Effects of sediment disturbance regimes on *Spartina* seedling establishment: Implications for salt marsh creation and restoration

Haobing Cao [ORCID],[1] Zhenchang Zhu,[2] Thorsten Balke,[3] Liquan Zhang,[1]* Tjeerd J. Bouma[2,4,5]*

[1]State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai, China
[2]Department of Estuarine and Delta Systems, and Utrecht University, NIOZ Royal Netherlands Institute for Sea Research, AC Yerseke, The Netherlands
[3]School of Geographical and Earth Sciences, University of Glasgow, Glasgow, UK
[4]Community & Conservation Ecology, Faculty of Science and Engineering, University of Groningen, Groningen, The Netherlands
[5]University of Applied Sciences, Vlissingen, The Netherlands

Abstract

Seedling establishment is an important process relevant for the restoration of salt marsh within the framework of sustainable coastal defense schemes. Recent studies have increasingly highlighted how the short-term (i.e., the day-to-day) sediment dynamics can form major bottlenecks for seedling establishment. Until recently, studies on quantifying the threshold values of such short-term sediment dynamics for marsh seedlings remain rare. As accretion/erosion trends and dynamics may differ greatly under global change, we study the effects of short-term sediment disturbance-regimes on seedling establishment of two globally distributed foundation species: *Spartina alterniflora* and *Spartina anglica*. Seedlings with different disturbance-free periods were exposed to a set of different accretion/erosion-regimes in the laboratory. Seedling survival appeared to be much more sensitive to erosion than accretion, seedlings with short disturbance-free periods were more sensitive than seedlings with longer ones, and *S. alterniflora* was more sensitive than *S. anglica*. Seedlings were less sensitive to gradual changes in sediment height (accretion/erosion) than to abrupt changes where time for morphological adjustment is lacking. Critical erosion depth (the maximum erosion that seedlings are able to withstand) was shown to mainly depend on sedimentation history. Our results confirm that the establishment of *Spartina* seedlings requires a flooding disturbance-free "window of opportunity" and that sediment disturbances affect their survival both directly and via morphological adjustment. These results provide fundamental insights into seedling establishment that can be used for designing engineering measures to create suitable conditions and enable marsh creation/restoration for nature goals or as part of coastal defense schemes under global change.

Accelerated sea level rise and the rising frequency and power of storms are expected to increase risk of coastal flooding in a warming climate (Donat et al. 2011; Lin et al. 2012; Cui et al. 2015). Coastal ecosystems such as intertidal salt marshes provide many valuable ecosystem services, such as enhancing biodiversity (Gedan et al. 2009), high primary productivity (Mitsch and Gosselink 2000) and contributing to coastal protection by dissipating waves and stabilizing shorelines (D'Alpaos 2011; Möller et al. 2014). Salt marshes are increasingly valued for their function of coastal protection, given the increasing flood risk and the growing coastal population (Nicholls et al. 2007). Unfortunately, salt marsh ecosystems have declined globally because of numerous pressures (e.g., land reclamation, coastal squeeze due to navigation, alterations in wetland drainage and sediment inputs, extreme events, etc.), and over 50% of salt marshes in the world have been lost in the last century (Silliman et al. 2009; Moreno-Mateos et al. 2012).

In recognition of habitat loss and the desire to utilize salt marshes for coastal protection (e.g., *see* Shepard et al. 2011, Bouma et al. 2014), there is a growing interest in conserving and re-creating salt marshes (Adam 2002; Mossman et al. 2012). Attempts to use marshes as a more sustainable way of protecting coastlines are being incorporated into large-scale practices in the U.S.A. and northern Europe (Mossman et al. 2012; Temmerman et al. 2013). However, salt marsh establishment at the desired locations may be difficult to achieve (Bouma et al. 2014), and active planting does not necessarily
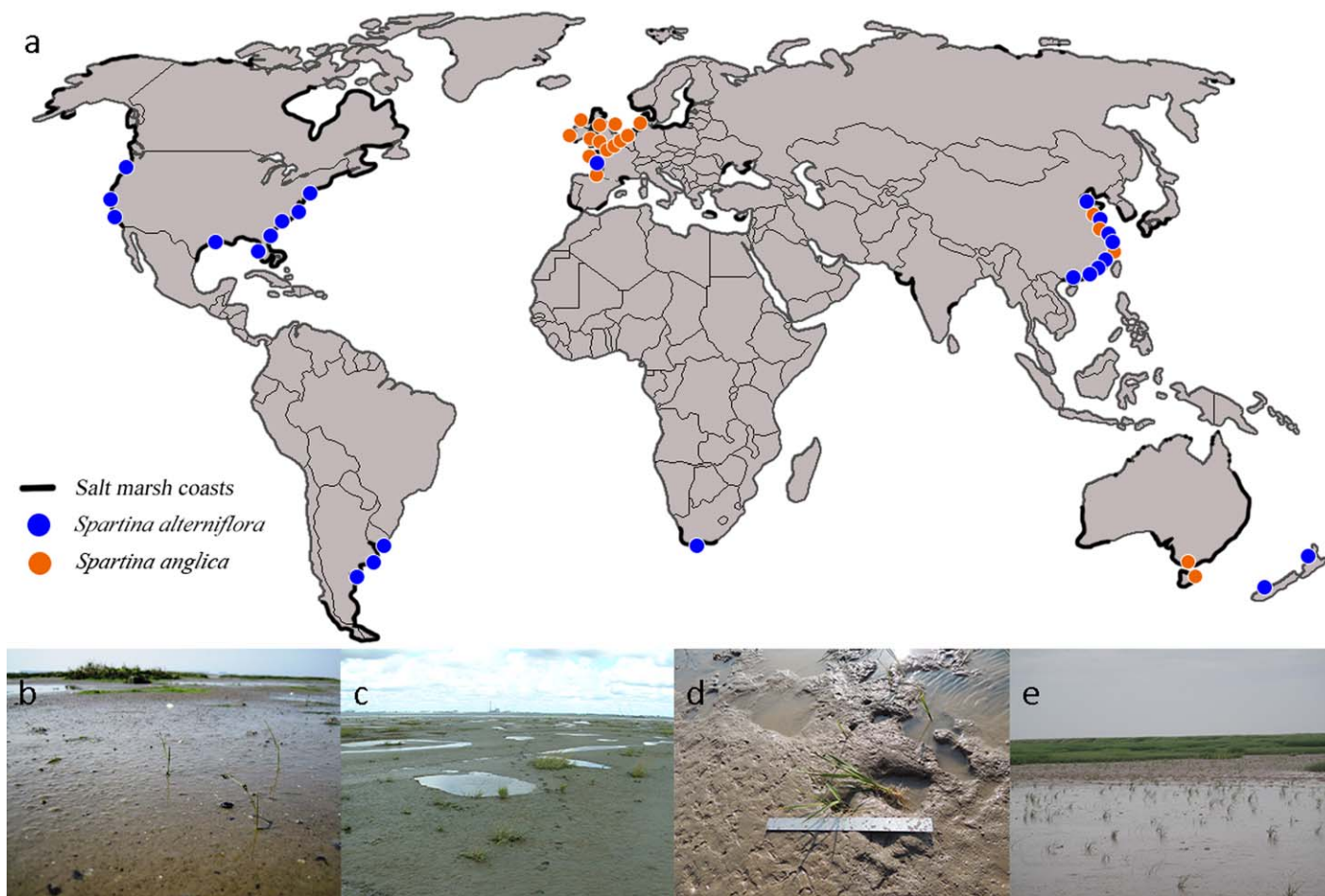
Fig. 1. (**a**) Distribution of *S. alterniflora* and *S. anglica* along the world coasts, which may not show the complete distribution. Photographs of (**b**) *S. anglica* seedlings established near the Oesterdam in the Oosterschelde; (**c**) *S. anglica* seedlings near tussocks in Hooge Platen, the Netherlands, and (**d, e**) expansion of *S. alterniflora* onto the mud flats that was initiated with seedling establishment in the Yangtze estuary, China.

lead to successful establishment of marshes (Moreno-Mateos et al. 2012; Mariotti and Fagherazzi 2013). As seedling establishment is one of the important processes relevant for initiating development of new salt marsh, especially at locations where the tidal flats are separated from existing marshes (which pre-empts colonization by clonal expansion), an in-depth understanding of the mechanisms of the establishment processes is necessary for salt marsh restoration (Bouma et al. 2009*a*, 2014, 2016; Friess et al. 2012).

Seedling establishment may be particularly important for the colonization of large bare tidal flats disconnected from existing vegetation, which may occur due to (1) the inherently cyclic nature of marsh dynamics, (2) rapid expansion of tidal flats, or (3) large-scale restoration (Broome et al. 1974; Laegdsgaard 2006; Bouma et al. 2016). In most cases, seedling establishment will be followed by lateral clonal growth and sward coalescence (van der Wal et al. 2008; Vandenbruwaene et al. 2011). Colonization of tidal flats by salt marsh seedlings is the result of biophysical interactions (Bouma et al. 2009*b*, 2016; Friess et al.

2012). Hydrodynamic forces and associated sediment dynamics often inhibit new seedling establishment (Callaghan et al. 2010; Hu et al. 2015*a*; Bouma et al. 2016), while the stochastic absence of physical disturbance, e.g., tidal current, wind waves and sediment dynamics, can facilitate recruitment events (Balke et al. 2014; Hu et al. 2015*b*). This has been highlighted by recent studies on "windows of opportunity (WO)," where a critical time interval without disturbance allows for seedlings to establish and gain enough strength to resist subsequent disturbances (Balke et al. 2014; Hu et al. 2015*b*). In this study, we focus on physical disturbance resulting from sediment dynamics and aim to quantify the effects of different sediment accretion/erosion regimes on seedling establishment (without considering marsh establishment via spreading of rhizomes and fragmentation), as this has been increasingly highlighted as key to the long-term persistence of salt marshes particularly in meso and macrotidal coastlines (*see* Bouma et al. 2009, 2016; Kirwan and Megonigal 2013). We study the response of two globally distributed foundation species in marshes: *Spartina alterniflora* and

Spartina anglica (Fig. 1; Chapman 1960; Essenlink et al. 2000; Kriwoken and Hedge 2000; Adam 2002; Isacch et al. 2006; An et al. 2007; Gedan et al. 2009; Angelini et al. 2011; and references therein).

Globally, accretion/erosion rates vary greatly among tidal flats, ranging from less than one to several tens of mm per year (Temmerman et al. 2012). Although part of this range may be related to the use of different measuring techniques and integration intervals (Nolte et al. 2013; Hu et al. 2015a), it is evident that regions differ in long-term accretion/erosion patterns, which may affect the lateral spread or retreat of marsh vegetation or "lateral vegetation dynamics" (Friess et al. 2012; Balke et al. 2013 for mangroves; Bouma et al. 2014, 2016). On top of the differences in long-term trends, the temporal variability in wave forcing may drive short-term erosion events (Hu et al. 2015a). Such short-term sediment dynamics may be especially influential during storms, with values of over 10 cm per event (cf. Hu et al. 2015a), with the exact amplitude most likely to be specific for both site and event. Given the combination of ongoing sea level rise (Kirwan and Temmerman 2009; Mariotti et al. 2010; Kirwan and Megonigal 2013) and increasing storminess (Donat et al. 2011), wave driven short-term sediment dynamics may be expected to increase in both magnitude and frequency (Hu et al. 2015a,b). It is currently unknown how increasingly energetic shorelines in a warming climate will affect lateral salt marsh dynamics (Mariotti and Fagherazzi 2010; Fagherazzi et al. 2012; Bouma et al. 2016).

The present experimental study aims to gain quantitative insight into how seedling survival is affected by short-term sediment dynamics, and to what extent this may be mitigated by morphological adjustments by the plant. In our mesocosm experiments, seedlings were exposed to a set of accretion/erosion regimes. To quantify the importance of having a disturbance-free period preceding accretion/erosion events, we applied two levels of initially disturbance-free periods: 2 and 9 d. Due to the potentially high dynamics of sediment during storm events (e.g., *see* Hu et al. 2015a), we used a large range of accretion/erosion rates to represent potential short-term sediment dynamics. To examine the maximum erosion the seedlings were able to withstand, we also determined the critical erosion depth (CED) in a flume. By using seedlings of the two most globally distributed pioneer marsh species (i.e., *Spartina alterniflora* and *S. anglica*; Fig. 1), we aim to contribute to a global perspective on salt marsh establishment under global climate change and to provide a basic data set for understanding and modeling the consequences of physical disturbance on tidal flats. Finally, we discuss our results in the context of marsh creation and restoration.

Material and methods
Seed germination and seedling growth conditions
S. alterniflora seeds were collected from salt marshes on Chongming Island (Yangtze estuary, China) in November 2013, and *S. anglica* seeds were collected from the Oosterschelde estuary (the Netherlands) in the same month. The collected seeds were air-dried and subsequently stored over winter in a 4°C refrigerator, while soaking in containers with sea water from Oosterschelde estuary until germination in April. April is the period when *Spartina spp.* seeds typically become active in the northern hemisphere (Schwarz et al. 2011, and personal field observations). Seeds were germinated in a climate chamber, which was kept at 25°C with 12 h d^{-1} light (550 μmol m^{-2} s^{-1} Photosynthetic Active Radiation; PAR). All seeds with a visible germ were identified as seedlings.

Seedlings were planted with an intact seed coat (to avoid damage when transplanting) into salt marsh sediment at 1 cm depth below the surface in individual PVC pots (practical choice, cf. Broome et al. 1974; Schwarz et al. 2015; Bouma et al. 2016). The pots (160 mm height and 110 mm inner diameter) were made from PVC pipes, with open bottoms that allowed for accretion/erosion treatments (*see* Han et al. 2012 for seagrasses, Balke et al. 2013 for mangroves). Within the pots, punctured polyethylene bags were used to line the bottom, allowing for drainage without losing the sediment. The sediment used in the pots (with a D50 of 31.58 μm) was collected from the top 20 cm of a salt marsh pioneer mudflat near Rilland-Bath, Oosterschelde estuary, the Netherlands. To prevent possible seedling loss due to grazing by benthic macro-invertebrates (Emmerson 2000), all collected sediment was put under airtight and waterlogged conditions for 2 weeks to kill the macrobenthos. Ten randomly chosen pots were sieved to ensure that this treatment was long enough to indeed kill all worms. The pots with sediment were watered with a mix of freshwater and water from the Oosterschelde that had a salinity of 15.83 ppt. All the pots were then left for a week to settle the sediment before adding the seedlings. The unoccupied volume on the top of the pots due to compaction was then replenished with some sediment before the seedlings were planted. The pots with buried seedlings were then transferred to the mesocosms described below.

Mesocosm experiments—technical aspects
We used 10 mesocosms, each consisting of 2 big tanks (with inner dimensions 110 × 95 × 60 cm) on top of each other (Fig. 2b): a top tank that contained plants and was used for tidal inundation, and a bottom tank that served as a water reservoir during low tide. The lower tanks were filled with the mixed brackish water as mentioned above. The pumps in the lower tanks were operated by a timer to flood the upper "experimental" tanks. An overflow return pipe was used to control inundation height, by providing return-flow of excess water to the lower tank. When the pump was switched off, the upper tank drained via the pump, causing a low tide in the upper "experimental" tanks. The tidal regime was set by the timer for a semi-diurnal 1.5 h flooding
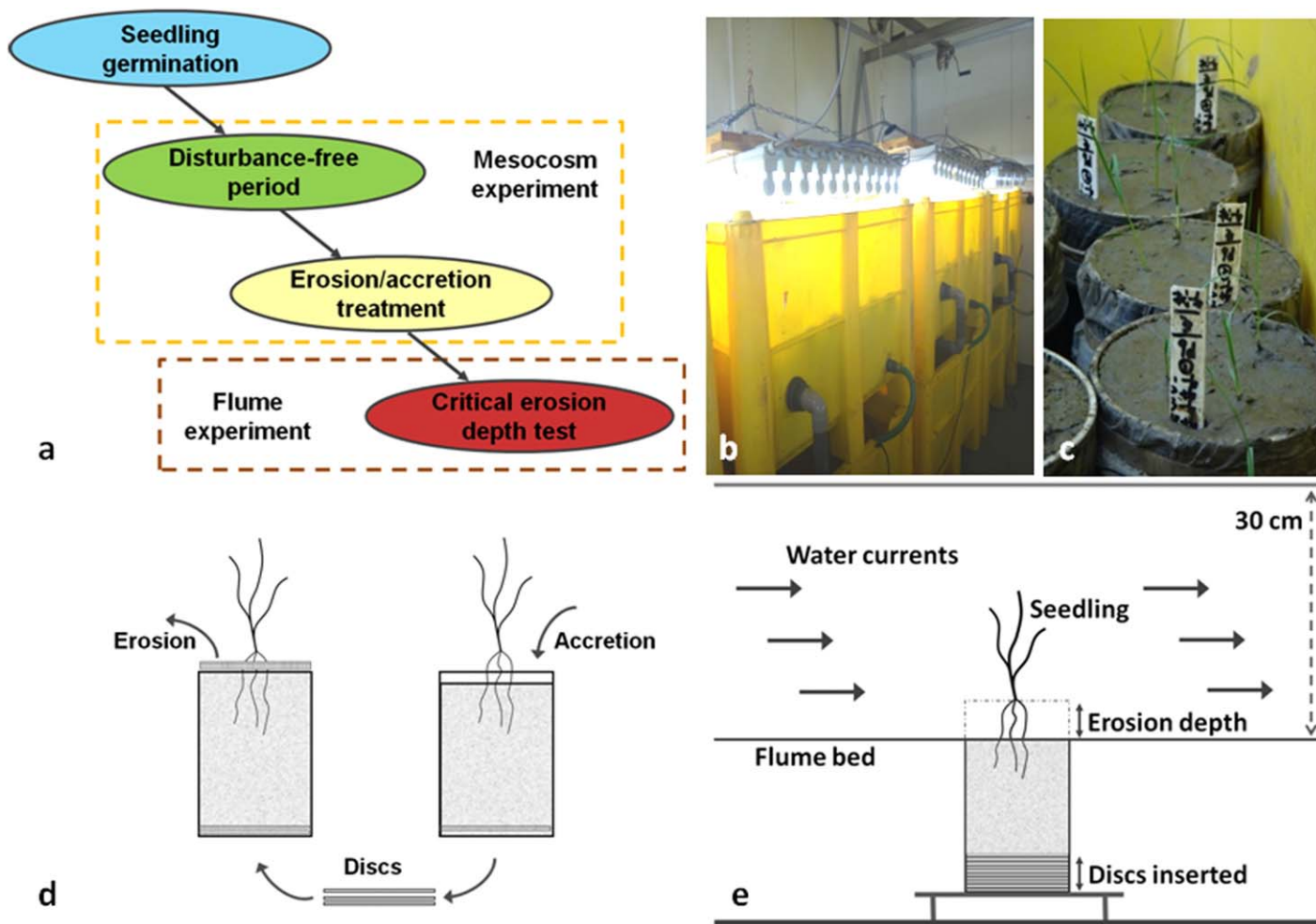
Fig. 2. Schematic diagrams and photographs showing the experiment setups. (**a**) The four steps in our experiment; (**b**) photographs of the meso-cosm setup and (**c**) seedlings in the upper experimental tanks during low tide; (**d**) erosion and accretion treatments; and (**e**) the test section of the flume, with a double bottom so that the upper edges of the pots could be kept level with the fume bed. The flume water depth was 30 cm with a constant current of 0.25 m s^{-1}. Note that the erosion depth equals the cumulative thickness of the discs inserted when applying the CED test.

of 50 cm in height in the upper tanks (3 h per day in total), thereby simulating the regular tidal regime of the pioneer zone in salt marshes (Schwarz et al. 2015).

Light to the mesocosms was provided by suspended fluorescent tubes arranged in parallel over the tanks (Fig. 2b) with 12 h d^{-1} (550 μmol m^{-2} s^{-1} PAR), and the temperature was thermostatically controlled in the climate room and maintained at 25°C during the day time and 18°C during night, which is approximately equivalent to the temperatures during seedling establishment in April and May at the field sites (Schwarz et al. 2011).

The pots containing seedlings of the two *Spartina* species (Fig. 2c) and the various accretion/erosion treatments were randomly assigned to the 10 upper mesocosm tanks. To compare the response of seedlings in the two different disturbance-free period groups, the two groups of seedlings were given a respite from regular artificial flooding in the

mesocosms for 2 d and 9 d, respectively, representing the 2 d and 9 d disturbance-free periods after germination. These two initial disturbance-free periods were chosen from among the durations of rest periods in a neap-spring tidal cycle, which have been considered to potentially provide WO for pioneer seedling settlement (Boorman 1999; Friess et al. 2012; Balke et al. 2014; Bouma et al. 2014).

Mesocosm experiments—accretion/erosion treatments

Three groups of sedimentation treatments were imposed weekly on seedlings and run for 6 weeks (Table 1): (1) "Constant Rate (CR)" consisting of constant net accretion/ erosion rates; (2) "Intermittent Supply (IS)" consisting of variable timing and amplitude of accretion/erosion events, in such a manner that the net cumulative changes were identical for all treatments; and (3) "Fluctuant Levels (FL)" consisting of regular fluctuations in accretion or erosion but with

Table 1. Sedimentation treatments every week during the 6-week course of the mesocosm experiments.

Treatment type		Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Total (mm)
		Treatments in 6 weeks (mm)						
Control	CK	0	0	0	0	0	0	0
Constant Rates treatments	CR–18	−18	−18	−18	−18	−18	−18	−108
(CR)	CR–12	−12	−12	−12	−12	−12	−12	−72
	CR–6*	−6	−6	−6	−6	−6	−6	−36
	CR–3	−3	−3	−3	−3	−3	−3	−18
	CR+3	3	3	3	3	3	3	18
	CR+6**	6	6	6	6	6	6	36
	CR+12	12	12	12	12	12	12	72
	CR+18	18	18	18	18	18	18	108
Intermittent Supply treatments	IS–18	−18	0	0	−18	0	0	−36
(IS)	IS–12	−12	0	−12	0	−12	0	−36
	IS–6*	−6	−6	−6	−6	−6	−6	−36
	IS+6**	+6	+6	+6	+6	+6	+6	+36
	IS+12	+12	0	+12	0	+12	0	+36
	IS+18	+18	0	0	+18	0	0	+36
Fluctuant Level treatments	FL–+18	−18	+18	−18	+18	−18	+18	0
(FL)	FL–+6	−6	+6	−6	+6	−6	+6	0
	FL+–6	+6	−6	+6	−6	+6	−6	0
	FL+–18	+18	−18	+18	−18	+18	−18	0

"–" and "+" represent erosion and accretion, respectively; "*" and "**" identify the same group of seedlings that were used in our experiments because of the overlapping design.

CS consisted of constant net accretion/erosion rates and different magnitudes of cumulative totals; IS consisted of same total erosion/accretion magnitudes but different rates and timing; FL had 0 total net erosion/accretion, but consisted of regular contrasting fluctuations in sediment level.

the sediment level returned to its previous state every week; that is, the FL treatments compared different amplitudes of disturbance without causing any net cumulative accretion/erosion. In total, we applied 1 control, 8 CR treatments, 6 IS treatments (with 2 overlaps with CR treatments), and 4 FL treatments (Table 1). Sediment erosion and accretion events were mimicked by adding or removing sediment from the top of the pots on a weekly basis (Fig. 2d; *see* Han et al. 2012 for seagrasses; Balke et al. 2013 for mangroves). Erosion was simulated by adding 3-mm-thick discs (1–6 discs according to the treatments, i.e., 3 to 18 mm erosion, *see* Table 1) underneath the pots and gently removing the pushed-up sediment by using a water spray (Fig. 2d). Accretion was simulated by removing discs that had been previously placed at the bottom of the pots and adding sediment on top around the plants (Fig. 2d). The previously placed polyethylene bags in the pots enabled us to smoothly lift the sediment cores up and down in the pots without affecting the roots.

Each sediment treatment was applied to 12 replicated seedlings per disturbance-free period group (in terms of flooding, 2 vs. 9 d). Hence, a total of 408 seedlings per *Spartina* species was used in our experiment (i.e., 12 replicates × 2 disturbance-free periods × 17 sediment treatments). All treatments and replicates were randomly assigned to the 10 mesocosms. Survival of the seedlings was surveyed weekly

and recorded as surviving, toppled (seedlings that had toppled over but still had visible live shoots or leaves) or dead. Immediately after the weekly monitoring had been completed, the next treatment was applied according to the schedule (Table 1).

Flume experiment—quantifying the critical erosion depth

At the end of 6 weeks, all seedlings that had survived the mesocosm treatments were put into a flume setup (Fig. 2e) in order to determine the CED for each seedling (*see* Balke et al. 2011, 2013 for mangroves; Bouma et al. 2016; Infantes et al. 2011 for seagrasses). The CED (in mm) was defined as the amount of sediment that needs to be eroded around the plants before toppling occurs. The CED, thus, is a quantitative measure for the resistance to future sediment disturbances. It was quantified by imposing step-wise incremental erosion, using the same method as used in the mesocosm experiment, but now with 1.5 mm discs to obtain higher resolution; the CED was thus calculated as the cumulative thickness of all discs added to the bottom of pots (Fig. 2e). Disc additions were continued until the seedlings toppled when exposed to the same current stress in a flume. We used a double bottom system into which we inserted the pots so that the upper edges of the pots were level with the bottom of the upper flume tank (Fig. 2e). The current velocity was
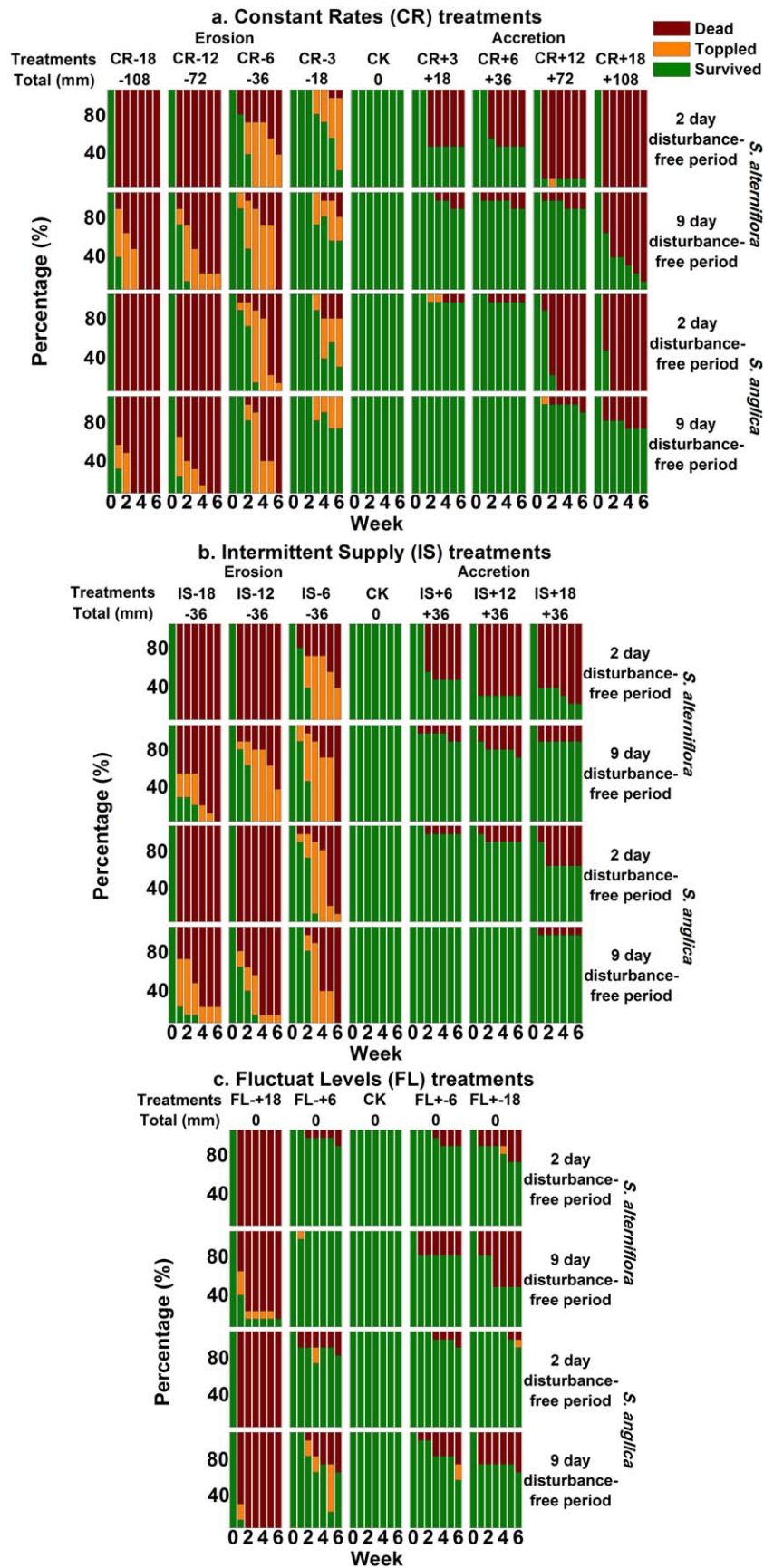
Fig. 3. Percentage of surviving, toppled and dead seedlings during the mesocosm experiments. (**a**) CR treatment groups, (**b**) IS treatment groups, and (**c**) FL treatment groups.

Table 2. Survival analysis of seedlings in the mesocosm experiment using the Cox regression analysis method. For each group of treatments, species, and disturbance-free period were set separately as fixed factors.

Treatments	Fixed factors		Variables	Cox regression of Survival d.f.	Cox regression of Survival Sig.
Constant treatments	Species	*S. alterniflora*	Disturbance-free period	1	.000
			Treatments	8	.000
		S. anglica	Disturbance-free period	1	.000
			Treatments	8	.000
	Disturbance-free period	2 d	Species	1	.022
			Treatments	8	.000
		9 d	Species	1	.166
			Treatments	8	.000
Intermittent treatments	Species	*S. alterniflora*	Disturbance-free period	1	.000
			Treatments	6	.000
		S. anglica	Disturbance-free period	1	.004
			Treatments	6	.000
	Disturbance-free period	2 d	Species	1	.008
			Treatments	6	.000
		9 d	Species	1	.477
			Treatments	6	.000
Fluctuated treatments	Species	*S. alterniflora*	Disturbance-free period	1	.930
			Treatments	4	.000
		S. anglica	Disturbance-free period	1	.134
			Treatments	4	.000
	Disturbance-free period	2 d	Species	1	.819
			Treatments	4	.000
		9 d	Species	1	.235
			Treatments	4	.000

chosen to mimic peak velocities typical for a *Spartina* pioneer zone (i.e., 0.25 m s^{-1} at a water level of 0.30 m, Bouma et al. 2005). Note that the constant flow rate used in our flume represents a simplified approach, which does not take into account the hydrodynamic force needed to impose erosion of the sediment used (Schwarz, et al. 2015; Mariotti et al. 2015). This allowed us to have well-defined erosion steps by imposing the erosion manually. The toppled seedlings were carefully cleaned, and the maximum root length and shoot height were measured to calculate the root-length/shoot-height ratio (referred to as the root-shoot ratio in the following sections).

Statistical analysis

Cox regression analysis was used to compare the differences in seedling survival according to sediment treatment, species and disturbance-free period in the mesocosm experiment. Both toppling and death of the seedlings were set as equal hazard events during this analysis. Species identity as well as the disturbance-free period before the treatments were set separately as fixed factors during analysis.

Three-way ANOVAs were performed for analyzing CED and root-shoot ratio with respect to the main effects of sediment treatment, species and disturbance-free period. The significance level of 5% was used in all analyses. All of the analyses were conducted with SPSS 18.0 software (SPSS, Chicago, IL, U.S.A.).

Results

Effects of accretion/erosion-regimes on the survival of seedlings

Among all the treatments, the control (i.e., without any accretion/erosion treatments) resulted in the highest survival rates (100%) throughout the mesocosm experiment (Fig. 3). For all the treatments, Cox regression analysis showed that the accretion/erosion-treatments significantly affected the survival of seedlings ($p < 0.01$, Table 2). The erosion treatments resulted in higher chances of toppling and mortality, on average, than the accretion treatments (Fig. 3).

When focusing on the effects of specific accretion/erosion treatments, it is clear that in the CR (Fig. 3a) and IS treatment groups (Fig. 3b), the hazards for both types of *Spartina*

seedlings became larger with increasing amplitude of the (erosion or accretion) application. Thus, a smaller amplitude in the accretion/erosion treatments resulted in higher survival (e.g., *see* Fig. 3b for erosion or accretion with 6 mm/ week). This is consistent with the observation that in the FL treatment groups, we observed almost 100% mortality for the seedlings that were exposed to the extremely high erosion event (i.e. large amplitude) during the first week of mesocosm establishment. For example, a sudden erosion of −18 mm and maintenance of this erosion level for 1 week (IS and FL −18) killed the seedlings as subsequent accretion was not able to rescue the seedlings (FL −+18) (Fig. 3b,c).

The importance of having a disturbance-free period was studied by comparing seedlings that had reached different disturbance-free times before the first accretion/erosion event was applied. As expected, the survival of seedlings with a 9 d disturbance-free period was found to be significantly higher than that of seedlings with a 2 d disturbance-free period in both CR and IS treatment groups (Fig. 3a,b) ($p < 0.01$, Table 2). No significant effect of the disturbance-free period was observed in the FL treatment groups (Fig. 3c).

When comparing *Spartina* species, the survival of *S. anglica* seedlings was higher than that of *S. alterniflora* seedlings after receiving the same cumulative accretion/erosion CR and IS treatments (Fig. 3a,b), with significant differences found for the 2 d disturbance-free seedlings ($p < 0.05$, Table 2) but not for the 9 d disturbance-free seedlings ($p > 0.05$, Table 2). No obvious trend across species was observed in the FL treatments (Fig. 3c).

Effect of accretion/erosion regimes on CED and seedling morphology

Three-way ANOVA analysis for the effects of (1) the sediment treatment, (2) species, and (3) disturbance-free period identified previous accretion/erosion treatments in the mesocosm experiment as the main factor significantly affecting the CED (the maximum erosion depth that seedlings can withstand without toppling) ($p < 0.05$). In contrast, no significant main effects were observed for either species or disturbance-free period ($p > 0.05$). We observed in CR and IS treatments that CED increased following previous accretion treatments (Fig. 4a,b), and the increase in CED was higher for CR than for IS treatments (Fig. 4a, b). However, no trends could be observed for any of the FL treatments (Fig. 4c). The effect of harsh erosion treatments on CED could not be quantified statistically due to high mortality (Fig. 4a–c).

The root-shoot ratio was significantly influenced by the constant sedimentation treatments ($p < 0.05$), with the root-shoot ratio being increased by non-lethal CR erosion and decreased by nonlethal CR accretion compared with the control groups (Fig. 5a), which indicates that plants reduced investment in roots when being stabilized by accretion. These responses explain why the absolute CED for erosive
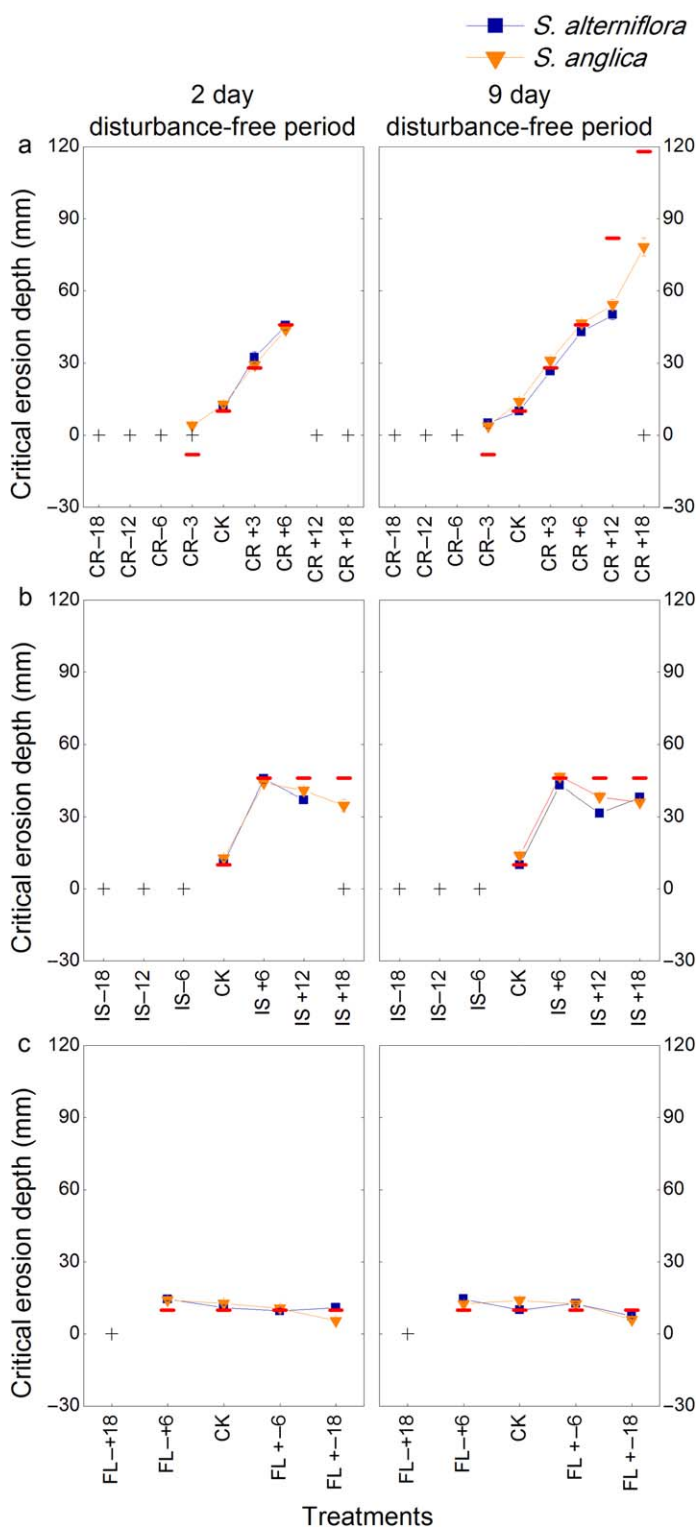

Fig. 4. The CED of surviving seedlings at harvest. (**a**) CR treatment groups, (**b**) IS treatment groups, and (**c**) FL treatment groups. The red dashes (short red horizontal lines) indicate the values where CED was equal to seedling burial depth based on accretion and erosion treatments alone. Note that the plus sign indicates groups with less than three surviving seedlings, and the error bars are not shown because they are smaller than the symbols used in the figure.
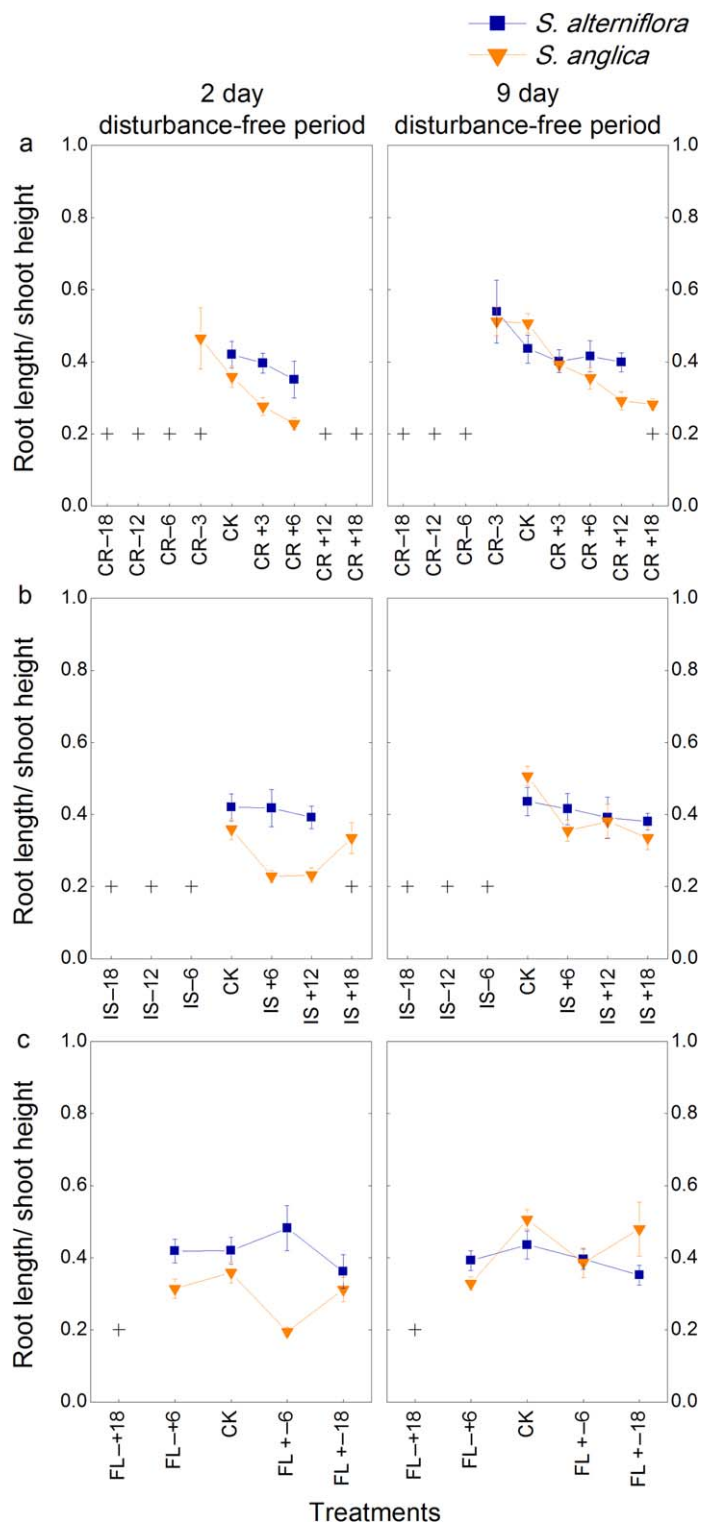
Fig. 5. The root/shoot ratio of the surviving seedlings. (**a**) CR treatment groups, (**b**) IS treatment groups, and (**c**) FL treatment groups. Note that the plus sign indicates treatment groups with less than three surviving seedlings.

treatments was higher than the expected CED value (i.e., seed burial depth based on cumulative changes after treatments) after non-lethal erosion treatments (e.g., CR-3, Fig. 4a) and lower than the expected CED value after nonlethal accretion treatments (e.g., CR + 3, Fig. 4a). The root-shoot ratio was not significantly affected by the IS and FL treatments ($p > 0.05$) (Fig. 5b,c).

Discussion

Successful restoration of salt marshes for coastal defense requires in-depth knowledge of the processes controlling seedling establishment on bare tidal flats. The present study is the first to quantify the effects of different accretion/erosion regimes on the establishment of two globally distributed foundation species of salt marshes: *S. anglica* and *S. alterniflora*. Our results indicate the following: (1) erosion strongly hampers seedling establishment, whereas accretion seems favorable in enhancing resistance to erosion (i.e., higher CED) and may only become adverse in extreme cases; (2) sedimentation regimes with similar net effects but with different temporal distributions may have different effects, with survival being higher when exposed to gradual changes than when exposed to abrupt ones; (3) a longer disturbance-free period is necessary for successful seedling establishment for both *Spartina* species; and (4) *S. anglica* was less sensitive to erosion/accretion dynamics than *S. alterniflora* in our experiments.

Importance of WO, short-term sediment dynamics and species

We observed that a longer disturbance-free period in terms of flooding (i.e., 9 d compared to 2 d) strongly enhanced seedlings survival, and the CED for seedlings that had already survived mesocosm treatments was significantly dependent on sediment disturbance history; the higher the sediment-accretion rate during mesocosm recruitment, the higher the critical erosion threshold that seedlings could resist later on, and vice versa. Such responses were slightly affected by the morphological adjustment of the root-shoot ratio (*see* Balke et al. 2013 for mangroves; Bouma et al. 2016). The fact that a 1 week difference in disturbance-free period in our experiment (i.e., 9 d compared to 2 d before starting sediment treatments) has significant impact on the survival of the seedlings quantitatively confirms the "window of opportunity (WO)" theory, which highlights the importance of having a disturbance-free hydroperiod for successful ecosystem establishment (Balke et al. 2014; Hu et al. 2015*b*). Moreover, because of the critical importance of seedling establishment in initiating a transition in state from bare mudflat to vegetation, our results support the finding that short-term sediment dynamics on the tidal flat determine long-term cyclic marsh dynamics (Bouma et al. 2016). Therefore, our results indicate that rapid germination and root growth during benign conditions are essential for

successful establishment of salt marsh ecosystems. Interestingly, the significant effect of species identity on seedling demographics with a 2 d disturbance-free period in our CS and IS treatment groups shows that *S. anglica* requires shorter WO than *S. alterniflora*. This may explain the highly successful global invasion of *S. anglica* (Watson 2008).

Obtaining such quantitative insights is important, as global-change processes may be expected to profoundly influence the presence of disturbance free periods and to impose more extreme disturbance events on tidal flats in the near future (Mariotti and Fagherazzi 2010, 2013). Even longer disturbance-free periods might be needed for seedling establishment, as the increasing frequency and intensity of both short-term perturbations (e.g., flood peaks) and long-term events (e.g., El Niño-Southern Oscillation) related to global change (Adam 2002; Brooks and Spencer 2010; Balke et al. 2014) are likely to lead to profound deviations in both disturbance-free periods and sediment stability (Brooks and Spencer 2010; Mariotti and Fagherazzi 2010, 2013; Balke et al. 2014). This may be particularly true for pioneer species, which are among the first plants that will have to cope with rising sea levels (Andersen et al. 2011). At the tidal flat scale, calm conditions may be present if the tidal mudflat has a suitable morphology and shape that can contribute to flooding attenuation over the tidal flat (Hu et al. 2015*b*). However, when facing high rates of changes in the seascape, time may be limited for geomorphological adjustment of tidal flats (Mariotti and Fagherazzi 2010; Fagherazzi, et al. 2012; Suykerbuyk et al. 2016). Thus, in order to (re)create salt marshes for long-term sustainable coastal protection under global change (Temmerman et al. 2013; Bouma et al. 2014), it is key to consider both present and estimated future sedimentation regimes before considering restoration projects, and where necessary, to engineer the site conditions to create—at least temporarily—disturbance-free periods that enable the primary establishment of pioneer species (Adam 2002; Watson 2008; Bouma et al. 2014, 2016). For example, engineering measures that can either temporarily reduce disturbances (e.g., reduce hydrodynamic forces, sediment dynamics or negative biotic interactions) or stabilize substrate for settlement, might offer useful ways to provide WO for marsh seedling establishment (Bouma et al. 2014).

Implications for salt marsh restoration in the face of global change

Our results highlight the significant impact that sediment disturbance plays on salt marsh seedling establishment. This suggests that selecting (or creating) field sites with benign sedimentary conditions is required for promoting salt marsh seedling establishment. However, the locations where wetland restoration is needed, especially in cases of desired coastal defense, are often wave-exposed areas with eroding tidal flats (Watson 2008; Kirwan and Megonigal 2013; Bouma et al. 2014; and references therein). Instead of trying to directly restore marshes at convenient (accreting) locations, future restoration projects should aim at restoring a suitable sedimentary environment that enables seedlings to establish (Balke et al. 2013 for mangroves; Bouma et al. 2016) at those locations where the tidal flats are disconnected from existing vegetation and human planting of marsh seedlings is needed.

Until recently, most of the research on sedimentary processes in salt marshes have been mainly related to the question of whether salt marsh accretion can outpace relative sea level rise (RSLR; Andersen et al. 2011; Suchrow et al. 2012, Temmerman et al. 2013; Cui et al. 2015). From a recent meta-analysis, it was concluded that salt marshes can keep up with RSLR if the effects of sediment availability balance those of SLR (Kirwan et al. 2016). Hence, our research focus needs to shift from drowning by RSLR to lateral marsh dynamics (Fagherazzi et al. 2012, 2013; Bouma et al. 2014) and how this is affected by sediment dynamics (Bouma et al. 2016). Creating favorable sedimentary conditions for seedling establishment at a tidal flat may be achieved by a range of engineering solutions. For instance, sedimentation fields have been constructed in the Wadden Sea coast for centuries, offshore barriers have been used in South-East England (Adam 2002; and references therein), and dredging-derived sediment slurry addition has been implemented in Louisiana (Mendelssohn and Kuhn 2003). Our detailed insights into the effects of sediment dynamics on seedling establishment provide arguments for carefully designing engineering measures that will create (at least temporarily) benign conditions with location-specific designs. This will enable us to improve salt marsh restorations under global climate change, at locations where we can most benefit from them with respect to coastal defense.

Conclusions

In order to successfully restore valuable salt marshes under global climate change, detailed mechanistic insight into seedling establishment is needed, especially at those locations where the tidal flats are disconnected from existing vegetation and human planting of *Spartina* tussocks is not desirable from a management perspective. This study highlights the critical importance of sediment dynamics for salt marsh vegetation establishment. *S. alterniflora* and *S. anglica* seedlings were shown to require a disturbance-free WO in terms of flooding to establish, while the history of the sediment disturbances also affected their survival both directly and indirectly via morphological adjustments by the seedlings. Our results provide fundamental insights that can be used for designing engineering measures to create suitable conditions, and to enable marsh creation/restoration for both nature conservation and coastal defense goals.

References

Adam, P. 2002. Saltmarshes in a time of change. Environ. Conserv. **29**: 39–61. doi:10.1017/S0376892902000048

An, S. Q., and others. 2007. *Spartina* invasion in China: Implications for invasive species management and future research. Weed Res. **47**: 183–191. doi:10.1111/j.1365-3180.2007.00559.x

Andersen, T. J., S. Svinth, and M. Pejrup. 2011. Temporal variation of accumulation rates on a natural salt marsh in the 20th century — the impact of sea level rise and increased inundation frequency. Mar. Geol. **279**: 178–187. doi:10.1016/j.margeo.2010.10.025

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. Bioscience **61**: 782–789. doi:10.1525/bio.2011.61.10.8

Balke, T., T. J. Bouma, E. M. Horstman, E. L. Webb, P. L. A. Erftemeijer, and P. M. J. Herman. 2011. Windows of opportunity: Thresholds to mangrove seedling establishment on tidal flats. Mar. Ecol. Prog. Ser. **440**: 1–9. doi:10.3354/meps09364

Balke, T., E. L. Webb, E. van den Elzen, D. Galli, P. M. J. Herman, and T. J. Bouma. 2013. Seedling establishment in a dynamic sedimentary environment: A conceptual framework using mangroves. J. Appl. Ecol. **50**: 740–747. doi:10.1111/1365-2664.12067

Balke, T., P. M. J. Herman, and T. J. Bouma. 2014. Critical transitions in disturbance-driven ecosystems: Identifying windows of opportunity for recovery. J. Ecol. **102**: 700–708. doi:10.1111/1365-2745.12241

Boorman, L. A. 1999. Salt marshes – present functioning and future change. Mangroves Salt Marshes **3**: 227–241. doi:10.1023/A:1009998812838

Bouma, T. J., M. B. De Vries, E. Low, G. Peralta, I. C. Tánczos, J. van de Koppel, and P. M. J. Herman. 2005. Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. Ecology **86**: 2187–2199. doi:10.1890/04-1588

Bouma, T. J., and others. 2009a. Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. Mar. Ecol. Prog. Ser. **388**: 293–297. doi:10.3354/meps08130

Bouma, T. J., M. Friedrichs, B. K. van Wesenbeeck, S. Temmerman, G. Graf, and P. M. J. Herman. 2009b. Density-dependent linkage of scale-dependent feedbacks: A flume study on the intertidal macrophyte *Spartina anglica*. Oikos **118**: 260–268. doi:10.1111/j.1600-0706.2008.16892.x

Bouma, T. J., and others. 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. Coast. Eng. **87**: 147–157. doi:10.1016/j.coastaleng.2013.11.014

Bouma, T. J., and others. 2016. Short-term mudflat dynamics drive long-1 term cyclic salt marsh dynamics. Limnol. Oceanogr. **61**: 2261–2275. doi:10.1002/lno.10374

Brooks, S. M., and T. Spencer. 2010. Temporal and spatial variations in recession rates and sediment release from soft rock cliffs, Suffolk coast, UK. Geomorphology **124**: 26–41. doi:10.1016/j.geomorph.2010.08.005

Broome, S. W., Woodhouse, J. R. Seneca. W. W., and E. D. 1974. Propagation of smooth cordgrass, *Spartina alterniflora*, from seed in North Carolina. Chesapeake Sci. **15**: 214–221. doi:10.2307/1350971

Callaghan, D. P., T. J. Bouma, P. Klaassen, D. van der Wal, M. J. F. Stive, and P. M. J. Herman. 2010. Hydrodynamic forcing on salt-marsh development: Distinguishing the relative importance of waves and tidal flows. Estuar. Coast. Shelf Sci. **89**: 73–88. doi:10.1016/j.ecss.2010.05.013

Chapman, V. J. 1960. Salt marshes and salt deserts of the world. Hill.

Cui, L. F., Z. M. Ge, and L. Q. Zhang. 2015. Vulnerability assessment of the coastal wetlands in the Yangtze Estuary, China to sea-level rise. Estuar. Coast. Shelf Sci. **156**: 42–51. doi:10.1016/j.ecss.2014.06.015

D'Alpaos, A. 2011. The mutual influence of biotic and abiotic components on the long-term ecomorphodynamic evolution of salt-marsh ecosystems. Geomorphology **126**: 269–278. doi:10.1016/j.geomorph.2010.04.027

Donat, M., D. Renggli, S. Wild, L. Alexander, G. Leckebusch, and U. Ulbrich. 2011. Reanalysis suggests long-term upward trends in European storminess since 1871. Geophys. Res. Lett. **38**: L14703. doi:10.1029/2011GL047995

Emmerson, M. 2000. Remedial habitat creation: Does *Nereis diversicolor* play a confounding role in the colonization and establishment of the pioneering saltmarsh plant, *Spartina anglica*?. Helgol. Mar. Res. **54**: 110–116. doi:10.1007/s101520050009

Essenlink, P., W. Zijlstra, K. S. Dijkema, and R. van Diggelen. 2000. The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. Biol. Conserv. **93**: 61–76. doi:10.1016/S0006-3207(99)00095-6

Fagherazzi, S., and others. 2012. Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. Rev. Geophys. **50**: RG1002. doi:10.1029/2011RG000359

Fagherazzi, S., G. Mariotti, P. L. Wiberg, and K. MacGlathery. 2013. Marsh collapse does not require sea-level rise. Oceanography **26**: 70–77. doi:10.5670/oceanog.2013.47

Friess, D. A., K. W. Krauss, E. M. Horstman, T. Balke, T. J. Bouma, D. Galli, and E. L. Webb. 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biol. Rev. Camb. Philos. Soc. **87**: 346–366. doi:10.1111/j.1469-185X.2011.00198.x

Gedan, K. B., B. R. Silliman, and M. D. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems.

Annu. Rev. Mar. Sci. **1**: 117–141. doi:10.1146/annurev.marine.010908.163930

Han, Q., T. J. Bouma, F. G. Brun, W. Suykerbuyk, and M. M. van Katwijk. 2012. Resilience of *Zostera noltii* to burial or erosion disturbances. Mar. Ecol. Prog. Ser. **449**: 133–143. doi:10.3354/meps09532

Hu, Z., W. Lenting, and T. J. Bouma. 2015*a*. Continuous monitoring bed-level dynamics on an intertidal flat: Introducing novel, stand-alone high-resolution SED-sensors. Geomorphology. **245**: 223–230. doi:10.1016/j.geomorph.2015.05.027

Hu, Z., J. van Belzen, D. van der Wal, T. Balke, Z. B. Wang, M. Stive, and T. J. Bouma. 2015*b*. Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: The importance of temporal and spatial variability in hydrodynamic forcing. J. Geophys. Res. Biogeosci. **120**: 1450–1469. doi:10.1002/2014JG002870

Infantes, E., A. Orfila, T. J. Bouma, G. Simarro, and J. Terrados. 2011. *Posidonia oceanica* and *Cymodocea nodosa* seedling tolerance to wave exposure. Limnol. Oceanogr. **56**: 2223–2232. doi:10.4319/lo.2011.56.6.2223

Isacch, J. P., C. S. B. Costa, L. Rodriguez-Gallego, D. Conde, M. Escapa, D. A. Gagliardini, and O. O. Iribarne. 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. J. Biogeogr. **33**: 888–900. doi:10.1111/j.1365-2699.2006.01461.x

Kirwan, M., and S. Temmerman. 2009. Coastal marsh response to historical and future sea-level acceleration. Quat. Sci. Rev. **28**: 1801–1808. doi:10.1016/j.quascirev.2009.02.022

Kirwan, M. L., and J. P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. Nature **504**: 53–60. doi:10.1038/nature12856

Kirwan, M. L., S. Temmerman, E. E. Skeehan, G. R. Guntenspergen, and S. Fagherazzi. 2016. Overestimation of marsh vulnerability to sea level rise. Nat. Clim. Change **6**: 253–260. doi:10.1038/nclimate2909

Kriwoken, L. K., and P. Hedge. 2000. Exotic species and estuaries: managing *Spartina anglica* in Tasmania, Australia. Ocean Coast. Manage. **43**: 573–584. doi:10.1016/S0964-5691(00)00047-8

Laegdsgaard, P. 2006. Ecology, disturbance and restoration of coastal saltmarsh in Australia: A review. Wetlands Ecol. Manage. **14**: 379–399. doi:10.1016/S0964-5691(00)00047-8

Lin, N., K. Emanuel, M. Oppenheimer, and E. Vanmarcke. 2012. Physically based assessment of hurricane surge threat under climate change. Nat. Clim. Change **2**: 462–467. doi:10.1038/nclimate1389

Mariotti, G., and S. Fagherazzi. 2010. A numerical model for the coupled long-term evolution of salt marshes and tidal flats. J. Geophy. Res. **115**: F01004. doi:10.1029/2009JF001326

Mariotti, G., S. Fagherazzi, P. L. Wiberg, K. J. McGlathery, L. Carniello, and A. Defina. 2010. Influence of storm surges and sea level on shallow tidal basin erosive processes. J. Geophys. Res. Oceans **115**: C11012. doi:10.1029/2009JC005892

Mariotti, G., and S. Fagherazzi. 2013. Critical width of tidal flats triggers marsh collapse in the absence of sea-level rise. Proc. Natl. Acad. Sci. USA **110**: 5353–5356. doi:10.1073/pnas.1219600110

Mariotti, G., K. Valentine, and S. Fagherazzi. 2015. Time-dependent behavior of a placed bed of cohesive sediment subjected to erosion and deposition cycles. Ocean Dyn. **65**: 287–294. doi:10.1007/s10236-014-0798-2

Mendelssohn, I. A., and N. L. Kuhn. 2003. Sediment subsidy: Effects on soil–plant responses in a rapidly submerging coastal salt marsh. Ecol. Eng. **21**: 115–128. doi:10.1016/j.ecoleng.2003.09.006

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands, 3rd ed. JohnWiley & Sons.

Möller, I., and others. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. Nat. Geosci. **7**: 727–731. doi:10.1038/ngeo2251

Moreno-Mateos, D., M. E. Power, F. A. Comin, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. PLoS Biol. **10**: e1001247. doi:10.1371/journal.pbio.1001247

Mossman, H. L., A. J. Davy, A. Grant, and C. Elphick. 2012. Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites?. J. Appl. Ecol. **49**: 1446–1456. doi:10.1111/j.1365-2664.2012.02198.x

Nicholls, R. J., P. P. Wong, V. R. Burkett, J. O. Codignotto, J. E. Hay, R. F. McLean, S. Ragoonaden, and C. D. Woodroffe. 2007. Coastal systems and low-lying areasm, p. 315–357. *In* M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson [eds.], Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Nolte, S., F. Müller, M. Schuerch, A. Wanner, P. Esselink, J. P. Bakker, and K. Jensen. 2013. Does livestock grazing affect sediment deposition and accretion rates in salt marshes?. Estuar. Coast. Shelf Sci. **135**: 296–305. doi:10.1016/j.ecss.2013.10.026

Schwarz, C., T. Ysebaert, Z. Zhu, L. Zhang, T. J. Bouma, and P. M. J. Herman. 2011. Abiotic factors governing the establishment and expansion of two salt marsh plants in the Yangtze Estuary, China. Wetlands **31**: 1011–1021. doi:10.1007/s13157-011-0212-5

Schwarz, C., T. J. Bouma, L. Zhang, S. Temmerman, T. Ysebaert, and P. M. J. Herman. 2015. Interactions between plant traits and sediment characteristics influencing species establishment and scale-dependent feedbacks in salt

marsh ecosystems. Geomorphology **250**: 298–307. doi: 10.1016/j.geomorph.2015.09.013

Shepard, C. C., C. M. Crain, and M. W. Beck. 2011. The protective role of coastal marshes: A systematic review and meta-analysis. PLoS One **6**: e27374. doi:10.1371/journal.pone.0027374

Silliman, B. R., T. Grosholz, and M. D. Bertness. 2009. Human impacts on salt marshes: A global perspective. Univ. of California Press.

Suchrow, S., N. Pohlmann, M. Stock, and K. Jensen. 2012. Long-term surface elevation changes in German North Sea salt marshes. Estuar. Coast. Shelf Sci. **98**: 71–83. doi: 10.1016/j.ecss.2011.11.031

Suykerbuyk, W., T. J. Bouma, L. L. Govers, K. Giesen, D. J. de Jong, P. Herman, J. Hendriks, and M. M. van Katwijk. 2016. Surviving in changing seascapes: Sediment dynamics as bottleneck for long-term seagrass presence. Ecosystems **19**: 296–310. doi:10.1007/s10021-015-9932-3

Temmerman, S., M. B. De Vries, and T. J. Bouma. 2012. Coastal marsh die-off and reduced attenuation of coastal floods: A model analysis. Glob. Planet. Change **92–93**: 267–274. doi:10.1016/j.gloplacha.2012.06.001

Temmerman, S., P. Meire, T. J. Bouma, P. M. J. Herman, T. Ysebaert, and H. J. De Vriend. 2013. Ecosystem-based coastal defence in the face of global change. Nature **504**: 79–83. doi:10.1038/nature12859

van der Wal, D., A. Wielemaker-Van den Dool, and P. M. J. Herman. 2008. Spatial patterns, rates and mechanisms of saltmarsh cycles (Westerschelde, The Netherlands). Estuar.

Coast. Shelf Sci. **76**: 357–368. doi:10.1016/j.ecss.2007.07.017

Vandenbruwaene, W., and others. 2011. Flow interaction with dynamic vegetation. patches: Implications for biogeomorphic evolution of a tidal landscape. J. Geophys. Res. Earth Surf. **116**: F01008. doi:10.1029/2010JF001788

Watson, E. B. 2008. Marsh expansion at Calaveras Point Marsh, South San Francisco Bay, California. Estuar. Coast. Shelf Sci. **78**: 593–602. doi:10.1016/j.ecss.2008.02.008

Conflict of Interest

None declared.