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

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ABSTRACT: Propagule dispersal is fundamental to the colonization of new habitats, metapopulation connectivity, and gene flow and thus enables saltmarsh 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 4 globally distributed saltmarsh species: *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*, and *Elymus athericus*. The results showed 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 saltmarsh 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 saltmarsh dispersal and establishment, allowing more accurate prediction of the distributional responses of saltmarsh species to climate change, thereby supporting appropriate management and restoration strategies.

KEY WORDS: Salt marsh · Seed dispersal · Dispersal unit · Buoyancy · Dispersal speed · Wave effect · Wind effect

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 for unique species (Barbier et al. 2011, Duarte et al. 2013). Unfortunately, global coastlines are facing accele-

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rated 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 saltmarsh 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 saltmarsh species and establish appropriate management and restoration strategies (Dethier & Hacker 2004, Friess et al. 2012, Shi et al. 2020).

Seed dispersal is a common long-distance dispersal strategy which is also used by saltmarsh species (Rand 2000, Shi et al. 2020). Saltmarsh 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 saltmarsh 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 & Pearson 1987, Bockelmann et al. 2003; for inflorescence see e.g. Strong & Ayres 2013; for fragments see e.g. Dethier & Hacker 2004, Minchinton 2006). These seed-containing units easily detach from the withered parent plant in autumn and winter through disturbance events (e.g. storms). 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 saltmarsh propagule dispersal ability, evidence suggests that they may be important for dispersal (Ingrouille & Pearson 1987, Bockelmann et al. 2003, Minchinton 2006, Strong & Ayres 2013). Therefore, we aimed to provide a more complete understanding of saltmarsh 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 a 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 that 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). Saltmarsh 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 dispersal speed and trajectory with tidal current velocities as a dominant control variable (Chambert & James 2009, van der Stocken et al. 2015, Cunnings et al. 2016, van der Stocken & Menemenlis 2017). 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, transport speed was slower under larger waves. In addition, the coupling of wind draft with hydrodynamic conditions has been 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 saltmarsh species under changing wave and wind conditions, even though it could represent a dominant dispersal mechanism in wind- and wave-dominated coastal environments.

In this study, we bridged 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. 1) of 4 globally distributed saltmarsh species (*Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*, and *Elymus athericus*; see Fig. 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 dispersal speed. The results of this study will contribute to the improvement of existing dispersal models and prediction of realistic distributional responses of saltmarsh species to global climate change, thereby supporting the establishment of appropriate management and restoration strategies for coastal saltmarshes.

2. MATERIALS AND METHODS

2.1. Plant materials

The saltmarsh species *Salicornia europaea* (hereafter *Salicornia*), *Scirpus maritimus* (*Scirpus*), *Spartina anglica* (*Spartina*), and *Elymus athericus* (*Elymus*) were selected as representatives of common functional species in salt marshes worldwide (Fig. 1; for

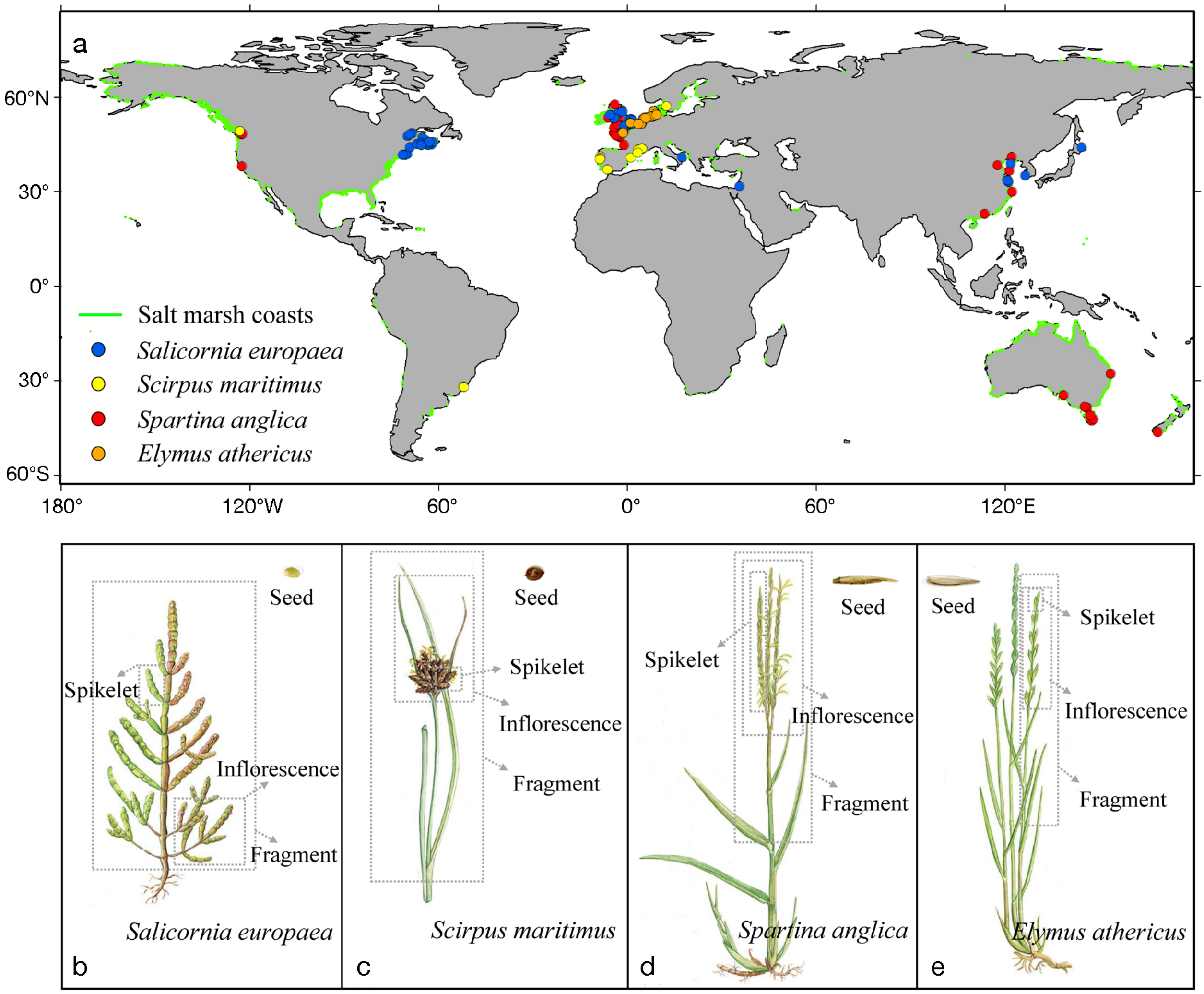

Fig. 1. (a) Distribution of *Salicornia europaea*, *Scirpus maritimus*, *Spartina anglica*, and *Elymus athericus* along global coasts based on literature records (may not show the complete distribution). The global salt marsh coasts shown here as a green line are based on occurrence data (surveys and/or remote sensing), available in the open-access data set (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 4 species. See Table 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)

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 and 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. 1). All species can disperse in the form of a single seed or as units containing seeds (Ingrouille & Pearson 1987, Bockelmann et al. 2003, Minchinton 2006, Strong & Ayres 2013). To determine how the dispersal units may affect their dispersal capability, seeds, spikelets, inflorescence, and plant fragments of these species were considered as 4 categories of dispersal units based on the number of seeds and their morphological characteristics (Fig. 1, Table 1).

Individual plants containing mature seeds of the 4 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 4 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 4 dispersal units of each species were used in flume experiments to determine the variation in dispersal speed under different 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. 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 7 tanks to simulate the floating process in still seawater (5 replications for each dispersal unit per species), and 40 additional containers were randomly placed in 7 tanks equipped with oscillatory shakers to simulate the floating process in moving seawater (Fig. 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 in 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 num-

Table 1. Morphological traits of the dispersal units (i.e. seed, spikelet, inflorescence, and fragment) of the 4 species used in this study. All morphological parameters were obtained through 100 measurements. The results are displayed as 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

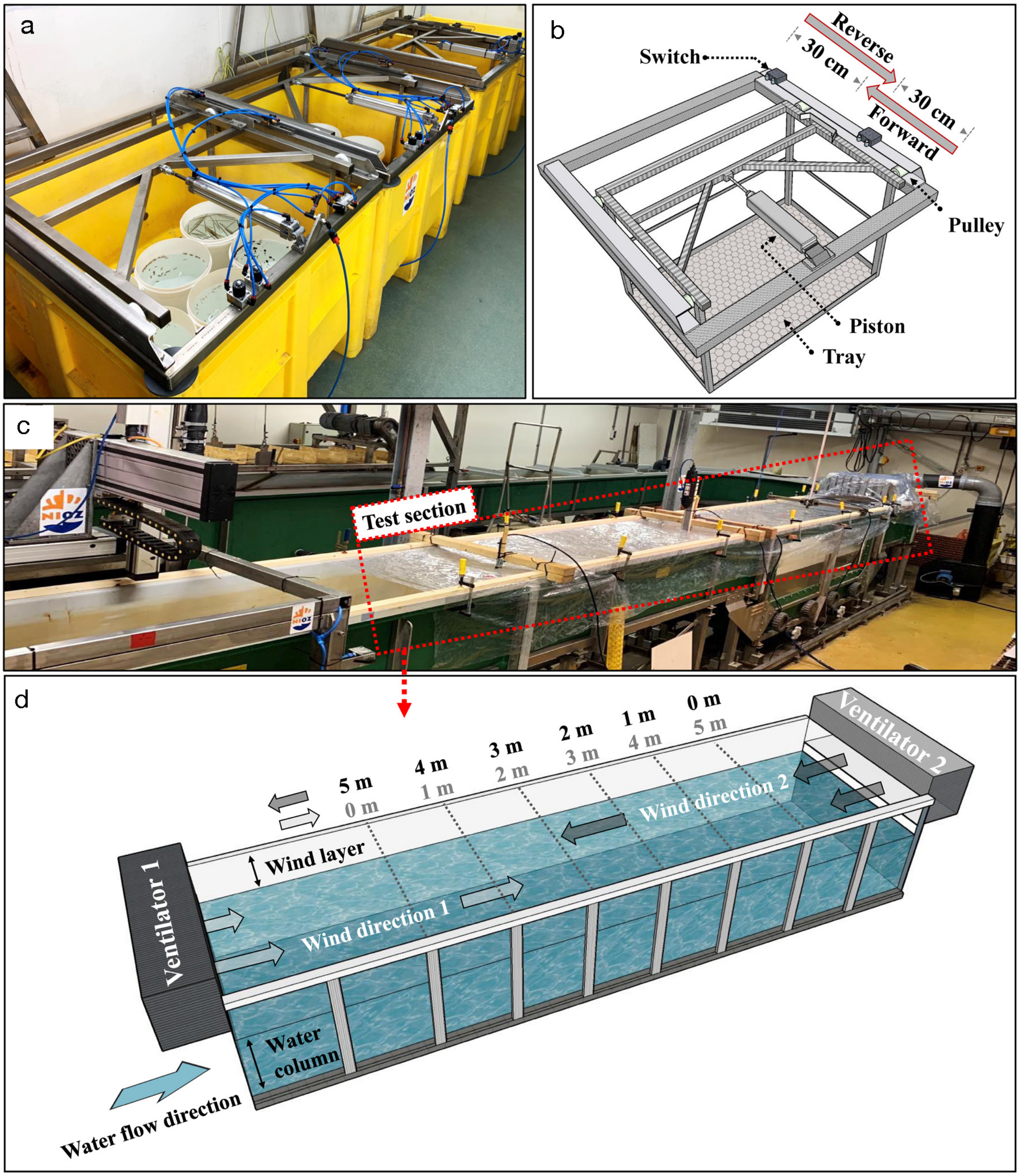

Fig. 2. Schematic diagrams and photographs showing the experiment setup. (a) Photograph of the mesocosm setup, which was designed to simulate the floating process of the dispersal units in moving seawater; (b) diagram of the oscillatory shaker that was used to create moving seawater. The shaker was driven 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 1 m (see dotted lines)

ber of seeds/spikelets used. During each monitoring period, the containers in the still water treatments were gently stirred to reduce surface tension (Favre-Bac et al. 2017).

2.3. Dispersal speed quantification in flume experiments

The racetrack flume facility (17.55 m long, 0.6 m wide, 0.45 m deep) at the Royal Netherlands Institute for Sea Research (NIOZ) was used for quantification of the dispersal speed of dispersal units containing seeds under varying hydrodynamic and wind conditions (Fig. 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). The flume was filled with seawater (salinity of 32) pumped directly 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 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. 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), pressure sensors (Druck PTX 1830; GE), and anemometers (AN100 CFM; Extech), 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 4 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 4 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; and

(4) waves and wind from the same direction: waves of 4 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 mm-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 effects 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 5760 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 dispersal speed. Runs in which the dispersal units touched the wall or bottom of the flume were not used.

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 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 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 2007, Lai et al. 2020). All statistical analyses were performed using R v.3.6.1 (https://www.r-project.org) and a significance level of 0.05.

3. RESULTS

3.1. Effects of flooding regimes on the buoyancy period

As expected, flooding regimes had a species-specific effect on the buoyancy of the dispersal units over time (Fig. 3). Overall, for the 3 pioneer species (i.e. *Salicornia*, *Scirpus*, and *Spartina*), both seeds and

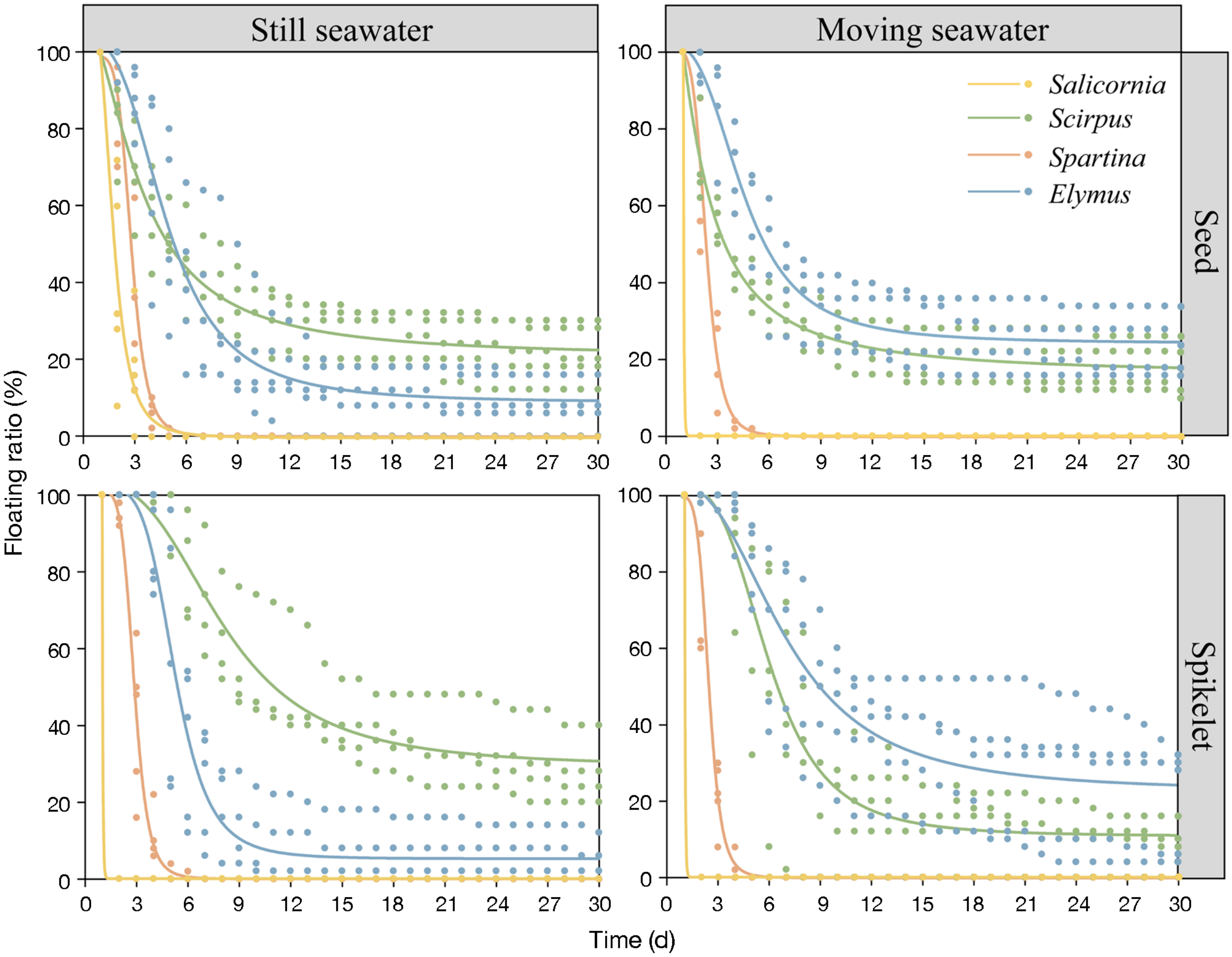

Fig. 3. Floating ratio of the seeds and spikelets of each species under different flooding regimes (i.e. still seawater vs. moving seawater) as a function of time. Solid circles: measured data; solid lines: the fitting curves based on the logistic function

spikelets tended to lose buoyancy more rapidly under moving seawater compared with still seawater (Fig. 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 increased under moving seawater (Fig. 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. 3). During the treatment with still seawater, the seeds of *Scirpus* lost 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. 3).

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* ($p < 0.01$).

3.2. Effects of currents and wind on the dispersal speed of different dispersal units

Currents had significant effects on dispersal speed regardless of the dispersal units, species, or wind directions. Dispersal speed linearly increased with increasing current velocity ($p < 0.001$; Fig. 4, Table S1 in the Supplement at www.int-res.com/articles/suppl/m678p063_supp.pdf). In the scenario in which the current and wind came 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. 4a). In addition, the dispersal speeds of the dispersal units for *Salicornia* were significantly different ($p < 0.05$; Table S1). The fastest dispersal speed was observed for a single seed; however, such a trend was not observed for other species ($p > 0.05$; Table S1). The dispersal speeds of different species were quasi-identical ($p > 0.05$; Fig. 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. 4b). The dispersal velocities of the dispersal units of all species were quasi-identical ($p > 0.05$; Table S2). Interestingly, the dispersal velocities varied significantly among species. The high tidal flat species (i.e. *Elymus*) exhibited the lowest dispersal speeds among the 3 pioneer species ($p < 0.05$), whereas *Salicornia* showed the fastest dispersal speed ($p < 0.05$; Fig. 4b).

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 S3), causing the transport of the dispersal units of all species to become notably slower than the speed of the prevailing current (Fig. 5a). As the wave magnitude increased, the overall deceleration effect of the waves on dispersal speed was alleviated, but this mitigation effect was not linear and varied among species (Figs. 5a & S1). Dispersal speeds of the dispersal units of each species also significantly differed ($p < 0.001$), except for the high tidal flat species *Elymus* (Fig. 5a, Table S3). However, variability among the dispersal units was species-specific and did not follow a common pattern or trend (Fig. 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. 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. 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. 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. 5b, Table S4). 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. 5b, Table S4). In addition, the dispersal speeds of the 4 species differed significantly ($p < 0.001$; Fig. 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. 5b).

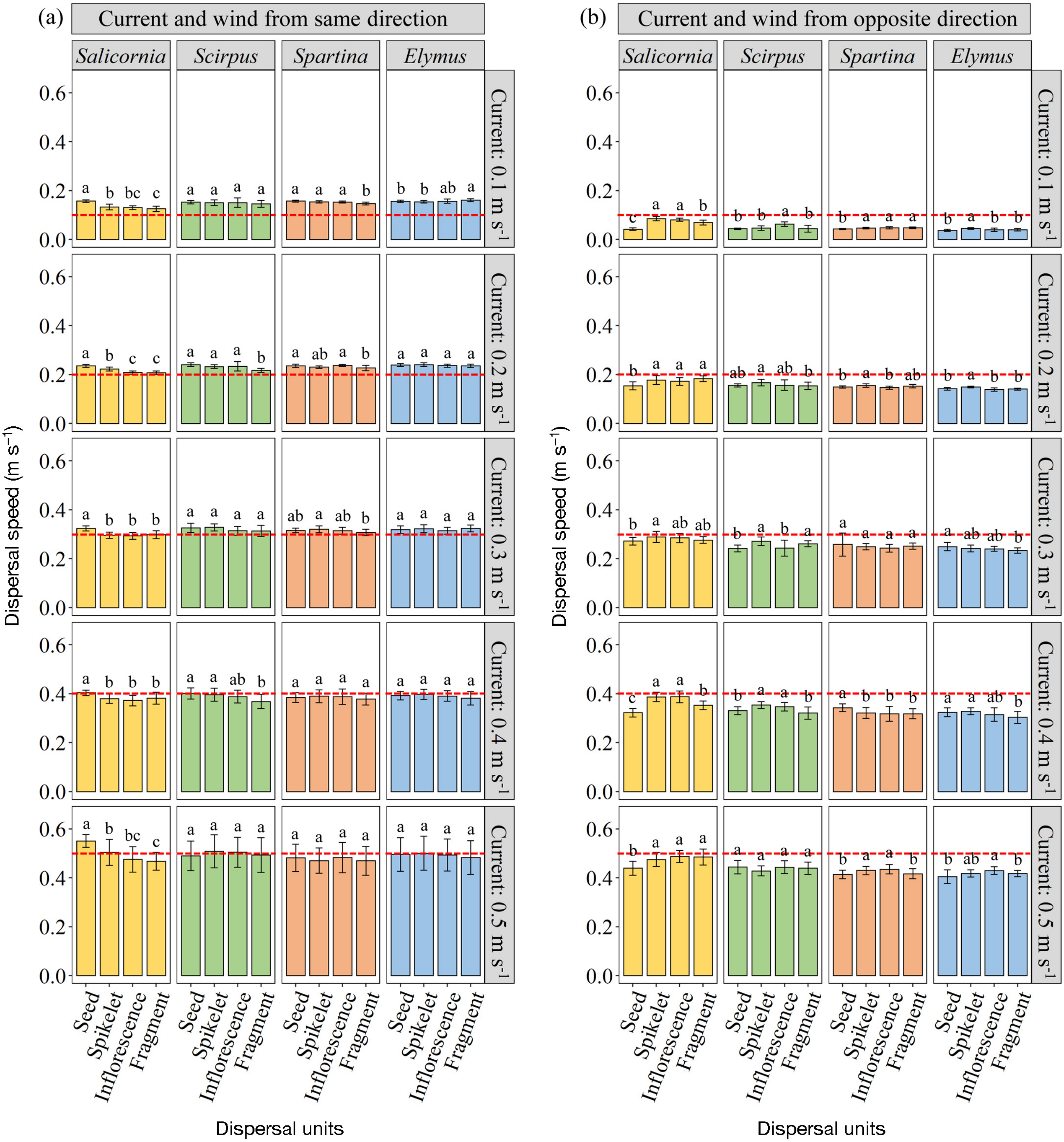

Fig. 4. Mean (±SD) dispersal speeds of 4 dispersal units (i.e. seed, spikelet, inflorescence, and fragment) per species under different current velocities and wind conditions. (a) Current velocities of 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1} were imposed with constant wind (3.0 m s^{-1}) in the same direction. (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

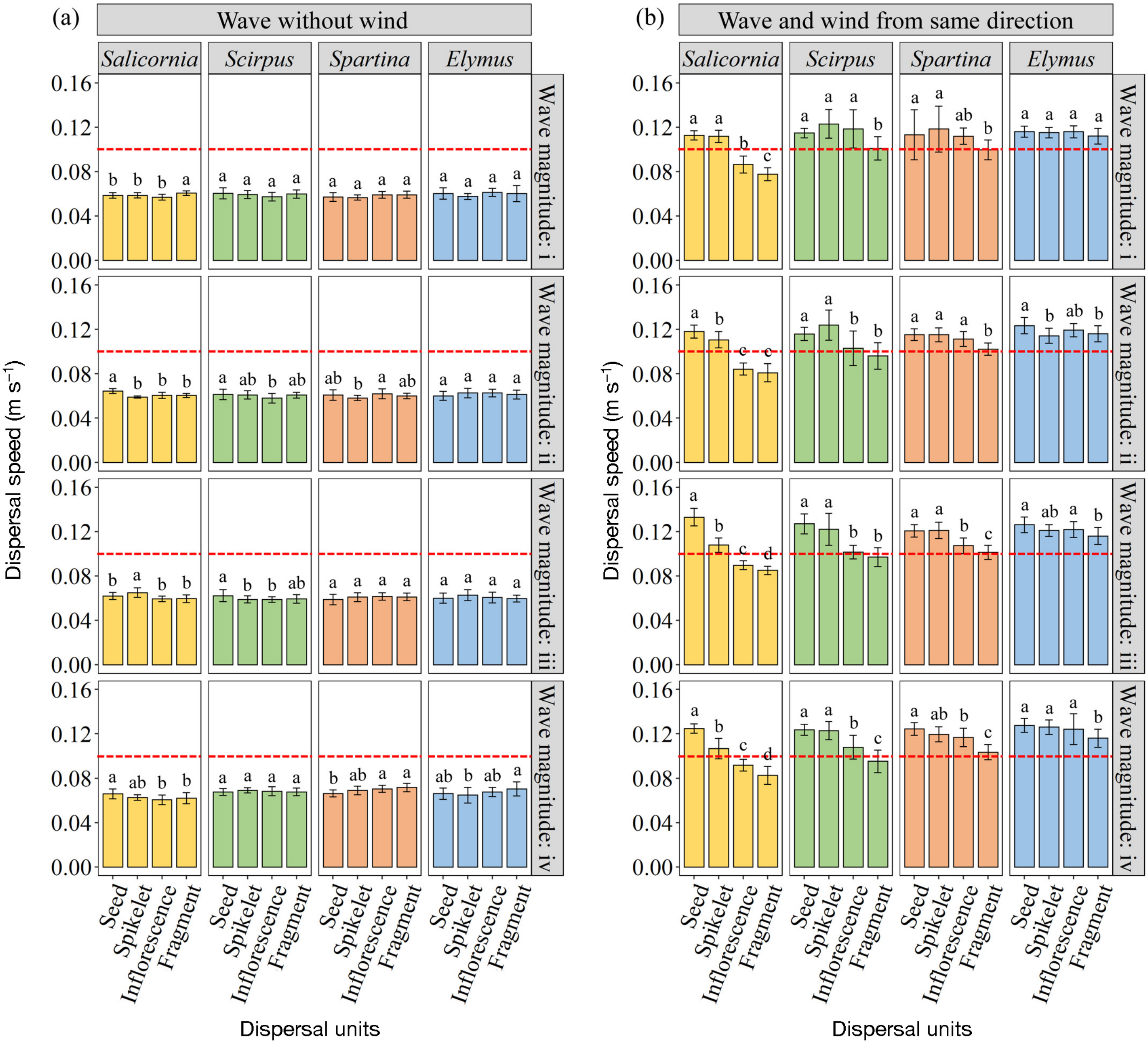

Fig. 5. Mean (±SD) dispersal speeds of 4 dispersal units (i.e. seed, spikelet, inflorescence, and fragment) per species under different wave magnitudes and wind conditions. (a) Waves of 4 magnitudes (**i**: wave height [*h*] = 4 cm, frequency [*f*] = 0.45 Hz; **ii**: *h* = 6 cm, *f* = 0.50 Hz; **iii**: *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 4 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

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). 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). 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). 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 3), 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 3). 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 3), 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 3).

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 for the floatability variation of seeds and spikelets of saltmarsh species in seawater with oscillatory flow regimes. The results show that moving seawater has a species-specific effect on 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 saltmarsh 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 saltmarsh seed motion and evaluate its poten-

Table 2. Results of the generalized linear models testing the effects of morphological characteristics on dispersal speeds under different current velocities (i.e. 0.1, 0.2, 0.3, 0.4, and 0.5 m s^{-1}) and wind conditions (speed of 0.3 m s^{-1} in the same direction as the current; speed of 0.3 m s^{-1} in the opposite direction to the current). Significance level: ***p ≤ 0.001; **p ≤ 0.01; *p ≤ 0.05

Model	Estimate	SE	*t*	p	Model	Estimate	SE	*t*	p
Current (0.1 m s^{-1}) and wind from the same direction					**Current (0.1 m s^{-1}) and wind from the opposite direction**				
Intercept	6.5696	0.0511	128.5090	<0.001***	Intercept	19.8265	0.7154	27.7140	<0.001***
Mass	0.5394	0.0609	8.8570	<0.001***	Mass	–2.3589	0.4700	–5.019	<0.001***
Shape	–0.0060	0.0012	–4.9480	<0.001***	Shape	0.0355	0.0191	1.8560	0.0655
Current (0.2 m s^{-1}) and wind from the same direction					**Current (0.2 m s^{-1}) and wind from the opposite direction**				
Intercept	4.2902	0.0197	217.4290	<0.001***	Intercept	6.4149	0.0824	77.8720	<0.001***
Mass	0.2345	0.0239	9.8300	<0.001***	Mass	–0.3555	0.0719	–4.9410	<0.001***
Shape	–0.0025	0.0005	–4.8720	<0.001***	Shape	0.0084	0.0022	3.7220	<0.001***
Current (0.3 m s^{-1}) and wind from the same direction					**Current (0.3 m s^{-1}) and wind from the opposite direction**				
Intercept	3.1658	0.0166	191.0800	<0.001***	Intercept	3.8915	0.0330	117.8830	<0.001***
Mass	0.1290	0.0186	6.9250	<0.001***	Mass	–0.0860	0.0252	–3.4080	<0.001***
Shape	–0.0013	0.0005	–2.5930	0.0102*	Shape	0.0034	0.0010	3.6080	<0.001***
Current (0.4 m s^{-1}) and wind from the same direction					**Current (0.4 m s^{-1}) and wind from the opposite direction**				
Intercept	2.5659	0.0162	158.1090	<0.001***	Intercept	2.9392	0.0270	108.8420	<0.001***
Mass	0.0555	0.0150	3.6970	<0.001***	Mass	–0.0688	0.0257	–2.6800	0.0080**
Shape	0.0005	0.0005	1.1290	0.2602	Shape	0.0034	0.0007	4.7360	<0.001***
Current (0.5 m s^{-1}) and wind from the same direction					**Current (0.5 m s^{-1}) and wind from the opposite direction**				
Intercept	2.0141	0.0238	84.7690	<0.001***	Intercept	2.3061	0.0147	156.4340	<0.001***
Mass	0.0565	0.0209	2.7030	0.0075**	Mass	–0.0903	0.0155	–5.8090	<0.001***
Shape	0.0011	0.0007	1.5810	0.1156	Shape	0.0019	0.0004	4.6680	<0.001***

Table 3. Results of the generalized linear models testing the effects of the morphological characteristics on the dispersal speeds under different wave magnitudes (i.e. **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) and wind conditions (no wind; speed of 0.3m s^{-1} in the same direction as the current). Note: A slow current of 0.1 m s^{-1} was applied to facilitate movement in one direction. Significance level: ***p ≤ 0.001; **p ≤ 0.01; *p ≤ 0.05

Model	Estimate	SE	*t*	p	Model	Estimate	SE	*t*	p
Wave (magnitude i) without wind					**Wave (magnitude i) and wind from the same direction**				
Intercept	17.0366	0.1680	101.4210	<0.001***	Intercept	8.6116	0.1221	70.5080	<0.001***
Mass	–0.1297	0.1331	–0.9740	0.3320	Mass	1.2237	0.1242	9.8500	<0.001***
Shape	0.0002	0.0104	0.0230	0.9820	Shape	–0.0064	0.0036	–1.7590	0.0802
Wave (magnitude ii) without wind					**Wave (magnitude ii) and wind from the same direction**				
Intercept	16.2921	0.1441	113.0770	<0.001***	Intercept	8.6294	0.0908	95.0660	<0.001***
Mass	0.0265	0.1085	0.2450	0.8070	Mass	1.3566	0.1134	11.9680	<0.001***
Shape	0.0107	0.0086	1.2490	0.2140	Shape	–0.0042	0.0015	–2.8680	0.0046**
Wave (magnitude iii) without wind					**Wave (magnitude iii) and wind from the same direction**				
Intercept	16.5845	0.1557	106.4920	<0.001***	Intercept	8.5366	0.0846	100.8690	<0.001***
Mass	–0.0068	0.0982	–0.0690	0.9450	Mass	1.1995	0.0869	13.8040	<0.001***
Shape	–0.0064	0.0096	–0.6740	0.5010	Shape	–0.0056	0.0025	–2.2570	0.025*
Wave (magnitude iv) without wind					**Wave (magnitude iv) and wind from the same direction**				
Intercept	14.9524	0.1209	123.6260	<0.001***	Intercept	8.2481	0.0877	94.0460	<0.001***
Mass	0.2872	0.1281	2.2410	0.0265*	Mass	1.5863	0.1189	13.3380	<0.001***
Shape	–0.0132	0.0028	–4.6560	<0.001***	Shape	–0.0056	0.0022	–2.5310	0.0121*

tial dispersal distance or range and thus contribute to the prediction of realistic distributional responses of saltmarsh species to a wide range of disturbance scenarios.

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 saltmarshes. As expected, both the seeds and spikelets of the 3 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 saltmarsh propagules may be rather imprecise because even a floating time difference of 1 d has a significant effect on dispersal distance, resulting in a significant shift in the magnitude and direction of 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 difference may underpin the importance of widely recognized research revealing that the environment of the mother plant serves as a regulator of the offspring's traits (so-called 'maternal effect'; Wolf & Wade 2009). Species in high tidal flat saltmarshes are typically exposed to much fewer inundations than the pioneer species in low tidal flats. Hence, high-marsh species may have evolved seed 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.

4.2. Relative role of dispersal units and abiotic conditions on dispersal speed

Saltmarsh 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 current velocity (Chambert & James 2009, van der Stocken et al. 2015, Cunnings et al. 2016, van der Stocken & Menemenlis 2017), 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 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 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 & Osland 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 saltmarsh species, such as the relative contribution of specific wave parameters including wavelength and wave period to the seed dispersal speed must be considered, particularly in future numerical models, to predict the saltmarsh 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 saltmarsh plants generally float on top of the water column and do not differ in terms of 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 & Jacobson 2005, https://globalwindatlas.info), which means that the effect of wind might be more prominent. Furthermore, our results emphasize the importance of wind direction, which can shift the role of wind during saltmarsh 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 for 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 trait but requires further scrutiny (Friess et al. 2012, van der Stocken et al. 2019a).

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 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 & Smallwood 1982, Pufal & Garnock-Jones 2010, Soons et al. 2017).

4.4. Implications for saltmarsh 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 2005, Bouma et al. 2014). Incorporating hydrology and natural regeneration via propagule establishment has the potential for faster recovery and more spatially extensive effects compared with man-made restoration attempts based on transplanting (Nilsson et al. 2010, Prach et al. 2015, Aavik & Helm 2018). The lateral expansion of transplants by clonal growth is slow compared to 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 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 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 saltmarsh 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 saltmarsh dispersal and thereby contributes to the design of ecological activities to maintain and restore saltmarshes and control invasive species.

Data Availability. The data that support the findings of this study are freely available in 4TU.Research Data at https://doi.org/10.4121/15177768.

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