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Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics

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Abstract

Our study aims to enhance process understanding of the long-term (decadal and longer) cyclic marsh dynamics by identifying the mechanisms that translate large-scale physical forcing in the system into vegetation change, in particular (*i*) the initiation of lateral erosion on an expanding marsh, and (*ii*) the control of seedling establishment in front of an eroding marsh-cliff. Short-term sediment dynamics (i.e., seasonal and shorter changes in sediment elevation) at the mudflat causes variation in mudflat elevation over time (δz_{TF}). The resulting difference in elevation between the tidal flat and adjacent marsh (ΔZ) initiates lateral marsh erosion. Marsh erosion rate was found to depend on sediment type and to increase with increasing ΔZ and hydrodynamic exposure. Laboratory and field experiments revealed that seedling establishment was negatively impacted by an increasing δz_{TF}. As the amplitude of δz_{TF} increases towards the channel, expanding marshes become more prone to lateral erosion the further they extend on a tidal flat, and the chance for seedlings to establish increases with the distance that marsh has eroded back towards the land. This process-based understanding, showing the role of sediment dynamics as explanatory factor for marsh cyclicity, is important for protecting and restoring valuable marsh ecosystems. Overall, our experiments emphasize the need for understanding the connections between neighbouring ecosystems such as mudflat and salt marsh.

Introduction

Salt marshes form an important element in coastal systems, providing habitat to unique plant and invertebrate communities (Irmler et al. 2002), and providing ecosystem services like hosting large numbers of migratory birds (Van Eerden et al. 2005; Laursen et al. 2009) and contributing to coastal defence by dissipating waves in front of sea defences (Möller 2006; Temmerman et al. 2013; Möller et al. 2014). Salt marshes are typically formed by two-way interactions between biological and physical processes, so-called biogeomorphic feedback. Salt-marsh vegetation traps sediments by reducing hydrodynamic energy (Leonard and Luther 1995; Bouma et al. 2005a; Temmerman et al. 2007, 2012), which causes the vegetation to grow better (Bruno 2000; Van Wesenbeeck et al. 2008) and hence to become more effective in trapping more sediment, thereby causing a positive feedback (Fagherazzi et al. 2012; Kirwan and Megonigal 2013). If vertical accretion exceeds sea-level rise, the decrease in inundation will cause succession from pioneer to low marsh and eventually high marsh vegetation types (De Leeuw et al. 1993; Adam 2002). If vertical sediment accretion is smaller than sea-level rise, marshes are at risk of drowning and suffer "coastal squeeze" when dikes prevent (high) marshes to recede inland (Doody 2004). Consequently, a large body of recent research has focused on the question whether vertical accretion rates on salt-marsh platforms can keep up with sea-level rise (Bartholdy et al. 2004; Kirwan and Temmerman 2009; Kirwan et al. 2010). In a recent meta-analysis, Kirwan et al. (2016) concluded that marshes can generally survive under a wide range of future sea-level scenarios. Recent modeling, however, indicates that the most important threat

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of sea-level rise to salt marshes may actually be posed by lateral erosion of salt marsh edges rather than drowning of salt marsh platforms (Mariotti and Fagherazzi 2010, 2013; Marani et al. 2011a; Kirwan et al. 2016). Low rates of sea-level rise result in small increases in water depths on the tidal flat in front of the salt marsh, thereby allowing for the persistence of effective wave attenuation over the tidal flat, minimizing lateral marsh erosion as only small waves reach the vegetated marsh edge. High rates of relative sea-level rise, on the other hand, increase the water depth over the tidal flats, thereby increasing the probability of wave propagation over the tidal flat and increasing the chance for marsh edge erosion (Mariotti and Fagherazzi 2010). The latter may be counteracted by enhanced sediment accretion if there is significant sediment supply (Mariotti and Fagherazzi 2010). Overall, obtaining a mechanistic understanding of the marsh edge dynamics is crucial for understanding the vulnerability to marsh loss in response to sea-level rise.

Marshes are dynamic ecosystems in which the position of the marsh edge experiences, on a decadal or longer time-scale, cyclic alternations between *(i)* an expansion-phase, characterised by lateral edge expansion onto the tidal flat which typically starts with seedling establishment, and *(ii)* a retreat-phase, characterised by lateral erosion in which a retreating cliff removes both the vegetation and the sediment-layer accumulated by the vegetation (Pye 1995; Allen 2000; Van der Wal et al. 2008; Chauhan 2009). The cyclic marsh dynamics may not always be apparent, as marshes may appear to be static due to the long time scales involved (decades to centuries). Although these cyclic dynamics have been recognised for a long time (Yapp et al. 1917; Gray 1972; Allen 2000), our understanding of the actual processes driving these dynamics remains poor. Existing studies on cyclic marsh loss by lateral erosion and marsh expansion by re-establishment of pioneer vegetation mainly use conceptual modeling (van de Koppel et al. 2005; Mariotti and Fagherazzi 2010; Tambroni and Seminara 2012) or large-scale empirical approaches, by relating remote sensing data of salt marsh retreat/expansion to datasets of hydro-meteorological forcing (Pye 1995; Cox et al. 2003; Van der Wal and Pye 2004; Van der Wal et al. 2008; Wang and Temmerman 2013). With respect to the initiation of lateral marsh erosion, at the landscape scale it has been attributed to changes in external forcing, such as increased shipping, shifted position of estuarine channels, wind-wave activity or sea-level rise (Allen 1989, 2000; Cox et al. 2003; Van der Wal and Pye 2004; Van der Wal et al. 2008). Alternatively, the initiation of marsh erosion has been described as an autonomous process that will inevitably occur due to the steepening of aging marsh edges, as vertical sediment accretion within the marsh vegetation is much faster than on the non-vegetated tidal flat in front of the marsh edge (van de Koppel et al. 2005; Chauhan 2009). Recent experimental studies on marsh edge erosion focus on processes affecting the erosion rate rather than the mechanisms inducing the initial erosional process (Feagin et al. 2009; Deegan et al. 2012; Silliman et al. 2012). Hence, none of the available studies give mechanistic insight in what process triggers the onset of lateral marsh erosion. Similarly, with respect to seedling establishment we also lack a mechanistic insight in the processes that enable/disable seedlings to establish (Bouma et al. 2009; Friess et al. 2012). We largely lack small-scale process studies that provide mechanistic insight in the *tipping points* (i.e., conditions initiating a shift in development) between salt marsh erosion and expansion. That is, we lack mechanistic insight in both *(i)* the actual processes that *initiate or prevent* lateral erosion on a laterally expanding marsh, as well as *(ii)* the processes that *enable or disable* seedlings to establish in front of a retreating cliff. The aim of the present study is to provide mechanistic insights in *(i)* the processes that induce or prevent the onset of lateral marsh erosion and *(ii)* the processes that enable or disable the onset of marsh expansion by seedling establishment. Present study thus does not focus on long-term, large-scale trends in physical forcing that ultimately constrain marsh evolution, but rather aims at understanding the short-term processes effectuating transitions in vegetation cover.

In a hydrodynamic analysis of four marshes differing in wind exposure and long-term development, Callaghan et al. (2010) demonstrated that the time-integrated sediment erosion rate due to wave forcing on the intertidal mudflat in front of a marsh was a factor of two higher for salt marshes that are laterally eroding than for laterally expanding marshes, regardless of the wind exposure. The long-term survival of seagrass meadows has also been recently related to sediment dynamics (Suykerbuyk et al., 2016). Previous studies have shown that on tidal mudflats, a seasonal cycle of sediment accretion and erosion exists, related to seasonal wind conditions (Herman et al. 2001; Yang et al. 2008). Callaghan et al. (2010) suggested that such seasonal variation in bed-level elevation of the tidal flat may cause the formation of a small cliff at the boundary between the dynamic bare mudflat sediment and the more stable vegetated marsh sediment. Recent studies also suggest sediment dynamics to play an important role in seedling establishment in various coastal wetlands (Han et al. 2012; Balke et al. 2013; Silinski et al. 2016). Hence, we expect that sediment dynamics on the mudflat, as they may occur at an even shorter time scale within a season, may hamper the establishment of pioneer seedlings. In this study, we want to test the following hypotheses, to mechanistically explain how mudflat sediment dynamics can determine the tipping points at which expanding marshes start to erode and eroding marshes can re-establish by seedlings:

i. Short-term sediment dynamics on tidal flats (δz_{TF}) can initiate lateral marsh erosion by creating a height differences between the tidal flat and the more stable marsh surface (ΔZ), with erosion rates depending on ΔZ, the

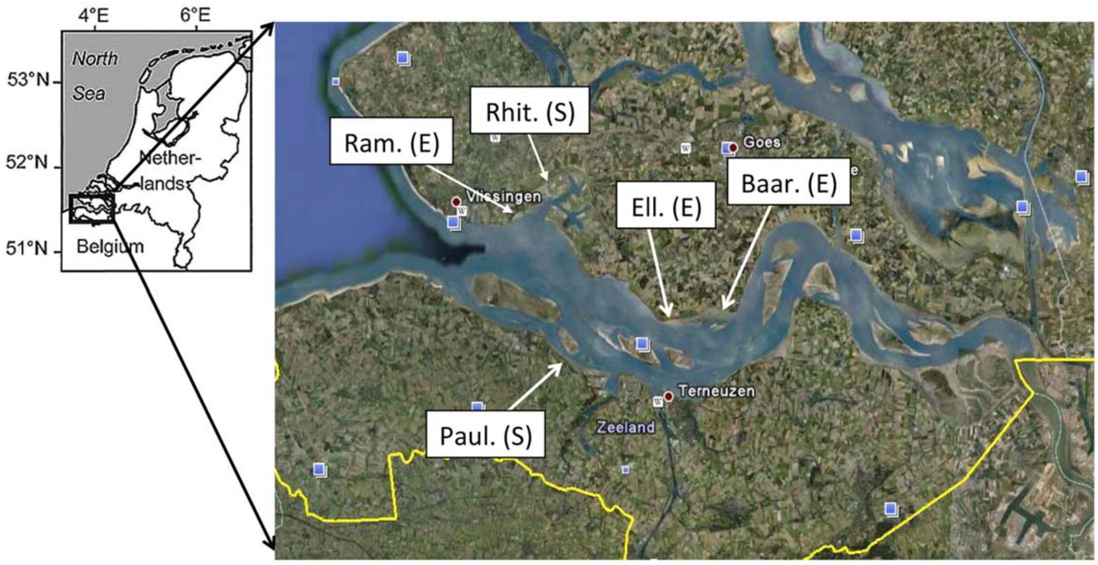

Fig. 1. Overview of the study sites used within the Western Scheldt estuary in SW Netherlands. Location names are abbreviated and sheltered and exposed sites are indicated with a capital E or S in brackets behind the location abbreviation. The 1st experiment at identifying mechanisms initiating marsh erosion was carried out at Ellewoutsdijk (Ell); for the 2nd experiment we collected sandy marsh cores from Rammekenshoek (Ram) and muddy marsh cores from Ellewoutsdijk (Ell) and placed these cores back at the exposed mudflat from Ellewoutsdijk and sheltered mudflat of Ritthem (Ritt). For the seedling establishment experiments, seedlings were planted at different distances from the marsh edge at Ellewoutsdijk (Ell), Baarland (Baar) and Paulinapolder (Paul). These marshes differ in wind exposure, as the main wind direction is South West (Callaghan et al. 2010).

marsh sediment type (stability) and the hydrodynamic exposure.

ii. The sediment dynamics on a tidal mudflat can result in short-term, within-season fluctuations in bed-level (δz_{TF}) that prevent seedlings from establishing when these bed-level changes (δz_{TF}) become too large.

iii. We hypothesise that the short-term sediment dynamics on a tidal mudflat (δz_{TF}) decrease from the seaside towards the land. This spatial trend explains both why lateral expansion towards the seaside (where δz_{TF} is larger) makes marshes increasingly vulnerable to lateral erosion, and why seedlings can only re-establish after a marsh-cliff has retreated landward to areas where δz_{TF} is small enough for seedlings to survive.

These hypotheses were tested by a combination of field and laboratory experiments. The outcomes are used to discuss implications for management aimed at preserving marshes.

Methods

Experiments related to hypothesis 1: mechanisms initiating lateral marsh erosion and factors affecting marsh-erosion rates

We carried out a manipulative field experiment to test the hypothesis that sediment dynamics on a tidal mudflat (δz_{TF}) can initiate a height difference (ΔZ), which can be the onset of subsequent marsh erosion. In the fall of 2011, we placed 4 cores (120 mm diameter; 200 mm height) with marsh vegetation on the tidal mudflat of Ellewoutsdijk (Scheldt estuary, SW Netherlands; Fig. 1). At this location, the tidal range is around 4 m and the elevation is 1.1 m above NAP (i.e., the Dutch ordinance level, which is close to local mean sea level). Tidal currents are proportional to tidal amplitude (Bouma et al. 2005b). At 1.1 m above NAP the maximum tidal currents as measured during spring tides is around 0.5 m s^{-1}, which is higher than typically observed in the pioneer zone where *Spartina* seedlings settle (i.e., around 0.25 m s^{-1}; Bouma et al. 2005b). This site is suitable to study initiation of marsh erosion, as it is close to where in the past a cliff was originally formed (Van der Wal et al. 2008) and because hydrodynamics are typically stronger in areas where colonisation occurs via clonal expansion rather than seedling establishment (cf. Silinski et al. 2016). The Ellewoutsdijk site is wind exposed, and typical wave conditions have been described in Callaghan et al. (2010) and Hu et al. (2015a). To show that it is the changes in bed elevation of the tidal flat (δz_{TF}) that causes marsh erosion, we inserted 2 cores directly into the tidal flat, whereas 2 other cores were surrounded by a concrete ring (230 mm outer diameter, 120 mm inner diameter and 35 mm high; Fig. 2). The concrete ring generated a fixed surrounding bed-level (i.e., $\delta z_{TF} = 0$), whereas the sediment around the cores without the concrete could freely accrete or erode (i.e., δz_{TF} is variable). After placing the cores 1 m apart, sediment heights of the mudflat and cores were regularly monitored using 1 m long Sediment Erosion Bars (Nolte et al. 2013). The SEB bars for these short-term measurements were specifically designed to allow measurements at small lateral intervals (i.e., we used a 2 cm interval on the cores and a 10 cm interval at the surrounding mudflat),

Fig. 2. Visual presentation of the concrete-rings-method, used to mimic a stabile non-eroding mudflat with a constant height (i.e., $\delta z_{TF} = 0$) adjacent to marsh sediment (i.e., the marsh core). A height difference between the mudflat and marsh core (ΔZ) can be created artificially by raising the core in the concrete ring, and mimics in a simplified way the height difference as will be obtained due to sediment dynamics on the tidal flat (δz_{TF}) adjacent to a marsh with more stable sediment.

so that we could measure elevation changes for *i)* the tidal flat and *ii)* the marsh core at several positions ($n = 5$). Per core, these measurements were averaged to a single value. The SEB bars were placed, making use of PVC-tubes with 0.1 m above-ground length and 0.55 m below-ground length. To minimize disruption during SEB measurements, we only walked on the landward side of the cores, using snowshoes.

In the second field experiment, we wanted to demonstrate that the rate of erosion strongly depends on the height difference between tidal flat and marsh vegetation (ΔZ), the sediment composition of the marsh cores, and the hydrodynamic energy in the system. We collected cores from a sandy marsh (median grain size 140 μm and silt content of 30%; Rammekenshoek, Scheldt estuary, SW Netherlands; Fig. 1) and a marsh with compacted, more fine-grained sediment (median grain size 80 μm and silt content of 40%; Ellewoutsdijk, Scheldt estuary, SW Netherlands; Fig. 1). These cores were placed at the marsh of Ritthem, which is completely sheltered by harbour dams (i.e., negligible waves), and the exposed marsh of Ellewoutsdijk (wave conditions described in Callaghan et al. 2010 and Hu et al. 2015a), both located in the Scheldt estuary, SW Netherlands (Fig. 1). All cores were surrounded by a concrete ring, in order to avoid any effects of changes in height in the tidal mudflat (i.e., $\delta z_{TF} = 0$), thus allowing us to fully focus on the erosion of the marsh cores. After placing the cores, the height of cores was monitored relative to the concrete ring, using the 1m-long Sediment Erosion Bars as described above. In both experiments, the concrete rings did not sink into the sediment during the duration of the experiment.

Experiments related to hypothesis 2: mechanism hampering seedling establishment

We tested the hypothesis that too large sediment dynamics on a tidal mudflat (i.e., too large δz_{TF}) will prevent seedlings from establishing by a combination of a series of mesocosm experiments and a field experiment. In our study, we focussed on the gramineae *Spartina anglica* Hubbard, which is a dominant pioneer species in NW European salt marshes. All mesocosm experiments were done in a climate room, where *Spartina* seedlings experienced a constant temperature of 18°C and light was supplied during 18 h d^{-1} with an average surface irradiance of 250 μmol photons m^{-2} s^{-1}. Using an automated pumping system, seedlings were inundated 2 times for 1 h d^{-1} with seawater of 15 PPM, with one inundation during the light period and one inundation during the dark period. *Spartina* seedlings were grown on locally collected sandy material, unless indicated differently.

In the 1st of three mesocosm experiments, we tested the effect of seed burial depth on seedling emergence, by burying *Spartina* seeds at a range of depths (5, 10, 15, 25, 45, 65 and 85 mm; $n = 10$), and monitoring emergence over a 42 day period. In a 2nd mesocosm experiment, we determined to what extent seed burial depth affects the seedling resistance to erosion events. That is, germinated *Spartina* seedlings were planted at a depth of 10, 20 and 40 mm (based on results of exp. 1), and after a 20 day period, the critical disturbance depth (CDD) was measured in a flume. The CDD was defined as the minimum erosion depth that causes a seedling to topple over when exposed to (tidal) current in a flume, as toppling over is expected to cause seedling mortality in the field. To mimic peak current velocities typical for the *Spartina* pioneer zone, the current was set at 0.25 m s^{-1} using a water level of 0.30 m, as observed during upcoming spring-tides when currents are strongest (Bouma et al. 2005b). The method used to apply step-wise erosion treatments to determine the CDD is explained in detail in Fig. 3a (cf. Balke et al. 2011; Infantes et al. 2011). In the 3rd mesocosm experiment, we measured how continuous accretion rates (3 and 6 mm wk^{-1}) or erosion rates (−3 mm wk^{-1}) affect the CDD. Accretion and erosion treatments were

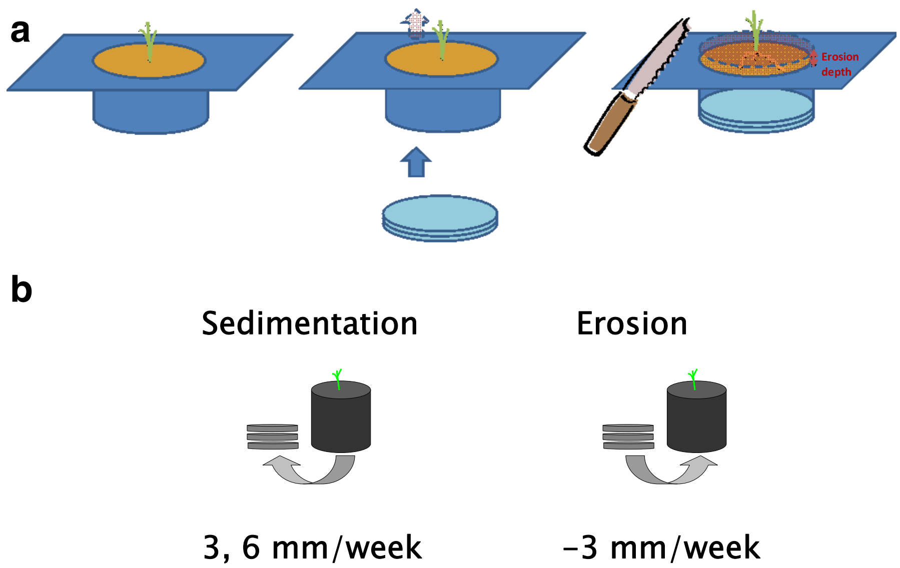

Fig. 3. Schematic representation of the method used to quantify the critical disturbance depth (CDD; 3a; cf. Balke et al. 2011, Infantes et al. 2011), and the method used to expose young *Spartina* seedlings to contrasting accretion and erosion rates (3b; cf. Han et al. 2012, Balke et al. 2013). Measuring the CDD involves step-wise insertion of discs, careful removal of the top sediment layer without harming the seedling, and at each step measuring if the seedling topples over when exposed (in a flume) to a mimicked upcoming tide when currents are highest [i.e., current set at 0.25 m s^{-1} using a water level of 0.30 m, based on field data from Bouma et al. (2005b)]. If a seedling topples over, the seedling is regarded to be lost under field conditions, so that the thickness of the inserted discs (= CDD) indicates the resistance of the seedling to disturbances from sheet erosion or sediment mixing. Applying continuous accretion rates of 3 and 6 mm wk^{-1} was achieved by removing pre-placed discs from the bottom of the pot and subsequent adding sediment on top of the pot, while applying a continuous erosion rate of −3 mm wk^{-1} was realised by adding discs at the bottom of the pot and carefully removing the top sediment layer without harming the seedling. To be able to measure the CDD and applying contrasting accretion and erosion rates requires pots that allow the insertion of discs at the bottom. Hence, the pots should have a constant diameter over its total length, and having an open bottom. Therefore, we used standard PVC drainage tubes, in which we placed a plastic bag to hold the sediment with the seedlings.

applied as explained in Fig. 3b (cf. Han et al. 2012; Balke et al. 2013). We planted germinated *Spartina* seedlings at 20 mm depth, and started the weekly sediment accretion and erosion treatments 7 days after planting. We used two types of sediment: muddy (median grain size 50 μm and silt content of 60%) vs. sandy (median grain size 230 μm and silt content of 0%). After a 49 day (i.e., after 6 weekly sediment accretion and erosion treatments) and 77 day (i.e., after 10 weekly sediment accretion and erosion treatments) period, the CDD was measured in a flume. These periods were chosen to represent two clearly different plant sizes.

In the field experiment, we monitored seedling survival at 3 mudflats in the Western Scheldt estuary (SW Netherlands; Fig. 1): Ellewoutsdijk (exposed; median grain size 50 μm and silt content of 60%), Paulinapolder (sheltered; median grain size 115 μm and silt content of 25%) and Baarland (exposed; median grain size 45 μm and silt content of 65%). With the majority of the wind coming from the South East, these three marshes differ in wind and thus wave exposure (for detailed information on wind statistics and the resulting wave climate see Fig. 4, Table 1 and Fig. 10 in Callaghan et al. 2010, who studied these specific sites) and consequently in sediment type. At each site, seedlings were planted at increasing distances from the marsh edge, where we expected sediment dynamics (δz_{TF}) to increase (see next section). At different distances the transplanted seedlings also have different elevations, thereby experiencing different inundation periods. Seedling survival was tracked from April to August 2009, and during this period the loss rates for each elevation were estimated using the maximum likelihood method assuming an exponential decay function. To identify which factors explained the survival of the transplanted seedlings, we carried out a step-wise multiple linear regression in which we included all known variables: elevation; wave fetch (cf. van der Wal et al. 2008); average wave height; wave height during stormy conditions (cf. Callaghan et al. 2010); the sediment dynamics approximated by the range [δz_{TF} = max(z)-min(z)] and the standard deviation ($\delta z_{TF} = \sigma z_t$ following Balke et al. 2013) of the sediment bed-level (measuring method is explained in next section). The estimated seedling loss rates were log transformed. All data used in the step-wise multiple linear regression are listed in digital appendix Table 1.

Measurements related to hypothesis 3: sediment dynamics (δz_{TF}) along the mudflat

We tested the hypothesis that the sediment dynamics on a mudflat decreases from the seaside towards the land, by

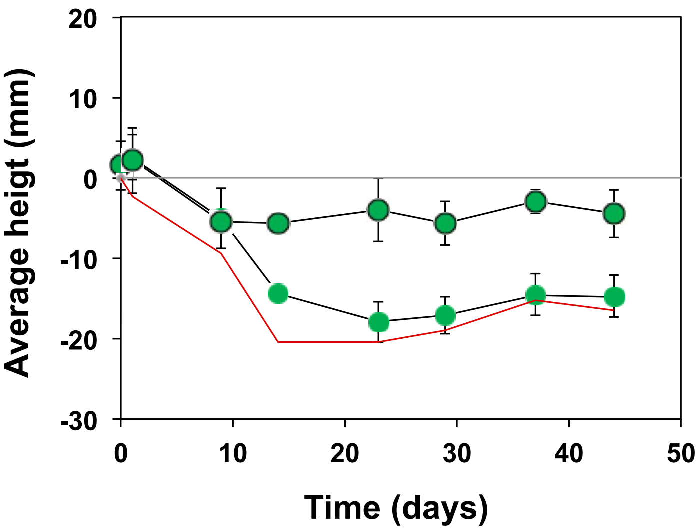

Fig. 4. Erosion of sediment cores originating from the salt marsh and placed on the mudflat. The surrounding of the core consisted either of a concrete ring (i.e., points with surrounding line) to keep the height of the surrounding 'sediment' fixed (i.e., $\delta z_{TF} = 0$), or consisted of mudflat that could freely accrete or erode (i.e., points without surrounding line). At placement (t0), marsh cores were level with the surrounding (i.e., $\Delta Z = 0$ at t0). The evolution of the elevation of the tidal mudflat (δz_{TF}) is indicated by the solid red line. The marsh cores that don't have a concrete ring followed the level of the tidal mudflat, whereas the marsh cores that are surrounded by a concrete ring have very limited erosion due to the absence of a ΔZ between the cores and their fixed (concrete) surrounding. This difference indicates that height changes of the tidal mudflat can initiate marsh erosion ($F = 81.09$, $p < 0.01$). [Color figure can be viewed at wileyonlinelibrary.com]

measuring the sediment dynamics for 3 mudflats in the Western Scheldt estuary (SW Netherlands; Fig. 1): Ellewoutsdijk, Paulinapolder and Baarland. At these sites, monthly changes in bed elevation were measured using SEB's, at the range of distances from the marsh edge where the seedlings were planted. Because these monthly measurements may have caused us to miss many bed-level modifications, we calculated the maximal difference between the lowest and highest observed bed-elevation and the standard deviation (following Balke et al. 2013) over the measuring period (April to August 2009) as proxy for the sediment dynamics at each location.

Statistical analyses

A repeated measures ANOVA was used to analyse if final elevation levels differed between marsh erosion treatments. Data was log-transformed when necessary to meet assumptions for the ANOVAs. Mauchly's method was used to test for Sphericity of data and Greenhouse-Geisser correction was used when the compound symmetry assumption (sphericity) did not hold. Differences at $p < 0.05$ were considered significant. For seedling establishment experiments in the laboratory we analyzed the data using linear regression. The seedling survival in the field experiment was analyzed using a stepwise multiple regression. Using this method, parameters that are directly correlated across field sites, will never come together within the regression model. Parameters that are correlated within field sites, but where the correlative relationship differs across field sites, can both end up in a single

Table 1. Concise overview of the definitions of all parameters used within this paper.

Abbreviation	Description of parameter	Usage
δz_{TF}	short-term sediment dynamics occurring on tidal flats, defined as the within-season changes in bed elevation on a tidal-flat	Figs. 4, 9, 10, 11
δz_M	short-term sediment dynamics occurring on a salt marsh, defined similar as for the tidal flat	Fig. 11
σz_t	the standard deviation of the measured sediment bed elevation on a tidal flat, during a period *t*. This approach focuses on representing the statistically average conditions (cf. Balke et al. 2013).	proxy δz_{TF} in regression
Max(z)-min(z)	the difference between the maximum and minimum elevation of the sediment bed-level, as observed within a given measuring period. This approach focuses on representing the extreme elevation changes.	proxy δz_{TF} in regression
ΔZ	the height difference in bed-level between the relative instable tidal flat and the more stable marsh surface	Figs. 4, 5, 11
CDD	the critical disturbance depth is defined as the minimum erosion depth that causes a seedling to topple over when exposed to current; proxy of seedling sensitivity to δz_{TF}	Figs. 3-11;
D	Burial depth of seed	Figs. 6, 7
E	Percentage of emergent seedlings	Fig. 6
NAP	the Dutch ordinance level, which is close to local mean sea level	Figs. 9, 10

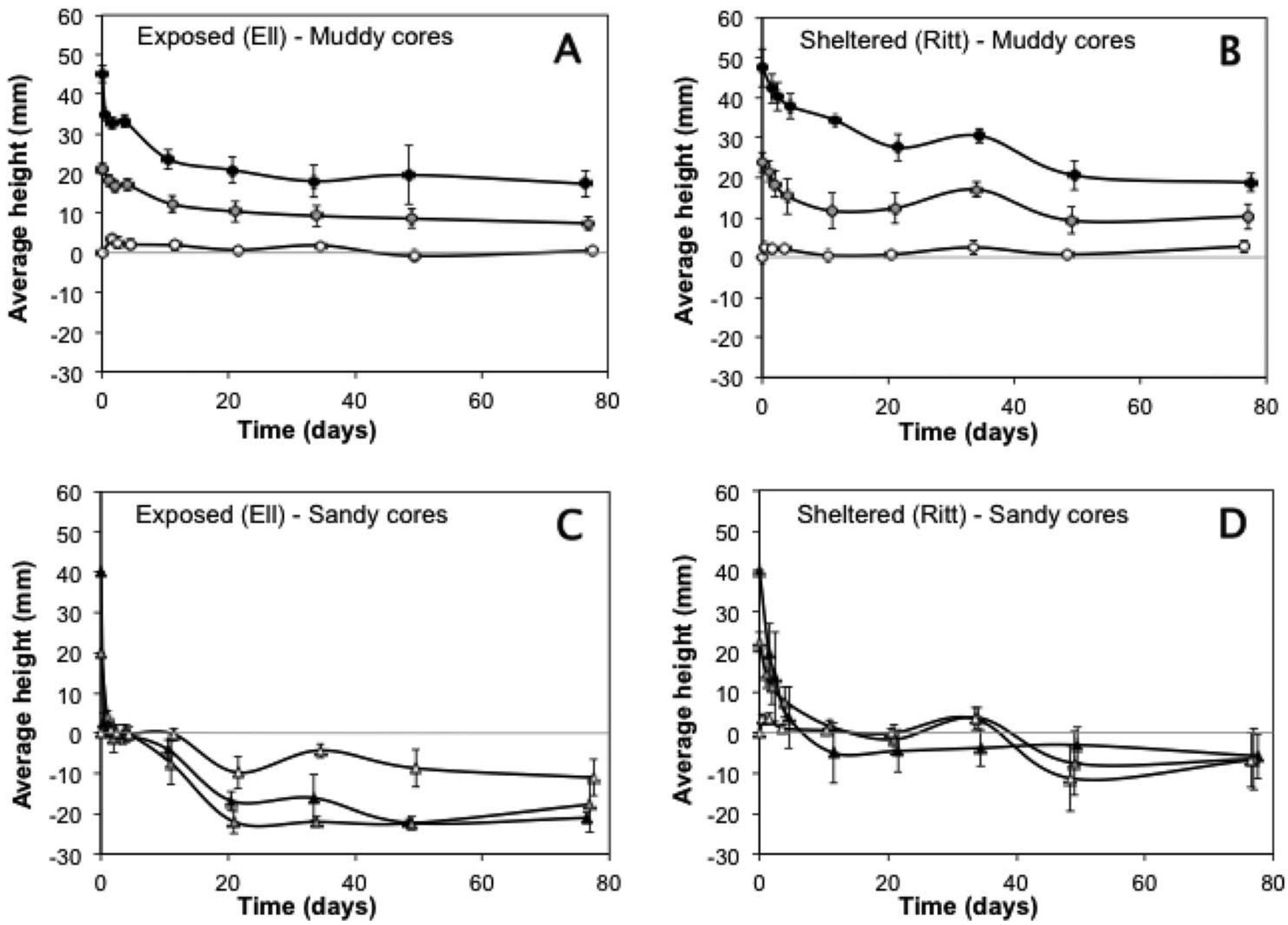

Fig. 5. Erosion of sediment cores originating from a muddy (top row; 5a and 5b) and sandy (bottom row; 5c and 5d) salt marsh and placed on the exposed marsh at Ellewoutsdijk (left row; 5a and 5c) and the sheltered marsh at Ritthem (right row; 5b and 5d). At placement ($t = 0$), cores were either 40 mm higher than (black symbols), 20 mm higher than (grey symbols) or level with (white symbols) the surrounding (i.e., $\Delta Z = 40$, 20 or 0 mm at t0). All cores were surrounded by a concrete ring to provide a fixed 'mudflat' height. Results demonstrate that *i)* larger height differences between marsh cores and the surrounding tidal flat (i.e., ΔZ) enhances erosion, *ii)* erosion especially of sandy cores (and to a much lesser extent muddy cores) is stronger at exposed than sheltered sites, and *iii)* sandy marshes erode more easily than muddy marshes. (a: $F = 27.64$, $p < 0.001$; b: $F = 44.29$, $p < 0.001$; c: $F = 0.99$, $p = 0.41$; d: $F = 0.65$, $p = 0.55$).

regression model, as they are independent in the whole data set. Results are presented as the mean ± standard errors. MATLAB (MathWorks, Inc.) was used for all analyses.

Results

Experiments related to hypothesis 1: mechanisms initiating lateral marsh erosion and factors affecting marsh-erosion rates

The first field experiments supported our hypothesis that sediment dynamics on a mudflat (δz_{TF}) can initiate marsh erosion (Fig. 4). The salt-marsh sediment cores that were surrounded by the concrete ring (i.e., $\delta z_{TF} = 0$) hardly eroded, whereas cores inserted into the mudflat without a fixed ring (i.e., $\delta z_{TF} =$ variable) closely followed the erosion of the surrounding tidal mudflat. Thus, the sediment dynamics of a tidal mudflat (δz_{TF}) can initiate erosion of the adjacent more-stable marsh sediment, and thereby form a key process in initiating marsh erosion. The second experiment, where we used salt-marsh cores taken from marshes with different sediment composition, showed that the height difference between tidal flat and the marsh sediment (i.e., core height; ΔZ), the sediment composition and the hydrodynamic energy are main determinants of salt-marsh erosion rates (Fig. 5). Erosion rates appeared to be lower at the sheltered site (Fig. 5b,d) than at the exposed site (Fig. 5a,c), which was particularly clear for the sandy cores (i.e., 5d vs. 5c) but less so for the muddy cores (i.e., 5b vs. 5a). At the sheltered site, the data showed that cores taken from marsh vegetation

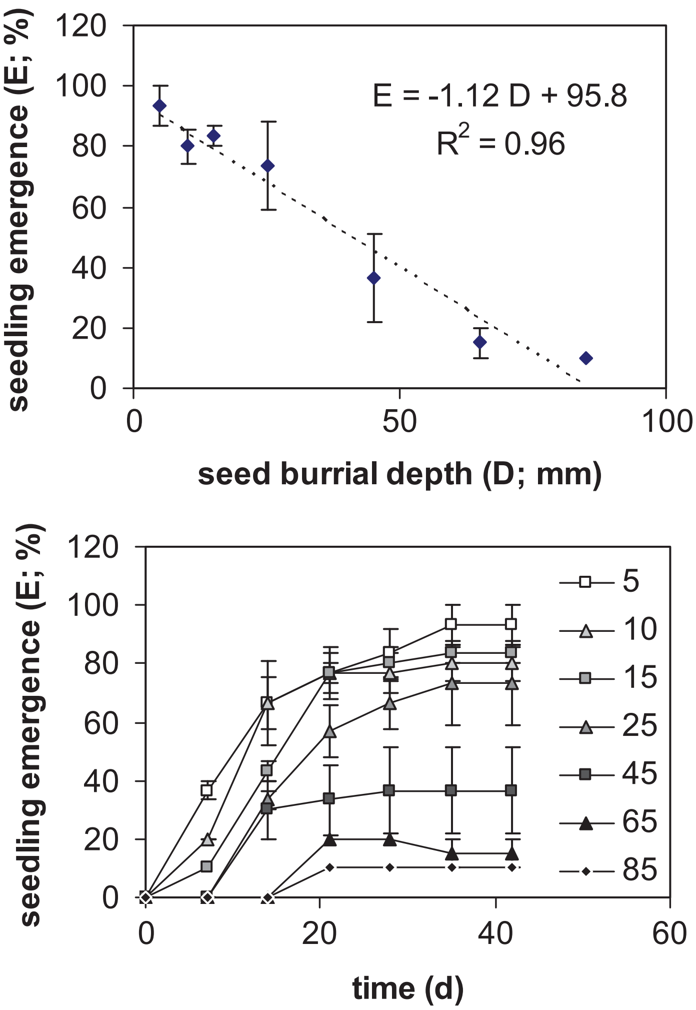

Fig. 6. Effect of burial depth of *Spartina anglica* seeds (D, mm) on the percentage of seedlings that emerge (E, %) (6a) and the time needed for seedlings to emergence (days) (6b). Error bars represent Standard Errors ($n = 10$ seeds), and the burial depth (mm) is in Fig. 6b represented by the symbols indicated within the figure.

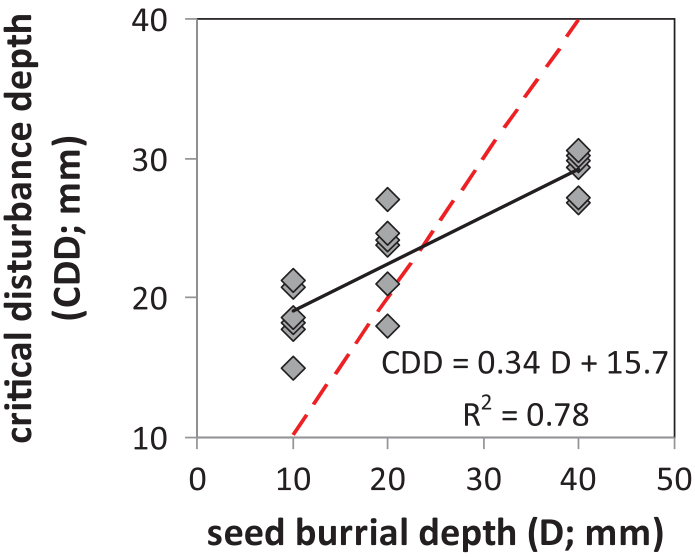

Fig. 7. Effect of seed burial depth on the Critical Disturbance Depth (CDD) for 20 days old seedlings. CDD is a measure for the resilience of a *Spartina anglica* seedling against erosion events, and was measured as indicated in Fig. 3. The red line indicates those values where CDD would equal the seed burial depth. [Color figure can be viewed at wileyonlinelibrary.com]

growing on sandy sediments (Fig. 5d) are easily eroded compared to cores taken from marshes growing on muddy sediment (Fig. 5b). The muddy cores (Fig. 5a,b) showed that a larger core height caused larger erosion, with virtually no erosion of the cores that were placed level with the concrete ring (Fig. 5a,b). This shows that larger height differences between muddy marsh and the surrounding tidal flat (i.e., ΔZ) enhances erosion rate, thereby forming a key process in cliff formation. In contrast to the muddy cores, the sandy cores (Fig. 5c,d) scoured till the level below the concrete ring, which was especially clear at the exposed site (Fig. 5c). In general the erosion effects showed quite comparable trends, except that effects were more pronounced at the high-energy site and for cores from the sandy marsh. At the exposed site the erosion of the sandy marsh cores occurred directly following placement of the core, implying that at exposed locations, sandy marshes are unlikely to create cliffs or at most very short-lived ones (Fig. 5c).

Experiments related to hypothesis 2: mechanism hampering seedling establishment

We tested the hypothesis that too large sediment dynamics on a mudflat (δz_{TF}) will prevent seedlings from establishing by a combination of a series of mesocosm experiments and a field experiment. The 1st mesocosm experiment showed that seed emergence linearly decreased with the seed burial depth, and that seeds that are buried deeper needed a longer time to emerge (Fig. 6). The 2nd mesocosm experiment demonstrated that seedlings that have emerged from seeds that were initially buried deeper, were more resistant to erosion events (Fig. 7). However, comparing the measured resistance to erosion to the expected value based on the burial depth alone (i.e., red dashed line in Fig. 7), it became clear that the deeply buried seedlings were less resistant than expected (i.e., below red dashed line) and the shallow buried seeds more than expected (i.e., above red dashed line). The latter suggests that growth responses over the 20 day period allowed seedlings to acclimate their morphology to the seed-burial depth, by investing less in roots when getting buried and more in roots when experiencing erosion. The 3rd mesocom experiment showed that seedlings, which were growing in a rapidly accreting environment, had a higher CDD and are thus more resistant to erosion events than seedlings developing in eroding environments (Fig. 8). However, over

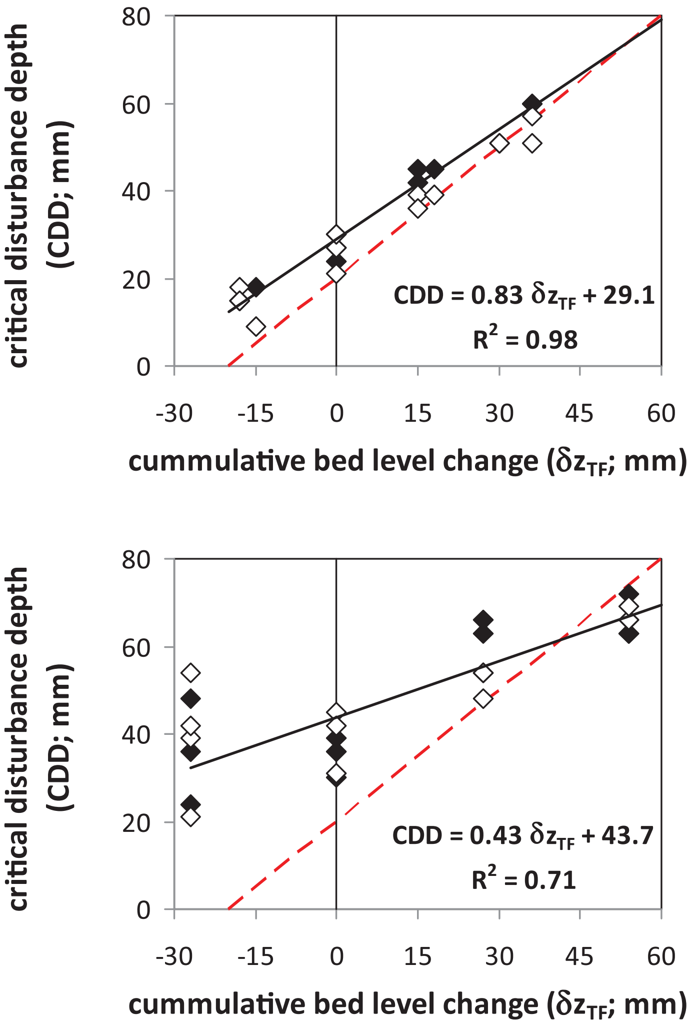

Fig. 8. Effect of sedimentation and erosion treatments (δz_{TF}) on Critical Disturbance Depth (CDD) on 50 (8a) and 80 (8b) days old seedlings (open symbol represents sandy sediment; filled symbols muddy sediment). Sediment accretion and erosion treatments and CDD measurements (i.e., a measure for seedling resilience to erosion events) were carried out as indicated in Fig. 3. The red line indicates those values where CDD would equal the seed burial depth *corrected* for subsequent accretion and erosion treatments. [Color figure can be viewed at wileyonlinelibrary.com]

time, the seedlings from eroding environment increase their CDD relatively more than the seedlings in the accreting environments (i.e., regression line for 90 days old plants in Fig. 8a had a smaller slope and larger intercept than the regression line for 50 days old plants in Fig. 8a). This means that differences in erosion resistance become smaller with time, again suggesting plastic growth responses to their sedimentary environment.

Overall, our mesocosm results showed that if CDD thresholds are surpassed by sheet erosion, seedlings can topple and get lost, and that the CDD depends on various factors such as seed burial depth (Fig. 7), past erosion and accretion events (Fig. 8), and plant age (Fig. 8), but to our surprise not sediment type (Fig. 8). It is however noted that the hydrodynamic energy needed in the field to actually surpass the CDD is likely to differ between sites, depending on the erodibility of the sediment present at a specific site. To further demonstrate that sediment dynamics on the mudflat (δz_{TF}) indeed play a key role in seedling establishment of salt marsh species, we analyzed the seedling survival in the field experiment with a step-wise multiple regression. The results from this regression indicated that seedling survival was controlled by two main factors: elevation (inundation period) and sediment dynamics ($R^2 = 0.59$, $p = 0.002$, Fig. 9). In areas with longer inundation periods stressing the plants, seedlings could resist smaller sediment dynamics on the mudflat (δz_{TF}). The latter implies that slower growing plants are more sensitive to δz_{TF}. Summarizing our field observations support the findings of the mesocosms experiments, by revealing that the sediment dynamics on the mudflat (δz_{TF}) indeed play a key role in seedling establishment of salt marsh species, and by showing that the CDD thresholds is dependent on local growth conditions.

Measurements related to hypothesis 3: sediment dynamics on the mudflat (δz_{TF} over time)

Our measurements of the sediment dynamics on the mudflat showed that δz_{TF} decreased in a site-specific way with distance from the seaside towards the land (Fig. 10). Regarding the scope of this paper, our transects had a limited length, so that we cannot show that this pattern in δz_{TF} persists all the way to the low water line. However, the pattern is very clear for that part of the mudflat that is relevant for salt marsh establishment, as defined by elevation and the associated inundation time.

Discussion

Salt marshes are known to have cyclic behaviour, with alternating phases of lateral expansion and retreat, which can be the result of either an autonomous process or can be related to long-term trends in external forcing (e.g., increased shipping, shifted position of estuarine channels, sea-level rise or altered sediment supply; for references see introduction). Present study does not focus on long-term trends that can constrain the marsh evolution, but rather focuses on the poorly understood short-term processes causing a shift from salt marsh expansion to lateral erosion and *vice versa*, causing a shift from lateral salt marsh erosion to expansion. To our knowledge, the present study is the first to experimentally demonstrate the role of short-term (seasonal and shorter) tidal mudflat sediment dynamics in forming tipping points for the long-term (decadal and longer) cyclic salt-marsh dynamics, by being the critical factor both for the seedling establishment success and for initiating lateral marsh erosion. A schematisation of present findings (Fig. 11) shows how the short-term sediment dynamics at

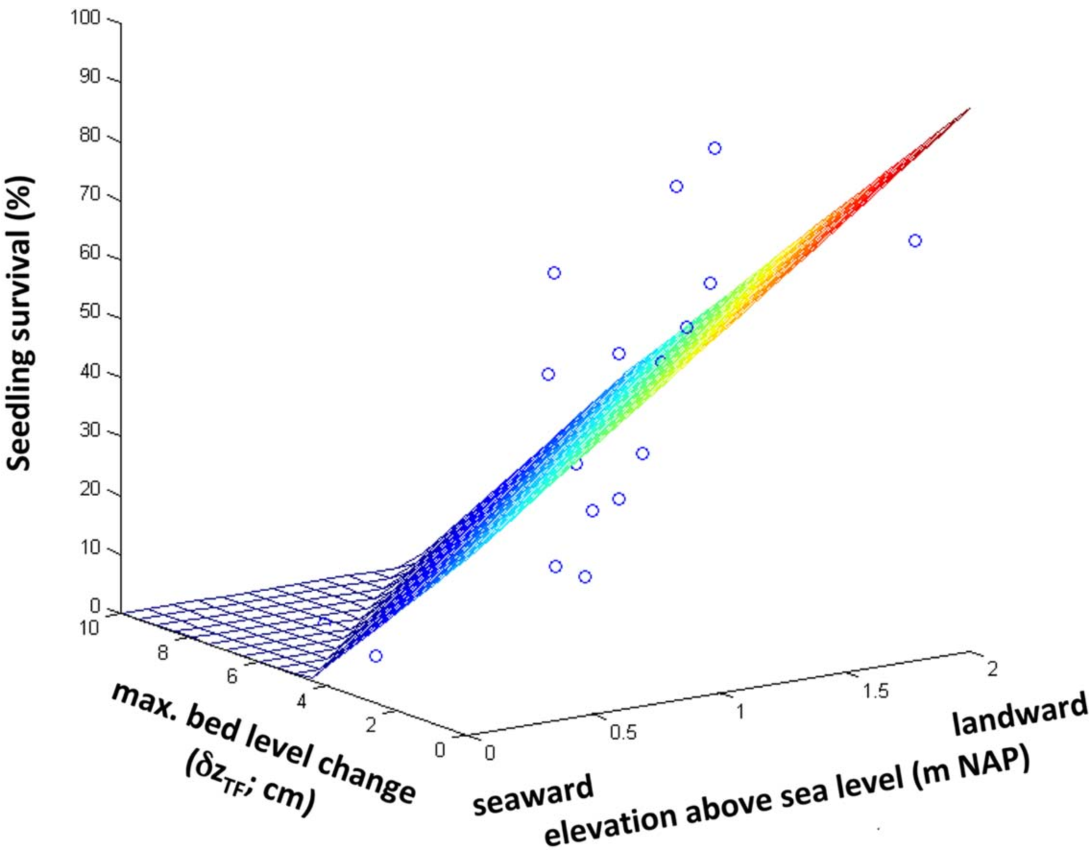

Fig. 9. Field measurements showing that seedling survival depends on a combination of the short-term sediment dynamics (δz_{TF}) and tidal elevation expressed relative to the Dutch ordnance level NAP which is close to local mean sea level ($R^2 = 0.59$, $p = 0.002$).

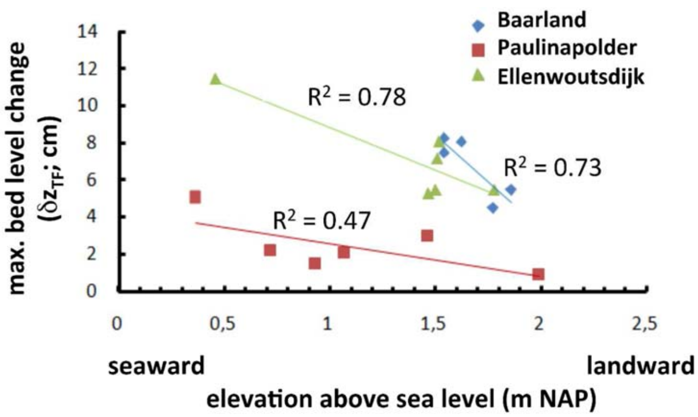

Fig. 10. Field measurements, demonstrating for three mudflats with contrasting exposure, that the amplitude of the short-term sediment dynamics at the mudflat (δz_{TF}) increases with inundation level. Inundation level increases for each site with distance away from mainland, and is expressed relative to the Dutch ordnance level NAP that is close to local mean sea level. [Color figure can be viewed at wileyonlinelibrary.com]

the mudflat (δz_{TF}) increases with distance away from the salt marsh (cf. Fig. 10). As a result, there is an increasing risk for marsh erosion to get initiated (cf. Figs. 4, 5) and decreasing chance for successful seedling establishment (cf. Figs. 7-9) with increasing distance seaward. That is, if the sediment dynamics (δz_{TF}) surpasses a certain maximum threshold, a laterally expanding marsh can transform into an eroding marsh with a retreating cliff, whereas if the sediment dynamics (δz_{TF}) decreases below a certain minimum threshold, new seedlings can start to establish in front of such retreating cliff (Fig. 11). Getting this process-based understanding of tipping points governing salt-marsh dynamics is highly important both for *i)* being able to translate ecological concepts (van de Koppel et al. 2005; Mariotti and Fagherazzi 2010; Tambroni and Seminara 2012) towards management measures aimed at preserving marshes and for *ii)* enhancing current insights in the importance of ecosystem connectivity at the landscape-scale (in our case the tidal flat and salt marsh) for the long-term dynamics of such ecosystems (cf. Gillis et al. 2014; Schuerch et al. 2014; van de Koppel et al. 2015). It is noted that although we identify the short-term tidal mudflat sediment dynamics as key-process for understanding the long-term cyclic salt-marsh dynamics, this does not imply that long-term changes in external forcing are unimportant. As discussed below these long-term trends may modify short-term tidal mudflat sediment dynamics.

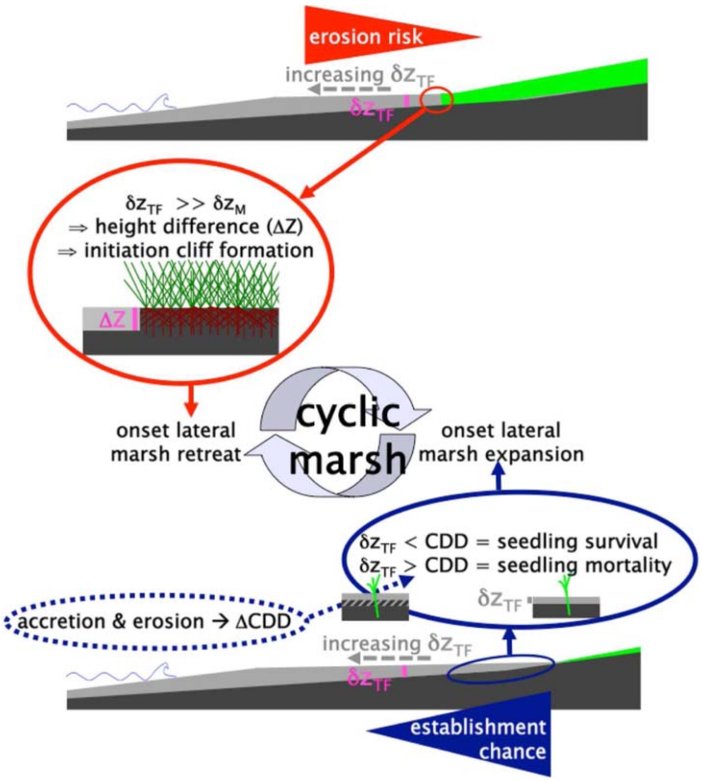

Fig. 11. Schematic representation of how the short-term sediment dynamics at the tidal mudflat (δz_{TF}) affect 2 key processes that determine the long-term development of a salt marsh and thereby its cyclic dynamics: initiation of marsh erosion (top half diagram) and seedling establishment (bottom half diagram). The dark grey line at the bottom of the schematised cross-section of the mudflat-marsh ecosystem indicates a stable sediment layer; the light grey line a sediment layer that may vary in depth over a short time period; the green line the marsh vegetation with a relative stable sediment; the blue wave the side from which the water front moves in during flood. When sediment dynamics at the tidal flat (δz_{TF}) occur next along a marsh with a relative stable bed (i.e., $\delta z_M \ll \delta z_{TF}$), a small height difference may be formed (ΔZ), which can be the onset of marsh erosion (Figs. 4, 5). If sediment dynamics (δz_{TF}) become too large, seeds cannot emerge by getting buried too deeply (Fig. 6) and seedlings cannot survive due to erosion exceeding a critical threshold causing seedling uprooting (Fig. 7–9). The critical disturbance/erosion depth (CDD) of seedlings will be affected both by the initial seed burial depth (Fig. 7) and subsequent sediment accretion and/or erosion rates (δz_{TF}) during the seedling growth (Fig. 8). Field measurements show that the amplitude of the sediment dynamics at the tidal mudflat (δz_{TF}) increases with distance away from the mainland (Fig. 10), and that as a result, chance for marsh erosion increases (Figs. 4 and 5) and seedling establishment decreases (Fig. 9) away from the mainland.

In spite of the many valuable ecosystem services that coastal vegetation provides (Costanza et al. 1997, 2008; Barbier et al. 2008, 2011), large areas of coastal vegetation have been lost over the last decades and continue to be threatened by global change processes and anthropogenic disturbances (Lozte et al. 2006; Orth et al. 2006; Duke et al. 2007; Waycott et al. 2009; Kirwan and Megonigal 2013). The (re-)establishment of coastal vegetation like seagrass and salt marsh (pioneer) species on bare flats appears to have low chances of success (e.g., see van Wesenbeeck et al. 2008; van Katwijk et al. 2009 and references therein), which has hampered the restoration of many coastal ecosystems (e.g., see for mangroves, Ellison 2000; Lewis III 2005; for salt marshes, Bakker et al. 2002; Hughes and Paramor 2004; for seagrass, Orth et al. 2006). By providing insight in the processes underlying the tipping points both for ecosystem re-establishment (i.e., seedling establishment) and impending ecosystem decline (i.e., lateral marsh erosion), scientists can provide direct guidelines to managers on which variables they have to monitor. In our case, we would advice managers of salt marshes to put emphasis on monitoring the short-term sediment dynamics on the adjacent mudflat (e.g., see Hu et al. 2015a, showing how innovative techniques allow monitoring the effects of sudden storm events on sediment levels), and request hydrodynamic models that can predict this specific parameter to understand future developments of the marsh (Hu et al 2015b). Also in designing restoration projects, process-based understanding on thresholds enables engineers to create the proper hydrodynamic conditions and thereby, more importantly, the proper sediment conditions to facilitate ecosystem dynamics. Attention for this aspect, however, should not obliterate the necessity to also include any long-term accretion or erosional trends when making restoration designs (Schuerch et al. 2014). Modelling of the short-term sediment dynamics on a mudflat is complicated, with limited formulations available, which are still poorly validated against observations (Shi et al. 2012, and references therein; but also see Hu et al 2015b for a novel modelling approach).

Present study identifies the hydrodynamically driven short-term sediment dynamics (δz_{TF}) as the main mechanism in explaining tipping points for the long-term cyclic salt-marsh dynamics, by its effect on seedling establishment and initiating lateral marsh erosion. This differs from the model studies by Mariotti and Fagherazzi (2010), which emphasize the importance of water depth for wave formation, but is not conflicting in that waves may be expected to be a main driver of sediment dynamics (cf. Hu et al. 2015a,b). A strength of present study is that it is based on field and flume observations, even though we do realise that the methods used to reach this conclusion are a simplified representation of reality. The initiation of lateral marsh erosion was studied on small cores, which will experience different hydrodynamic forces than a true marsh edge, and are likely to have different erosion behaviour than a marsh edge. However, sediment cores have proven to provide useful insights in mechanisms controlling marsh erosion (Feagin et al. 2009). Moreover, the present observation shows that the erosion of the sandy marsh cores at the exposed site was extremely fast (Fig. 5c), and was thereby in agreement with field observations showing that sandy *Spartina* tussocks eroded too fast to see a cliff at locations, whereas muddy *Spartina* tussocks did form a cliff (van Hulzen et al. 2007). It also agrees with the findings of Deegan et al. (2012), who showed that sediment type is a main factor in determining the erodibility of marshes. Our conclusion on the importance of mudflat dynamics for generating a height difference that forms the onset of lateral erosion, confirms the model-based hypothesis raised by Callaghan et al. (2010). The laboratory-flume experiments in which we mimicked the effect of sediment erosion on the toppling of seedlings, either planted at different depths or grown in contrasting sedimentary environments, also represents a strongly simplified approach. However, the basic principle was confirmed by an extensive field experiment. Moreover, the flume approach has also proven to be applicable for understanding the establishment of mangrove and seagrass seedlings (Balke et al. 2011; Infantes et al. 2011). Hence, we believe that these simplified methods applied are valid to demonstrate the fundamental mechanisms. Interestingly, these laboratory-flume experiments enable relating these short-term processes to long-term trends in sediment supply, by showing the effects of gradual accretion and erosion on seedling establishment. Similar effects of long-term trends in sediment supply may be expected to affect the cliff formation process via the short-term sediment dynamics, but have not been accounted for in our study.

The present result, indicating that short-term sediment dynamics on the tidal flat determine the long-term cyclic behaviour of the marsh, emphasises the importance of understanding the connectivity between ecosystems. Whereas this has been well recognised for processes like, e.g., nutrient fluxes across ecosystems and organismal exchange, this is still relatively poorly realised for other processes such as the reduction of hydrodynamic energy between adjacent systems (see review by Gillis et al. 2014). Connectivity between ecosystems may generate reciprocal positive interactions between adjacent ecosystems, with implications for ecosystem stability (Gillis et al. 2014). Both modelling by, e.g., Mariotti and Fagherazzi (2010) and Hu et al. (2015c), observational studies by, e.g., Schuerch et al. 2014 and the present experimental study emphasize that understanding the connections at the landscape scale between mudflats and salt marshes, is crucial for understanding tipping points driving ecosystem dynamics such as the cyclic behaviour of salt marshes. This connectivity has so far been insufficiently emphasized in earlier studies, which were more focussed on the process of marsh erosion itself (Feagin et al. 2009; Deegan et al. 2012; Silliman et al. 2012). Similar to the modelling work of Mariotti and Fagherazzi (2010), present study emphasizes the importance of including the mudflat in predicting the effect of sea-level rise on salt marsh stability, in addition to the large body of work aimed at vertical marsh accretion (for review, see Kirwan and Temmerman 2009). In addition to Mariotti and Fagherazzi (2010, 2013), who emphasized the importance of water depth over the mudflat in attenuating waves reaching the marsh edge, in the present study we want to emphasize the importance of understanding how the latter affects the sediment dynamics on the tidal flats. It may be speculated that with sea-level rise, an enhanced water depth over the mudflat may allow bigger waves to impose more stress on the mudflat sediment during storms, thereby creating the risk that the critical ΔZ for initiating lateral marsh erosion and the critcal δz_{TF} for seedling establishment move landwards, enhancing coastal squeeze. This process may be counteracted by sediment accretion, if long-term sediment supply is high enough to prevent enhanced water depth over the mudflat.

In order to be able to integrate tidal marshes in long-term coastal defense schemes (Temmerman et al. 2013), it is key to know for a particular location how far a marsh can laterally extend before it will start to erode and retreat, and how far a cliff will laterally retreat (i.e., how much marsh is left) before the marsh pioneer species can re-establish again. At this moment, little is known about the factors determining the amplitude over which a marsh laterally expands and erodes, and how this may differ between locations (van der Wal et al. 2008). The present study implies that differences in the spatial distribution of the short-term mudflat dynamics provide the underlying mechanism explaining differences in the amplitude over which different marshes laterally expand and erode on a decadal scale. This provides us with the challenge to both develop reliable modeling of the short-term sediment dynamics across sites and obtain data sets that allow testing of such models, to further improve our understanding of cyclic marsh dynamics in different estuaries and coastlines.

In conclusion, present study indicates that short-term sediment dynamics on the tidal flat (δz_{TF}) are the driving mechanism that connects the long-term cyclic behaviour of the marsh to (changing) large-scale physical forcing. Hence our findings call for a better spatially explicit understanding of sediment dynamics on tidal flats, as a key parameter for driving ecosystem dynamics, affecting more systems than only salt marshes (see Suykerbuyk et al., 2015). We hence challenge scientists to go beyond hydrodynamic characterization of field sites. Although hydrodynamics in conjunction with sediment properties determine the extent that sediment dynamics will occur, it is the sediment dynamics themselves that we need to quantify in order to predict the key ecological processes of seedling establishment and the initiation of cliff erosion.

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Conflict of Interest

None declared.

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