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The role of tides and winds in shaping seed dispersal in coastal wetlands

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Abstract

Global changes such as sea level rise and enhanced storminess motivate the use of saltmarshes as nature-based flood defenses. Yet, it remains poorly understood about how shifted environmental conditions may shape processes governing long-term stability of saltmarshes. Here, we integrated data from in situ measurements and field experiments in several Dutch salt marshes to probe the impacts of changes in tides and winds on seed arrival and seed retention on adjacent tidal flats, which is key to marsh regeneration following wave-driven lateral erosion. The results show that both the quantity and viability of the seeds transported toward adjacent tidal flats relate positively with the peak water level of each tide. Spring tides are more powerful in seed dispersal than neap tides, and storm-induced extreme water levels can serve as "Window of Opportunity" that deliver disproportionately higher amounts of viable seeds than average conditions. Seed retention decreased with growing onshore wind speed. Storm-induced strong wave disturbance can function as "Windows of Risk" that wipe out seeds on tidal flats at wind-exposed marshes. This study highlights the importance of variability in tides and winds for regulating the potential of seed-based marsh recovery on adjacent tidal flats and thus their resilience to lateral degradation. These findings are relevant for assessing the long-term marsh stability and sustainability of nature-based coastal defenses with saltmarshes under global environmental changes.

Recent years have seen a paradigm shift from conventional engineered flood defenses towards innovative, nature-based solutions with coastal wetlands such as saltmarshes (Cheong et al. 2013; Temmerman et al. 2013; Barbier 2014). Saltmarshes have displayed their high efficiency in reducing storm-wave impacts (Moller et al. 2014; Vuik et al. 2016) meanwhile remaining highly stable during severe storms (Moller et al. 2014; Spencer et al. 2016). Although global changes such as sea level rise and enhanced storminess motivate the use of saltmarshes as natural defenses (Cheong et al. 2013; Temmerman et al. 2013; Bouma et al. 2014), it remains poorly understood how shifted conditions associated with these events may shape processes in relation to marsh stability in the long run. This knowledge gap imposes uncertainties in the sustainability of nature-based flood defense by saltmarshes.

One of the key processes that governs long-term marsh stability is vegetation regeneration at the seaward marsh edge, where lateral erosion often occurs due to wave attacks (Deegan et al. 2012; Silliman et al. 2012; Leonardi et al. 2016). Lateral erosion is a common mechanism of long-term marsh degradation (Deegan et al. 2012; Silliman et al. 2012; Leonardi et al. 2016), with lateral retreat rates of up to several meters per year (van der Wal et al. 2008). As seen in many marshes, a resilient marsh edge can recover the lost area by revegetation of saltmarsh pioneer plants (Allen 2000; van der Wal et al. 2008; Chauhan 2009). Many mesotidal and macrotidal marshes have shown cyclic alternations between lateral erosion and revegetation on decadal or longer time scales (Allen 2000; van der Wal et al. 2008; Chauhan 2009). Although marsh revegetation, in some areas predominantly, can be the result of clonal extension from the existing vegetation (Allison 1995; Angelini and Silliman 2012), seedling recruitment often yields rapid vegetation expansion on tidal flats over extensive areas (Gray et al. 1991; Zhu et al. 2012; Strong and Ayres 2013). Regeneration from seeds (Fig. 1a) is especially important in mesotidal and macrotidal systems where clonal expansion is not possible at the presence of a

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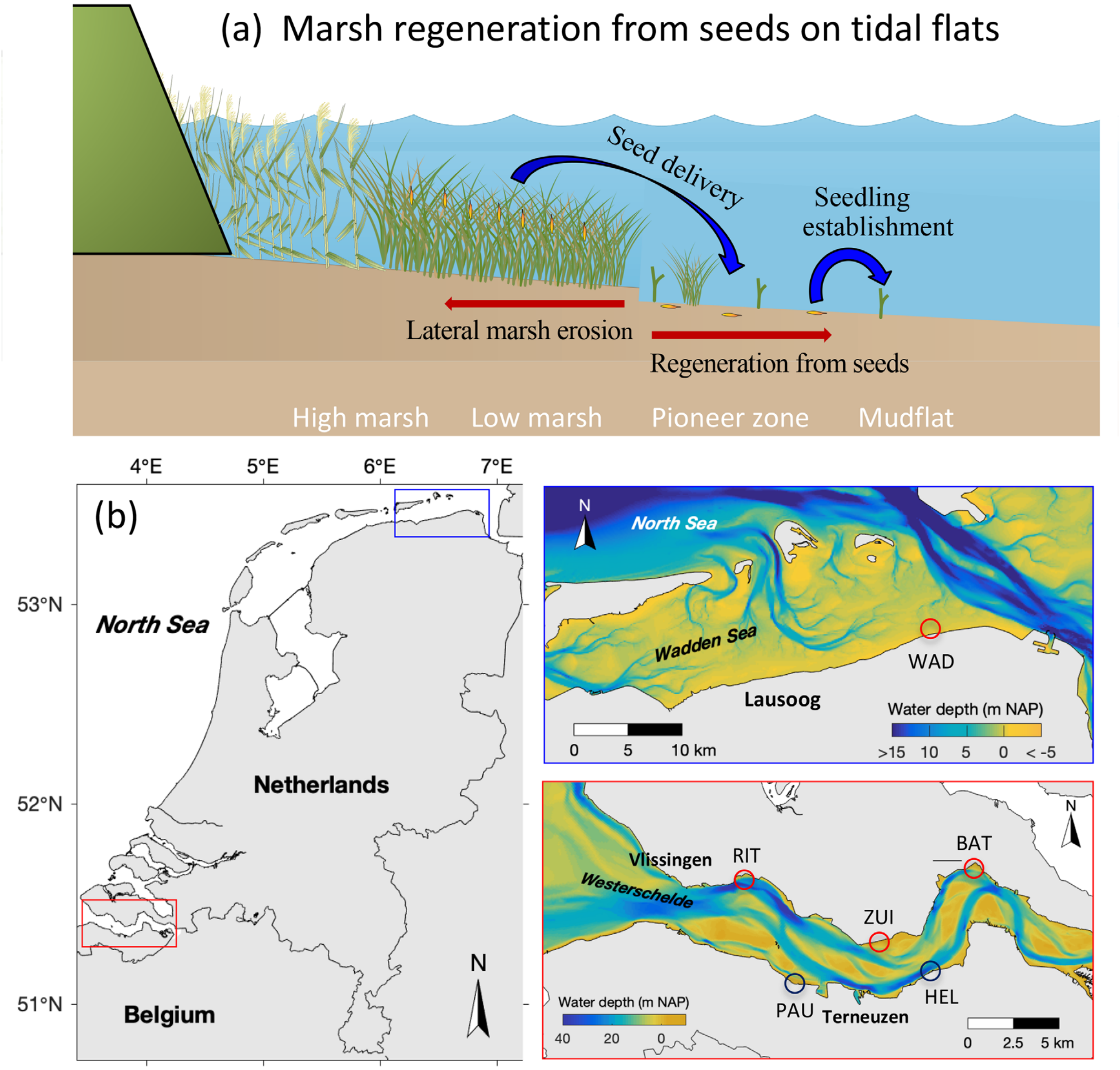

Fig. 1. (**a**) Seed-based marsh regeneration on tidal flats. (**b**) Geographic locations of the study sites in the Wadden Sea coast (WAD) and in the Westerschelde: Paulinapolder (PAU), Ritthem (RIT), Zuidgors (ZUI), Hellegatpolder (HEL), and Bath (BAT). The wind exposure, geographic coordinates and sampling regimes are present in Table 1. The relatively wind-exposed sites are marked with red circles whereas the relatively wind-sheltered sites are denoted with blue circles

high cliff at the marsh edge. Seedling establishment, by and large, plays a key role in ensuring marsh resilience to lateral degradation and thus long-term marsh stability.

Seedling establishment can be limited by seed processes (e.g., seed production, dispersal, retention, and survival) and/or seedling processes (e.g., seedling emergence and survival). Although previous studies mostly concerned thresholds and window of opportunities involved in seedling survival (Friess et al. 2012; Hu et al. 2015; Cao et al. 2018), recent studies underscore the importance of effective seed dispersal (quantity × quality) for enabling seedling establishment on tidal flats (Zhu et al. 2014, 2020*a*; van Regteren et al. 2019). Effective seed dispersal includes the delivery of viable seeds by tides to the desired location (i.e., adjacent mudflats) and seed retention at this location (Friess et al. 2012; Zhu et al. 2014). The latter has been increasingly recognized as a critical bottleneck to seedling establishment (Groenendijk 1986; Houwing 2000; Zhu et al. 2014). Seed removal from tidal flats by waves and the resultant sediment erosion during the winter impedes seedling establishment in the spring, even with suitable conditions for seedling growth and survival (van Regteren et al. 2019). Since waves in tidal habitats are driven primarily by winds, shifted wind conditions due to climate change may alter the pattern of seed retention, thereby affecting marsh revegetation capacity. Moreover, given the capacity of storms in modifying both tides and winds, storms may have major impacts on both the quantity and the quality of seed dispersal in relation to vegetation recovery on tidal flats. Within this

Table 1. An overview of experiments/surveys and associated sites included in the analyses of this study. These sites are Paulinapolder (PAU), Ritthem (RIT), Zuidgors (ZUI), Hellegatpolder (HEL), Bath (BAT), and a Wadden Sea marsh (WAD) as shown in Fig. 1b.

Survey/experiments	Methods	Site	Coordinates	Wind exposure	Period
Seed quantity and viability in plants	Field survey and lab test	PAU	51.352 N, 3.722 E	Sheltered	September 2011, September 2012, September 2013
		RIT	51.458 N, 3.659 E	Exposed	
Seaward seed transport	Field survey with floatable nets	PAU	51.352 N, 3.722 E	Sheltered	November 2013–February 2014
		RIT	51.458 N, 3.659 E	Exposed	
Wave forcing under varying wind conditions during seed dispersal season	In situ measurements with wave sensors	BAT	51.403 N, 4.195 E	Sheltered	November 2014-April 2015, November 2015–April 2016, October 2016–February 2017
		HEL	51.367 N, 3.952 E	Exposed	
		WAD	53.464 N, 6.738 E	Exposed	January 2015–April 2015, October 2016–February 2017
Seed persistence under varying wind conditions during seed dispersal season	Reanalysis of published data collected in a manipulated seed bank experiments (Zhu et al. 2014)	PAU	51.352 N, 3.722 E	Sheltered	January–May 2012
		ZUI	51.388 N, 3.845 E	Exposed	

context, there is a pressing need to understand how changes in tides and wind conditions may shape both tide-driven seed transport and subsequent seed retention.

In this paper, we investigated (1) how tidal variability may affect seed delivery of salt marsh pioneer species towards the adjacent tidal flats and (2) the response of subsequent seed retention to changing wind conditions, using cordgrass (i.e., *Spartina* spp.), a globally common marsh pioneer species (Strong and Ayres 2013) as a model. Based on the results from these two processes, we further explored how storms may shape effective seed dispersal (quantity × quality) of cordgrass by modifying the tides and wave conditions. Such information is essential to assess the long-term marsh stability under global environmental changes, with important implications for implementing sustainable nature-based flood defenses by saltmarshes.

Methods

Study sites and general setup

We integrated data from various field surveys and experiments on different salt marshes and adjacent tidal flats in the Netherlands (Fig. 1b; Table 1), including one site along the Wadden Sea coast, and five sites in the Westerschelde estuary: Paulinapolder, Ritthem, Zuidgors, Hellegatpolder, and Bath. The pioneer vegetation at all sites consists mainly of common cordgrass, *Spartina anglica*, which often forms monocultures in the low marsh that has elevations ranging from 60 to 200 cm NAP (Nieuw Amsterdams Peil, Dutch Ordnance Level, close to mean sea level, van der Wal et al. 2008). This species flowers from July to October and seeds ripen within 12 weeks. Seed release starts from autumn, extending through the winter and early spring of the following year, which concurs with the stormy season in the Netherlands (Huiskes et al. 1995). Seeds can move either landward or seaward with the tides. The current study focused on seaward seed delivery in relation to lateral marsh regeneration, where the tides transport the seeds from the marsh toward the tidal flats (Huiskes et al. 1995), with most seeds deposited on tidal flats close to the marsh (Zhu et al. 2014).

The combined dataset covers all relevant processes at the seed stage for cordgrass regeneration on tidal flats, including seed production, seed release, seed delivery and seed retention (Table. 1). At site Paulinapolder and Ritthem in the Westerschelde, seed numbers and seed viability in plants along an elevation gradient were quantified to detect the seed production pattern, followed by a survey of seed release dynamics. At these two sites, surveys of the quantity and quality of seaward transported seeds under varying tide heights were also conducted, to detect the effects of tidal variability on effective seed delivery toward the adjacent tidal flats. Since seed retention on tidal flats was mainly determined by wave actions driven primarily by winds (Zhu et al. 2020*a*), we further combined wind data with existing in situ measured wave data on tidal flats during the dispersal season to detect the relation between wave forcing and wind conditions. Wave measurements were conducted at three field sites including two Westerschelde marshes Hellegatpolder and Bath, which differ in wind exposure (van der Wal et al. 2008), as well as a marsh along the Wadden Sea coast (Fig. 1b), where winter storms occur more frequently (Zhu et al. 2020*b*). In addition, we reanalyzed the published data (Zhu et al. 2014) of seed retention on tidal flats at two Westerschelde marshes Paulinapolder and Zuidgors during winter to examine the relation between seed retention and wind conditions.

Impacts of tidal variability on seaward seed delivery

Quantity and viability of seeds in plants

As cordgrass often displays zonal variation in seed production and seed viability (Marks and Truscott 1985; Mullins and Marks 1987; Xiao et al. 2009), we conducted field surveys on cordgrass seed production along the elevation gradient at site Paulinapolder and Ritthem (Fig. 1b). At each site, we selected a ca. 20-m wide cross-marsh transect spanning from the upper to the lower limit of cordgrass zone. Along this transect, four sampling zones (Supporting Information Table S1) were established. Within each zone, we sampled five 1 × 1 m quadrates of comparable elevations. The flowering inflorescences within each quadrate were excised and transported to the lab in plastic bags. This was conducted first in 2011 and repeated in 2012 and 2013, at the beginning of November when most of the seeds were still on the plants.

In the lab, seeds were released from the inflorescences and counted, after which seed production (no. m^{-2}) was determined for each quadrate, respectively. The gathered seeds from each quadrate were separately placed into mesh storage bags submersed in seawater, labeled, and stored in a 4°C fridge for 3 months, after which seed viability was determined by germination tests in a climate room with a constant temperature of 25°C. The germination tests terminated when no more germinated seeds could be seen for 1 week. Seed viability was calculated as the percentage of seeds germinated.

In addition, we established six permanent plots (50 × 200 cm) both in the higher (> 140 cm NAP) and lower part (< 140 cm NAP) of cordgrass marsh to survey the seed release dynamics. These plots were randomly selected and at least 5 m apart. The number of seeds remaining on the plants (no. m^{-2}) was monthly determined by (i) counting flowering inflorescence per m^2 and (ii) quantifying the number of seeds per inflorescence. The former was done within each plot, whereas for the latter we sampled 10 inflorescences for each plot. This survey was conducted at both Paulinapolder and Ritthem, which started in September 2013 and ended in April 2014 when all the seeds were gone from the plants.

Quantity and viability of seaward transported seeds

Tides are characterized by fluctuating water level with time. Water level determines not only the extent of the seed source area, but also the inundation duration, that is, the time available for seed delivery. Hence, we quantified the response of seaward seed delivery to changing peak water level, by conducting field surveys at site Paulinapolder and Ritthem using floatable seed trapping nets adapted from the design in Huiskes et al. (1995). Such nets proved very effective in trapping cordgrass seeds that disperse via floating in the water column (Koutstaal et al. 1987; Huiskes et al. 1995; Xiao et al. 2016). The survey was done between November 2013 and February 2014 to capture the main seed dispersal season. Monthly monitoring on seed release at these sites confirms that most of the seeds have been released within this period (Supporting Information Fig. S1a). One severe storm occurred during the survey season, which yielded a major storm surge (Supporting Information Fig. S1b). We were, however, not able to measure seed transport during that event due to logistic problems.

In total, 12 tides were sampled, including 3 spring tides and 2 neap tides (Supporting Information Fig. S1b; Table S2). Peak water levels were between 164 and 332 cm NAP for site Paulinapolder and ranged from 142 to 307 cm NAP for site Ritthem (Supporting Information Fig. S1b). On the tidal flats of each site, three permanent steel poles (ca. 3 m above ground) were established along the shoreline with 10 m apart, and each was 5 m away from the marsh edge. For each pole, we deployed one seed trapping net (mesh size 100 μm) through a steel ring. The net was initially placed with its opening (68 cm × 24 cm) facing the marsh edge, which can adjust its orientation with the current direction and move up and down the pole with the tides (Huiskes et al. 1995).

For each survey, the nets were deployed during the low tide and recovered on the next day (after two tidal periods). Recovery of nets after only one tidal period was not possible, due to logistic problems of field survey during the night. For each survey, the number of captured cordgrass seeds by each net was counted and averaged for the three nets. Divided by two (tides), the number of seeds captured per net was then calculated to quantify seaward seed transport by each tide. Seeds captured from all three nets were pooled together and stored in a 4°C fridge for 3 months to keep them dormant (Zhu et al. 2016). After that, the viability of the seeds captured during each survey was determined by germination tests to examine the quality of seaward transported seeds. When the total number of seeds was less than 800, all the seeds were tested, else we used a sub sample of ca. 800 seeds. Seed viability (%) was calculated as the portion of germinated seeds.

Data analysis

Generalized linear models (GLMs) were employed to detect the response of seed quantity and seed viability in plants to changing elevation, respectively, with “site” and “year” as category factors. When there were significant effects of “site” and “year” on seed quantity or seed viability in plants, we fit the data separately for each site and each year. GLMs were also used to test how the quantity and quality of seeds of seaward transported seeds vary with fluctuating peak water level, respectively, with “site” as a category factor. We specified "poisson" family for the seed quantity data and "binomial" family for the seed viability data, given a Poisson or negative binomial distribution of these data. When necessary, we refitted the model using "quasi-binomial" to account for the over-dispersion. All the statistical analyses were done in R (version 4.02, http://www.R-project.org) using the R Stats Package, applying a significance level of $\alpha = 0.05$.

As statistics displayed significant effects of "peak water level" and "site" on seed quantity and seed viability (Table 2), we further quantified the relations between seed quantity/viability and peak water level for each site. To achieve this, we fit the data with different models including linear, exponential, logarithmic, quadratic functions, and then picked a model based on the goodness (R^2) of each fit. This was done for both response variables (seed quantity and seed viability in plants) and both sites (Paulinapolder and Ritthem). Quadratic functions were eventually adopted due to the higher R^2 than any other functions in all cases (Table S3). Combining the resultant regression equations, and the time-series data of peak water level during each tide, we modeled the temporal dynamics of seaward seed transport during September 2013 to April 2014 (i.e., seed dispersal season) for each site. To compare the potential of the seaward transport of viable seeds under varying peak water levels of the tide, we also computed the number of viable seeds captured per net during one tide by multiplying the corresponding seed quantity with seed viability captured per net during each tide.

Response of seed retention on tidal flats to changing wind conditions

Wave-induced bed shear stress under varying wind conditions

Previous study has shown that seed retention at the tidal flat surface decreased with increased wave-induced bed shear stress, that is, a measure of the friction force imposed on the sediment surface by waves (Zhu et al. 2020*a*). To examine the relation between wave-induced bed shear stress and wind conditions, we analyzed in situ measured wave data at sites Hellegatpolder, Bath, and the Wadden Sea marsh with varying wind exposure (Table 1). Wave measurements were conducted using pressure sensors (OSSI-010-003C; Ocean Sensor Systems, Inc.). The measurement at Hellegatpolder and Bath covered three winter periods whereas it was done for two winter periods at the Wadden Sea marsh (Table 1).

Every sensor was mounted on a pole inserted on the tidal flat next to the marsh edge, approximately 5 cm above the tidal flat surface. The measuring interval and period were 15 and 7 min, respectively. The wave analysis was based on pressure fluctuations, measured with a frequency of 5 Hz. The recorded pressure readings were converted to water level fluctuations, from which we derived water depth, significant wave

Table 2. Analysis of deviance table of the GLMs on the quantity and viability of seeds in plants as well as the quantity and viability of seeds captured by nets, respectively. "Quasi-poisson" GLM family was applied to seed quantity data and "quasi-binomial" GLM family for seed viability data.

Response variable	Source	Df	Deviance	Resid. Df	Resid. Dev	Pr (> Chi)
(a) Seed quantity in plants	Site	1	16,542.8191	158	329,124.59	<0.001***
	Elevation	1	23,949.5513	157	305,175.04	<0.001***
	Year	2	125,841.417	155	179,333.62	<0.001***
	Site : elevation	1	195.239619	154	179,138.38	0.677
	Site : year	2	10,131.4504	152	169,006.93	0.011*
	Elevation : year	2	3573.75244	150	165,433.18	0.204
	Site : elevation : year	2	3879.09795	148	161,554.08	0.178
(b) Seed viability in plants	Site	1	0.54524328	158	13.36	<0.001***
	Elevation	1	2.19853225	157	11.16	<0.001***
	Year	2	4.78287836	155	6.38	<0.001***
	Site : elevation	1	0.29447641	154	6.08	<0.001***
	Site : year	2	3.07838372	152	3.00	<0.001***
	Elevation : year	2	0.16520587	150	2.84	0.010*
	Site : elevation : year	2	0.01830123	148	2.82	0.603
(c) Seed quantity captured by nets	Site	1	946.254164	22	7616.43	0.014*
	Peak water level	1	4714.37765	21	2902.05	<0.001***
	Site : peak water level	1	6.1405535	20	2895.91	0.844
(d) Seed viability captured by nets	Site	1	0.62728135	22	1.26	<0.001***
	Peak water level	1	0.55173432	21	0.71	<0.001***
	Site : peak water level	1	0.00188681	20	0.71	0.826

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

height and peak wave period (Callaghan et al. 2010; Vuik et al. 2018; Zhu et al. 2020*a*). These parameters were then used to determine time-averaged bed shear stress imposed by waves ($\tau_{\text{wave\_avg}}$, Pa), using the method described in Zhu et al. 2020*a*. We calculated $\tau_{\text{wave\_avg}}$ for each tide and distinguished it between two scenarios: (1) onshore winds dominated and (2) offshore winds dominated. We decided whether the wind direction is onshore or offshore by calculating the included angle between the wind direction and a seaward arrow perpendicular to the shoreline. The wind is regarded as "onshore" when the included angle is between 90° and 180° and else (0°–90°) as "offshore." The dominant wind direction during each tide is defined as the wind direction for the strongest winds during that period. Hourly wind speed and wind direction data were obtained from the nearby weather stations, which are Vlissingen for the two Westerschelde salt marshes Hellegatpolder and Bath, and Lauwersoog for the Wadden Sea marsh, respectively (Fig. 1b).

Seed retention under varying wind conditions

To detect the relation between seed retention and wind conditions, we reanalyzed the dataset in a published paper (Zhu et al. 2014) where manipulated seed bank experiments were done in 2012 at two Westerschelde marshes Paulinapolder and Zuidgors that differ in wind exposure (Fig. 1b). In their experiments, cordgrass seeds were deployed at different depths of the sediment on tidal flats near the marsh and recovered in 4 weeks to quantify the effects of seed burial on seed retention. Their analysis demonstrated that seed retention was generally low at the tidal flat surface and grew nonlinearly with increased seed burial depth (Supporting Information Fig. S2). In the current study, we extended the analysis by determining the relationship between seed retention and wind conditions (wind speed and direction). To achieve this, we combined seed retention data from Zhu et al. 2014 with the hourly wind speed and wind direction data obtained for both sites from the nearby weather station Vlissingen (Fig. 1a).

The seed retention experiment at each site was repeated four times (January–February, February–March, March–April, and May–June) during the period from January to June in 2012. This period was within the stormy season and covered the stage during which seeds need to stay in site before they germinate. One severe storm (Southwest wind) took place during the experiment in January (January–February). Site Zuidgors was exposed to the storm wind whereas Paulinapolder was relatively sheltered. For both sites, three burial depths (on the surface, 1.5 and 3.0 cm) were used in the first two experiments (January–February and February–March), whereas an extra depth (0.5 cm) was added for the last two experiments (March–April and May–June). For each experiment, 45 preprepared layered seed bank cores were monthly deployed recovered, with each core having five cordgrass seeds placed at each burial depth (for details, *see* Zhu et al. 2014). Seed retention (%) was calculated as the percentage of seeds that stayed in site.

Statistics

Analysis of covariance was applied to detect the dependence of time-averaged bed shear stress imposed by waves ($\tau_{\text{wave\_avg}}$) on wind speed and wind direction (onshore winds or offshore winds dominated), with "averaged wind speed" as the dependent variable, "site" and "wind direction" as category factors. Where needed, we conducted log transformation to improve data normality. Due to the binomial distribution of seed retention data, we employed GLMs (family = "binomial") to examine the response of seed retention to wind speed, with "seed burial depth" as a category factor. Data from the two sites (Paulinapolder and Zuidgors) were pooled together to ensure enough data points for the model fits. When necessary, we refitted the model using "quasi-binomial" family to account for the overdispersion. To test whether wind direction affects the relation between seed persistence and wind speed, we repeated the analysis three times, using (1) averaged onshore wind speed, (2) averaged offshore wind speed, and (3) averaged wind speed (including both onshore and offshore winds).

Results

Seed delivery toward the adjacent tidal flats

Seed production surveys at the wind-sheltered site Paulinapolder and the wind-exposed site Ritthem indicated that, despite clear year-to year variations, both seed quantity and seed viability in plants increased significantly with raised marsh elevation (Table 2a,b; Fig. 2). Surveys of seaward seed delivery at the same sites further showed that both the quantity and viability of seaward transported seeds increased significantly with elevated peak water level of each tide (Table 2c,d; Fig. 3). There were also clear differences of seaward seed delivery between sites. Compared with site Ritthem, the quantity and viability of seeds captured by the seed trapping nets were both higher at site Paulinapolder (Fig. 3), where cordgrass produced more seeds with higher viability in the year (2013) when the seed transport survey was conducted (Figure 2).

For both sites, predictions of seaward delivery of viable seeds revealed a pulsed pattern of seaward seed transport over time during the dispersal period, where spring tides are more powerful in seed dispersal than neap tides (Fig. 4). Moreover, the episodic extreme water levels due to storm surges were predicted to deliver a much higher number of viable seeds toward the adjacent mudflats (Fig. 4).

Seed retention at the adjacent tidal flats

Analyses of wave forcing in relation to seed retention on tidal flats showed that the time-averaged wave-induced bed shear stress ($\tau_{\text{wave\_avg}}$) during each tide was dependent on both wind speed and wind direction (onshore or offshore winds)

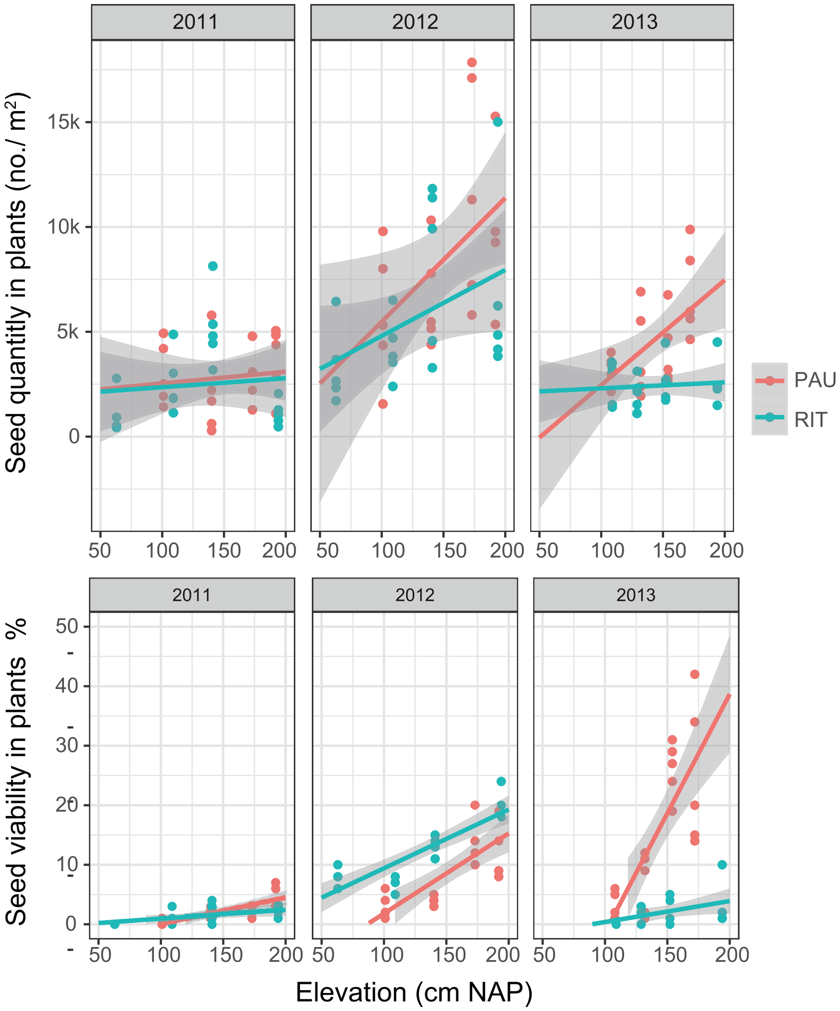

Fig. 2. Seed quantity and seed viability in plants along the elevation gradient at the wind-sheltered site Paulinapolder (PAU) and the wind-exposed site Ritthem (RIT) in 2011, 2012, and 2013. Despite between-sties and year-to-year variation, both seed quantity (no. m^{-2}) and seed viability (%) in plants increased significantly (Table 2a,b) with elevated ground height

(Table 3; Fig. 5). When the site was exposed to the wind (onshore winds dominated), $\tau_{\text{wave\_avg}}$ rises rapidly with increasing wind speed. Stormy weather (Beaufort wind force scale ≥ 6) yielded much greater $\tau_{\text{wave\_avg}}$ than normal conditions, as seen at all three field sites (Hellegatpolder, Bath, and the Wadden Sea marsh). By contrast, $\tau_{\text{wave\_avg}}$ under stormy weather was generally comparable with that during normal weather conditions when offshore winds dominated, despite a slight increasing trend of $\tau_{\text{wave\_avg}}$ with amplified averaged wind speed (Fig. 5).

Since seed retention decreases with increasing $\tau_{\text{wave\_avg}}$ (Zhu et al. 2020*a*), enlarged onshore wind speeds are expected to lower seed retention as a result of increased $\tau_{\text{wave\_avg}}$. Analysis of the seed bank experiments confirmed that seed retention at the tidal flats declined significantly with the growth of averaged wind speed (Table 4a; Supporting Information Table S4a). This decreasing trend was highly significant for onshore winds (Fig. 6a; Table 4b; Supporting Information Table S4b), whereas there was no significant relationship between seed retention and averaged offshore wind speed (Fig. 6b; Table 4c; Supporting Information Table S4c).

Seed burial depth alone had significant effects on seed burial, whereas there were no significant interactive effects between seed burial depth and averaged wind speed regardless of wind direction (Table 4). The decreasing trend of seed retention with increased speed of onshore winds was more obvious for seeds on the surface and buried at 0.5 cm than those buried deeper (Fig. 6a). For the seed retention data from surface seeds, an outlier (data point in triangle) occurred when there was a severe storm (Beaufort wind force scale ≥ 8) during the experiment. Although the averaged onshore wind speed was not so high during this period, all surface seeds were lost, and

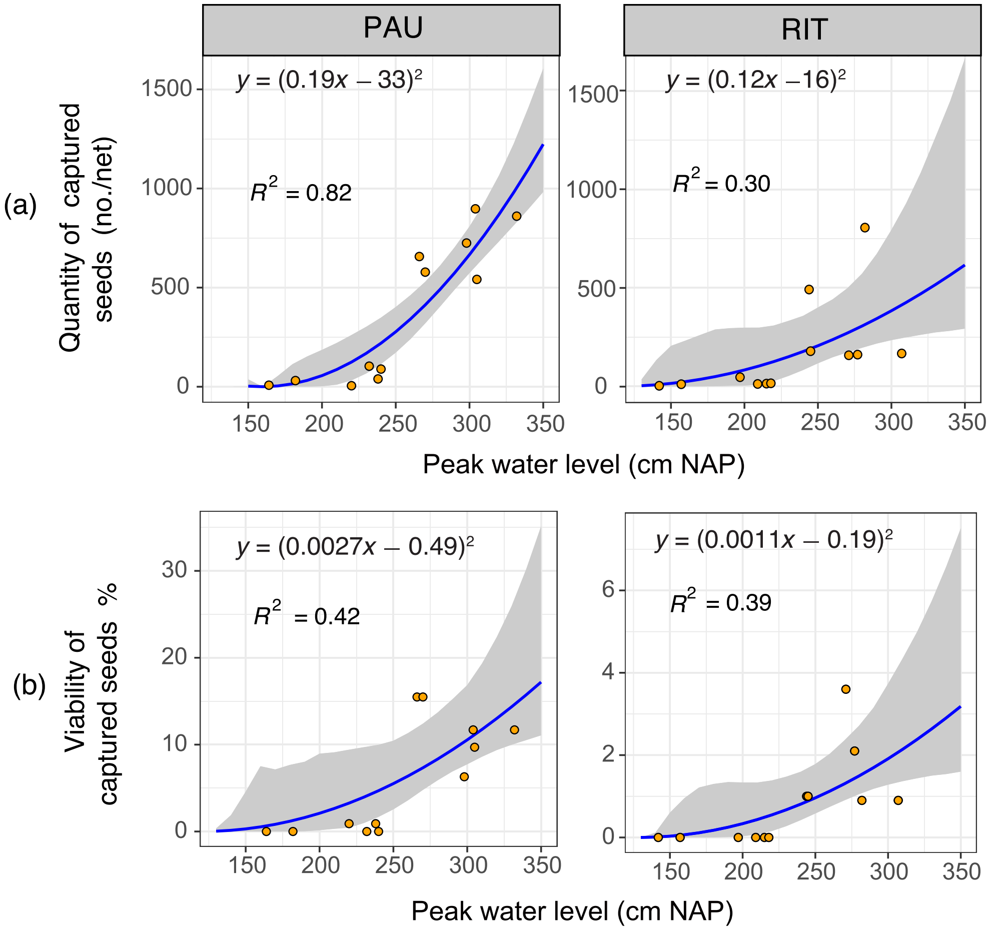

Fig. 3. For both the wind-sheltered site Paulinapolder (PAU) and the wind-exposed site Ritthem (RIT), the quantity and the viability of the seaward transported seeds captured in the floatable nets at increased significantly with elevated peak water level of the tide (Table 2c,d). For each relationship, we fit a curve with the equation: $y = (a * x + b)^2$.

even 25% of the seeds buried at the depth of 1.5 cm were also eroded (Fig. 6a).

Discussion

Tides and winds are both important seed dispersal drivers (Chambers and Macmahon 1994). Using cordgrass as an example, this study for the first time demonstrates the role of tides and winds in regulating seed dispersal in relation to lateral marsh regeneration, including the quantity and viability of delivered seeds as well as the quality of seed delivery (i.e., seed retention). The results reveal that spring tides are much more efficient in seed transport than neap tides, and storm surges deliver disproportionately higher numbers of viable seeds from the marsh towards the tidal flats than average conditions. Moreover, seed retention on tidal flats is controlled by winds. Increase of onshore wind speeds leads to enhanced seed removal by wave forcing on tidal flats.

The current study stresses the relevance of tidal pulsing in shaping seed transport in saltmarshes, supporting the flood pulse theory (Boedeltje et al. 2004; Gurnell et al. 2006; Vogt et al. 2006). The disproportionate impacts of spring tides and storm surges on seed delivery in tidal systems resembles high-flow periods in rivers that have major contribution to the seed dispersal of riparian plants (Boedeltje et al. 2004; Vogt et al. 2006). More importantly, our results additionally demonstrate that such high magnitude events influence not only the quantity but also the quality (i.e., viability) of seed dispersal.

Our findings suggest that storms may occasionally open “Windows of Opportunity” (WoO) for massive delivery of viable seeds toward the mudflats in front of a wind-sheltered marsh (Fig. 7a). WoO are highly relevant for plant regeneration in the disturbance-prone environments like coastal wetlands (Balke et al. 2014), where pioneer seedling establishment is often difficult due to harsh physical conditions such as wave disturbance and sediment erosion (Hu et al. 2015;

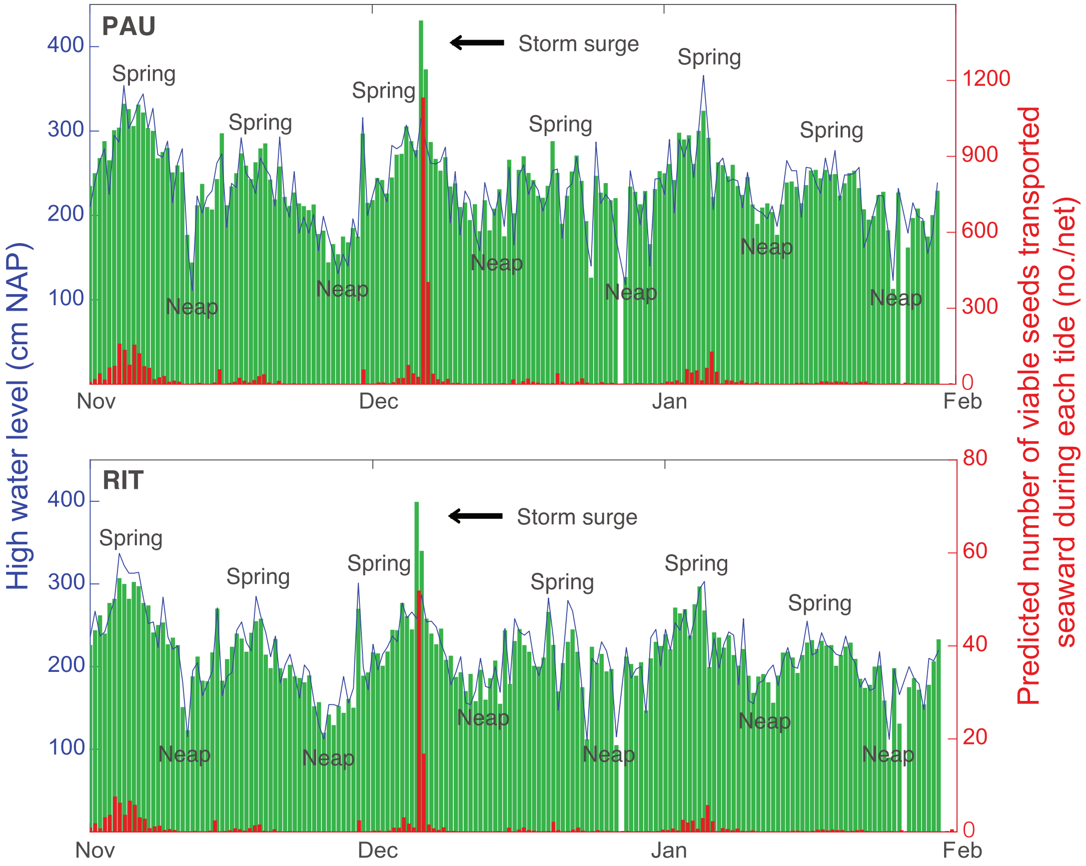

Fig. 4. Predicted (blue line) and measured (green bars) peak water level of each tide at wind-sheltered site Paulinapolder (PAU) and the wind-exposed site Ritthem (RIT) from November 2013 to February 2014, and the predicted temporal dynamics of effective seaward seed delivery (red bars). The latter was calculated as the number of viable seeds captured per net after each tide, based on the equations shown in Fig. 3.

Table 3. ANOVA table for the ANCOVA on time-averaged bed shear stress induced by waves.

Response variable	Source	Df	Sum Sq	Mean Sq	F value	Pr (> F)
Time-averaged bed shear stress induced by waves ($\tau_{\text{wave\_avg}}$)	Site	2	11.84	5.92	43.79	<0.001***
	Averaged wind speed	1	86.78	86.78	641.92	<0.001***
	Wind direction	1	41.66	41.66	308.13	<0.001***
	Site : averaged wind speed	2	18.71	9.35	69.19	<0.001***
	Site : wind direction	2	6.87	3.43	25.4	<0.001***
	Averaged wind speed : wind direction	1	21.91	21.91	162.06	<0.001***
	Site : averaged wind speed : wind direction	2	0.78	0.39	2.88	0.056
	Residuals	880	118.97	0.14		

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Bouma et al. 2016; Cao et al. 2018). Previous studies focused mainly on WoO associated with early-stage seedling survival on tidal flats, such as periods of free inundation (Balke et al. 2011; Balke et al. 2014), low hydrodynamic forcing, and limited sediment variability (Hu et al. 2015; Poppema et al. 2019). Here we stress that WoO exist for both seed and seedling stages, as successful seedling establishment entails not only suitable conditions for seedling growth and survival,

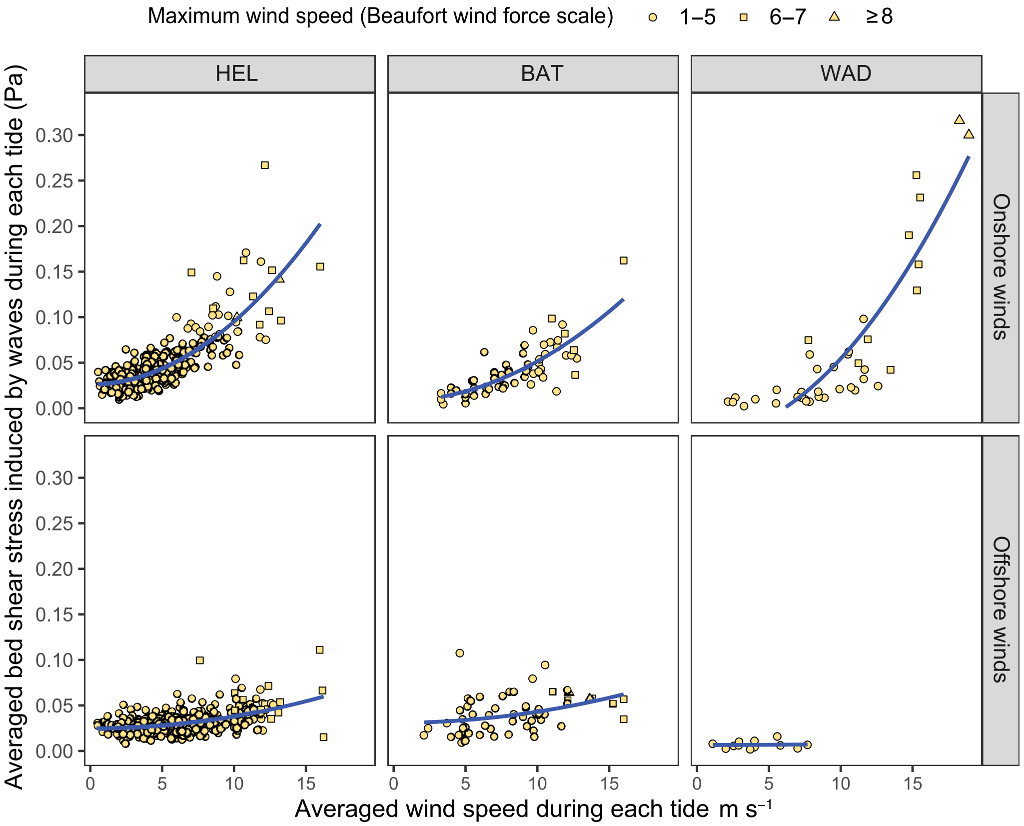

Fig. 5. Relation between the time-averaged bed shear stress induced by waves and the averaged wind speed and wind direction scenarios (onshore winds or offshore winds dominated) during each tide. For each panel, the data points were fit with a quadratic function: $y = a * x^2 + b$. Waves data were collected during the seed dispersal season (October–April) at tidal flats in front of the marsh at the wind-sheltered site Hellegatpolder and wind-exposed site Bath in the Westerschelde, as well as a more wind-exposed site along the Wadden Sea coast (WAD) (Fig. 1b; Table 1).

Table 4. Analysis of deviance table of the GLMs (family = "quasi-binomial") on seed retention on the tidal flats in front of the marsh.

Response variable	Source	Df	Deviance	Resid. Df	Resid. Dev	Pr (> chi)
(a) Seed retention	Seed depth	1	16.30	26.00	3.86	<0.001***
	Averaged wind speed	1	0.58	25.00	3.28	0.034*
	Seed depth : averaged wind speed	1	0.03	24.00	3.25	0.614
(b) Seed retention	Seed depth	1	16.30	26.00	3.86	<0.001***
	Averaged onshore wind speed	1	1.69	25.00	2.18	<0.001***
	Seed depth : averaged onshore wind speed	1	0.00	24.00	2.17	0.901
(c) Seed retention	Seed depth	1	16.30	26.00	3.86	<0.001***
	Averaged offshore wind speed	1	0.43	25.00	3.44	0.096
	Seed depth : averaged offshore wind speed	1	0.04	24.00	3.40	0.632

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

but also that good seeds are present at the right place and time (Zhu et al. 2014).

Strong waves during severe storms, however, could pose "Windows of Risk" for wind-exposed marshes (Fig. 7b). Low seed availability due to seed removal at the tidal flats during the winter has been recognized as a critical bottleneck constraining plant establishment at tidal flats (Groenendijk 1986; Houwing 2000; Zhu et al. 2014). Previous field studies showed that waves dislodged seeds from the tidal flat surface without burying them, and seed retention decreased with increasing bed shear stress induced by waves (Zhu et al. 2020*a*, 2021). We found that storm-enlarged bed shear stress impedes seed retention on mudflat surface and can even erode buried seeds from tidal flats, yielding

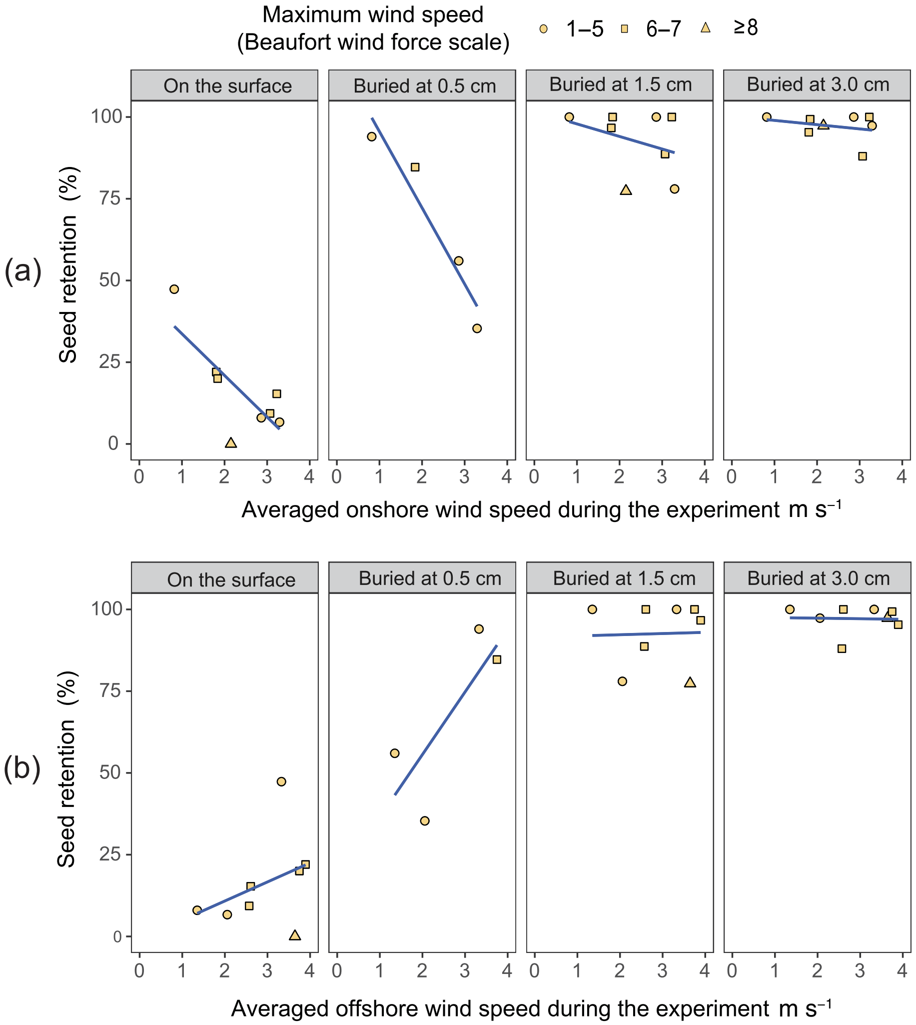

Fig. 6. (**a**) The retention of seeds on the surface or buried at different depths decreased significantly with the increase of averaged onshore wind speed during each experimental period (Table 4b). For the retention of surface seeds, an outlier (data point in triangle) occurred when a severe storm (Beaufort wind force scale ≥ 8) took place during the experiment. (**b**) There was no significant relationship between seed retention and averaged offshore wind speed (Table 4c).

ineffective seed dispersal and declines of seed availability for plant regeneration on tidal flats. Although extreme high water levels during storms can enhance seed delivery, the tidal flats were not conducive to seed deposition and retention due to strong waves. In this case, a large quantity of seeds was transported but did not end up at desired locations (i.e., adjacent tidal flats), resulting a net loss of seeds from the system. The eroded seeds may be transported seaward to distant places or washed ashore, with a net landward transport (Huiskes et al. 1995). The landward transported seeds can either be added into driftline materials deposited near/on the dike (Wolters and Bakker 2002) or trapped by the standing vegetation (Chang et al. 2008). A previous field study on seed rain patterns showed that the highest density of captured seeds within saltmarsh vegetation was found during a stormy period (Chang et al. 2007). Storms tend to redistribute the seeds from the relatively more exposed areas (e.g., tidal flats) toward the relatively more sheltered places (e.g., within vegetation), where seedling establishment is, however, less meaningful due to the lack of niches (Deng et al. 2009).

The likely enhanced storminess (Knutson et al. 2010; Lin et al. 2012) under climate change and associated extreme sea levels (Wahl et al. 2017) motivates the use of saltmarshes as nature-based coastal defense (Cheong et al. 2013; Temmerman et al. 2013; Barbier 2014). This study, however, suggests that increased storminess may decline seed availability on tidal flats for the regeneration of wind-exposed marshes, by incurring more “Windows of Risk” of ineffective seed dispersal that could weaken marsh resilience. This impairs long-term marsh persistence as well as their coastal defense functions. To avoid being caught in a “Catch 22” situation like this, human assistance may help improve marsh resilience to lateral

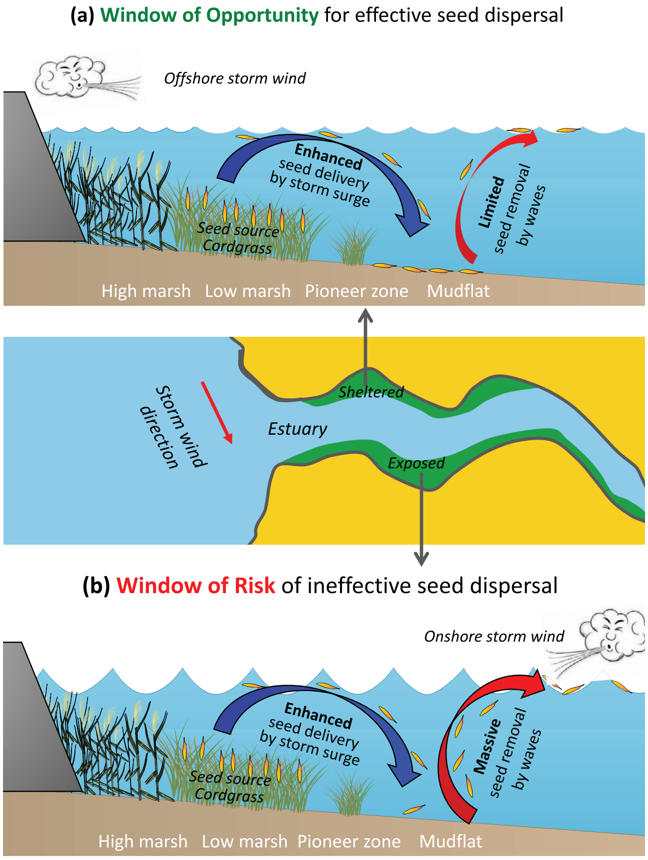

Fig. 7. (**a**) For wind-sheltered marshes, storms can serve as "Windows of Opportunity" for effective seed dispersal: enhanced seed delivery toward adjacent tidal flats by storm surge + limited seed removal by waves. This can increase seed availability for marsh regeneration on tidal flats. (**b**) For wind-exposed marshes, storms can function as "Windows of Risk" of ineffective seed dispersal: enhanced seaward delivery + massive seed removal by waves. A large quantity of seeds was transported but did not end up at desired locations (i.e., adjacent tidal flats), resulting a net loss of seeds from the system.

degradation. For instance, at wind-exposed sites, seeds of target plants could be deliberately buried to a moderate depth after the stormy season to enhance seed availability for plant regeneration at tidal flats. Other measures may include biodegradable structures that help shield the seeds from hydrodynamics and stabilize the sediment during the winter to improve seed persistence (Temmink et al. 2020).

For wind-sheltered marshes, more frequent and stronger storms may enhance seed-based marsh regeneration on tidal flats by opening up more "Windows of Opportunity" for effective seed dispersal. This effect can enhance marsh resilience and may even facilitate the expansion of wind-sheltered marshes. Although these marshes are not so relevant for wave attenuation during storms, they are still valuable for coastal protection. Given that storm surges can also occur and cause failure of engineered structures at wind-sheltered sites, marshes at these sites can mitigate the impacts of coastal flooding due to the breaching of engineered defenses (Zhu et al. 2020*b*).

As this work is a postanalysis that integrates relevant data from available sources rather than a preplanned study for specific sites, seed delivery surveys and seed retention experiments were not conducted at the same sites. This flaw hampers the quantification of combined effects of tides and winds on effective seed dispersal of cordgrass toward tidal flats for each site. However, the data integration approach is valid in this study, as we aim at detecting general principles instead of site-specific knowledge. Although the study sites differ in parameters such as seed production, tide heights and wind exposure, we do not expect large differences in terms of general principles governing the patterns and processes in relation to seed dispersal, hydrodynamics, and winds. Moreover, we also ensured that the data of one parameter was measured for at least two sites to account for variations between sites.

Overall, the current study provides novel insights into how variability in tides and winds as well as extreme events may regulate the potential of seed-based marsh recovery on adjacent tidal flats. We specifically highlight the role of storms in shaping key ecological processes associated with the resilience of saltmarshes to lateral degradation, either by opening up "Window of Opportunity" or incurring "Window of Risk" (Fig. 7). In the face of changing storminess and growing need of nature-based flood defense by coastal wetlands under global change, such knowledge is relevant for assessing long-term marsh stability and the sustainability of nature-based coastal defenses with saltmarshes.

Data availability statement

The datasets used in this paper are available upon request.

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Conflict of Interest

None declared.

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