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

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HIGHLIGHTS

- Saltmarsh seedlings show a unique trade-off to resist hydraulic disturbances.
- Dislodged saltmarsh seedling as a potential mode for long-distance dispersal
- Windows of opportunity regulate the re-establishment potential of dislodged seedlings.
- Seed-seedling transition is not a single-line process but a cyclical behavior.
- "Wheel of Recruitment" is proposed to inform resilience study and marsh restoration.

GRAPHICAL ABSTRACT
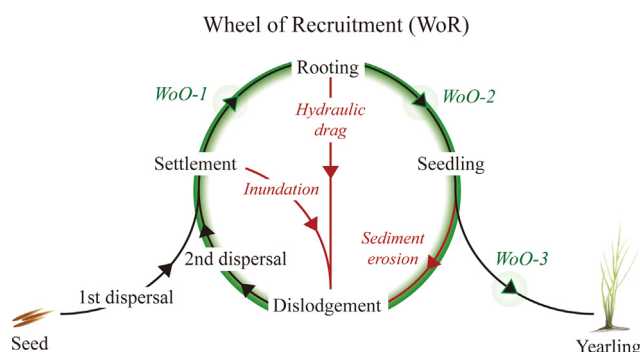
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ABSTRACT

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 saltmarsh restoration potentials. However, the resilience of these recruits, especially through recovery, remains poorly understood. Here, two contrasting globally occurring saltmarsh 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

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important for forecasting resilience and persistence of biogeomorphic systems such as salt marshes under global change and for guiding life cycle informed restoration.

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. S1). 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 saltmarsh 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, saltmarsh 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 saltmarsh 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 et al. (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., 2019). We speculate that the inundation-free period (the WoO-1; Fig. S1) 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 saltmarsh 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. S1) 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. S1) 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 saltmarsh 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 saltmarsh restoration.

2. Materials and methods

2.1. Quantifying the dislodgement resistance of establishing seedlings in a flume

To quantify species-specific demand in the length of WoO-1 (Fig. S1) and species-specific entanglement between seedling growth and disturbance pulses during WoO-2 and WoO-3 (Fig. S1), 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 saltmarsh 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. 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
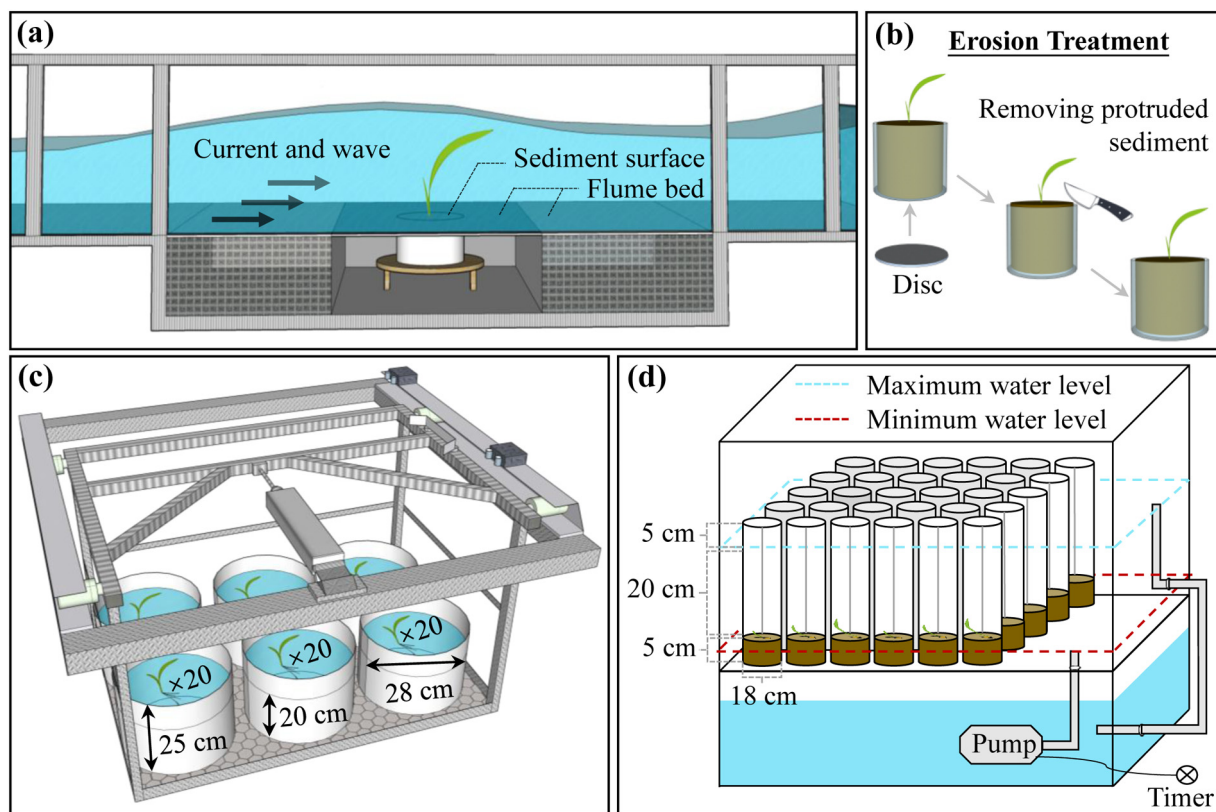
Fig. 1. Schematic representation of the study: (a) Flume setup used to quantify the critical conditions that seedlings can resist prior to being dislodged (results in Figs. 3 and 4). The test unit (made of PVC pipe, filled with sediment and a planted seedling) was placed on the deepened bottom to keep 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. 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). 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. 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.

stormy events at the front of the saltmarsh 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 2 min, 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. 1b). A BSS of $0.28\ N\ m^{-2}$ (representing the hydraulic disturbances typical for saltmarsh pioneer zone; Callaghan et al., 2010) was then applied and maintained for 2 min.
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.

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. 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 saltmarsh 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 S1 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 ($R = N/20 \times 100\ \%$, where N is the number of floating seedlings and 20 refers to the total number of seedlings used).

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. S1). 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. 1d; cf. Cao et al., 2018). These tanks were placed in a climate chamber where light was provided for $12\ h\ d^{-1}$ ($550\ \mu mol\ photons\ m^{-2}\ s^{-1}$), 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. 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 allows 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.

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.

3. Results

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. 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. 2a, b, d). *S. europaea* had a significantly faster evolution rate of the root-shoot ratio compared with *S. anglica* ($P < 0.001$; Fig. 2c), suggesting that during the early morphological development of *S. europaea*, relatively more is invested in root elongation.

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 S2). The surficial seedlings for both species with a root length of <3 mm would automatically float up when submerged (Fig. 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. 3a; related to WoO-2). Based on the regression equation for root extension listed in Fig. 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}).

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. 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. 3b). These results indicate that the surficial seedlings of the annual
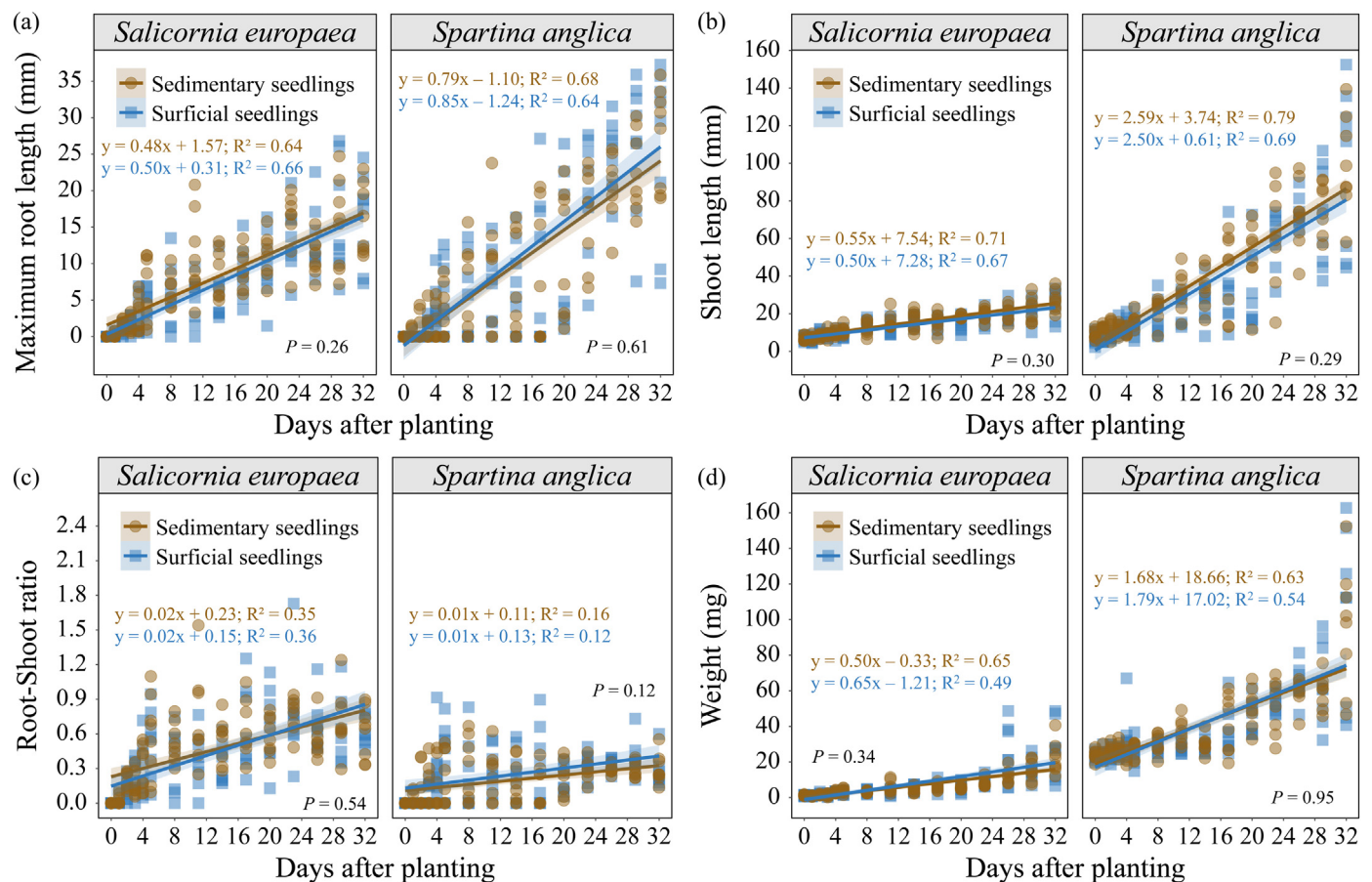

Fig. 2. Maximum root length (a), shoot length (b), root-shoot ratio (c), and weight (d) of the seedlings of *Salicornia europaea* and *Spartina anglica* as a function of time since transplanting under two establishment scenarios without and with 5 mm sediment burial. Without burial is denoted as superficial 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 seedlings vs. sedimentary seedlings).
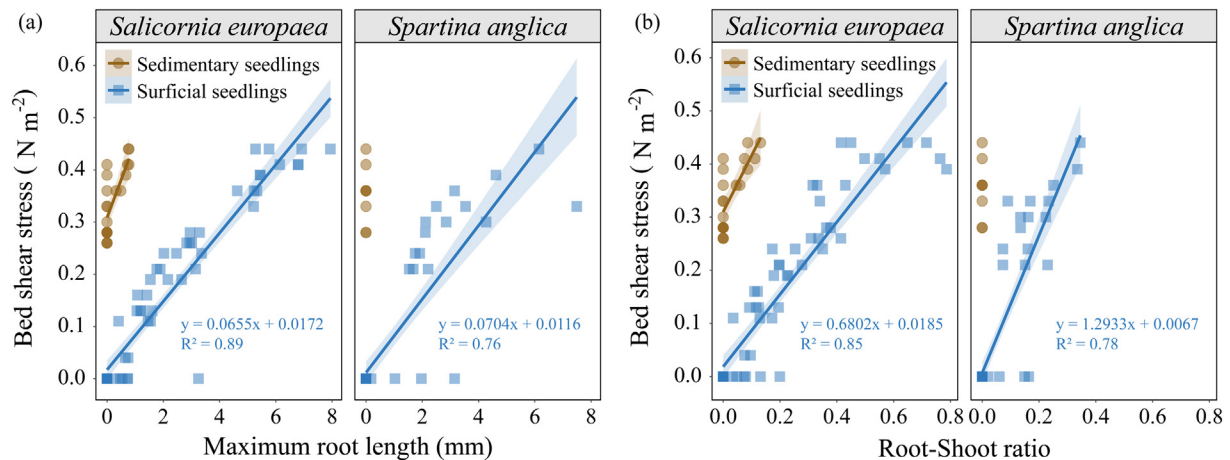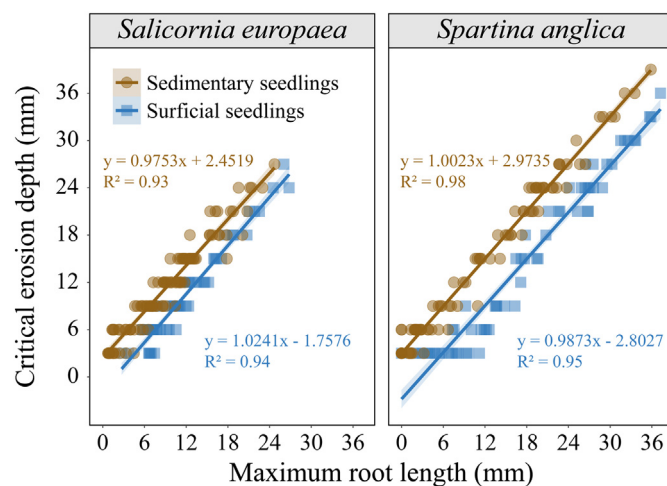
Fig. 3. The hydrodynamic disturbance (expressed as bed shear stress, BSS; methods cf. Fig. 1a) that required to be surpassed to dislodge seedlings with different root lengths (a) and root-shoot ratios (b) under two establishment scenarios: without (blue; superficial seedlings) and with (brown; sedimentary 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. 4).

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. 3). In contrast, for *S. anglica*, the 5 mm sediment burial prevented the seedlings from being dislodged (Fig. 3).
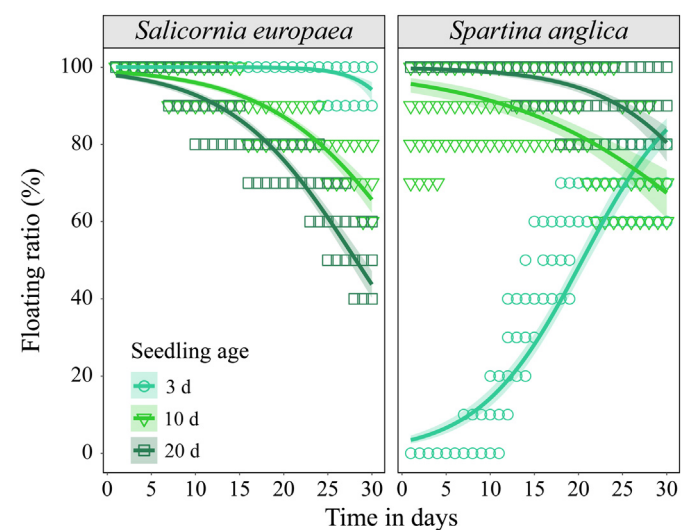
For seedlings that resisted the maximum BSS imposed in the flume, their dislodgement required sediment erosion in addition to drag. According to the results from multiple linear regressions, only changes in the root length significantly affected the critical erosion depth required to be surpassed to dislodge seedlings (Table S2). 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. 4).

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 S3; Fig. 5). For *S. europaea*, the older the seedlings that were dislodged, the faster their ability to float weakened ($P < 0.001$; Table S3; Fig. 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. 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 S3; Fig. 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. 5b).

Fig. 4. The critical erosion depth (methods cf. Fig. 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.

Fig. 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. 1c).

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. S1), but showed a species-specific pattern ($P < 0.05$; Fig. S2). 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. 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. 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. 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 disledged at 3-days-old having the fastest and highest settling
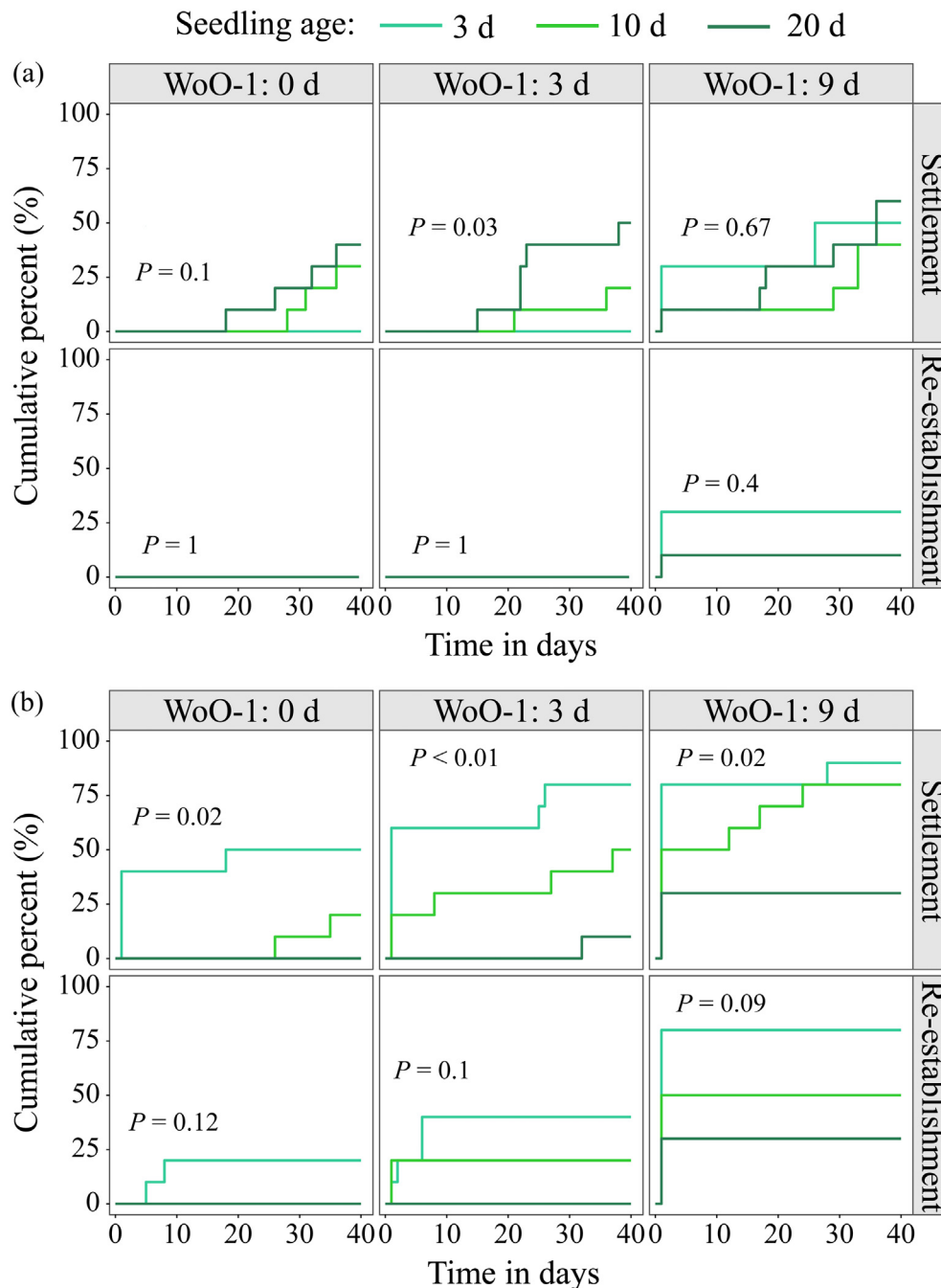
Fig. 6. Settlement and re-establishment percentage over a period of 40 days for seedlings in three age classes (3 d, 10 d, 20 d; referring to seedlings dislodged at different stages) of *Salicornia europaea* (a) and *Spartina anglica* (b). Settlement refers to staying on the sediment surface and no longer floating while re-establishment means rooting into the sediment. Tidal systems (methods in Fig. 1d) were used to impose an inundation-free period of 0 d, 3 d, and 9 d (WoO-1; Fig. S1). 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.

ratio (Fig. 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. 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. 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. 6b).

4. Discussion

This study aims to unravel saltmarsh 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 4.4). The present findings are highly important for *i)* modeling and forecasting the future resilience and persistence of saltmarsh under global change and for *ii)* guiding life cycle informed restoration to obliterate potential risks.

4.1. Trade-off and sedimentary superiority associated with seedling resistance

In line with our expectations, the young saltmarsh seedlings show a unique trade-off between root and shoot production to resist hydraulic disturbances (related to WoO-2; Fig. S1). 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).

### 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 saltmarsh 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., 2019). 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., 2019). Otherwise observational studies in the absence of such technical innovations might easily turn into looking for a needle in a haystack.

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. S1). 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. 7c), rather than through physiological processes such as loss of buoyancy (Fig. 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., 2016; Fivash et al., 2020).
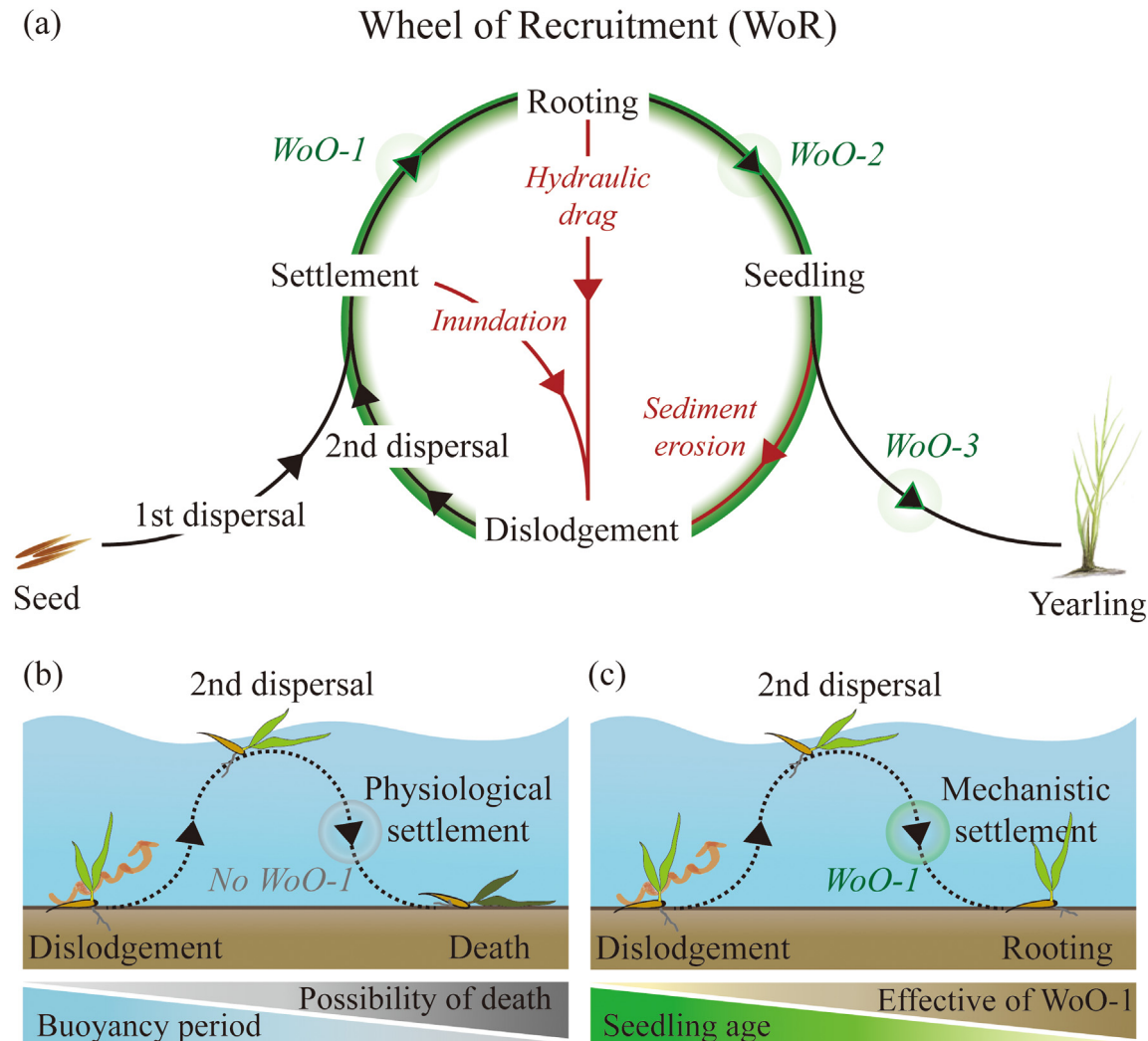
Fig. 7. (a) Schematic diagram of the proposed Wheel of Recruitment (WoR): a short-term cyclic behavior affiliated with the critical early stages of saltmarsh pioneer development. The WoR emphasizes that dislodgement during seed-seedling transition is not the end of yearling recruitment, but a potential 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. S1. 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.

4.4. Wheel of recruitment: neglected cyclic behavior at early saltmarsh life cycle

Cyclic behavior is a common feature of complex systems with periodic disturbance (Stallins, 2006; Beninca 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 (Beninca 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. 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. 7a). The dislodgement of young seedlings in spring kick-starts the

WoR, while the sequence of disturbance-free/low periods (WoO, Fig. S1) provides the flywheel driving this cyclic behavior (Fig. 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.

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).

CRediT authorship contribution statement

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

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157595.

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