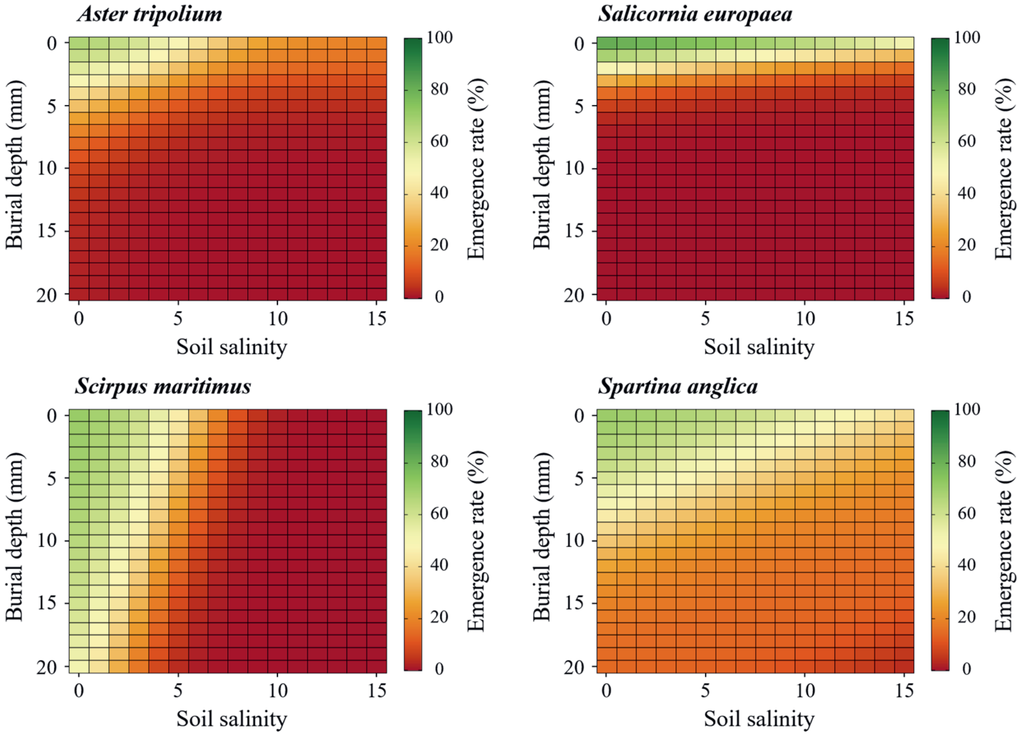

Fig. 4.6 Modeling results of the developed machine learning predictors on seedling emergence probability in potential restoration practices. These practices were parametrically characterized with broad variation in critical factors (i.e., burial depth and soil salinity) governing seedling emergence.

4.4 Discussion

4.4.1 Linking restoration failures to stage-specific bottlenecks

Quantifying demographic losses across all early life stages of establishing plants is an essential step in determining the stages that are most likely to inhibit recruitment and thus limit seed-based restoration (Statton et al., 2017; Kettenring and Tarsa, 2020). Major recruitment bottlenecks in coastal wetlands have been widely attributed to individual loss/death during seedling establishment and survival (Balke et al., 2011; Statton et al., 2017; Hu et al., 2021). In contrast, this study focused on demographic processes prior to seedling establishment. Our broad-scale experiments showed that a substantial loss of superficial seeds (75%–100% in most locations) would be routinely incurred following sowing, suggesting that seed retention rather than seedling establishment was perhaps the principal bottleneck to recruitment in seed-based restoration. This finding supports earlier arguments (e.g., James et al., 2011; Larson et al., 2015) that high mortality later in life may be insignificant in determining plant abundance, when mortality early in life is also considered. This finding also corroborates the recently advocated view that seed availability is a non-negligible recruitment limitation in coastal wetlands (van Regteren et al., 2019; Zhu et al., 2020a). In contrast with related studies that attribute low seed availability to naturally low seed yields or dispersal limitations (Broadhurst et al., 2016; Kettenring and Tarsa, 2020), our study revealed that hydrodynamic intensity and sediment erosion were the dominant drivers of low seed availability after sowing.

Once seeds are retained, e.g., due to burial by benthos or due to high sediment accretion (Friess et al., 2012; Marion et al., 2021), our large-scale seedling emergence experiments suggest that unequal emergence probability is a key driver of recruitment variation across species. Moreover, surficial seeds of species such as *S. europaea* and *S. anglica* were shown to be able to emerge under a wide range of environmental conditions. This implies that such emergence limitations could be circumvented through management such as species selection during the early planning stages of restoration. Although salinity was shown to be tied to seed germination (Rand, 2000; van Regteren et al., 2020), our results revealed its lingering implications for subsequent seedling emergence. Unlike hydrodynamic intensity and bed-level dynamics which dominate seed retention and are highly spatiotemporally heterogeneous, soil salinity typically has little within-site variability (van Regteren et al., 2020), suggesting the feasibility of avoiding the emergence limitations further by site suitability assessment.

4.4.2 Burying seeds to amplify restoration output

Broadcast sowing to the soil surface has been widely adopted to achieve rapid and large-scale restoration (Marion and Orth 2010; Kettenring and Tarsa, 2020). However, our findings imply that this approach tends to fail in coastal wetlands due to substantial seed loss after sowing. Restoration efforts typically compensate for high seed losses with bet-hedging strategies such as a large seed supply (Marion and Orth 2010; Statton et al., 2017) or multi-year sowing (Groves and Brudvig, 2019), ignoring the possibility that excessive seed collection may risk damage to donor populations, which in turn counteract the intended effects of restoration (Balestri and Lardicci, 2012; Kettenring and Tarsa, 2020). This study offers a robust rationale for adopting proper seed burial as an alternative, with the greatest likely returns for improving seed retention and thus more efficient restoration with limited seed supply. The optimum seed burial depths varied across species as a consequence of differences in emergence probability.

Sowing seeds to the depths ideal for species involved are common with restoration practices in terrestrial systems (Palma and Laurance, 2015; Kildisheva et al., 2016), yet very few efforts have been made in coastal wetlands due to the technical difficulties involved in quickly burying large quantities of seeds (Marion and Orth 2010; Marion et al., 2021). Potential seed-planting approaches that have been attempted include drill seeding (Zilverberg et al., 2014) and dispenser injection seeding (Tan et al., 2020). However, the labor-intensive nature renders them impractical for large-scale restoration efforts (Kettenring and Tarsa, 2020). Hydroseeding with a slurry as part of dredging projects may offer opportunities for this purpose and has been attempted in salt marshes (Thorne et al., 2019; Saunders et al., 2020), although it cannot precisely control the seed-planting depths. Moreover, this approach may be limited in application in coastal wetlands that require “clear” water, such as in seagrass habitats (Thorne et al., 2019). Marion et al. (2021) reported a machine that allows burying seeds into specific depths in hectare-sized plots at sandy sites; unfortunately, its applicability to muddy sites has not been robustly validated. Therefore, technological advancement in ecosystem-specific seed-planting methods/machinery is urgently needed to attain the goals of large-scale restoration in coastal wetlands.

4.4.3 Hitting restoration targets based on a priori predictions

Experimental studies providing in-depth insights into recruitment bottlenecks, in tandem with modeling approaches, represent an important step contributing to cultivating predictive capabilities prior to restoration initiation (Brudvig et al., 2017; Barnard et al., 2019). This study given the first attempt to apply field data-driven machine learning to identify recruitment bottlenecks associated with seed-based restoration in coastal wetlands. The ANN exemplified here has a high overall prediction accuracy, reflecting the highlighted value of this and similar algorithms (e.g., classification and regression tree, random forest) in improving the predictability of restoration ecology (Barnard et al., 2019; Hu et al., 2021), although comparisons between multiple algorithms are pending in future research. It is important to note that the predicted retention and/or emergence probability in our study may not represent the long-term population trajectory in a restoration context. Constrained by a sequence of threshold effects related to windows of opportunity (cf., Balke et al., 2011), the number of seedlings eventually established appear to constitute a small fraction of available seeds/seedlings (Hu et al., 2015; Statton et al., 2017). However, it is possible that the few survivors could result in rapid population growth due to potentially high reproductive output (Friess et al., 2012). This suggests that more information is required for predicting long-term restoration outcomes, but our study provides the underlying research framework needed for this purpose. We advocate an integrative research approach that includes broad-scale experiments on outcome variability, model exploration of root causes, and field data-driven predictions on site-specific bottleneck(s). Although such an approach requires significant investment, especially when focusing on broader demographic processes in restored populations (e.g., survival of seedlings and adults), it appears to be the next indispensable step toward a future of predictive restoration (Brudvig et al., 2017).

4.5 Conclusions

Our results demonstrate that early life-stage transitions significantly impact the outcomes of seed-based restoration in coastal wetlands, with seed retention as the principal bottleneck responsible for demographic plummets, and seedling emergence being the critical bottleneck driving cross-species variability. To improve restoration efficiency, hydrodynamic intensity, bed-level dynamics, and soil salinity should be included in assessment metrics for site suitability. Furthermore, small steps in strategic management were shown to drive giant leaps in restoration output. For example, burying seed would significantly reduce seed loss, and species selection would elude the emergence limitation. In particular, this study exemplifies the value of data-driven techniques in predicting variability in restoration outcomes based on site conditions. The resulting a priori expectations can help practitioners position restoration in areas most likely to be successful and inform strategic management to overcome recruitment bottlenecks. Despite these advances, it remains difficult to determine the long-term demographic trajectory of restored populations. A logical next step would be to develop field data-driven predictors oriented toward life-stage transitions after seedling emergence using the advocated integrative research approach.

4.6 Supporting information

Table S4.1. An overview of the characteristics of the field locations.

Location	Abbreviation	Coordinates	Elevation (m NAP)	Water depth (max, m)	Grain size (D50, µm)
Dortsman	Dort	51.5731 N, 4.009 E	1.14	1.13	127.98
Rattekaai	Ratt	51.4389 N, 4.1669 E	1.10	1.18	109.02
Zandkreek	Zand	51.5414 N, 3.8972 E	0.74	1.93	44.59
Baarland-Hollow	Baar_Hol	51.3914 N, 3.8721 E	1.85	0.80	40.16
Baarland-Hummock	Baar_Hum	51.3914 N, 3.8721 E	1.95	0.70	47.41
Zuidgors	Zuid	51.3906 N, 3.8512 E	2.30	0.34	28.63
Hoofdplaat	Hoof	51.3719 N, 3.6817 E	1.38	1.49	51.23
Baalhoek	Baal	51.3569 N, 4.1042 E	1.92	1.27	61.24
Ketenisse-Hollow	Kete_Hol	51.2848 N, 4.3132 E	2.89	0.24	53.65
Ketenisse-Hummock	Kete_Hum	51.2848 N, 4.3132 E	2.94	0.19	48.88

Table S4.2 An overview of the characteristics of studied species and their seeds. Seed traits were obtained through 100 measurements and are displayed as mean ± SD. Overview of site characteristics are shown in Table S4.1.

Traits	Species			
	Aster tripolium	*Salicornia europaea*	*Scirpus maritimus*	*Spartina anglica*
Life cycle	Perennial	Annual	Perennial	Perennial
Major niche	Brackish	Salt	Brackish	Salt
Seed length (mm)	6.53 ± 0.64	1.10 ± 0.09	3.35 ± 0.39	18.13 ± 1.77
Seed width (mm)	1.57 ± 0.21	0.75 ± 0.11	2.36 ± 0.28	2.10 ± 0.34
Seed mass (g)	0.0035 ± 0.001	0.0002 ± 0.00001	0.0050 ± 0.0009	0.0100 ± 0.003
Distribution at study sites	Zuid, Baal, Kete	Dort, Ratt, Baar. Zuid, Hoof, Baal	Baal, Kete	Dort, Ratt, Zand, Baar, Hoof, Baal

Table S4.3. Two-way ANOVA results on the differences in seed retention and seedling emergence across species and among locations in the field experiments.

Response variable	Deviance source	df	*F*	*P*
Seed retention	Location	1	62.140	< 0.001
	Species	1	0.002	0.962
Seedling emergence	Location	1	91.720	< 0.001
	Species	1	256.830	< 0.001

Table S4.4. Results of pairwise correlation analysis testing the autocorrelation between the random variables that may have an effect on seed retention. Autocorrelation was evaluated with absolute Pearson's coefficient |ρ| > 0.7.

	Elevation	Hydrodynamic intensity	Bed-level dynamics
Elevation	1	-0.727	0.206
Hydrodynamic intensity	-0.727	1	-0.292
Bed-level dynamics	0.206	-0.292	1

Table S4.5. Results of candidate general linear mixed-effects models filtering the autocorrelated random variables that may have an effect on seed retention.

Model	AIC	BIC	logLik	Deviance	df.resid
Seed retention ~ 1 + Buried depth + Bed-level dynamics + Elevation + (1 | Microsite)	3288.3	3323.2	-1639.1	3278.3	7995
Seed retention ~ 1 + Buried depth + Bed-level dynamics + Hydrodynamic intensity + (1 | Microsite)	3265.3	3300.3	-1627.7	3255.3	7995

Table S4.6. Results of pairwise correlation analysis testing the autocorrelation between the random variables that may have an effect on seedling emergence. Autocorrelation was evaluated with absolute Pearson's coefficient |ρ| > 0.7.

	Salinity	pH	Water content	Organic content	Grain size	Elevation
Salinity	1	-0.317	0.495	0.296	-0.175	-0.548
pH	-0.317	1	-0.181	0.042	-0.273	0.104
Water content	0.495	-0.181	1	0.568	-0.543	0.089
Organic content	0.296	0.042	0.568	1	-0.769	0.412
Grain size	-0.175	-0.273	-0.543	-0.769	1	-0.426
Elevation	-0.548	0.104	0.089	0.412	-0.426	1

Table S4.7. Results of candidate general linear mixed-effects models filtering the autocorrelated random variables that may have an effect on seedling emergence.

Model	AIC	BIC	logLik	Deviance	df.resid
Seedling emergence ~ 1 + Species + Burial depth + Salinity + PH + Water content + Elevation + Grain size + (1|Microsite)	551.2	601.6	-266.6	533.2	1991
Seedling emergence ~ 1 + Species + Burial depth + Salinity + PH + Water content + Elevation + Organic content + (1|Microsite)	550.9	601.3	-266.5	532.9	1991

Table S4.8. Variable estimates from the final model for explaining seed retention variability, with random variables selection done by dropping terms individually from the full model.

Variables	Estimate	SE	*z*	*P* (Drop1)	Include (Drop1)	*P* (BH)	Include (BH)	*P* (Holm)	Include (Holm)
(Intercept)	4.114	0.539	7.638						
Burial depth	0.564	0.019	28.956	0.000	Yes	0.000	Yes	0.000	Yes
Hydrodynamic intensity	-0.151	0.012	-12.379	0.000	Yes	0.000	Yes	0.000	Yes
Bed-level dynamics	1.299	0.287	4.521	0.000	Yes	0.000	Yes	0.000	Yes

Table S4.9. Variable estimates from the final model for explaining seedling emergence variability, with random variables selection done by dropping terms individually from the full model.

Variables	Estimate	SE	*z*	*P* (Drop1)	Include (Drop1)	*P* (BH)	Include (BH)	*P* (Holm)	Include (Holm)
(Intercept)	2.151	2.614	0.823						
Species	-0.928	0.115	-8.082	0.000	Yes	0.000	Yes	0.000	Yes
Burial depth	-0.575	0.055	-10.380	0.000	Yes	0.000	Yes	0.000	Yes
Salinity	-0.239	0.070	-3.402	0.001	Yes	0.003	Yes	0.001	Yes
pH	-0.007	0.308	-0.024	0.981	No	1.000	No	0.981	No
Water content	0.010	0.030	0.342	0.732	No	1.000	No	0.855	No
Organic content	0.071	0.100	0.713	0.476	No	1.000	No	0.668	No
Elevation	0.525	0.337	1.558	0.119	No	0.470	No	0.206	No

Table S4.10. Structure and performance of the developed artificial neural network (ANN) predictors on seed retention and seedling emergence.

Object	Structure			Performance (10-folds cross validation; Mean±STD)		
	Number of hidden layers	Number of neurons	Subset	R^2	RMSE	Accuracy (%)
ANN predictor on seed retention						
All species	2	(4, 1)	Validation	0.85 ± 0.05	0.22 ± 0.03	78 ± 3
			Testing	0.84 ± 0.06	0.23 ± 0.04	77 ± 4
ANN predictor on seedling emergence						
Aster tripolium	1	3	Validation	0.84 ± 0.06	0.08 ± 0.02	92 ± 2
			Testing	0.84 ± 0.07	0.08 ± 0.02	92 ± 2
Salicornia europaea	1	5	Validation	0.96 ± 0.02	0.08 ± 0.01	92 ± 1
			Testing	0.96 ± 0.02	0.08 ± 0.01	92 ± 1
Scirpus maritimus	1	3	Validation	0.71 ± 0.06	0.10 ± 0.03	90 ± 3
			Testing	0.71 ± 0.06	0.10 ± 0.03	90 ± 3
Spartina anglica	1	3	Validation	0.84 ± 0.05	0.12 ± 0.02	88 ± 2
			Testing	0.84 ± 0.05	0.12 ± 0.02	88 ± 2

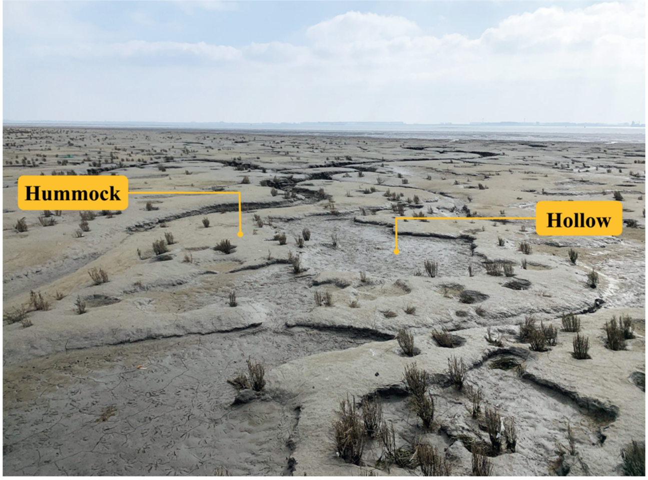

Fig. S4.1 A photo exemplifying the micro-topography structures (i.e., hummock and hollow) in Baarland and Ketenisse. The hummocks and hollows were considered in our study as different micro-habitats with contrasting physical settings, which may result in variability in seed retention and seedling emergence.

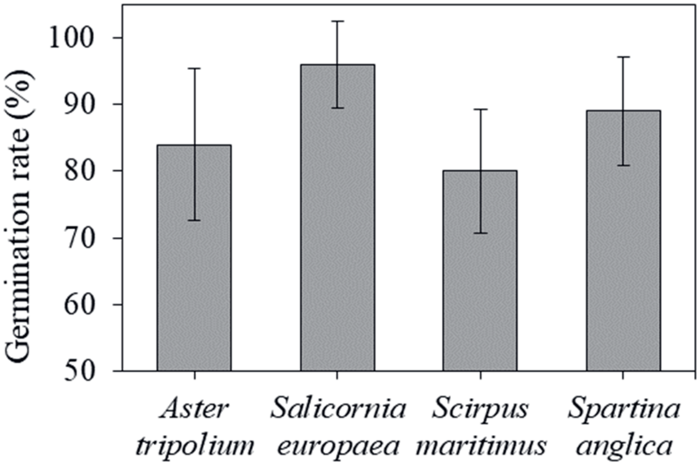

Fig. S4.2 Pre-test results of germination rates for seeds of studied species (i.e., *Aster tripolium*, *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*) under ideal laboratory conditions. The same batch of seeds was used for seedling emergence experiments in the field.

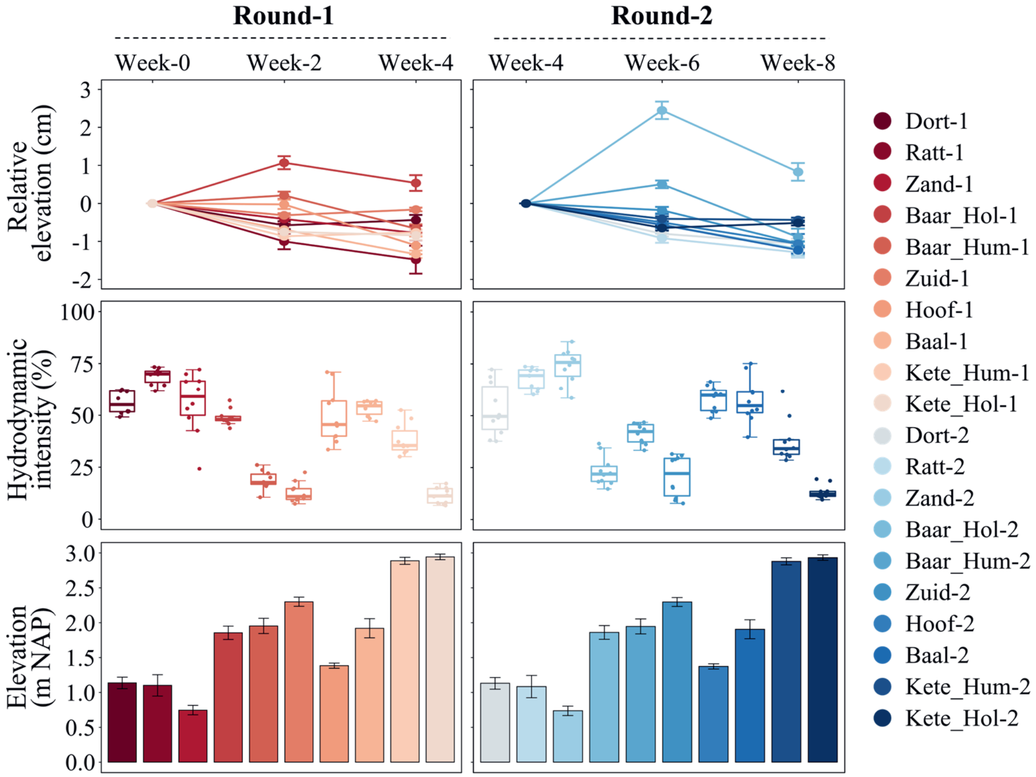

Fig. S4.3 Overview of environment characteristics involved in the field seed retention experiment, including elevation, hydrodynamic intensity, sedimentary dynamics (i.e., relative elevation changes). This experiment was replicated twice and each round lasted four weeks. See the methods section of the main text for relevant monitoring methods. Numbers in the legend represent experimental rounds (i.e., round-1 and round-2) at different periods.

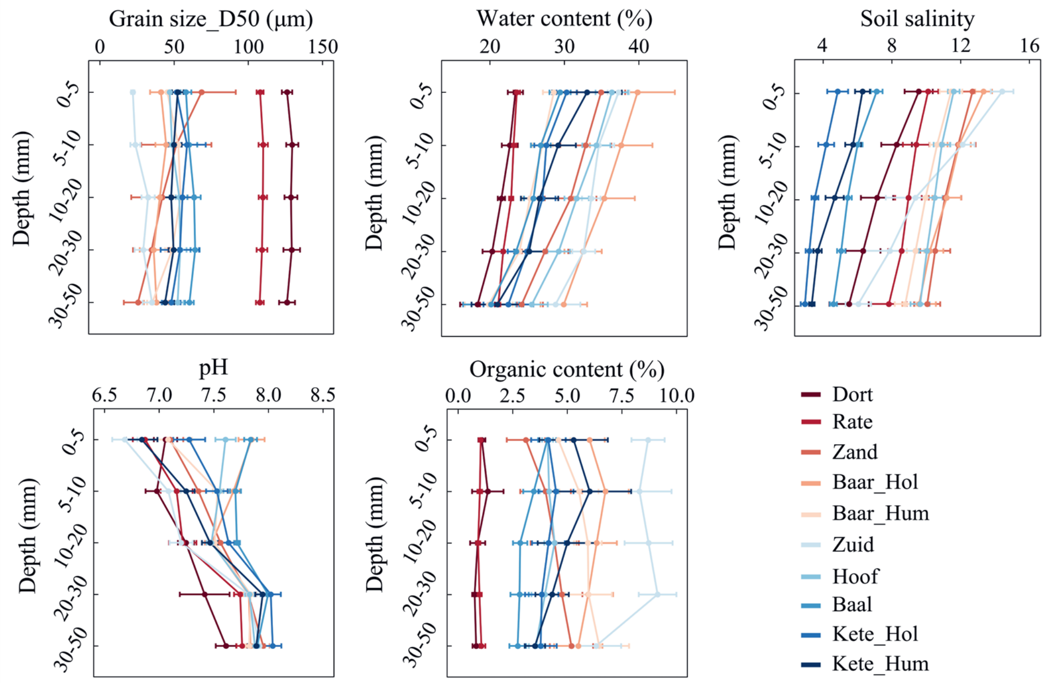

Fig. S4.4 Depth profile changes in grain size, water content, soil salinity, pH, and organic content. These sediment parameters were considered most likely to affect seedling emergence in field experiments. See the methods section of the main text for relevant monitoring methods.

Appendix S1. Overview of physical conditions at all study locations

The average elevation among the 10 locations covered a range of 0.7 – 2.9 m (NAP), with little within-location variation (< 2 cm) between the two rounds of seed retention experiments (Fig. S4.3). The overall span (between 6.6% and 85.7%) of hydrodynamic intensities was similar in the two rounds of experiments, but significant fluctuations were observed among and within the locations (Fig. S4.3). All locations showed an overall sediment regime (after 4 weeks) of slight erosion with relative elevation change varied from -0.2 cm to -1.5 cm, except for Baarland-hollow where relative elevation increased by 0.5 cm and 0.8 cm in the first and second round of experiments respectively (Fig. S4.3).

The 10 locations also exhibited contrasting sediment characteristics (Fig. S4.4). Grain size (D50) covered a range of 16.9 – 145.3 μm. No obvious change trend of grain size was found within the 5 cm depth profile at all locations. Water content ranged from 10.4% to 53.1% and gradually decreased within the 5 cm depth profile at all locations. Soil salinity covered a range of 2.1 – 15.7 and was negatively correlated with depth at all locations. The range of soil pH was 6.4 – 8.2. An overall increasing trend of pH was observed within the 5 cm depth profile at all locations. Organic content ranged from 0.5% to 11.9% and varied little within a 5 cm depth profile at each location.

Appendix S2. ANN for the prediction of seed retention

The formula for seed retention (SR) in the ANN is shown as:

$$SR = G(W_3 \times G(W_2 \times G(W_1 \times \mathrm{X} + b_1) + b_2) + b_3)$$

The input vector (scaled using min-max normalization) is:

$$\mathrm{X} = \begin{bmatrix} \dfrac{HI - 6.593674}{79.108286} \\ \dfrac{BC + 3.8}{6} \\ \dfrac{D}{30} \end{bmatrix}$$

where *HI* is Hydrodynamic intensity (%), *BC* is Bed-level dynamics (cm), *D* is sowing depth (mm).

The weight matrix of the 1st hidden layer is:

$$W_1 = \begin{bmatrix} 1.18336 & 3.39064 & 28.89337 & 9.23076 \\ 0.00313 & 1.43065 & -2.99985 & -192.25203 \\ 4.69717 & 1.24299 & 5.29735 & 10.50688 \end{bmatrix}$$

and its bias is:

$$b_1 = \begin{bmatrix} 0.258 \\ -0.34471 \\ -12.58661 \\ 101.08984 \end{bmatrix}$$

The weight matrix of the 2nd hidden layer is:

$$W_2 = \begin{bmatrix} 5.05586 \\ -4.03266 \\ 0.55407 \\ 0.46493 \end{bmatrix}$$

and its bias is:

$$b_2 = -2.58784$$

The weight matrix of the output layer is:

$$W_3 = 28.86082$$

and its bias is:

$$b_3 = -5.68285$$

Appendix S3. ANN for the prediction of seedling emergence

The formula for seedling emergence (SE) of ***Aster tripolium*** in the ANN is shown as:

$$SE_{Aster} = \left(G(W_2 \times G(W_1 \times \mathrm{X} + b_1) + b_2)\right) \times 0.95$$

The input vector (scaled using min-max normalization) is:

$$\mathrm{X} = \begin{bmatrix} \frac{S - 2.10655}{13.56825} \\ \frac{D}{30} \end{bmatrix}$$

where *S* is soil salinity, *D* is sowing depth (mm).

The output vector (scaled) is:

$$SE_{Aster\_out} = \begin{bmatrix} \frac{SE_{Aster}}{0.95} \end{bmatrix}$$

The weight matrix of the hidden layer is:

$$W_1 = \begin{bmatrix} 0.25783 & 5.18989 & -1.23278 \\ 13.2371 & 2.21846 & 18.02181 \end{bmatrix}$$

and its bias is:

$$b_1 = \begin{bmatrix} -3.60015 \\ -1.11468 \\ -1.30425 \end{bmatrix}$$

The weight matrix of the output layer is:

$$W_2 = \begin{bmatrix} -2.81424 \\ -3.73301 \\ -2.16739 \end{bmatrix}$$

and its bias is:

$$b_2 = 2.71337$$

The formula for seedling emergence (SE) of ***Salicornia europaea*** in the ANN is shown as:

$$SE_{Salicornia} = \left(G(W_2 \times G(W_1 \times \mathrm{X} + b_1) + b_2)\right) \times 0.95$$

The input vector (scaled using min-max normalization) is:

$$\mathrm{X} = \begin{bmatrix} \dfrac{S - 2.10655}{13.56825} \\ \dfrac{D}{30} \end{bmatrix}$$

where *S* is soil salinity, *D* is sowing depth (mm).

The output vector (scaled) is:

$$SE_{Salicornia\_out} = \left[\frac{SE_{Salicornia}}{0.95}\right]$$

The weight matrix of the hidden layer is:

$$W_1 = \begin{bmatrix} -0.07929 & -0.99017 & 0.27062 & 0.63237 & 0.44454 \\ -7.91371 & -7.17094 & 6.90233 & 6.14132 & -9.66168 \end{bmatrix}$$

and its bias is:

$$b_1 = \begin{bmatrix} 0.263 \\ 0.3993 \\ 0.58987 \\ 0.04023 \\ -0.5153 \end{bmatrix}$$

The weight matrix of the output layer is:

$$W_2 = \begin{bmatrix} 2.40533 \\ 4.42563 \\ -3.41657 \\ -3.74554 \\ 3.84928 \end{bmatrix}$$

and its bias is:

$$b_2 = 0.27728$$

The formula for seedling emergence (SE) of ***Scirpus maritimus*** in the ANN is shown as:

$$SE_{Scirpus} = \left(G(W_2 \times G(W_1 \times \mathrm{X} + b_1) + b_2)\right) \times 0.95$$

The input vector (scaled using min-max normalization) is:

$$\mathrm{X} = \begin{bmatrix} \frac{S - 2.10655}{13.56825} \\ \frac{D}{30} \end{bmatrix}$$

where *S* is soil salinity, *D* is sowing depth (mm).

The output vector (scaled) is:

$$SE_{Scirpus\_out} = \left[\frac{SE_{Scirpus}}{0.95}\right]$$

The weight matrix of the hidden layer is:

$$W_1 = \begin{bmatrix} 4.48293 & 5.38425 & 4.38916 \\ 1.8097 & 2.75017 & 2.02579 \end{bmatrix}$$

and its bias is:

$$b_1 = \begin{bmatrix} -2.03204 \\ -2.98431 \\ -2.22513 \end{bmatrix}$$

The weight matrix of the output layer is:

$$W_2 = \begin{bmatrix} -2.40885 \\ -5.14767 \\ -2.12475 \end{bmatrix}$$

and its bias is:

$$b_2 = 1.77351$$

The formula for seedling emergence (SE) of ***Spartina anglica*** in the ANN is shown as:

$$SE_{Spartina} = \left(G(W_2 \times G(W_1 \times \mathrm{X} + b_1) + b_2)\right) \times 0.95$$

The input vector (scaled using min-max normalization) is:

$$\mathrm{X} = \begin{bmatrix} \dfrac{S - 2.10655}{13.56825} \\ \dfrac{D}{30} \end{bmatrix}$$

where *S* is soil salinity, *D* is sowing depth (mm).

The output vector (scaled) is:

$$SE_{Spartina\_out} = \begin{bmatrix} \dfrac{SE_{Spartina}}{0.95} \end{bmatrix}$$

The weight matrix of the hidden layer is:

$$W_1 = \begin{bmatrix} -6.36779 & 5.42381 & 0.36149 \\ -20.92713 & 4.44144 & 9.10115 \end{bmatrix}$$

and its bias is:

$$b_1 = \begin{bmatrix} 19.54878 \\ -1.39525 \\ -1.63026 \end{bmatrix}$$

The weight matrix of the output layer is:

$$W_2 = \begin{bmatrix} 1.82987 \\ -1.97305 \\ -2.30893 \end{bmatrix}$$

and its bias is:

$$b_2 = 0.45741$$

5

Unraveling the wheel of recruitment for salt-marsh seedlings: resistance to and recovery after dislodgement

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Abstract

Elucidating bottlenecks at critical life stages and quantifying associated resilience (including resistance and recovery) to physical processes are central in inform restoration and attain sustainable development of coastal biogeomorphic ecosystems. Seedling establishment is a key life stage determines salt marsh restoration potentials. However, the resilience of these recruits, especially through recovery, remains poorly understood. Here, two contrasting globally occurring salt marsh species, namely *Salicornia europaea* and *Spartina anglica*, were employed to generate insights in *i*) seedling resistance against dislodgement, and *ii*) seedling recovery potential after dislodgement. Regarding resistance, we found that 1) root-shoot antagonism characterizes the growth rate of seedling resistance to dislodgement through hydraulic disturbance, 2) the root length determines seedling resistance to dislodgement through sheet erosion; 3) a 5 mm sedimentary setting amplifies seedling resistance without inhibiting their morphological evolution. Regarding recovery, we found that 4) dislodged seedlings have a high probability for achieving long-distance dispersal; 5) seedling age and the inundation-free period regulate the re-establishment potential of dislodged seedlings. Overall, *S. anglica* showed stronger resilience than *S. europaea*, characterized by stronger seedling resistance against dislodgement and higher re-establishment potential. Our results on seedling resilience suggest that seedling dislodgement is not an end-of-life cycle but a new spin on the "Wheel of Recruitment", a proposed short-term cyclic behavior with alternating phases of seedling dislodgement, dispersal, and (re-)establishment. The Wheel of Recruitment concept is important for forecasting resilience and persistence of biogeomorphic systems such as salt marshes under global change and for guiding life cycle informed restoration.

5.1 Introduction

Salt marshes are a typical example of coastal biogeomorphic systems, in that they are similar to seagrasses (Infantes et al., 2011), mangroves (van der Stocken et al., 2019), reefs (Temmink et al., 2021) and tidal flats (Murray et al., 2019), belong to the most valuable, but also the most fragile ecosystems worldwide (Temmerman et al., 2013; Möller et al., 2014; Temmink et al., 2020). Understanding the mechanisms driving the life cycles of such coastal biogeomorphic systems is an indispensable cornerstone for decision-making in restoration ecology (Trevor Caughlin et al., 2019; Temmink et al., 2021). This is particularly important with the loss of these ecosystems accelerating under global change (Leonardi et al., 2016; Parkinson et al., 2017; Pannozzo et al., 2021). For vegetated biogeomorphic systems such as salt marshes, completion of the life cycle through seed dispersal, seedling establishment, adult plant expansion, and subsequent reproduction is a key benchmark (Friess et al., 2012; Temmink et al., 2021). Variations in resilience, including resistance and recovery, at different life stages explain different evolutionary trajectories for this benchmark (De Battisti, 2021; Schoutens et al., 2021). Most resilience studies have focused on larger vegetation units (Bouma et al., 2009; Altieri et al., 2013; Leonardi et al., 2016), but few have tracked the resilience of salt marshes with a focus on individual seedlings. Examining ecosystem resilience at the individual seedling level is especially important in the meso- and macro-tidal marsh systems in Europe and SE-Asia, where marsh recruitment primarily occurs through seedling establishment (Redelstein et al., 2018; Zhao et al., 2021a).

Understanding seedling resilience implies unraveling the potential to either resist or to recover from different stress types (Leonardi et al., 2016; De Battisti, 2021). Dislodgement is regarded as the main fatal process for young seedlings and it can be triggered primarily through wave-induced bed shear stress and sediment scouring (Cao et al., 2018; Schoutens et al., 2021; Marion et al., 2021). Tidal currents are the main driver of long-distance dispersal following dislodgement (van der Stocken et al., 2019; Zhao et al., 2021b). To resist and survive a dislodgement event, seedling development needs to occur during a sequence of disturbance-free/low periods, which are referred to as “Windows of Opportunity” (WoO; see detailed framework composition in Fig. 1.4). These critical windows involve a species-specific and time-varying entanglement between stochastic disturbance pulses versus seedling resistance (Balke et al., 2011; Hu et al., 2015a, 2021). The WoO framework has been extensively cited to explain the critical transitions induced by seedling establishment in salt marshes (Balke et al., 2014; Hu et al., 2015a; Schwarz et al., 2018). However, we lack experimental studies to quantify 1) the species-specific temporal evolution of seedling resistance against dislodgement, namely the WoO resistance requirements, and 2) the re-establishment potential of dislodged seedlings, namely the WoO recovery requirements. This quantitative understanding is indispensable in predicting salt marsh resilience at critical pioneer development stages and supports the application of the WoO framework in optimizing the development of life cycle informed restoration protocols (see Temmink et al., 2021 for an example).

With respect to species-specific temporal evolution of seedling resistance to dislodgement, the root extension rate can determine the increase in seedling resistance for mangrove species (Balke et al., 2011, 2013). This may also be a key determinant in salt marshes (Cao et al., 2018; Redelstein et al., 2018; Hu et al., 2021). In contrast with mangroves, salt marsh seedlings have a specific emergence regime of shoot (i.e., embryo bud, which develops into leaves) sprouting prior to root growth (Wijte and Gallagher, 1996). This implies that the aboveground part of the plant may influence seedling resistance before or during root-anchoring taking effect. A recent flume study revealed that the lift-off threshold for salt marsh plant seeds dropped considerably after shoot emergence during germination (Zhao et al., 2021a). Experimental studies encompassing multiple seagrasses species also indicate that seedlings with the same root length and larger leaves are more likely to be dislodged (Wicks et al., 2009; Infantes et al., 2011). Despite emerging studies and practices focusing on the mechanism underlying successful seedling establishment in salt marshes (e.g., Fivash et al., 2020; Qiu et al., 2021; Schoutens et al., 2021), there is a lack of studies examining the extent to which the root anchoring force is offset by other seedling organs.

After being dislodged, seedlings appear to remain healthy and grow during transport in the water column (Huiskes et al., 1995; Koch et al., 2010). Minchinton (2006) reported secondary displacement of established *Salicornia europaea* seedlings, with substantial dispersal distances occurring by rafting on wracks. Huiskes et al. (1995) captured tide-borne seedlings of *Scirpus maritima* and *Atriplex hastata* in nets and documented that these seedlings would grow into adult plants at the floodmark line within marshes. Zhao et al. (2021a) reported a rapid vegetation recruitment event in tidal flats without local seed banks and attributed this to the secondary dispersal and (re-)establishment of young seedlings from adjacent populations. There have been no studies undertaken that have determined the period for which dislodged seedlings can maintain buoyancy and the chance of them re-establishing after dispersal. If dislodged seedlings can drift for a long time without losing vigor and become successfully re-established, they may be a viable conduit for local recovery and/or long-distance colonization at new locations (Bohrer et al., 2005; Friess et al., 2012; van der Stocken et al., 2019a). We speculate that the inundation-free period (the WoO-1; Fig. 1.4) within the WoO framework (cf. Balke et al., 2011) is an indispensable propellant to kick-start both seedling establishment and seedling re-establishment. However, the stochastic nature of seedlings being dislodged and the variability of their dispersal period may cause the output of dislodged seedlings to vary in terms of their physiological and physical properties, making them different from seeds involved in the primary establishment. These differences in the physiological and physical properties may in turn affect the probability of final re-establishment by modifying the length of the required WoO-1. Furthermore, owing to variability in the life history and the growth rate (Schwarz et al., 2018; Yando et al., 2019), different species may vary in their ability to recover post-disturbance.

In this study, we aim to enhance our mechanistic understanding of salt marsh resilience by quantifying variability in the resistance and recovery of individual seedlings in relation to the seedling size, deepening our knowledge on the relevant life cycle processes and informing restoration. To obtain generic insights, we used two globally common pioneer marsh species as a model, namely the annual *Salicornia europaea* and the perennial *Spartina anglica*. *Firstly*, racetrack flume experiments were conducted to quantify the critical (free/low) hydraulic conditions and erosion depths that the seedlings can resist before being dislodged (related to the three sequential WoO; Fig. 1.4) under two potential seedling establishment scenarios, and to evaluate how functional traits such as root-shoot ratio influence their dislodgement susceptibility. *Secondly*, we determined the dispersal ability of seedlings being dislodged at various ages through a mesocosm study, in which the water motion experienced under floating conditions was mimicked by employing oscillatory shakers. *Thirdly*, we determined the possibility of re-establishment of dislodged seedlings under inundation-free periods (the WoO-1; Fig. 1.4) of varying lengths, through another mesocosm study using tidal-mimic systems. *Finally*, we integrated our results into a conceptual framework identified as the “Wheel of Recruitment”, to elucidate short-term cyclic behavior that occurs in the early stage of salt marsh establishment. Overall, our study advocate for more attention to the role of young seedlings in the resilience and persistence of salt marshes under global changes, and to aid prediction potential for life cycle informed salt marsh restoration.

5.2 Materials and methods

5.2.1 Quantifying the dislodgement resistance of establishing seedlings in a flume

To quantify species-specific demand in the length of WoO-1 (Fig. 1.4) and species-specific entanglement between seedling growth and disturbance pulses during WoO-2 and WoO-3 (Fig. 1.4), seeds of *S. europaea* and *S. anglica* were collected from salt marshes at the Westerschelde estuary (southwestern Netherlands) in November 2019. The seeds of *S. europaea* were air-dried and stored dry in a fridge at 4 °C (Redelstein et al., 2018), while the seeds of *S. anglica* were soaked in containers with seawater and stored wet in the same fridge (Cao et al., 2018). In April 2020, seeds of each species were germinated in growth chambers until visible shoot emerged. The seedlings were then transplanted individually into sediment-filled PVC pots (15 cm in height and 12 cm in diameter, with removable bases), under two treatments that mimicked potential seedling establishment scenarios: (*i*) seedlings were placed at the sediment surface (hereafter, the surficial seedlings); (*ii*) seedlings were planted at 0.5 cm depth of sediment (hereafter, the sedimentary seedlings). The sediment (with a D50 of 31.58 μm) was collected from the top 20 cm of a salt marsh pioneer mudflat in the Westerschelde estuary, and was defaunated by inducing anoxia with airtight tanks and then by sieving through a 3 mm sieve. These growth pots were placed under natural climate conditions in a greenhouse with day and night temperatures of approximately 21 °C and 15 °C, respectively. Daily watering was undertaken to ensure healthy growth of the seedlings. Eight pots under each growing scenario for each species were randomly selected and subjected to daily flume tests for the first five days, and the tests were then undertaken every three days for the next 27 days. A total of 448 pots were used in the experiment.

The flume facility comprised an oval racetrack with a length of 17.5 m and a width of 0.6 m (more details see Bouma et al., 2009), which was filled to a depth of 0.33 m with seawater at a salinity of 32. A test section in the straight portion of the flume was equipped with a double bottom into which we inserted the pots so that the sediment surface was flush with the flume bed and the seedlings were exposed (Fig. 5.1a). At the end of the test section, a wave damper was equipped to minimize wave reflections. A series of hydraulic treatments were mimicked in the flume, by adjusting the wave height in a range from 1 to 9 cm and the wave period ranging from 1.5 to 4 s while maintaining a constant flow velocity of 2.5 cm s^{-1}. The wave peddle in the flume did not fully reach down to the flume-floor to enable the continuous flow to be combined with wave generation. With this design, the peddle movement does not transfer all the energy into wave generation, due to “water leakage” underneath the wave peddle. This means that the translation of the settings of the wave peddle into wave characteristics is more complex than for wave-flumes where the peddle does reach the flume floor. To ensure that all the flume settings are directly comparable, all the treatments were parameterized as maximum bed shear stress (BSS) of the waves and current, according to the method described in Balke et al. (2011). The maximum BSS that could technically be achieved was 0.44 N m^{-2}, which is close to the time-averaged BSS observed during stormy events at the front of the salt marsh edge in the Westerschelde estuary (Callaghan et al., 2010). The flow velocity and wave parameters required to define the varied BSS scenarios were obtained and calibrated by using acoustic doppler velocimeters (Nortek AS, Oslo, Norway) and pressure sensors (Druck PTX 1830, GE, USA), respectively. These hydrodynamic settings do not represent the full range of hydrodynamic conditions as they may be found in the field, but the BSS-parametrization is sufficient to provide mechanistic insight on how seedling dislodgement can be triggered by waves.

In each flume test, a five step experimental protocol was implemented, with the test being terminated as soon as the seedling was dislodged:

1) The potted seedling was submerged into flume and slowly placed into the test section.
2) If no dislodgement occurred, a BSS of 0.04 N m^{-2} was applied and it was maintained for two minutes, which was a time step that proved to be sufficient for dislodging fragile seedlings (Balke et al., 2011).
3) If no dislodgement occurred, the BSS was increased in a stepwise manner up to 0.44 N m^{-2}, with each increment being held during two min time steps.
4) If no dislodgement occurred at the maximum BSS of 0.44 N m^{-2}, erosion treatment was applied by adding 3 mm PVC disc from the bottom into the pot and removing the protruded sediment (Fig. 5.1b). A BSS of 0.28 N m^{-2} (representing the hydraulic disturbances typical for salt marsh pioneer zone; Callaghan et al., 2010) was then applied and maintained for two minutes.
5) If no dislodgement occurred, step four was repeated until dislodgement occurred.

To evaluate how morphological traits influence the dislodgement resistance of the seedlings, maximum root length (mm; using vernier caliper), shoot length (mm; using vernier caliper), and wet weight after blotted dry (g; using electronic balance) of each dislodged seedling was measured after the flume test.

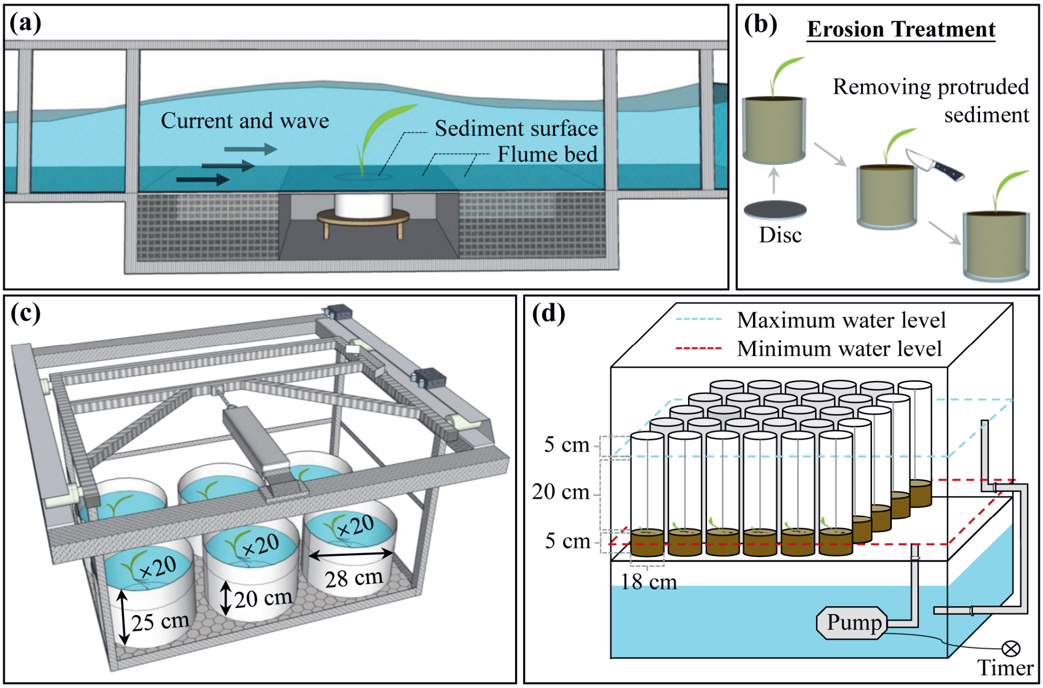

Fig. 5.1 Schematic representation of the study: (a) Flume setup used to quantify the critical conditions that seedlings can resist prior to being dislodged (results in Fig. 5.3 and 5.4). The test unit (made of PVC pipe, filled with sediment and a planted seedling) was placed on the deepened bottom to keep the sediment surface level with the flume bed so that the planted seedling was exposed to disturbances from currents and waves, which were parameterized as bed shear stress (BSS). (b) Method for quantifying the critical erosion depth of seedlings that can resist the maximum BBS applied in this flume in the absence of erosion (results in Fig. 5.4). By placing discs underneath the sediment, the seedling and sediment becomes slightly raised. This allows a thin layer of sediment to be removed, thereby mimicking sheet erosion before the pots are placed back into the flume. (c) Oscillatory shaker system (analogue to Zhao et al., 2021b) used to determine the floating time of the dislodged seedlings (results in Fig. 5.5). The oscillatory shaker was used to mimic the water motion under floating conditions. (d) Tidal system setup that was used to evaluate the potential of dislodged seedlings to re-establish under contrasting tidal settings

(results in Fig. 5.6). The cylinders represent independent experimental units and the gray solid lines on their side indicate slits for tidal water exchange. All the experimental units were lined with nets to prevent small seedlings from flowing out of the cylinders through the slits.

5.2.2 Quantifying the floating ability of dislodged seedlings over time (mesocosm exp. I)

To determine the dispersal ability vs. time of seedlings dislodged at varied ages, their floating period was monitored in seawater-filled (salinity of 32) cylindrical containers (25 cm in height, 28 cm in diameter), which were placed in tanks equipped with oscillatory shakers (Fig. 5.1c). The shakers moved the containers back and forth, 30 cm in opposite directions over a period of 2.6 s, generating water fluctuations with an average frequency of 0.38 Hz. This was undertaken to mimic the wave-related condition typical of the salt marsh fronts in the Westerschelde estuary (Callaghan et al., 2010). The water fluctuations generated in the presence of waves have been shown to slow down the drift process for dispersal units associated with currents (Zhao et al., 2021b). Wave action may also reduce the period that a dispersal unit remains buoyancy (Zhao et al., 2021b). Thus, including the effect of waves when quantifying the floatability of seedlings will provide more realistic data compared with that of a still water environment.

Prior to the tests, seeds of *S. europaea* and *S. anglica* were germinated to seedlings under the same settings and conditions used for the flume experiment. The seedlings were cultivated in growing pots until the specific ages of 3 d, 10 d, and 20 d. Seedlings of each age were dug out to simulate naturally occurring dislodgement and were then sorted by sight. They were then selected according to uniform size for testing (see table S5.1 for detailed parameters). A total of 100 seedlings from each age class per species were randomly placed in five containers with five replications. The number of floating seedlings in each container was monitored daily for a month and was used to calculate the floating ratio (R = N / 20 × 100%, where N is the number of floating seedlings and 20 refers to the total number of seedlings used).

5.2.3 Determining the re-establishment potential of dislodged seedlings (mesocosm exp. II)

We assessed if the dislodged seedlings can successfully re-establish if they are exposed to a sufficiently long inundation-free period (WoO-1, Fig. 1.4). Following the method used in the flume experiment and mesocosm exp. I, seedlings of *S. europaea* and *S. anglica* were obtained from the three age classes of 3 d, 10 d, and 20 d, referring to seedlings dislodged at different stages. These seedlings were subjected to varied WoO-1 to examine their potential to become re-established after being dislodged: (1) daily flooding, (2) three days without flooding, and (3) nine days without flooding.

The semi-diurnal 2 h tide inundation environment was mimicked in six two-layer stacked mesocosm tanks with the upper tank as experimental chamber, and the lower tank being used as the water reservoir. Seawater with a salinity of 32 could be automatically interchanged between these two tanks using a pump with a timer (Fig. 5.1d; cf. Cao et al., 2018). These tanks were placed in a climate chamber where light was provided for 12 h d^{-1} (550 µmol photons m^{-2} s^{-1}), and the temperature was controlled at 25 °C during the day and 20 °C during the night. A total of 180 PVC pots of 18 cm in diameter and 30 cm in height were placed in the six experimental tanks, to form independent experimental units (Fig. 5.1d). The bottom 5 cm of these pots were filled with preprocessed sediment following the same pre-treatment protocol used in the flume experiment. For the water interchange, slits were cut around the pots except for the bottom 5 cm, and they were lined with nets with a mesh size of 100 μm to prevent any smaller seedlings from escaping. An overflow return pipe inside the experimental tank maintained the water level at a maximum of

25 cm, so that the flooding depth within the pots was 20 cm above the sediment, leaving the top of the pots 5 cm above the water surface.

The six experimental tanks each containing 30 pots were assigned to one of the three treatments, namely (1) daily flooding, (2) three days without flooding, and (3) nine days without flooding. These sets of flooding-free periods (WoO-1 with a length of 0 d, 3 d, and 9 d) were chosen to represent the full spectrum of conditions in the salt marshes at the Westerschelde estuary. Daily flooding is a common scenario for most pioneer zones, three days without flooding occurs regularly in areas with relatively high elevations, while nine days without flooding represents an extreme scenario (Balke et al., 2014; Cao et al., 2018). Seedlings of the two species from the three age classes were randomly assigned to the 60 pots under the same treatment, with 10 replications for each age class per species under each treatment. The seedlings were initially placed on the sediment surface, and the mimicked tidal cycle allow the (positively buoyant) seedlings to periodically come into contact with the sediment. The status of the seedlings during inundation included floating, settlement (i.e., staying upon sediment surface), or re-establishment (i.e., rooting in the sediment), and were then monitored daily for 40 days. To determine whether the seedlings had settled or re-established, the pot was gently agitated. If the seedlings had not re-established, they would move around on top of the sediment when the pot was agitated.

5.2.4 Statistical analysis

For the data regarding the morphological trait evolution of seedlings over time from the flume experiments, the Pairwise Wilcoxon rank-sum test was used to test the difference between surficial seedlings and sedimentary seedlings. To assess which morphological trait(s) best explain the critical conditions required for the seedlings to be dislodged, multiple linear regressions were used with bed shear stress or the critical erosion depths as the response. For the data obtained from the mesocosm exp. I, the Pairwise Wilcoxon rank-sum test was used to test the difference in the floating ratio between the two species. For each species, the effect of the seedling ages on the floating ratio was analyzed by using a generalized linear model (GLM) with “binomial” family for the proportion data, following by a post hoc multiple comparison analysis among the seedling ages using the “multcomp” package (Hothorn et al., 2008). In the mesocosm exp. II, Kaplan–Meier survival analyses were performed using the “survival” package (Therneau, 2009) to estimate the time taken before the dislodged seedlings settling or re-establishing in the sediment. A log-rank test was used to compare the settlement and re-establishment between the two species. The same analysis was undertaken to compare the settlement and re-establishment between the seedling ages as well as between the flooding-free periods. All the statistical analyses were performed using R (v4.1.0; https://www.r-project.org) and with a significance level of 0.05.

5.3 Results

5.3.1 Morphological evolution of seedlings over time

On average, two and three days after transplanting were required for the surficial seedlings of *S. europaea* and *S. anglica* to grow their first root, respectively, while the first root of sedimentary seedlings that were buried by 5 mm of sediment was visible after one day for both species. Thereafter, seedling growth vs. time showed a species-specific linear pattern and was not significantly affected by the establishment scenarios applied in this study, namely without and with 5 mm sediment burial ($P > 0.05$; Fig. 5.2). The *S. anglica* seedlings were found to have a significantly faster growth rate in the root length, shoot length, and weight than *S. europaea* ($P < 0.01$; Fig. 5.2a, b, d). *S. europaea* had a significantly faster evolution rate of the root-shoot ratio compared with *S. anglica* ($P < 0.001$; Fig. 5.2c), suggesting that during the early morphological development of *S. europaea*, relatively more is invested in root elongation.

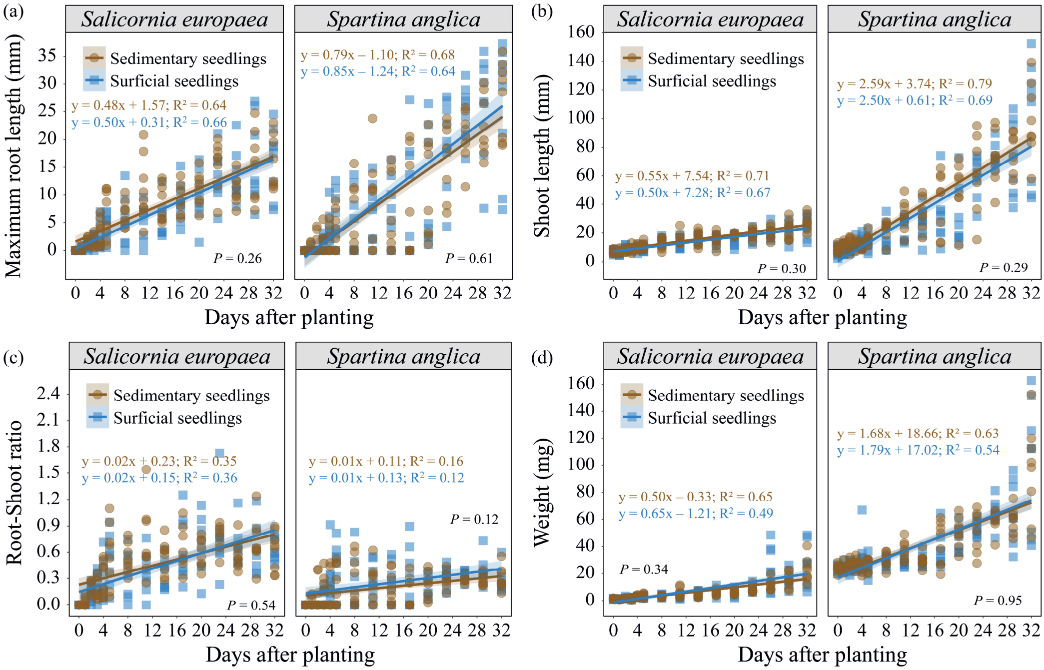

Fig. 5.2 Maximum root length (a), shoot length (b), root-shoot ratio (c), and weight (d) of the seedlings of *Salicornia europaea* and *Spartina anglica* as a function of time since transplanting under two establishment scenarios without and with 5 mm sediment burial. Without burial is denoted as superficial seedlings (blue) and with 5 mm sediment burial is denoted as sedimentary seedlings (brown). All the morphological parameters for each species under each scenario were measured for eight dislodged seedlings after each flume run (N = 112 for each species under each scenario). *P*-values at the facets denote the significance level in the seedling morphological parameters of each species between establishment scenarios (i.e., surficial seedings vs. sedimentary seedlings).

5.3.2 Critical conditions that seedlings can resist before being dislodged

In the scenario without sediment burial, the root length and the root-shoot ratio were the morphological parameters that best predicted the critical BSS that surficial seedlings can resist before being dislodged (Table S5.2). The surficial seedlings for both species with a root length of less than 3 mm would automatically float up when submerged (Fig. 5.3a; related to WoO-1). *S. europaea* surficial seedlings with a root length exceeding 6.5 mm and *S. anglica* surficial seedlings with a root length exceeding 6.1 mm could no longer be dislodged under the maximum BSS (i.e., 0.44 N m^{-2}) applied in the flume (Fig. 5.3a; related to WoO-2). Based on the regression equation for root extension listed in Fig. 5.2a, this critical root length would be reached on average after 12.4 days for *S. europaea* and after 8.6 days for *S. anglica*. Therefore, the growth rate (N m^{-2} d^{-1}) of seedling resistance against BSS due to root development can be calculated by dividing the maximum BSS (N m^{-2}) by the average growth period (d) required for the seedling to resist it. *S. europaea* was found to be slower in developing seedling resistance against BSS (i.e., 3.5×10^{-2} N m^{-2} d^{-1}) than *S. anglica* (i.e., 5.1×10^{-2} N m^{-2} d^{-1}).

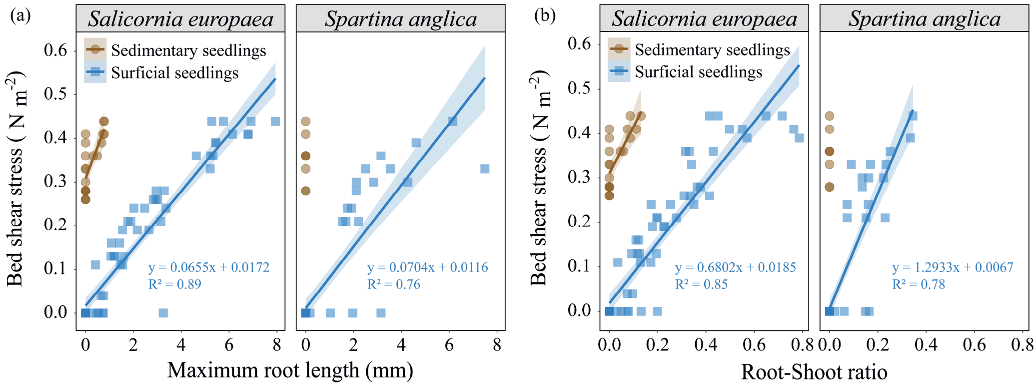

Fig. 5.3 The hydrodynamic disturbance (expressed as bed shear stress, BSS; methods cf. Fig. 5.1a) that required to be surpassed to dislodge seedlings with different root lengths (a) and root-shoot ratios (b) under two establishment scenarios: without (blue; superficial seedlings) and with (brown; sedimentary

seedlings) 5 mm sediment burial. The maximum BSS applied in the flume was 0.44 N m^{-2}, and sediment erosion was required for dislodgement of seedlings that can resist this maximum BSS (data shown in Fig. 5.4).

Seedlings with the same root length but a longer shoot (i.e., lower root-shoot ratio) are more likely to be dislodged than seedlings with a shorter shoot (i.e., higher root-shoot ratio). Surficial seedlings of *S. europaea* with a root-shoot ratio above 0.62 could no longer be dislodged under the maximum BSS (Fig. 5.3b), while surficial seedlings of *S. anglica* required a smaller threshold for the root-shoot ratio (i.e., 0.34) to resist the maximum BSS (Fig. 5.3b). These results indicate that the surficial seedlings of the annual *S. europaea* were less resistant to being dislodged than those of the perennial *S. anglica* under hydrodynamic force from the waves and current.

In the scenario with 5 mm of sediment burial, no seedlings floated up autonomously regardless of the species. Above a root length of 0.8 mm and a root-shoot ratio of 0.15, the *S. europaea* seedlings could not be dislodged by the maximum BSS applied in the flume (Fig. 5.3). In contrast, for *S. anglica*, the 5 mm sediment burial prevented the seedlings from being dislodged (Fig. 5.3).

For seedlings that resisted the maximum BSS imposed in the flume, their dislodgement required sediment erosion in addition to drag. According to the results from multiple linear regressions, only changes in the root length significantly affected the critical erosion depth required to be surpassed to dislodge seedlings (Table S5.2). Under a constant BSS of 0.28 N m^{-2}, the critical vertical erosion depth (related to WoO-3) required for seedlings dislodgement was correlated linearly to the maximum root length, regardless of the species and the growth scenarios (Fig. 5.4).

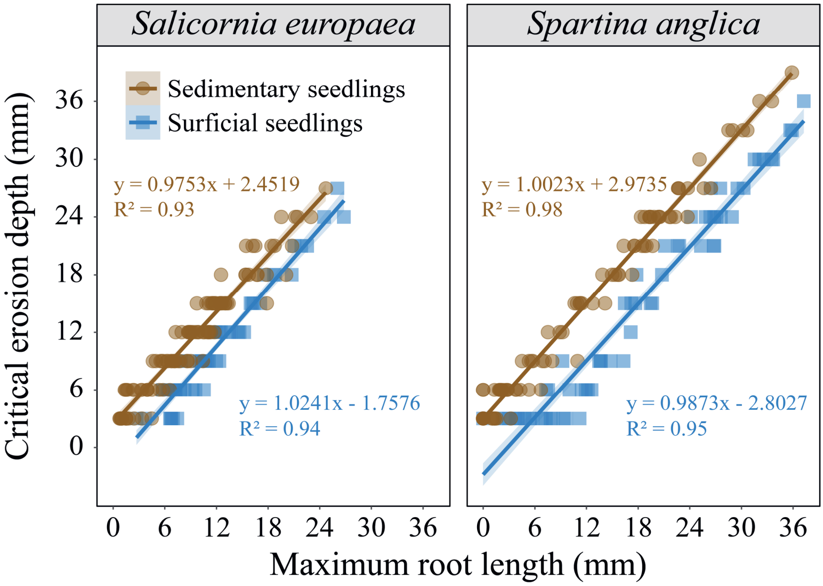

Fig. 5.4 The critical erosion depth (methods cf. Fig. 5.1b), required for the dislodgement of seedlings that can resist the maximum BSS applied in the flume, as a function of the maximum root length under two establishment scenarios: without (blue; superficial seedlings) and with (brown; sedimentary seedlings) 5 mm of sediment burial.

5.3.3 Seedling floatability in relation to the seedling age at dislodgement

Dislodgement timing (expressed as seedling ages) had a marked impact on seedlings floatability, regardless of the species ($P < 0.001$; Table S5.3; Fig. 5.5). For *S. europaea*, the older the seedlings that were dislodged, the faster their ability to float weakened ($P < 0.001$; Table S5.3; Fig. 5.5a). 30 days after dislodgement, 90%, 70%, and 40% of *S. europaea* seedlings dislodged at 3-days-old, 10-days-old, and 20-days-old remained buoyant, respectively (Fig. 5.5a). However, an opposite trend was recorded for *S. anglica*. The seedlings dislodged at an older age (i.e., 20-days-old) had a significantly longer floating period compared to those dislodged at other ages (i.e., 3-days-old and 10-days-old; $P < 0.001$; Table S5.3; Fig. 5.5b). It is noted that the *S. anglica* seedlings dislodged at the youngest age (3-days-old) stayed at the bottom without floating during the first few days, and became positively buoyant over time (Fig. 5.5b).

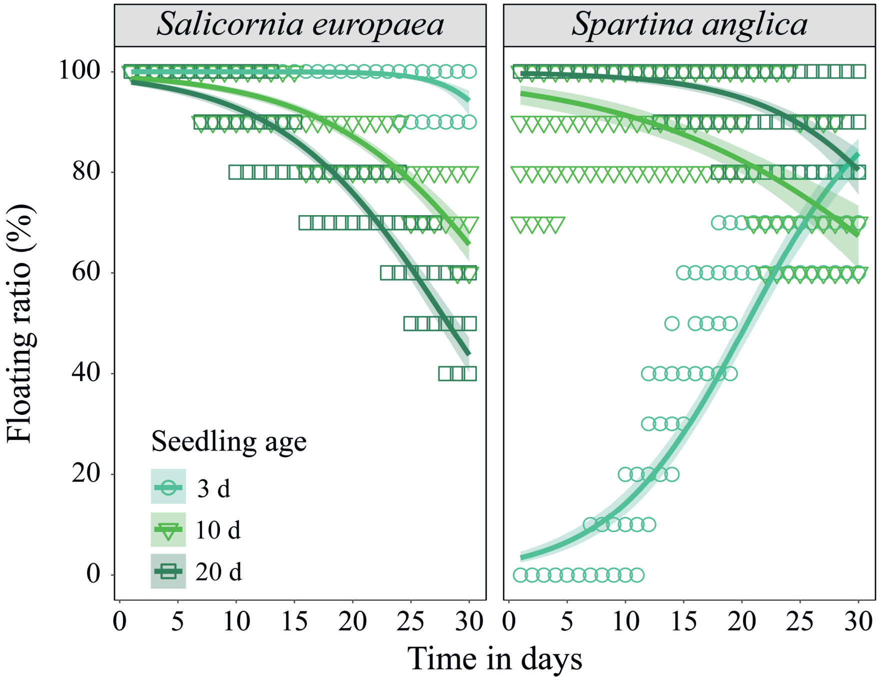

Fig. 5.5 Dispersal ability (indicated by the floating ratio over time) of seedlings dislodged at different ages (i.e., 3-days-old, 10-days-old, and 20-days-old) for *Salicornia europaea* and *Spartina anglica*. The floatation time was quantified while the dislodged seedlings were kept in an oscillatory shaker to mimic the water motion experienced under floating conditions (methods cf. Fig. 5.1c).

5.3.4 Re-establishment potential of dislodged seedlings

The potential for the seedlings to settle and re-establish after dislodgement was significantly affected by the ages of the dislodged seedlings and the length of the WoO-1 (i.e., inundation-free period; Fig. 1.4), but showed a species-specific pattern ($P < 0.05$; Fig. S5.1). Settlement is defined as staying upon the sediment surface, while re-establishment is defined as rooting in the sediment.

For *S. europaea*, the settlement was most likely to happen in the seedlings that dislodged at a greater age (Fig. 5.6a). Of the settled seedlings under the scenarios with WoO-1 of 0 and 3 d, most did so from 15 d after experiencing tidal flooding, but none of them established successfully by the end of the 40 day experiment (Fig. 5.6a). While under the scenario with WoO-1 of 9 d, some seedlings (30 % of 3-days-old seedlings, 10% of 10-days-olds seedlings and 20-days-olds seedlings) settled within the first days and were successfully re-established at the end of the 40 day experiment (Fig. 5.6a).

For *S. anglica*, the seedlings dislodged at varied ages settled at significantly different rates regardless of the length of WoO-1 ($P < 0.05$), with the seedlings dislodged at 3-days-old having the fastest and highest settling ratio (Fig. 5.6b). Under the scenario with WoO-1 of 0 day, only seedlings that were dislodged at 3-days-old managed to establish during the 40 days but with a lower rate of 20% (Fig. 5.6b). Under the scenarios with longer WoO-1 (i.e., 3 and 9 days), only seedlings that had settled within the first few days managed to re-establish, which was positively affected by the length of WoO-1. That is, the settling rate of seedlings increased over time, but the re-establishment rate of the settled seedlings remained stable at the level reached during the first days (Fig. 5.6b). The establishment rate of the seedlings in the scenario with WoO-1 of 9 d was higher than that of the scenario with WoO-1 of 3 d (Fig. 5.6b).

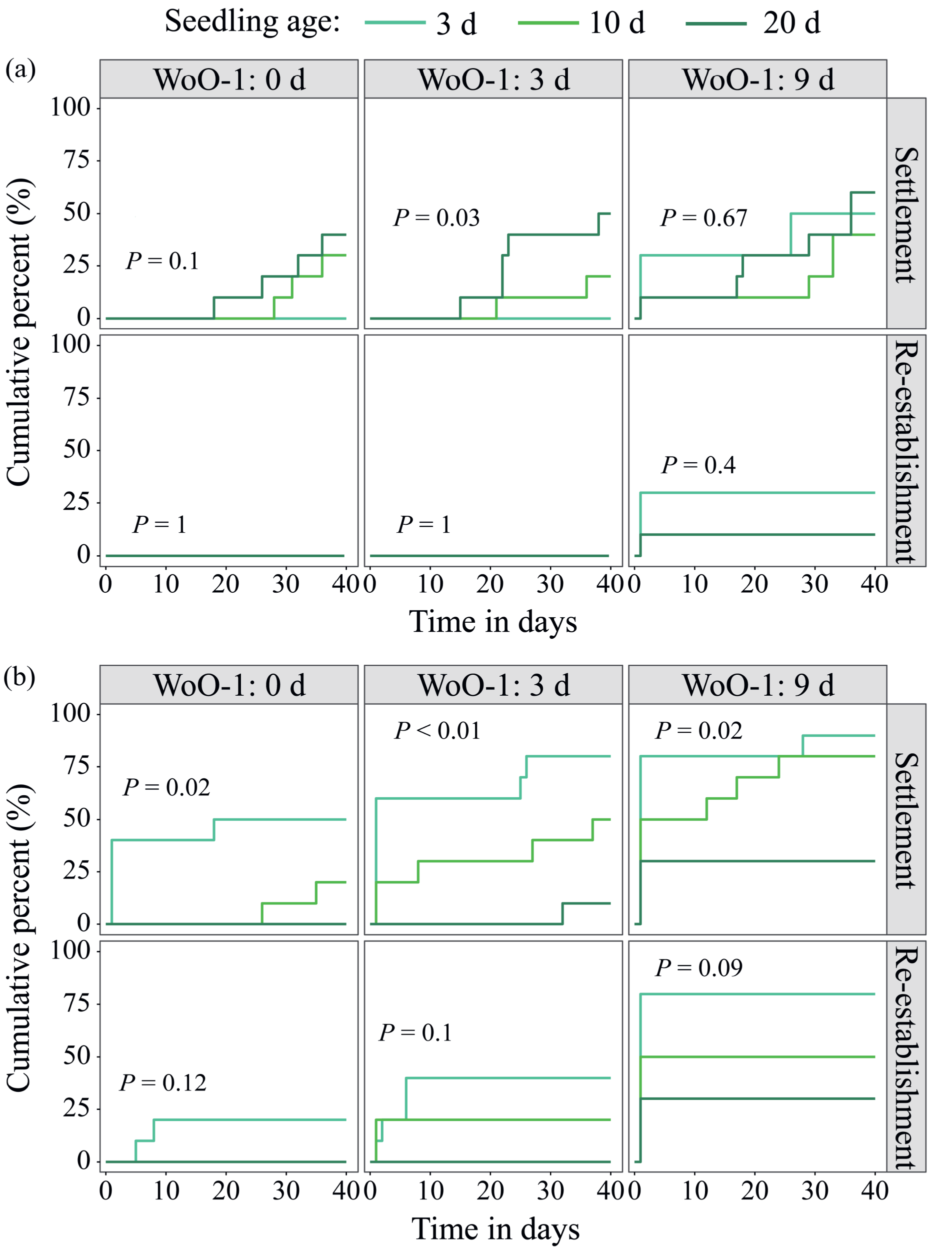

Fig. 5.6 Settlement and re-establishment percentage over a period of 40 days for seedlings in three age classes (3 d, 10 d, 20 d; referring to seedlings dislodged at different stages) of *Salicornia europaea* (a) and *Spartina anglica* (b). Settlement refers to staying on the sediment surface and no longer floating

while re-establishment means rooting into the sediment. Tidal systems (methods in Fig. 5.1d) were used to impose an inundation-free period of 0 d, 3 d, and 9 d (WoO-1; Fig. 1.4). The 3-days-old *S. anglica* seedling were initially negatively buoyant (i.e., stay on sediment surface) but could float later on. It was only when the 3-days-old *S. anglica* seedlings remained on the sediment surface throughout the experiment or settled down following floating, that they were considered as have settled. *P*-values at facets denote the significance level in the settling or re-establishment rate between seedlings of each species dislodged at different ages.

5.4 Discussion

This study aims to unravel salt marsh resilience in the critical pioneer development stage, by quantifying the growth rate of seedling resistance against dislodgement and by revealing the mechanism underlying the recovery of dislodged seedlings. Our process-based analyses indicate that the early life cycle of salt marshes may derive additional cyclic behavior, with alternating phases of seedling dislodgement, dispersal and (re-)establishment, which can be conceptually integrated into a "Wheel of Recruitment" (section 5.4.4). The present findings are highly important for *i*) modeling and forecasting the future resilience and persistence of salt marsh under global change and for *ii*) guiding life cycle informed restoration to obliterate potential risks.

5.4.1 Trade-off and sedimentary superiority associated with seedling resistance

In line with our expectations, the young salt marsh seedlings show a unique trade-off between root and shoot production to resist hydraulic disturbances (related to WoO-2; Fig. 1.4). This trade-off is derived from the special germination regime of the shoot sprouting prior to the root (Wijte and

Gallagher, 1996; Zhao et al., 2021a). By first investing maternal reserves in growing shoots, seedlings may enhance their potential to fix carbohydrates during photosynthesis, supporting a higher growth rate (Mašková and Herben, 2018). However, in a hydrodynamic-dominated environment, this comes at the price of diminished root-anchoring and less resistance to dislodgement from currents and waves. Similar phenomena regarding the entanglement between the aboveground and underground parts that determine seedling establishment have also been reported in seagrass (Wicks et al., 2009; Infantes et al., 2011) and in terrestrial (Mašková and Herben, 2018) systems, indicating that the potential antagonism of the aboveground part cannot be excluded. This provides a credible explanation for why rooted seedlings can still be dislodged in the absence of hydraulic drag, as was the case in our flume experiments. That is, the anchoring force of the root was offset by the positive buoyancy of the shoot.

Our flume study results show that a burial depth of 5 mm almost completely restrains the seedlings from dislodgement under the applied maximum BSS, without affecting the evolution of their morphological characteristics. Bouma et al. (2016) and Cao et al. (2018) reported that sediment burial will cause seedlings to invest less in root growth, resulting in less resistance. However, burial too deep may prevent the shoots from emerging (Bouma et al., 2016; Jørgensen et al., 2019; Abbas et al., 2020). Sediment dynamics may also inhibit the seedlings from establishing (Hu et al., 2021; Marion et al., 2021). This suggests that there is an optimal burial depth, which enables the seedlings to retain an upstanding position without triggering unfavorable morphological domestication. The superiority of shallow burial in promoting seedling establishment has also been demonstrated in other coastal systems (e.g., see Infantes et al., 2011 for seagrass and Balke et al., 2013 for mangrove). This type of shallow burial can arise as part of natural biotopographical processes such as bioturbation from burrowing benthos or the movement of sand waves (Green and Coco, 2014; Roche et al., 2016). In the absence of such natural processes, artificial means to create a similar environment prone to gradual sediment accretion offer interesting research pathways with key applications in enhancing seedling resistance (e.g., see Fivash et al., 2021 for a novel approach).

5.4.2 Dislodged seedling as a potential mode for long-distance dispersal

After dislodgement, the seedlings are expected to drift with the tidal currents so that the floating period primarily determines their potential travel distance (Koch et al., 2010; Cornacchia et al., 2019). According to our mesocosm exp. I, most of the dislodged salt marsh seedlings remained positively buoyant for 30 days. This indicates a considerable time window for dislodged seedlings to achieve long-distance dispersal and recruitment. Longer dispersal ranges are favorable in creating more opportunities for genetic mixing (Bohrer et al., 2005; Rouger and Jump, 2014), which fundamentally affects the metapopulation genetic structure and diversity and over time leads to stronger resilience against disturbance (Friess et al., 2012; van der Stocken et al., 2019a). This long-distance dispersal potential from dislodged seedlings may be particularly important for species with a limited seed dispersal ability such as *S. europaea* whose seeds maintain buoyancy only for a few hours (Huiskes et al., 1995). Emerging studies suggest that the spatial settlement pattern of positive buoyancy dispersal units, such as dislodged seedlings, depends on the theoretical buoyancy-dependent potential, in combination with the tidal direction, flow velocity, and landscape elements that may trap these dispersal units (Ruiz-Montoya et al., 2012; Wang et al., 2018; Zhao et al., 2021a). For example, seedlings that are dispersed landward during high tide may be captured by vegetation and re-establish nearby. More field evidence is indispensable for determining the exact or approximate dispersal distances of dislodged seedlings. However, acquisition data on this requires innovations in techniques that can be used to track the movement trajectories of seedlings along shorelines or in the marine environment (van der Stocken et al., 2019a).

Otherwise observational studies in the absence of such technical innovations might easily turn into looking for a needle in a haystack.

5.4.3 Condition-specific re-establishment potential of dislodged seedling

If tide-drifted dispersal units, such as the dislodged seedlings, settle in areas near or far from the donor population, the outcomes of our mesocosm exp. II suggest that the possibility of successful re-establishment is regulated by the inundation-free period (WoO-1; Fig. 1.4). This kind of WoO-1 enables the dislodged seedlings to stay on the sediment surface and to root (Balke et al., 2011; Hu et al., 2015a). However, the effectiveness of WoO-1 was shown to differ with varied settlement states and ages for the dislodged seedlings. Seedlings are required to settle through mechanistic processes such as rooting (Fig. 5.7c), rather than through physiological processes such as loss of buoyancy (Fig. 5.7b). The latter basically means the decay of seedling vitality (Stafford-Bell et al., 2015; Thomson et al., 2015), which in turn impairs the effectiveness of WoO-1 in promoting rooting. Compared with older seedlings, younger seedlings are able to root more rapidly, once they come into contact with the sediment (Redelstein et al., 2018).

For simplicity, the tidal inundation cycle was employed as the only physical driver in our study, which is key to initiating waterborne propagules such as the dislodged seedlings to come into contact with the sediment bed (Lai et al., 2018). In nature, the superficial sediment layers on natural tidal flats would be dynamic with sediment entrainment, dispersal, and settlement (Green and Coco, 2014). The resulting shallow burial from such motion may assist the seedlings to settle (Jørgensen et al., 2019; Marion et al., 2021), thereby amplifying the chances of seedling re-establishment. Microtopographic structures, such as hummocks and hollows, have been proven to trap and retain dispersal units (Fivash et al., 2020; Qiu et al., 2021). This potentially helps the dislodged seedlings to retain the state of settlement for longer to promote re-establishment. Other factors that may enhance trapping of dislodged seedlings include the presence of benthic algae, interception of plants, covering of plant wrack, and bioturbation behavior of benthic animals (Stafford-Bell et al., 2015; Zhu et al., 2016a; Fivash et al., 2020).

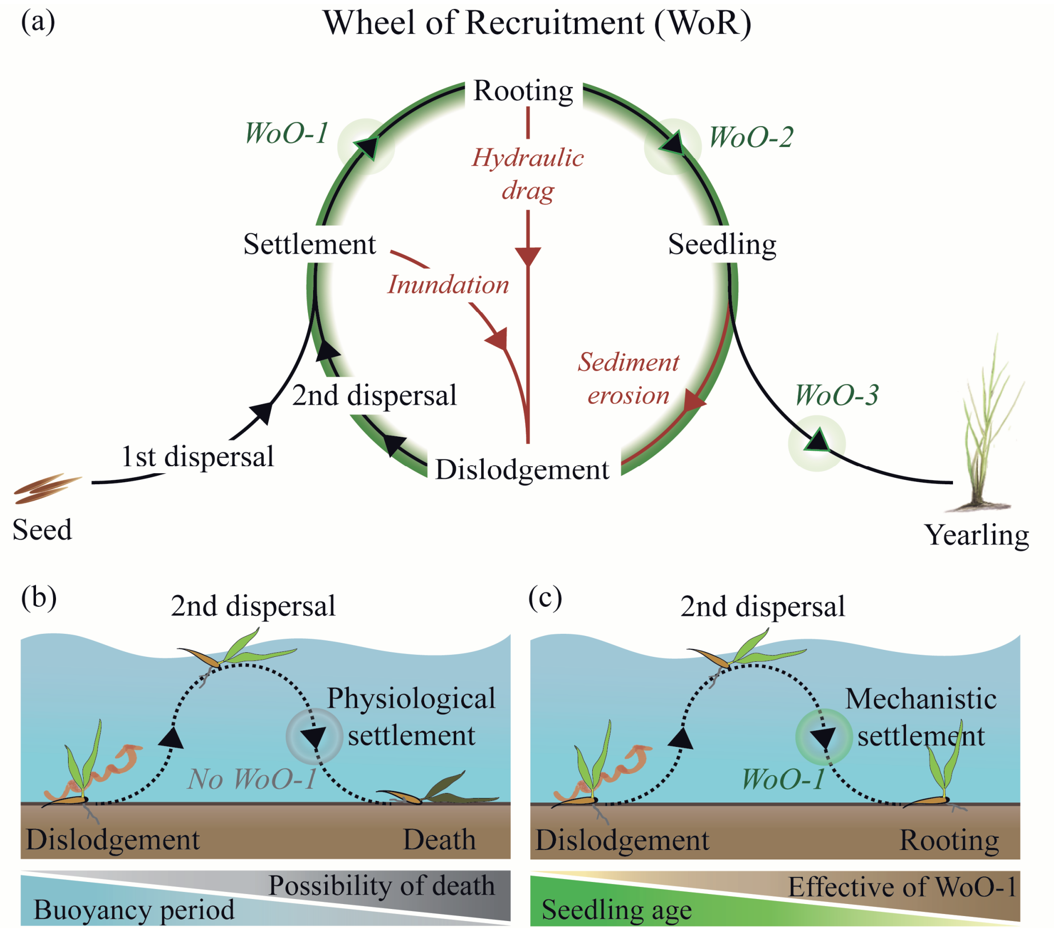

Fig. 5.7 (a) Schematic diagram of the proposed Wheel of Recruitment (WoR): a short-term cyclic behavior affiliated with the critical early stages of salt marsh pioneer development. The WoR emphasizes that dislodgement during seed-seedling transition is not the end of yearling recruitment, but a potential starting point of a new life cycle. The black font indicates the stages or processes related to yearling recruitment; the red italic font indicates the

external disturbances that impede the seed-seedling transition; the green italic font indicates the conditions that empower the seeds/seedlings to resist corresponding disturbance and complete the transition. WoO: Windows of opportunity, which refers to stochastic periods during which external disturbances are temporarily absent or diminished. For detailed descriptions of WoO-1, 2, 3 refer to Fig. 1.4. Note: we assume that *i*) dislodged seedlings can successfully re-establish if they live through the stage of initially rooting with the assistance of WoO-1, *ii*) subsequent seedling resistance related to WoO-2 and WoO-3 would also apply to the re-established seedlings. (b) Schematized mechanism of failed seedlings re-establishment. Without WoO-1, the drifting seedlings settle through physiological processes with a loss of buoyancy, which means loss of vitality or death. (c) Schematized mechanism of successful seedlings re-establishment. The appearance of WoO-1 provides the dislodged seedlings with more time to settle through mechanistic processes, namely rooting and achieving successful establishment. The effectiveness of WoO-1 was shown to differ with the varied ages of the dislodged seedlings.

5.4.4 Wheel of recruitment: neglected cyclic behavior at early salt marsh life cycle

Cyclic behavior is a common feature of complex systems with periodic disturbance (Stallins, 2006; Benincà et al., 2015). Well-known examples form the coast are the long-term cyclic succession over a period of years between bare rock, barnacles, crustose algae, and mussels in the rocky intertidal community (Benincà et al., 2015) and the long-term cyclic alternations over a period of years between lateral erosion and vegetation expansion in salt marshes (van der Wal et al., 2008). In this study, the reported potential of seedling resistance and recovery suggests a neglected cyclic behavior affiliated with the critical early stages of pioneer development (Fig. 5.7a). Seedling dislodgement following the initial establishment attempt from seed does not necessarily purport the end of vegetation recruitment. It may also be the start of a new spin on the Wheel of Recruitment (WoR; Fig. 5.7a). The dislodgement of young seedlings in spring kick-starts the WoR, while the sequence of disturbance-free/low periods (WoO, Fig. 1.4) provides the flywheel driving this cyclic behavior (Fig. 5.7a). The WoR is characterized as short-term with a period of days to weeks, depending on the age of the seedling being dislodged and the length of WoO. For older seedlings or individual plants dislodged later in growing season (e.g., during summer), WoR may no longer apply as the effectiveness of WoO in promoting re-rooting drops considerably with seedling age.

In dynamic coastal environments, the proposed WoR would trigger short-term and effectively chaotic trajectories of the paradigm life cycle (cf. Temmink et al., 2021), because it produces more opportunities for shaping plant resilience by amplifying the potential of recovery after disturbance. Similar short-term cyclic behaviors related to specific life stages have also been inferred from other ecosystems, such as vegetative fragments dispersal and re-establishment in seagrass beds (Lai et al., 2018) and freshwater streams (Cornacchia et al., 2019), or the resprouting of snapped trees in tropical rainforest (Curran et al., 2008). These examples suggest that the WoR-like processes affiliated to specific life stages may be relatively common in ecosystems where WoO appears following stochastic disturbance pulses (e.g., mangrove, Balke et al., 2011; river floodplain, Sarneel et al., 2014; dune, Lichter, 2000). Our findings illustrate the potential of this short-term cyclic behavior to strengthen system resilience, suggesting that the related mechanism insights are essential to improve our understanding of the life cycle and ecosystem persistence.

5.4.5 Implications for Restoration Practice

Mechanistic insight into the processes that enable/disable seedling (re-)establishment has direct relevance for restoration decision-making (Bouma et al., 2016; Yando et al., 2019; Schoutens et al., 2021). The present species-specific data regarding seedling resistance can be used in biophysical models (e.g., Hu et al., 2015a, 2021; Schwarz et al., 2018) to predict long-term habitat suitability for restoration. Present findings also emphasize that it is important to measure short-term sediment dynamics (e.g., see Hu et al., 2015b, 2020 and Willemsen et al., 2022 for state-of-the-art approaches) during the critical period of seedling establishment at the target site to optimize restoration designs. A less-exposed sedimentary field is ideal for seedling establishment, considering its performance in enhancing seedling resilience (Jørgensen et al., 2019; Marion et al., 2021). Furthermore, our results suggests that management and restoration schemes could benefit from ameliorating seedling resilience through creating WoO. One possible avenue is to employ artificial assistance measures such as biodegradable temporary structures (Temmink et al., 2020) to enhance seedling resistance and create a temporary low-stress condition during which seedlings can establish and grow enough to advance to the next life cycle stage (Fivash et al., 2021; Temmink et al., 2021).

5.5 Supporting information

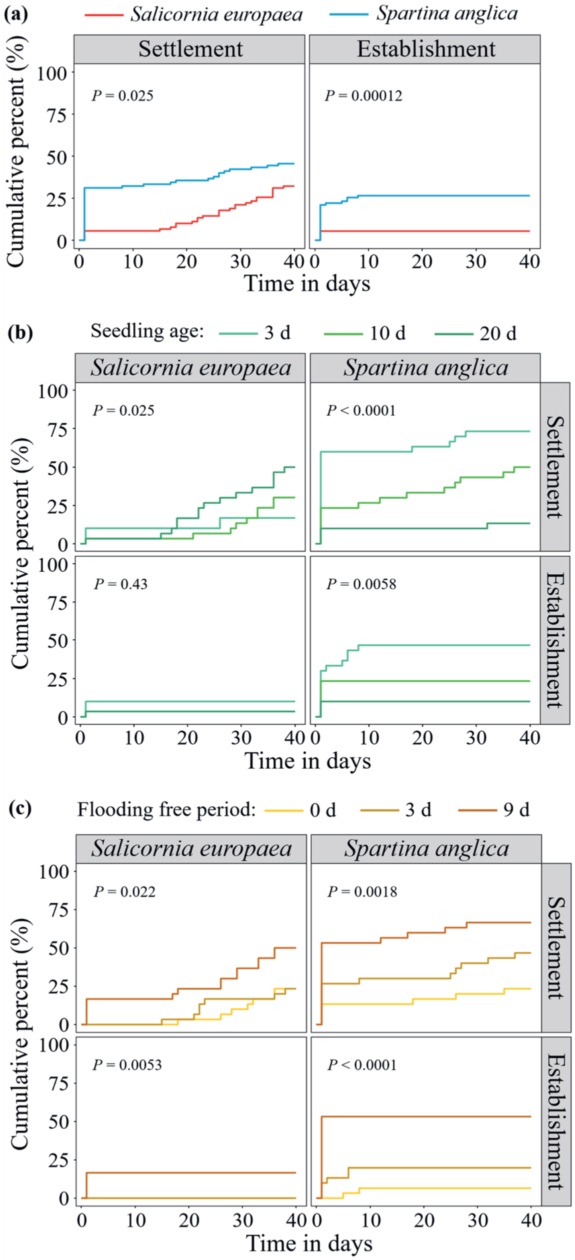

Fig. S5.1 Variations in settlement and re-establishment percent (during a period of 40 days) of the dislodged seedlings of *Salicornia europaea* and *Spartina* *anglica* among species (a), seedling ages (b), and flooding-free periods (c). *P*-values at facets denote the significance level of the difference in seedling settlement or re-establishment percent among the corresponding variable.

Table S5.1. Seedling characteristics of *Salicornia europaea* and *Spartina anglica* at three age classes (3 d, 10 d, 20 d; referring to seedlings dislodged at different stages) used in mesocosm experiment 1 and 2. All morphological parameters are displayed as the mean ± standard deviation. Different lowercase letters denote significant differences between age classes.

	Age classes		
Salicornia europaea	3-days-old 	10-days-old 	20-days-old 
Weight (mg)	1.31 ± 0.46 c	5.26 ± 1.61 b	11.97 ± 4.39 a
Shoot length (mm)	8.76 ± 1.07 c	11.73 ± 2.13 b	18.37 ± 2.75 a
Root length (mm)	1.24 ± 0.66 c	6.63 ± 3.41 b	9.49 ±3.84 a

	Age classes		
Spartina anglica	3-days-old 	10-days-old 	20-days-old 
Weight (mg)	24.76 ± 3.56 c	30.85 ± 4.80 b	40.73 ± 4.69 a
Shoot length (mm)	8.20 ± 2.78 c	21.72 ± 8.30 b	45.49 ± 10.46 a
Root length (mm)	0.00 ± 0.00 c	5.13 ± 2.01 b	25.82 ± 7.46 a

Table S5.2. Results of the multiple linear models testing effects of morphological factors on the critical bed shear stress and critical erosion depth required by seedling dislodgement.

Models	Estimate	Std. error	t-value	p-value
Effect on bed shear stress				
Intercept	-0.003	0.014	-0.217	0.829
Root length	0.399	0.081	4.932	<0.001***
Shoot length	0.013	0.012	1.021	0.310
Weight	0.461	0.482	0.957	0.340
Root-Shoot ratio	0.280	0.088	3.164	0.002**
Effect on critical erosion depth				
Intercept	2.206	0.393	5.614	<0.001***
Root length	9.017	0.450	20.035	<0.001***
Shoot length	0.210	0.178	1.184	0.237
Weight	-12.475	13.707	-0.910	0.363
Root-Shoot ratio	-1.193	0.888	-1.344	0.180

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

Table S5.3. Results of the generalized linear models testing effects of seedling age on their floating rate.

Models	Estimate	Std. error	t-value	p-value
Salicornia europaea				
Main effect				
Intercept	1.017	0.010	97.45	<0.001***
Seedling age	0.399	0.081	4.932	<0.001***
Multiple comparisons				
3-days-old : 10-days-old	-0.107	0.014	-7.827	<0.001***
3-days-old : 20-days-old	-0.195	0.014	-14.284	<0.001***
10-days-old : 20-days-old	-0.088	0.014	-6.457	<0.001***
Spartina anglica				
Main effect				
Intercept	0.358	0.020	18.23	<0.001***
Seedling age	0.033	0.002	21.77	<0.001***
Multiple comparisons				
3-days-old : 10-days-old	0.490	0.022	22.258	<0.001***
3-days-old : 20-days-old	0.587	0.022	26.680	<0.001***
10-days-old : 20-days-old	0.097	0.022	4.421	<0.001***

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

6

General discussion

6. General discussion

6.1 Towards a holistic understanding of salt marsh recruitment processes

Recruitment of most salt marsh species involves a sequence of transitions through the seed and seedling stages, during which underlying variations in demographic proportions would significantly modulate the trajectories and outcomes of recruitment (Larson et al., 2015; Kettenring and Tarsa, 2020). The well-known key life stage involved in salt marsh recruitment include primary seed dispersal, secondary seed dispersal, seed retention, seedling emergence, seedling rooting, and seedling survival (Fig. 1.5; Friess et al., 2012). In this thesis, we extended this paradigm (Fig. 6.1) and demonstrated that the salt marsh recruitment process is much more complex than we have long recognized. By means of field investigations and experiments, mesocosm experiments, and flume studies, we revealed the following three distinct types of secondary dispersal across seed and seedling stages:

- **Type-I**: Seed re-movement due to hydrodynamics and sheet erosion (Chapter 4).
- **Type-II**: Seed entrainment due to lower lift-off threshold after germination (Chapter 3).
- **Type-III**: Seedling dislodgement by hydraulic drag and sediment scouring (Chapter 5).

Secondary dispersal of Type-I is included within the well-known recruitment paradigm (Fig. 6.1; Table 6.1) and has long been considered to be directly connected with the post-dispersal seedling establishment (Friess et al., 2012; van der Stocken et al., 2019a). The seeds involved in this process tend to be negative buoyancy due to saturating with seawater during primary dispersal (Chang et al., 2008). Therefore, secondary dispersal of Type-I is characterized by short-distance near-surface movements induced by strong hydrodynamic disturbances (e.g., storm; Zhu et al., 2020a). For buried seeds in particular, entrainment of the whole sediment layer above the seeds was required to initiate secondary dispersal of Type I (Ruiz-Montoya et al., 2012; Zhu et al., 2014, 2021). Secondary dispersal of Type-II and Type-III follow Type-I in sequence and are attached to the process of seedling emergence and seedling establishment, respectively (Fig. 6.1; Chapters 3 and 5). Both may cascade to subsequent life stages, causing varying degrees of demographic variability and having disproportionate impacts on recruitment outcomes (detailed in sections 6.1.1 and 6.1.2).

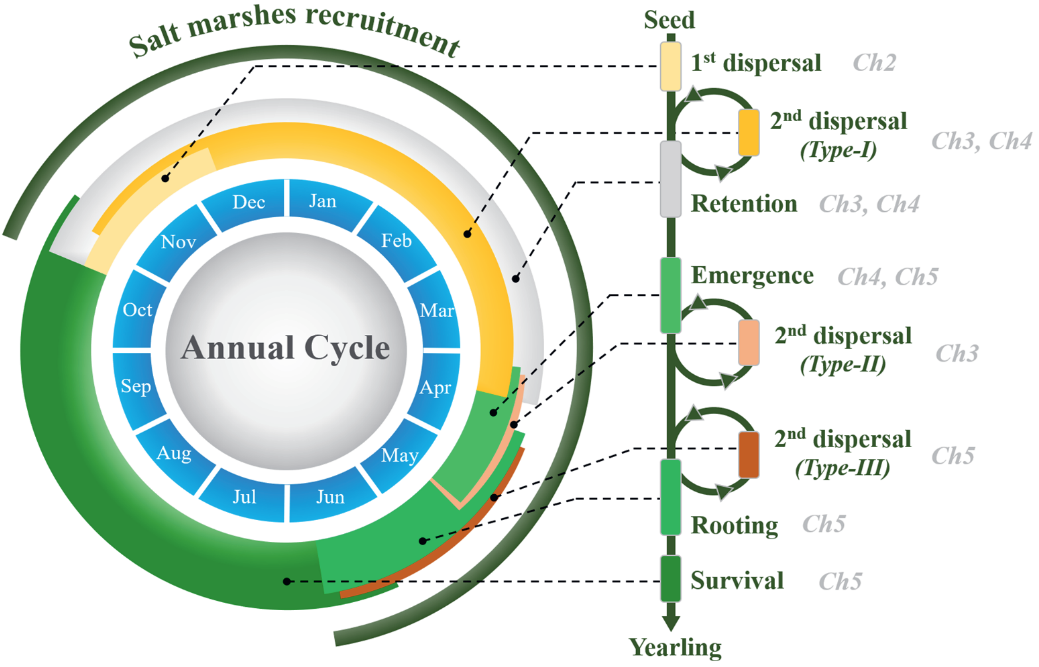

Fig. 6.1 Schematic diagram of the extended annual life cycle associated with seed-based salt marsh recruitment and relation with the thesis chapters. Based on the well-known life-cycle paradigm (see Fig.1.5), three types of secondary seed/seedling dispersal attached to varied life stages were revealed and summarized in this thesis. *Type-I* refers to seed re-movement due to hydrodynamics and sheet erosion. *Type-II* refers to seed entrainment due to a lower lift-off threshold after germination. *Type-III* refers to seedling dislodgement by hydraulic drag and sediment scouring. All three types of secondary dispersal can lead to seed(ling) loss in local populations, while may

also contribute to seed availability and seedling establishment in nearby and/or distant populations with condition-dependent potential. Abbreviations indicate thesis chapters, e.g., Ch2 refers to Chapter 2.

6.1.1 Secondary dispersal induced by seed germination

Following secondary dispersal of Type-I, seeds may retain at microsites, e.g., due to plant interception, sediment accretion, or bioturbation (Chang et al., 2008; Zhu et al., 2016a; Marion et al., 2021), and subsequently transform into germinated seeds. With the emergence of embryo shoot (which develops into a leaf), seed traits, especially the density, will change significantly (Coops and van der Velde, 1995; Finch-Savage and Leubner-Metzger, 2006). This would enable the negatively buoyant seeds to float again during tide inundation (Chapters 3 and 5). Meanwhile, the extension of buds enlarges its contact area with the tidal component, making the seed more sensitive to drag force (Darnell et al., 2015). As a result, the lift-off current threshold required for seed displacement dropped, dramatically increasing the likelihood of secondary seed dispersal in calm tides (Chapter 3). This is particularly significant for shallowly buried seeds (e.g., 5 mm), as they would slide out of the substrate under the coupling of drag force and buoyancy without requiring sheet erosion (Chapter 3; Koch et al., 2010). All together indicated the great potential for secondary seed dispersal after germination (i.e., Type-II; Table 6.1), implying that the movement of salt marsh seeds may be much more frequent in spring than previously anticipated. Such secondary seed dispersal may be one reason for the sharp drop in native-scale seed available in the spring when there are in absence of high-energy hydrodynamic events (e.g., storms; Chapter 3; van Regteren et al., 2019; Yuan et al., 2020).

On the other hand, by integrating remote sensing analysis, seed bank surveys, and in situ monitoring of physical conditions, we demonstrated that the massive secondary seed dispersal and seedling establishment would occur together over spring in the Yangtze estuary, China (Chapter 3). This suggests that secondary dispersal of Type-II may also be one of the main driving processes leading to sudden salt marsh recruitment in nearby or distant mudflats (Chapter 3; Table 6.1). Relative to Type-I, secondary dispersal of Type-II would benefit salt marsh recruitment in two ways: (1) Larger dispersal distances allowed by long-term floating period (days to months; Chapters 2 and 5). The enhanced dispersal capacity would expand the distribution range of the current population (Friess et al., 2012; van der Stocken et al., 2019b) and potentially contribute to the genetic complexity of nearby and/or distant populations (Bohrer et al., 2005; Rouger and Jump, 2014), although the potential dispersal distance remains to be quantified. (2) More opportunities for settlement and establishment. The enlarged seed shape after germination may magnify the possibility of seeds being intercepted or trapped by landscape elements (e.g., plants and topography; Chang et al., 2008; Xie et al., 2019; Qiu et al., 2021). Furthermore, the protruded root(s) during germination will make it easier for seeds to adhere to sediment particles after secondary dispersal (Koch et al., 2010), thereby may accelerating the anchorage and shortening the length of the desired windows of opportunity (Fig. 1.4; cf. Balke et al., 2011; Hu et al., 2021).

6.1.2 Secondary dispersal following seedling dislodgement

If the seeds were added to the persistent soil bank and have successfully emerged, the follow-up biggest risk for the emerging seedlings during establishment and survival is being dislodged (Balke et al., 2011, 2014; Bouma et al., 2016) and subject to water-borne dispersal (i.e., Type-III; Chapter 5). Seedling dislodgement and dispersal typically occurs when the drag force from tidal currents and waves overwhelms the anchoring force of seedlings (Balke et al., 2011; Hu et al., 2015a). In scenarios where erosion occurs, seedlings' anchoring ability would be drastically attenuated by the exposure of their roots, thus resulting in dislodgment under weaker drag forces (Cao et al., 2018;

Marion et al., 2021). Such secondary dispersal following seedling dislodgement is directly responsible for massive seedling loss at the native scale (Table 6.1; Chapter 5). However, seedling displacement and dispersal during establishment does not necessarily entail the end of salt marsh recruitment. In Chapter 5, we provided solid evidence through mesocosm experiments that the dislodged seedlings have a high probability of leaving their donor habitat to achieve long-distance dispersal based on the prolonged positive buoyancy and establishing again in distant mudflats. This finding suggests that secondary dispersal following seedling dislodgement (i.e., Type-III; Table 6.1) is an unrecognized mode for local marsh recovery and/or long-distance recruitment of new habitats (Bohrer et al., 2005; van der Stocken et al., 2019a).

After secondary dispersal of Type-III, the dislodged seedlings would arrive at a sink site and coming into contact with the sediment bed at low tide (Lai et al., 2018). The possibility of successful re-establishment of the dislodged seedlings was found to be species-specific and dependent on the age of seedlings being dislodged and the length of windows of opportunity (cf. Fig. 1.4; Chapter 5). Additionally, landscape elements that assist seed retention and establishment (after secondary dispersal of Type-I and/or Type-II) are expected to similarly benefit the settlement and re-establishment of dislodged seedlings, although few have been tested and verified rigorously. The factors or processes worth exploring include e.g., burial by benthos or having a high sediment accretion (Marion et al., 2021), the presence of benthic algae (Fivash et al., 2020), interception of existing plants (Chang et al., 2008), trapping of heterogeneous micro-topographic structures (Xie et al., 2019; Qiu et al., 2021), and covering of plant wrack (Stafford-Bell et al., 2015). Even though the successful re-establishment of dislodged seedlings may be event-driven and rare, secondary dispersal of Type-III shows great potential to drive genetic mixing in a long-distance manner (Bohrer et al., 2005; Rouger and Jump, 2014), which would fundamentally affect the genetic diversity of metapopulations and contribute to greater resilience to physical disturbances (Friess et al., 2012; van der Stocken et al., 2019a). This would be particularly important for species with limited seed dispersal capacity such as *Salicornia europaea*, whose seeds can only remain afloat for a few hours (Huiskes et al., 1995; Chapter 2).

Table 6.1 A general summary of the secondary dispersal processes involved in seed-based salt marsh recruitment. These processes will cause seed/seedling loss from native populations, but may also contribute to increasing seed/seedling availability in nearby and/or distant populations. Asterisks (*) indicate the degree of the impact based on empirical speculation, with more asterisks indicating a greater likelihood of forming risk or providing opportunity.

Secondary dispersal	Applicable objects	Drive process	Features	Impacts			Implications for restoration
				on native populations	on nearby populations	on distant populations	
Type-I	Wet seeds (*Negative buoyancy*)	Hydrodynamic and sheet erosion	Near-bed short-distance movement	Risk ***** (*Continued seed loss from late fall to early spring*)	Opportunity * (*Less seed available due to difficulty in retention*)	Opportunity * (*Few seeds arrival due to limited dispersal distance*)	Bottleneck induced by seed loss (*Can be overcome by seed burial or habitat regulation*)

Continued Table 6.1

Type-II	Germinated seeds (*Negative buoyancy turns to positive buoyancy during germination*)	Lower seed lift-off threshold after germination (*Species specific*)	Short or long-distance drifting (*Depends on buoyant state*)	Risk *** (*Rapid seed loss in spring*)	Opportunity ***** (*Massive seeds arrive collectively; Relatively easy to be retained; Synchronized with seedling establishment*)	Opportunity *** (*Many seeds arrive collectively; Relatively easy to be retained; Synchronized with seedling establishment*)	Bottleneck induced by seed loss (*Can be overcome by habitat regulation*) Options for large-scale restoration in areas without seed sources (*Add germinated seeds before WoO in spring*)
Type-III	Dislodged seedlings (*Positive buoyancy*)	Weak seedling resistance against hydraulic drag and sediment scouring (*Species specific*)	Long-distance drifting	Risk ** (*Seedling loss in spring and early summer*)	Opportunity * (*Few seedlings stay due to persistent buoyancy*)	Opportunity ** (*Seedlings can arrive but require specific conditions for re-establishment*)	Bottleneck induced by seedling loss (*Can be overcome by sediment burial, aggregated planting, and habitat regulation*)
Note					Importance for genetic diversity and resilience		See details in section 6.4

6.2 The relative importance of abiotic conditions in salt marsh recruitment

6.2.1 The role of currents, waves, and sediment erosion in salt marsh recruitment

Salt marsh species are hydrochorous (i.e., their seeds are dispersed by water), which determines that the hydrodynamics of tidal motion serve as the main abiotic driver affecting the trajectory and outcome of dispersal events (Chang et al., 2008; Friess et al., 2012; Shi et al., 2020). By means of flume experiments, we revealed a simple linear additive effect of tide current on primary seed dispersal in salt marshes (Chapter 2). This echoes the results found in other coastal systems (e.g., mangrove and seagrass), that is, seed dispersal speed would change in synchrony with current velocity in the same increments under the current-only scenario (van der Stocken et al., 2015; Cunnings et al., 2016; van der Stocken and Menemenlis, 2017). Our flume study further revealed a drastic slowdown of seed dispersal speed relative to the prevailing current component, due to the orbital movement caused by wave action (Chapter 2). The increase in wave magnitude was shown to dampen this slowdown in a non-linear manner (Chapter 2). Furthermore, through mesocosm experiments, we found that the floating ability of seeds would also be significantly affected under wave-driven oscillatory flow regimes, with a faster loss in buoyancy for especially pioneer salt marsh species (Chapter 2). All together convey a clear message that the existing assessments of primary seed dispersal in salt marshes may be rather imprecise by ignoring the effects of waves. Gaining insights into wave effects is particularly ecological significant, given the increased wave intensity in future climate change scenarios (Silinski et al., 2015; Hanley et al., 2020; Krauss and Osland, 2020). The resulted data in Chapter 2 can be integrated into numerical models to more accurately predict variability in salt marsh dispersal and recruitment in wave-dominated coastal environments.

After primary dispersal, the movement (i.e., secondary dispersal) or nonmovement (i.e., retention) of seeds in a temporary settlement site is also highly related to the hydrodynamics of tidal motion (Koch et al. 2010; Friess et al., 2012; Zhu et al., 2020a). Using a unidirectional flow flume, we quantified the lift-off velocity threshold for seeds to kick-start secondary dispersal (of both Type-I and Type-II; Fig. 6.1) and found that increasing current velocity resulted in a nonlinear acceleration of the lift-off ratio for settled seeds (Chapter 3). Although not verified in this study, secondary seed dispersal should also benefit from the wave-dominated bed shear stress, which has been documented to vertically entrain tiny particles, such as settled seeds and sediment grains (Carthey et al., 2016; Dorrell et al., 2018). Once lifted, the seeds are expected to be transported by currents to other locations (Chapter 3; Chang et al., 2008). Similarly, based on large-scale field experiments, we demonstrated a non-linear negative correlation between seed retention and hydrodynamic intensity and revealed an inevitable loss of seeds in erosion-prone sites (Chapter 4). Only by settling in microsites with stable or accretion-prone sediment regimes, is it possible for the seeds to achieve persistent retention and then transition to the next recruitment stages (Chapter 4).

During seedling establishment processes (i.e., emergence, rooting, and survival; Fig. 1.2), the impacts of tidal motion are mainly reflected in the dragging and even uprooting of seedlings by currents and waves (Hu et al., 2015a; Schoutens et al., 2021). The inhibitory effects of hydrodynamics on seedling establishment would be dramatically amplified as erosion occurs (Chapter 5). The final establishment outcome depends on the entanglement between the stochastic disturbance pulses and the resistance of seedlings at that time (Poppema et al., 2019; Hu et al., 2015a, 2021). By quantifying both the maximum shear stress and the critical erosion depths that the seedlings can resist before being dislodged, we found that seedlings' resistance against hydrodynamics and erosion increases linearly as seedlings develop, but with species-specific patterns (Chapter 5). This study provides quantitative support for the application of the windows of opportunity framework (Balke et al., 2011, 2014) in salt marsh ecosystem, such as predicting the establishment probability of seedlings under varied restoration scenarios (for one example see Hu et al., 2021).

6.2.2 The role of sediment accretion in salt marsh recruitment

Recent studies on seedling recruitment appear to be more inclined to reveal the effects of short-term sediment dynamics (i.e., daily vertical accretion and erosion; Balke et al., 2013; Cao et al., 2018; Hu et al., 2021), which have been documented as a major factor driving long-term salt marsh dynamics (Bouma et al., 2016; Fagherazzi et al., 2020). Sediment erosion typically occurs simultaneously with high-energy hydrodynamic disturbances (Shi et al., 2012; Hu et al., 2015b), thus inhibiting establishment by increasing the probability of seed/seedlings being dislodged (Chapter 5; Hu et al., 2015a; Schoutens et al., 2021). Instead, with sediment availability, the occurrence of accretion tends to be accompanied by relatively weak hydrodynamic disturbances (Masselink et al., 2007; Fagherazzi et al., 2012). Supported by the results from large field experiments and mesocosm experiments, this study underscores the superiority of slightly sediment burial (e.g., 5 mm), which showed great potential in inhibiting the onset of secondary dispersal of seeds (Chapter 4), germinated seeds (Chapter 3), and established seedlings (Chapter 5). This would be beneficial for successful recruitment as it promotes the possibility of seed/seedling retention at the microsite, which is the condition precedent for the transition of seeds to subsequent recruitment stages (van der Stocken et al., 2019a; Wang et al., 2019).

However, the incessant accretion of sediments can terminate the recruitment process by inhibiting seedling emergence (Chapter 4). The erratic emergence possibility was attributed to the fact that too deep burial can deplete seed resource reserves and suffocate punctured seedlings (Balke et al., 2013; Bouma et al., 2016; Zhao et al., 2020a). The emergence-related burial threshold has shown to be species-specific (Boorman et al., 2001; Abbas et al., 2020), and species with larger seeds appear to be able to tolerate deeper sediment burial (Chapter 4). Furthermore, existing research and our flume study suggested the lingering implications of sediment accretion on subsequent recruitment stages (Chapter 5). For example, during establishment, seedlings would neutralize the potential impact of shallow burial based on their morphological plasticity (e.g., Jørgensen et al., 2019) and induce higher critical erosion depths to consolidate their persistence and survival (Chapter 5; Cao et al., 2018). While in the case of excessive accretion surpassing the tolerance threshold of seedlings, they would inevitably die due to blocked physiological functions (e.g., hypoxia; Jørgensen et al., 2019; Fagherazzi et al., 2020).

We recognize that natural sediment disturbance is not a gradual process and that each individual disturbance event may feed back into seedling morphology (Balke et al., 2013; Suykerbuyk et al., 2016; Cao et al., 2018), thereby indirectly altering the establishment/survival possibility of seedlings during subsequent stages. In general, seedlings perform better with gradual changes in sediment regimes than with sudden ones (Cao et al., 2018). Collectively, this study highlights the significance of slight sediment burial (e.g., 5 mm), which can promote seed/seedling retention without inhibiting seedling emergence and establishment, in salt marsh recruitment (Chapter 3, 4, 5). This kind of shallow burial is realistically available as part of natural biotopography processes, such as bioturbation from burrowing benthos (Roche et al., 2016), the resuspension of sediments (Li et al., 2019), or the movement of sand waves (Green and Coco, 2014).

6.3 The relative importance of biotic traits in salt marsh recruitment

6.3.1 Variation in recruitment potential across species

Several dominant landscape-forming salt marsh species were considered in this thesis, including *Aster tripolium, Elymus athericus, Salicornia europaea*, *Scirpus maritimus*, *Scripus mariqueter*, *Spartina anglica*, and *Spartina alterniflora*. Two to four of them were employed as model species in each chapter to uncover the mechanisms underlying different recruitment processes. Significant across-species differences were detected in all recruitment processes except seed retention, which was overwhelmingly dominated by physical conditions (Chapter 4). The species inhabiting the high tidal-flat (e.g., *E. athericus*) appear to have a stronger ability in primary seed dispersal than pioneer species thanks to their longer buoyancy periods (Chapter 2). This underscores the potential of mother plant's living environment in regulating offspring's traits, i.e., the so-called maternal effect (cf. Wolf and Wade, 2009). Among the pioneer species, *Spartina* spp. showed relatively better performance in initiating secondary seed dispersal (of Type-II; Chapter 3), seedling emergence potential (Chapter 4), and seedling establishment possibility (Chapter 5). Moreover, seedlings of *Spartina* spp. are more likely to re-establish after dislodgement, suggesting a stronger resilient to physical disturbances than other species (Chapter 5). These process-based insights help explain the highly successful invasion of *Spartina* spp. across the globe (Liu et al., 2018). Of particular note, *S. europaea* has the smallest seeds and its seedlings were found to has the lowest probability to establish in accretion-prone tidal-flat, where even 5 mm of sediment burial may completely inhibit seedling emergence (Chapter 4). This lethal effect offsets the superiority of sediment burial in promoting seed retention (see description in section 6.2.2).

6.3.2 The role of plant traits in salt marsh recruitment

Plant traits are widely recognized as a universal unit of comparison to assess and predict the heterogeneity of performance across species in homogeneous environments (Martínez-Garza et al., 2013; Larson et al., 2015). Existing studies on salt marshes have primarily linked plant traits to their ecological engineering capabilities, such as attenuating waves and stabilizing sediment (Bouma et al., 2005, 2010; De Battisti et al., 2019; Schulze et al., 2019), with little insight into how differences in plant traits affect underlying demographic processes, especially in early life stages. It is indispensable to establish the relationship between seed/seedling trait variation and their transition potential among recruitment stages, towards a general trait-based framework for (pre-)evaluating recruitment outcomes in natural or restored salt marshes (Friess et al., 2012; Hu et al., 2015a, 2021).

The nature of keeping growth over time complicates the question of which seed/seedling traits affect recruitment possibility, leading to different traits dominating different recruitment processes (Larson et al., 2015; Statton et al., 2017). In wave-dominated salt marsh habitats, the mass and shape of seeds were identified as the critical morphological factors that govern their dispersal speed (Chapter 2). Both factors were related to seed buoyance by changing seed density, thus may further affect the dispersal distance of seeds (Chapter 2; Erfanzadeh et al., 2010; van der Stocken et al., 2019a). Regarding secondary dispersal of type II (Fig. 6.1), the simultaneous changes in shoot length and seed density during germination determine the lift-off velocity threshold that kick-start the displacement of seeds (Chapter 3). Species with the largest seed size were found to have the strongest potential in seedling emergence (both for surficial seeds and buried seeds; Chapter 4), implying that emergence probability would also be influenced by seed traits like the contained seed resource reserves (Kettenring and Whigham, 2018). Unlike mangroves (e.g., Balke et al., 2011), the length of windows of opportunity (refer to Fig. 1.4) required for salt marsh seedling establishment was not only determined by the extension of root length, but also highly related to the root-shoot ratio of the seedlings (Chapter 5). This is attributed to the special germination regime of salt marsh seeds, whereby the shoot sprouts prior to the root (Chapter 3; Wijte and Gallagher, 1996). In general, seedlings with the same root length but longer shoot lengths (i.e., lower root-shoot ratios) are more difficult to achieve successfully establishment than that with shorter shoot lengths (i.e., higher root-shoot ratios), due to the greater risk of being uprooted (Chapter 5).

6.4 Implications for salt marsh conservation and restoration

The fast intensification rate of climate change-related and anthropogenic stressors in tandem with the slow rate of natural recovery suggest that there is a pressing necessity for salt marsh restoration on a global scale (Parkinson et al., 2017; Silliman et al., 2019; Saunders et al., 2020). This becomes even more ecologically significant when salt marsh restoration is targeted for nature-based applications such as coastal defense, climate stability, or carbon sequestration (Bouma et al., 2014; Zhu et al., 2020a; Macreadie et al., 2021; Temmink et al., 2022). The recruitment processes are condition precedents for (re)covering vegetation in degraded or new habitats, yet are often problematic due to the complex multidimensional bio-physical interactions inherent in the salt marsh ecosystem (Cao et al., 2018, 2020; van Regteren et al., 2019, 2020). Mechanistic studies that reveal more comprehensive understanding of salt marsh recruitment processes and provide insights into thresholds associated with each step of recruitment process represent a first but critical step towards amplifying restoration output. Such knowledge may guide the restoration participants to obliterate potential risks involved in the precarious recruitment stages and optimize restoration design (Friess et al., 2012; Bouma et al., 2016; Saunders et al., 2020).

This study suggests that seed-based recruitment in natural or restored salt marshes can be limited by several sequential bottlenecks, including the low seed/seedling persistence due to secondary dispersal that occurs in multiple stages (i.e., secondary dispersal of Type-I, Type-II, Type-III; Table 6.1; Chapters 3, 4, and 5), and the erratic seedling emergence and survival possibility (Chapters 4 and 5). To improve the efficiency of seed-based salt marsh restoration, we suggest practitioners prioritize the following two suitability assessments of target sites before starting any restoration efforts:

1) The short-term sediment regime during the critical period of seedling establishment (i.e., late March to early June). Sites characterized by accretion-prone are ideal, as e.g., 5 mm of sediment burial has been proven

in this study to be superior in promoting seed retention by circumventing all types of secondary dispersal, without inhibiting subsequent seedling emergence for most species (Chapters 3, 4 and 5).

2) The occurring likelihood of windows of opportunity (cf. Fig. 1.4). Sites with sufficiently long periods of calm low-stress conditions would benefit seedling establishment by ameliorating seedling's resistance to dislodgement and enabling seedling recovery after dislodgement (Chapter 5).

Generally, relatively higher restoration efficiencies can be expected when restoration activities are implemented in suitable sites that meet the above two metrics (Bouma et al., 2016; Hu et al., 2021). However, it is important to note that these two metrics for assessing site suitability are species-specific. The optimal sedimentary condition depends on the burial depth threshold related to seedling emergence of the target species (Chapter 4). Similarly, the effectiveness of the window of opportunity is not equal and depends on the species-specific growth rate of seedlings' resistance (Chapter 5). This study provided quantitative data on these stage-specific thresholds for several common salt marsh species (Chapters 3, 4 and 5), contributing to cultivating modeling-based assessment capabilities prior to restoration initiation (see examples in Hu et al., 2015a, 2021). In contrast to process-based models, data-driven models based on machine learning techniques, such as artificial neural networks, were exemplified in this study to have great application potential in predicting bottleneck effects involved in seed-based recruitment processes (Chapter 4). This data-driven approach can achieve independent and rapid prediction based on easily obtained or published data (Chapter 4; Goldstein et al., 2019; Hu et al., 2020), but also can serve as components to provide data-supported parameterizations for the so-called hybrid models (e.g., Plant et al., 2016; Hu et al., 2021).

If salt marsh restoration is required in unsuitable sites with limited sediment supply and/or lack of windows of opportunity, artificial assistance measures need to be employed as lever by which to tip the system into a state favoring seed-based recruitment (Temmink et al., 2020; Fivash et al., 2021). That is, on the basis of identifying the critical factors dominating the recruitment bottlenecks (e.g., the three types of secondary dispersal which lead to seed/seedling loss; Chapters 3, 4 and 5), such bottlenecks perhaps can be circumvented by artificially enhancing the inhibitory factors and/or weakening the facilitators, thereby amplifying the restoration output. Based on the information resulting from this study, the following three potential avenues are suggested for this purpose:

(i) Creating less-exposed sedimentary fields through engineering measures, such as the construction of offshore barriers and the supply of dredging-derived sediment slurry (Temmerman et al., 2013; Hu et al., 2021). The less-exposed sedimentary fields would contribute to increasing seed persistence and subsequent seedling establishment opportunities by inhibiting all types of secondary dispersal during seed and seedling stages (i.e., secondary dispersal of Type-I, Type-II, Type-III; Table 6.1; Chapters 3, 4, and 5). See Thorne et al. (2019) and Saunders et al. (2020) for cases of large-scale restoration based on this approach. For restoration practices that cannot rely on engineering measures, sowing seeds to the depths ideal for target species may be a cost-effective alternative to indirectly create the less-exposed "sedimentary fields". Potential seed-sowing methods worth trying include drill seeding (Zilverberg et al., 2014) and dispenser injection seeding (Tan et al., 2020), both have been successfully applied to seagrass restoration. However, the labor-intensive nature rendered them impractical for large-scale restoration efforts (Kettenring and Tarsa, 2020).

(ii) Attenuating local hydrodynamic intensity and associated sediment scouring (or sheet erosion) by mimicking emerging traits in a sustainable manner (see examples in Temmink et al., 2020 and Fivash et al., 2021), with the greatest likely returns on reducing the possibility of secondary seed/seedling dispersal (Chapters 3, 4, and 5) and thus more efficient restoration. This purpose would also be achieved indirectly by creating complex micro-topographic structures, which have been proven to be effective in providing "barriers" or "shelters" for seeds/seedlings, thereby effectively trapping and retaining seeds/seedlings (Xie et al., 2019; Qiu et al., 2021) as well as accelerating seedling growth (Fivash et al., 2020).

(iii) Achieving "jump" recruitment by transplanting aggregated seedlings to circumvent the recruitment bottleneck induced by seed re-movement and entrainment (i.e., secondary dispersal of Type-I and Type-II; Chapters 3 and 4). This approach would also reduce the likelihood of seedlings being dislodged (i.e., secondary dispersal of Type-III; Chapter 5) by harnessing self-facilitation (Silliman et al., 2015; Fischman et al., 2019). In addition, this study detected significant variation across species in seed dispersal potential (Chapters 2, 3 and 4) and seedling resistance against physical disturbance (Chapter 5). This implies that the outcomes of such "jump" recruitment would be further amplified through species selection during the early designing stages. The priority should be given to species that perform better in seedling resistant against dislodgement, such as *Spartina* spp. (Chapter 5).

In addition to pursuing successful seedling recruitment, ensuring the long-term sustainability of the restored ecosystem is equally important (O'Brien et al., 2021; Wilsey, 2021). The latter emphasizes the significance of recovering genetic diversity in restoration efforts (Aavik and Helm, 2018; Freitag et al., 2021), as higher genetic diversity enables the establishment of self-supporting communities that are resilient to climate-related disturbances (Nef et al., 2021; O'Brien et al., 2021). Therefore, the assessment of restoration effects requires integrating the restored habitats into a larger ecological matrix and gaining insights into the dispersal capacity and gene flow of established populations (Aavik and Helm, 2018). This study provides quantitative data regarding salt marsh seed dispersal potential, especially under the coupled effects of tidal currents, waves, and wind (Chapter 2). Such data can be used in existing dispersal models, which helps to (*i*) pre-assess the potential connectivity of the target sites to surrounding habitats during the restoration planning stage; (*ii*) more accurately predict and track the dispersal of established populations at the landscape scale during the restoration monitoring stage. In general, habitat connectivity and long-distance dispersal imply potential gene flow and more genetic complexity among multiple populations (Binks et al., 2019; van der Stocken et al., 2019b), although rigorous validation based on molecular tools remains indispensable. Finally, this study underscored that salt marsh dispersal is much more complex and frequent than previously anticipated by revealing two types of neglected secondary dispersal processes (i.e., Type-II and Type-III, Table 6.1; Chapters 3 and 5). While such secondary dispersal will routinely result in the loss of seeds/seedlings from local natural or restored populations, it may also contribute to seed/seedling availability in nearby or distant populations and may yield more opportunities to shape population resilience (Chapter 5; Benincà et al., 2015). This is highly relevant to the maintenance of long-term restoration effectiveness and underscores the necessity of integrating these neglected processes into existing dispersal models and into the long-term evaluation framework of restoration efforts.

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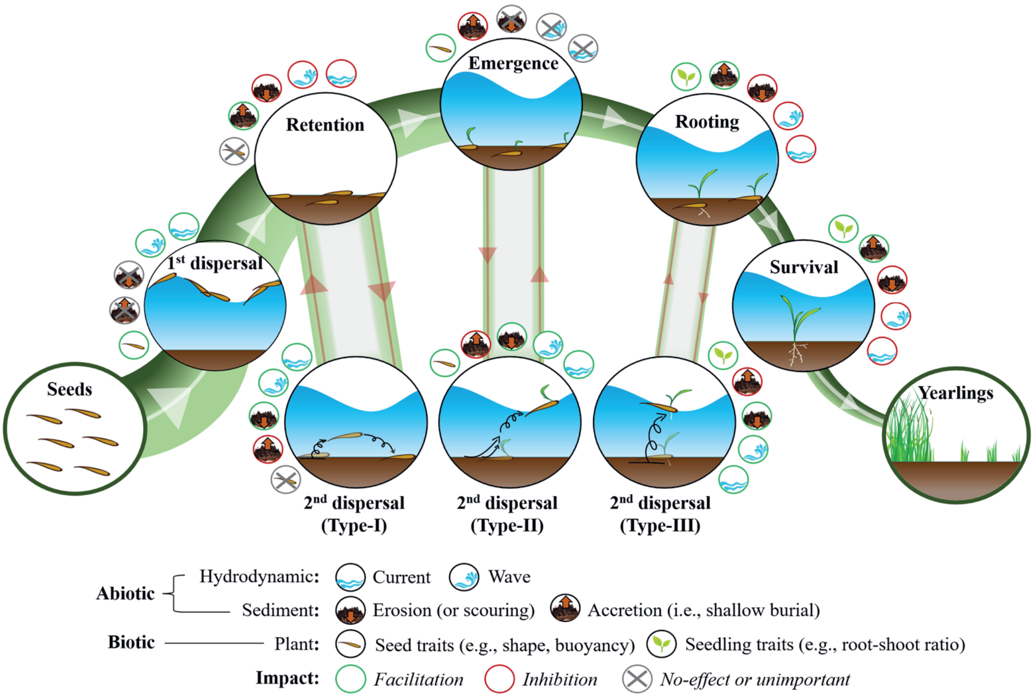
Summary

Life processes involved in seed-based saltmarsh recruitment & impacts of abiotic and biotic factors



Salt marshes are among the most valuable ecosystems, but currently suffering from massive habitat shrinkage. There is growing interest in the application of combined salt marshes and engineering structures as a hybrid strategy to mitigate flood risk. Combining with the provision of multiple other ecological functions, they are also increasingly accepted as a broad Nature-based Solution contributing to climate stability. As a result, conservation and restoration practices oriented toward salt marsh ecosystems are in full swing around the world. However, outcomes of such practices were often elusive because of the erratic demographic loss or mortality during the early recruitment stages. Mechanistic insights into the underlying processes that enable or disable vegetation recruitment are thus indispensable cornerstones

for decision-making in salt marsh conservation and restoration.

Relative to asexual reproduction through tillering and cloning, significant advantages exist in rapidly establishing foundational vegetation and building population genetic diversity through seed-based recruitment strategies. More importantly, the seed-based approach is widely recognized as the most cost-effective way to achieve large-scale restoration. In this study, through the lens of several globally occurring salt marsh species, we provide integrated experimental insights in the relative importance of biotic and abiotic factors in dominating seed-based salt marsh recruitment, from primary seed dispersal, secondary seed dispersal, seed retention, seedling emergence, and seedling rooting to seedling survival.

After detaching from parent plant, the dispersal potential of seeds is primarily constrained by buoyancy period, which not only varied among species but also among dispersal units of the same species (Chapter 2). In wind- and wave-dominated environments, the dispersal speed of seeds would vary greatly depending on the wave magnitude, wind direction, as well as dispersal units' type and morphology, thus resulting in more complex dispersal pathways as compared to that dominated by the prevailing current (Chapter 2). The floating seeds would end up in microsites due to loss of buoyancy, interception of landscape elements and burial of sediments, with their subsequent re-movements (i.e., secondary dispersal of Type-I) typically tied to high-energy hydrodynamic disturbance and associated erosion events rather than biotic traits (Chapter 4). In spring, however, seeds would adjust their lift-off threshold, driven by regaining buoyancy (due to reduced density) and increasing the surface-drag forces (due to extended bud) during germination, thereby greatly increasing the probability of seed entrainment (i.e., secondary dispersal of Type-II) during calm hydrodynamic events (Chapter 3). Such secondary dispersal can occur even when the seeds are partly buried, and may benefit rapid seedling establishment on tidal flats occurring within the same time window by increasing seed availability from marshes toward the tidal flats

(Chapter 3).

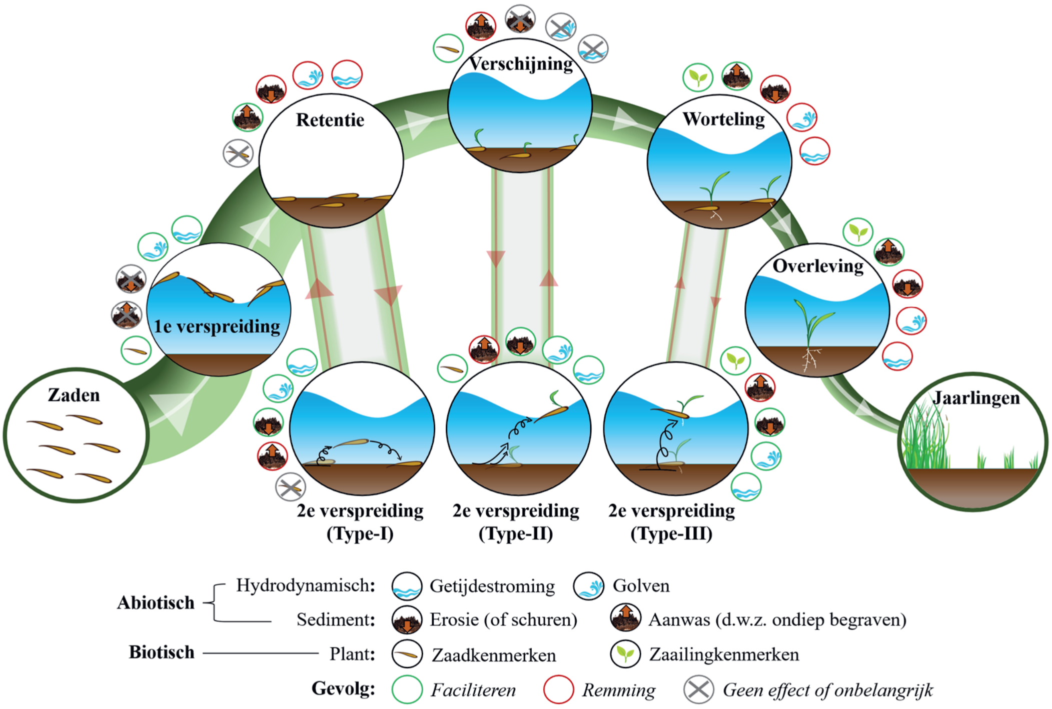
Once seeds can be retained, soil salinity have overwhelming effect on subsequent seedling emergence (Chapter 4). For buried seeds, sediments in the upper layer that aided seed retention may turn into the culprit in bringing the seedling establishment to an abrupt halt, once the species-specific burial thresholds are surpassed and thereby hampering seedling emergence (Chapter 4). Thus, seed burial depths ideal for particular species needs to be met to allow both seed retention and successful seedling emergence. However, seedling dislodgement would still occur at any point during rooting, depending on species-specific and time-varying entanglement between stochastic disturbance pulses versus seedlings' resistance (Chapter 5), underscoring the significance of Windows of Opportunity (WoO; i.e., disturbance-free/low periods) for recruitment outcomes. In the early stages of establishment, root-shoot antagonism characterizes the growth rate of seedlings' resistance to dislodgement by hydraulic disturbances. Subsequently, root length seizes the dominance and determines seedlings' resistance to dislodgement by sediment erosion (Chapter 5). Shallow burial by sediments (e.g., 5 mm) during rooting would disproportionately strengthen the overall resistance of seedlings and amplify the effectiveness of WoO (Chapter 5).

Seedling displacement due to insufficient resistance (i.e., secondary dispersal of Type-III) does not necessarily purport the end of recruitment. Since dislodged seedlings are positively buoyant and able to sustain growth in water columns, they have the potential to drift with tidal currents over long distances (Chapter 5). After arriving at a new settlement site, these dislodged seedlings may repeat similar processes, including retention, (re-)rooting, and survival, under analogous regulatory mechanisms as the initial establishment from seeds (Chapter 5). Of particular note, the effectiveness of WoO in promoting rooting here is further regulated by the age of seedlings being dislodged, with seedlings dislodged at a younger age more likely to achieve re-establishment (Chapter 5).

Overall, this study contributes to the holistic understanding of both opportunities and bottlenecks involved in seed-based salt marsh recruitment. We dissected the processes related to the successful transition from seeds to seedlings, with two neglected efficient chaotic trajectories (i.e., secondary dispersal of Type-II and Type-III) of the well-known recruitment paradigms being revealed for the first time. This demonstrates that the seed-based recruitment in salt marshes is much more intricate than previously expected. Furthermore, we provide insight into the critical factors that have overriding effects on each recruitment process and highlight the variability of their impacts across species and among sites. The results provide guidelines and valuable first-hand data for future model efforts to simulate salt marsh evolution and identify demographic stages that drive recruitment failures. More importantly, this mechanistic process study can be translated into practical guidelines for effective conservation and restoration of salt marshes through seed-based or seedling-based approaches, thereby contributing to incorporating salt marshes in nature-based applications such as coastal defense, climate stability, or carbon sequestration.

Samenvatting

Levensprocessen die betrokken zijn bij op zaden gebaseerde kwelderrekrutering & effecten van abiotische en biotische factoren



Buitendijkse met planten begroeide getijde moerassen, in Zeeland schorren genaamd, en in het noorden kwelders genoemd, behoren tot de meest waardevolle ecosystemen ter wereld. De afgelopen decennia hebben we wereldwijd een sterke afname van hun areaal gezien. Er is momenteel een groeiende belangstelling om schorren/kwelders in combinatie met dijken, als hybride kustbeschermingsstrategie te gebruiken, om daarmee kosteneffectief overstromingsrisico te verminderen. Omdat schorren ook een hoge natuurwaarde hebben en in nog tal van andere ecosysteemdiensten voorziet (bijvb. koolstof opslag), zijn ze aantrekkelijk om toe te passen als nature-based kustbescherming die bijdraagt aan bredere doelstellingen zoals biodiversiteitherstel en klimaatstabiliteit. Daarom wordt wereldwijd ingezet op schor herstel en beheer. De uitkomst van dergelijke inspanningen waren vaak moeilijk te voorzien door niet voorzien verlies en/of zaailing sterfte tijdens de vroege kolonisatie. Mechanistisch inzicht in alle onderliggende processen die de vestiging van schor/kwelder planten mogelijk maakt, is dan ook een onmisbare hoeksteen om verder te komen in het succesvol herstellen en behouden van schorren/kwelders.

Ten opzichte van de ongeslachtelijke voortplanting door middel van uitlopers en andere vormen van klonale verspreiding, bieden op zaadverspreiding gebaseerde rekruteringsstrategieën aanzienlijke voordelen. Zaadverspreiding resulteert namelijk in snelle vestiging en het potentieel verhogen van genetische diversiteit binnen de populatie. Bovendien worden op zaadverspreiding gebaseerde restauratie benaderingen in het algemeen gezien als de meest kosteneffectieve manier om grootschalige restauratie te bereiken. In dit proefschrift bieden we mechanistisch inzicht in het relatieve belang van biotische en abiotische factoren die sturend zijn in de op zaden gebaseerde schorvestiging. De uitkomsten zijn veralgemeniseerd door experimenten te doen met meerdere wereldwijd voorkomende dominante kweldersoorten, en daarbij te kijken naar alle stappen in het proces: primaire zaadverspreiding, secundaire zaadverspreiding, zaadretentie, zaailing kiemen, zaailing vestiging en overleving.

Na het loslaten van de moederplant, wordt het verspreidingspotentieel van zaden voornamelijk beperkt door de periode dat de zaden kunne drijven. Die periode varieerde niet alleen tussen soorten, maar ook tussen de verschillende verspreidingseenheden binnen een soort (hoofdstuk 2). In een door wind en golven gedomineerde omgeving zal de verspreidingssnelheid van zaden sterk variëren, afhankelijk van de golfgrootte, windrichting, en het type verspreidingseenheid met bijbehorende morfologie. Dit maakt dat in de aanwezigheid van wind de verspreiding veel complexer te voorspellen is dan wanneer er alleen getijdestroming aanwezig is (hoofdstuk 2). Drijvende zaden kunnen op microsites terechtkomen door verlies van drijfvermogen, de interactie met landschapselementen en door begraving. Hierdoor zal een volgende verplaatsingen vanaf zo'n microsite (d.w.z. secundaire verspreiding van Type I) doorgaans alleen optreden tijdens hoogenergetische hydrodynamische verstoring (denk aan stormen) mat daarbij behorende erosie. Biotische eigenschappen zijn dan ook minder belangrijk voor secundaire verspreiding Type I (hoofdstuk 4).

In het voorjaar kunnen zaden hun drijfvermogen herwinnen doordat ze opdrogen en kiemen, wat resulteert in een lagere dichtheid (= drijfvermogen) en een groter frontaal oppervlak waarop water kan aangrijpen (= drag). Hierdoor neemt de kans toe dat een zaad ook tijdens kalme hydrodynamische omstandigheden (dus in de afwezigheid van een storm) wordt meegenomen door het water (d.w.z., secundaire verspreiding van Type-II; Hoofdstuk 3). Dergelijke secundaire verspreiding kan zelfs plaatsvinden wanneer de zaden gedeeltelijk zijn begraven. Secundaire verspreiding kan snelle vestiging van zaailingen op een onbegroeide getijdeplaat veroorzaken, door kiemende zaden vanuit een schor te exporteren (Hoofdstuk 3).

Zodra zaden worden vastgehouden op een plek, dan hebben lokale omstandigheden zoals het zoutgehalte van de bodem een overweldigend effect op hoeveel zaailingen opkomen (hoofdstuk 4). Als zaden begraven zijn, dan kan de bodemlaag die eerst hielp om het zaad op zijn plaats te houden, de opkomst van een zaailing gaan hinderen. Elke soort heeft namelijk een soort-specifieke maximale begravingsdiepte, waaronder een zaad te weinig energie heeft om nog boven de grond uit te groeien (hoofdstuk 4). Elke soort heeft dus een ideale begravingsdiepte, waarbij zaden enerzijds niet gemakkelijk wegspoelen, maar anderzijds nog wel succesvol kunnen opkomen. Wortelende zaailingen kunnen nog steeds van de bodem losraken. De kans daarop hangt af van de lengte van de verstoringsvrije periode (d.w.z., geen stormen) in relatie tot de soort en de grote van de zaailing, wat het belang van Windows of Opportunity (WoO; d.w.z. storingsvrije/lage perioden) voor succesvolle vestiging benadrukt. Aanvankelijk bepaald de wortel-scheut verhouding hoe gemakkelijk zaailingen losraken. Voor grotere zaailingen is de wortellengte de dominantie factor die de weerstand tegen losraken door erosie bepaald (Hoofdstuk 5). Ondiepe begraving (bijv. 5 mm) zou de algehele weerstand van zaailingen tegen wegspoeling enorm versterken en daarmee de kans op het benutten van een WoO voor zaailingvestiging enorm vergroten (Hoofdstuk 5).

Het losraken en door water verplaatsen van zaailingen betekent niet noodzakelijk het einde van zo’n zaailing. Doordat losgeraakte zaailingen drijfvermogen hebben, zijn ze in staat om in de waterkolom te blijven groeien. Daardoor kunnen ze zich drijvend met de getijstromen potentieel over grote afstanden verplaatsen (Hoofdstuk 5). Nadat ze op een nieuwe vestigingsplaats zijn aangekomen, kunnen deze losgeraakte zaailingen zich her-vestigen, waarbij processen zoals retentie, (her)worteling en overleving opnieuw een rol spelen. Hierbij zijn de regulerende mechanismen dan ook analoog aan de sturende processen tijdens de initiële vestiging uit zaden (d.w.z. secundaire verspreiding van Type-III; hoofdstuk 5). Een geschikte WoO voor het wortelen is hierbij bijzonder belangrijk, waarbij de de wortelgroei sterk af hangt van de leeftijd waarop de zaailing zich verplaatste. Zaailingen die op jongere leeftijd beginnen aan secundaire verspreiding Type-III, hebben een grotere kans hebben om zich opnieuw succesvol te vestigen (hoofdstuk 5).

Samenvattend draagt dit promotieonderzoek sterk bij aan het verkrijgen van een meer holistisch inzicht in zowel de kansen en knelpunten die sturend zijn bij de vestiging van schorren/kwelders uit zaden. Door het analyseren van de processen die verband houden met de succesvolle overgang van zaden naar zaailingen, zijn twee nieuwe types van secundaire verspreiding onthuld: Type-II en Type-III. De op zaden gebaseerde rekrutering in schorren/kwelders is dus ingewikkelder is dan eerder gedacht. Door inzicht te beiden in welke factoren een doorslaggevende effecten hebben op elk fase van de vestiging en daarbij de variabiliteit tussen soorten en locaties mee te nemen, zijn de resultaten waardevol voor het modeleren van schorontwikkeling en daarmee (locatie specifiek) de bottlenecks voor vestiging te identificeren. Bovendien kunnen de resultaten van de mechanistische processtudie worden vertaald naar praktische richtlijnen voor effectief beheer en herstel van schorren/kwelders door middel van op zaden (of zaailingen) gebaseerde benaderingen. Hiermee draagt dit promotieonderzoek direct bij aan kwelders integreren in op de natuur gebaseerde toepassingen zoals kustverdediging, klimaatstabilisatie of koolstofvastlegging.

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Curriculum vitae

Zhiyuan Zhao was born on December 10, 1992, in Shandong Province, China. In September 2012, he started his undergraduate studies at Ludong University, majoring in life sciences, and earned his Bachelor's degree in June 2016. In September 2016, he joined the State Key Laboratory of Estuarine and Coastal Research (SKLEC) of East China Normal University (ECNU) as a master student and majored in wetland ecology. For the next two years, he worked on the invasive species *Spartina alterniflora*, mainly studying their invasion mechanism as well as prevention and control technology. In September 2018, he got the opportunity to join a dual diploma doctoral research program, still majoring in wetland ecology but switching to study the dispersal and establishment mechanism of salt marsh pioneer species. He spent his first year of PhD at SKLEC, after which he came to Royal Netherlands Institute for Sea Research (NIOZ) to continue his PhD study for 3 years at the department of Estuarine and Delta Systems. He will then defend his thesis at Utrecht University.

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