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Tidal marsh dynamics in a changing climate

A study on the mechanisms of pioneer establishment and erosion

Schordynamiek in een veranderend klimaat
Een onderzoek naar de mechanismen van pioniersvestiging en erosie
(met een samenvatting in het Nederlands)

Proefschrift

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Chapter 1

1. General Introduction

1.1 Tidal marsh ecosystems in a changing climate

Tidal marshes (Fig. 1.1) are major, widely distributed, intertidal habitats that belong to the most valuable bio-geomorphic ecosystems on earth (Adam 2002; Barbier et al. 2011). These habitats host a number of macrophytes that can be found within a gradient of inundation and salinity stress (Adam 2002; Perillo et al. 2009). The ecosystem services of tidal marshes in terms of high primary productivity (Mitsch and Gosselink 2000), biodiversity conservation (Gedan et al. 2009), carbon sequestration (Kirwan et al. 2012a,b; Burden et al. 2013), wave attenuation (Möller et al. 2014), storm surge mitigation (Wamsley et al. 2010; Stark et al. 2015), and formation of high foreshores by sediment trapping (Kirwan and Megonigal 2013; Temmerman and Kirwan 2015) are of vital importance for a wide range of marine-intertidal communities and the growing coastal human population (Nicholls et al. 2007; Temmerman et al. 2013).

Fig. 1.1 Tidal marsh ecosystem at the interface of land and sea; photo taken by Haobing Cao at the Yangtze estuary.

In the face of global climate change with induced sea level rise and storm surges, tidal marshes are increasingly valued for their function of coastal protection, making them been appreciated as an important component of sustainable coastal protection schemes (Shepard et al. 2011; Temmerman et al. 2013; Bouma et al. 2014). Although there is strong evidence that tidal marshes can keep pace with sea level rise due to sediment-trapping plant-growth feedbacks (Kirwan et al. 2013, 2016), marsh ecosystems are experiencing a worldwide decline due to large-scale, anthropogenic and climatological disturbances (Gerdan et al. 2009; Silliman et al. 2009; Temmerman et al. 2012; Kirwan and Megonigal 2013; Schepers et al. 2017). The decline of these highly valuable ecosystems emphasize the needs to conserve and restore them. The latter requires in-depth mechanistic understanding on both tidal marsh establishment and dynamics under external and internal stressors (Fagherazzi et al. 2013; Bouma et al. 2014; van Belzen et al. 2017).

1.2 Tidal marsh dynamics

Being a typical biogeomorphic ecosystem occurring at the dynamic interface of land and sea, tidal marshes are subject to changing environmental conditions (Adam 2002). As a consequence of interactions between physical and biological processes (Callaghan et al. 2010; Mariotti and Fagherazzi 2010), tidal marshes have long been recognized to have cyclic dynamics at the tidal flat/vegetation boundary with alternating phases of lateral expansion and erosion at different spatial and temporal scales (Yapp et al. 1917; Gray 1991; Adam 2002; van der Wal et al. 2004, 2008; van de Koppel et al. 2005; Chauhan 2009; Bouma et al. 2016).

Fig. 1.2 Tidal marsh expansion and erosion at the pioneer zone. Left, seedling establishment followed by lateral clonal growth; right, cliff erosion at a marsh edge. Photos taken by Haobing Cao.

1.2.1 Tidal marsh establishment and expansion

In many coastal areas around the world, the development of tidal marsh ecosystems often starts with pioneer species colonization on a bare intertidal flat though seedling establishment (Friess et al. 2012). This process is regarded as the first critical threshold that needs to be surpassed to initiate the shift from bare tidal flat to vegetated state (Wang and Temmerman 2013; Balke et al. 2014; Bouma et al. 2009, 2016). Colonization of tidal flats by salt marsh seedlings is the result of bio-physical interactions and thus often problematic (Bouma et al. 2009, 2016; Friess et al. 2012). For example, wave stress and associated sediment dynamics often inhibit new seedling establishment (Callaghan et al. 2010; Hu et al. 2015a; Bouma et al. 2016). To be able to successfully establish, marsh seedlings need a disturbance free/low period (referred to as "Windows of Opportunity", Balke et al. 2014; Hu et al. 2015b; Bouma et al. 2016) to become strong enough to resist stochastic physical disturbances.

Once seedlings have established, further marsh expansion can be expected by subsequent lateral clonal growth to patchy patterns (van der Wal et al. 2008; Vandenbruwaene et al. 2011). After exceeding a critical biomass or density threshold (Van Wesenbeeck et al. 2008; Bouma et al. 2009a), positive feedbacks between vegetation growth and sediment trapping will enhance the stability of vegetation state, forming a closed vegetation cover that dissected by drainage channels (Allen, 2000; van de Koppel et al. 2005; Temmerman et al. 2007). The presence of such closed marsh vegetation with channel networks constitute basic pathways for the exchange of water, nutrient, and sediment supply of the marshes, and are thus important for the long-term persistence of tidal marsh ecosystems under sea level rise (Perillo et al. 2009; Schwarz et al. 2014a, b; Temmerman and Kirwan 2015; Kirwan et al. 2016). However, quantitatively studies are current largely lacked on how physical stresses may affect tidal marsh establishment and how marsh dynamics may interact them in a changing climate.

1.2.2 Tidal marsh erosion

When a tidal marsh is under erosion or retreat, the discontinuity at the tidal flat and vegetation boundary is typically visible as a pronounced cliff at the edge of the marsh plateau (van de Koppel et al. 2005; Callaghan et al. 2010; Mariotti and Fagherazzi 2010). The formation and retreat of such cliffs are attributable to a variety of extrinsic and intrinsic variations at different scales (Fagherazzi et al. 2013; Wang et al. 2017). For instance, while wave density can extrinsically determine the hydrodynamic energy that reaches the marsh edge (Marani et al. 2011; Möller et al. 2014; Wang et al. 2017), soil type and the presence of vegetation may intrinsically influence erodibility at the marsh edge (Feagin et al. 2009; Mudd et al. 2010; Lo et al. 2017; Wang et al. 2017). In many cases, cliff erosion is followed by a runaway reaction of piping, soaping, and vegetation collapse, which may modify the rate of marsh regression and ultimately the total extension of marsh ecosystems along the coastline (van de Koppel et al. 2005; Mariotti and Fagherazzi 2010). Recent studies indicate that plants are particularly influential for geomorphic processes, and different dominant plant species may produce species-specific signatures in the organization and development of the landscape features (Corenblit et al. 2011, 2018; Schwarz et al. 2018) Therefore, it is tempting to understand how the differences in marsh expansion traits may drive cliff formation and evolution.

1.3 Knowledge gapes in tidal marsh dynamic

Notwithstanding the increasing understanding of tidal marsh dynamic mechanisms, there is still much to be learnt. This is especially true in an era of changing climate with increasing uncertainty on the resilience of tidal marsh ecosystems to environment variations (Kirwan et al. 2009, 2013; Marani et al. 2011; van Belzen et al. 2017). Currently, attempts to use tidal marsh ecosystems as a sustainable way of coastal protection are far from success (Mariotti and Fagherazzi 2013; Bouma et al. 2014). The main knowledge gaps that hamper large-scale application to date remain in ability to account quantitatively for both short-term and long-term dynamics of marsh ecosystems (Bouma et al. 2014, 2016).

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 stress, as well as short-term sediment dynamics related to waves, is expected to increase in both magnitude and frequency (Hu et al. 2015a, b). It is an intriguing question and an important practical problem how increasingly energetic shorelines in a changing climate will affect both short-term and long-term tidal marsh dynamics (Mariotti and Fagherazzi 2010; Fagherazzi et al. 2012; Bouma et al. 2016). Therefore, it is important to address **Question 1: What are the effects of contrasting sediment disturbance regimes on seedling establishment? What is the importance of disturbance intensity, disturbance frequency and the length of an initial disturbance-free period?** Similarly, surprisingly little is known on the direct mechanisms that limit or allow primary marsh establishment under wave stress (Silinski et al. 2015, 2018) and wave-induced sediment disturbance (Bouma et al. 2016). It is also necessary to understand **Question 2: What are the effects of wave stress on the establishment of seedling of pioneer marsh species? Do species from different locations along an estuarine salinity gradient respond differently in their morphology and biomechanical traits?**

Recent studies highlight the importance to have a self-organized diverse landscape in the resilience of many coastal ecosystems (Rietkerk and van de Koppel 2008; Liu et al. 2014; van de Koppel et al. 2012, 2015). In tidal marshes, drainage channels inserting in marsh vegetation can enhance landscape stabilization with scale dependent feedbacks (Schwarz et al. 2014a, b, 2018; Temmerman and Kirwan 2015; Kirwan et al. 2016). Whereas previous studies have mainly focused on how plant traits contribute to channel formation or evolution (Temmerman et al. 2007, Vandenbruwaene et al. 2013; Bouma et al. 2013; Schwarz et al. 2018), it is equally important to understand the inverse mechanism. Topographic heterogeneity and channel related surface drainage relief may initiate vegetation establishment and further contribute to the evolution towards a mature marsh. Hence, it is needed to understand **Question 3: How is the establishment of pioneer marsh plants in poorly consolidated muddy systems affected by channel related surface drainage relief, and is**

this age-dependent?

With respect to marsh erosion, many experimental and modelling studies have provided considerable advances in identifying and quantifying both extrinsic (e.g., wind waves) and intrinsic factors (e.g., sediment properties, the presence of vegetation) in understanding marsh-cliff retreat mechanisms (Feagin et al., 2009; Fagherazzi et al. 2012; Francalanci et al. 2013; Lo et al. 2017; Wang et al. 2017). However, very few studies so far have focussed on how species-specific plant traits influence dynamics and evolution of this biogeomorphic landscape. If the differences in traits drive different long-term dynamics of tidal marshes, especially in the critical cliff formation process, it is important to understand these relations. Therefore, it is interesting to investigate **Question 4: How do species clonal expansion traits at the marsh edge affect the likelihood of the presence of cliffs? Do such clonal expansion traits respond to different sediment properties?**

1.4 Thesis outline

In order to enhance our mechanistic understanding on marsh dynamics and bridge the afore mentioned knowledge gapes, this thesis has taken the pioneer tidal marsh as focal system and combined both laboratory and field experiments to address the above 4 questions in chapters 2 to 5:

Chapter 2) is related to Question 1: What are the effects of contrasting sediment disturbance regimes on seedling establishment? What is the importance of disturbance intensity, disturbance frequency and the length of an initial disturbance-free period?

The chapter examines the effects of short-term sediment disturbance-regimes on seedling establishment of two globally distributed foundation marsh species: *Spartina alterniflora* and *Spartina anglica*. Seedlings of them were exposed to a set of different accretion/erosion-regimes in the laboratory, following two different disturbance-free periods.

Chapter 3) is related to Question 2: What are the effects of wave stress on the establishment of seedling of pioneer marsh species? Do species from

different locations along an estuarine salinity gradient respond differently in their morphology and biomechanical traits?

Using a newly developed plant-shaking mesocosm that mimicked water-imposed wave drag forces, the effect of wave stress on seedling survival was studied for three marsh pioneer species that are dominant along the salinity gradient: *Spartina anglica*, salt to brackish; *Scirpus maritimus*, brackish; and *Phragmites australis*, brackish to fresh). For the surviving plants, the effect of waves on their morphology and biomechanical properties was examined.

Chapter 4) is related to Question 3: How is the establishment of pioneer marsh plants in poorly consolidated muddy systems affected by channel related surface drainage relief, and is this age-dependent?

By means of a manipulative field experiment, the impact of surface drainage and sediment level relative to mean sea level on the survival of marsh seedlings from three different age classes, as well as the growth performance of mature marsh tussocks, were examined The manipulative experiment was done by building “mega-marsh organ” mesocosms, which are designed for a theoretically undrainable, recently deposited and poorly consolidated muddy system, to investigate (1) if poor surface drainage forms a critical threshold for initial seedling establishment, while not affecting seedlings at a larger stage, and (2) if the strength of this threshold depends on the level of inundation stress.

Chapter 5) is related to Question 4: How do species explicit clonal expansion traits at the marsh edge affect the likelihood of the presence of cliffs? And do such clonal expansion traits respond to different sediment properties?

This chapter describes a controlled mesocosm experiment to compare the clonal expansion traits of three marsh pioneer species that are dominant along the salinity gradient (same species as Chapter 3). This was followed by a flume experiment examining how species-specific expansion strategies like clonal step length may on the one hand respond to the sedimentary environment, and on the other hand drive cliff dynamics.

Chapter 2

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

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Abstract

Seedling establishment is an important process relevant for the restoration of salt marsh within the frame work 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 adjust mentis 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.

2.1 Introduction

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 saltmarshes 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 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. 2009a, 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. 2009b, 2016; Friess et al. 2012). Hydrodynamic forces and associated sediment dynamics often inhibit new seedling establishment (Callaghan et al. 2010; Hu et al. 2015a; 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. 2015b). 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. 2015b). 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 macro tidal coastlines (see Bouma et al. 2009b, 2016; Kirwan and Megonigal 2013). We study the response of two globally distributed foundation species in marshes: *Spartina alterniflora* and *Spartina anglica* (Fig. 2.1; 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 Fagherazzi2010; Fagherazzi et al. 2012; Bouma et al. 2016).

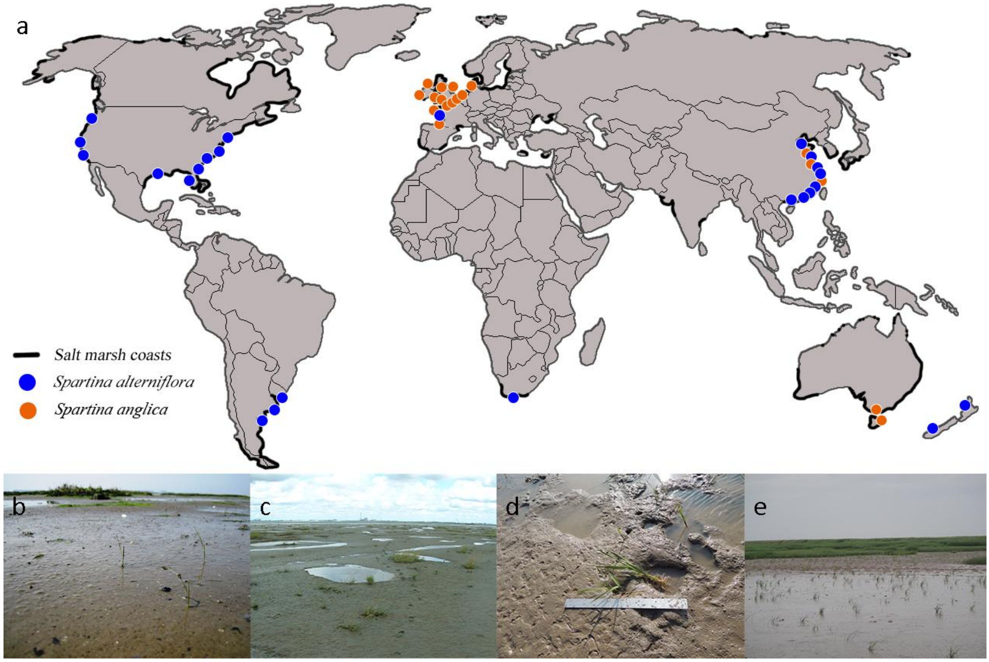

Fig. 2.1. (a) Distribution of *Spartina alterniflora* and *Spartina anglica* along the world coasts, which may not show the complete distribution. Photographs of (b) *Spartina anglica* seedlings established near the Oesterdam in the Oosterschelde; (c) *Spartina anglica* seedlings near tussocks in Hooge Platen, the Netherlands, and (d & e) expansion of *Spartina alterniflora* onto the mud flats that was initiated with seedling establishment in the Yangtze estuary, China.

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: 2and 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., *S. alterniflora* and *S. anglica*; Fig. 2.1), 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 modelling the consequences of physical disturbance on tidal flats. Finally, we discuss our results in the context of marsh creation and restoration.

2.2 Material and methods

2.2.1 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 48C 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℃ 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 D_{50} 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.

2.2.2 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. 2.2b): 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 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).

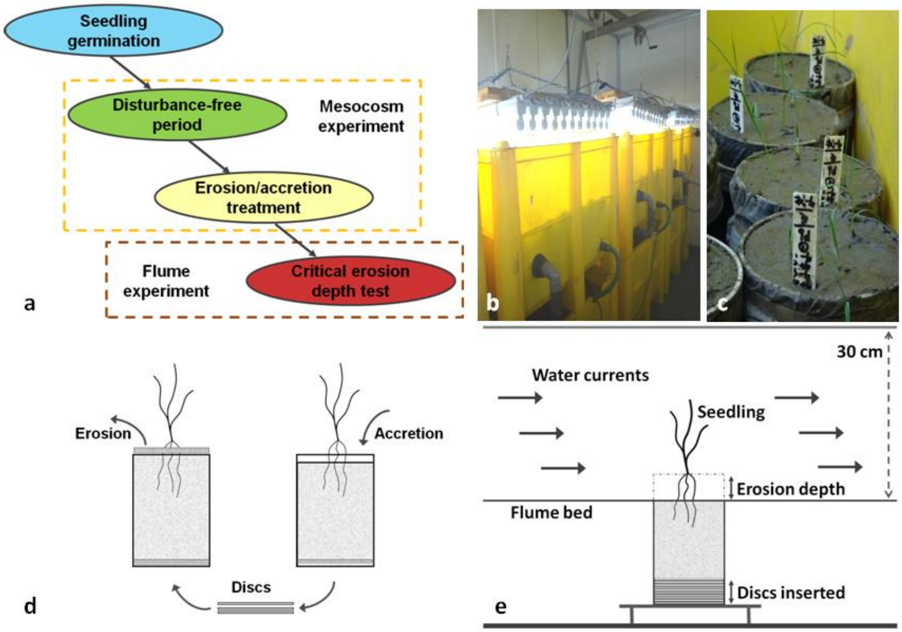

Fig. 2.2. Schematic diagrams and photographs showing the experiment setups. (a)The four steps in our experiment; (b) photographs of the mesocosm setup and (c) seedlings in the upper experimental tanks during low tide; (d) erosion and accretion treatments; and (e) the test section of the flume, with a 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.

Light to the mesocosms was provided by suspended fluorescent tubes arranged in parallel over the tanks (Fig. 2.2b)with 12 h d^{-1} (550 μ mol m^{-2} s^{-1} PAR), and the temperature was thermostatically controlled in the climate room and maintained at 25℃ during the day time and 18℃ 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. 2.2c) 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 2d 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).

2.2.3 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 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 2.1). 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 2.1) underneath the pots and gently removing the pushed-up sediment by using a water spray (Fig. 2.2d). 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. 2.2d). 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 were used in our experiment (i.e., 12 replicates × 2 disturbance-free periods × 17 sediment treatments). All treatments and replicates were randomly assigned to the 10mesocosms. 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 2.1).

Table 2.1. Sedimentation treatments every week during the 6-week course of the mesocosm experiments.

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

2.2.4 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. 2.2e) in order to determine the CED for each seedling (see Balkeet al. 2011, 2013 for mangroves; Bouma et al. 2016; Infanteset 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. 2.2e). 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. 2.2e). The current velocity was chosen to mimic peak velocities typical for a *Spartina* pioneer zone (i.e., 0.25 ms^{-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).

2.2.5 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 analysing 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.).

2.3 Results

2.3.1 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. 2.3). 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. 2.3).

When focusing on the effects of specific accretion/erosion treatments, it is clear that in the CR (Fig. 2.3a) and IS treatment groups (Fig. 2.3b), 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. 2.3b 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. 2.3b, c).

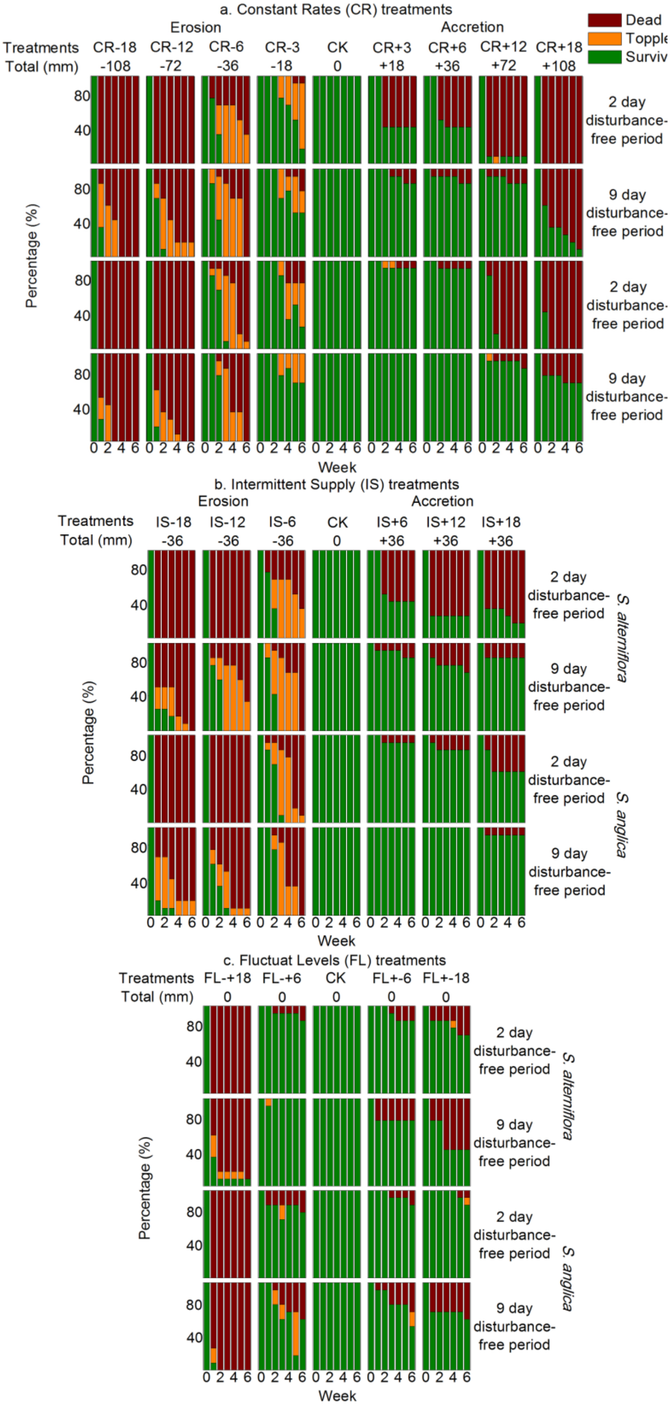

Fig. 2.3. Percentage of surviving, toppled and dead seedlings during the mesocosm experiments. (a) Constant Rate (CR) treatment groups, (b) Intermittent Supply (IS) treatment groups, and (c) Fluctuant Level (FL) treatment groups.

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. 2.3a,b) ($p<0.01$, Table 2.2). No significant effect of the disturbance-free period was observed in the FL treatment groups (Fig. 2.3c).

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. 2.3a,b), with significant differences found for the 2 d disturbance-free seedlings ($p<0.05$, Table2.2) but not for the 9 d disturbance-free seedlings ($p>0.05$,Table 2.2). No obvious trend across species was observed in the FL treatments (Fig. 2.3c).

2.3.2 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. 2.4a, b), and the increase in CED was higher for CR than for IS treatments (Fig. 2.4a, b). However, no trends could be observed for any of the FL treatments (Fig. 2.4c). The effect of harsh erosion treatments on CED could not be quantified statistically due to high mortality (Fig. 2.4a, b and 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

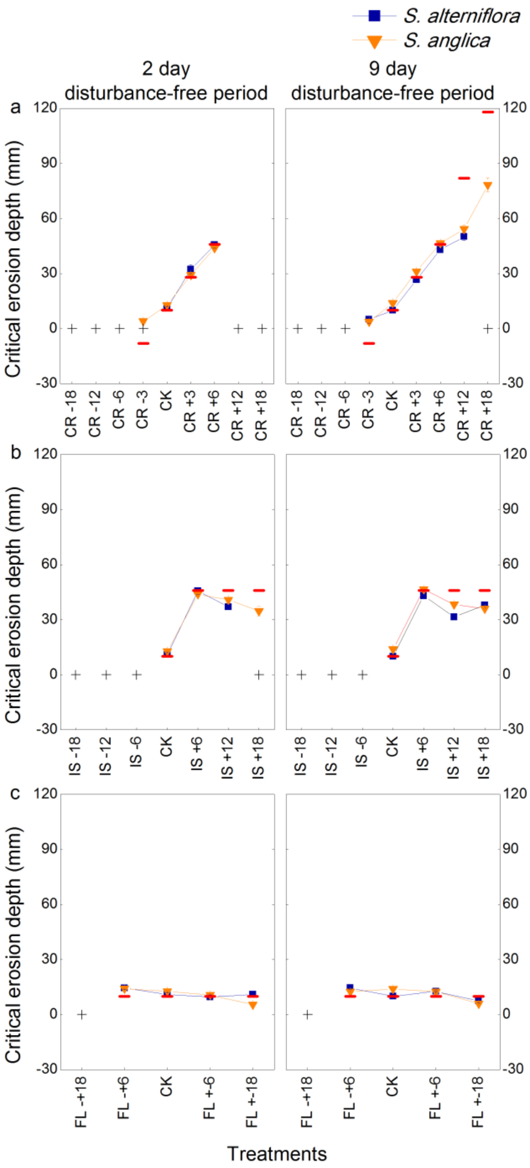

Fig. 2.4. The critical erosion depth (CED) of surviving seedlings at harvest. (a) Constant Rate (CR) treatment groups, (b) Intermittent Supply (IS) treatment groups, and (c) Fluctuant Level (FL) treatment groups. The red dashes (short red horizontal lines) indicate the values where CED was equal to seedling 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.

with the control groups (Fig. 2.5a), which indicates that plants reduced investment in roots when being stabilized by accretion. These responses explain why the absolute CED for erosive 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.2.4a) and lower than the expected CED value after non-lethal accretion treatments (e.g., CR+3, Fig. 2.4a). The root-shoot ratio was not significantly affected by the IS and FL treatments (*p*>0.05) (Fig. 2.5b, c).

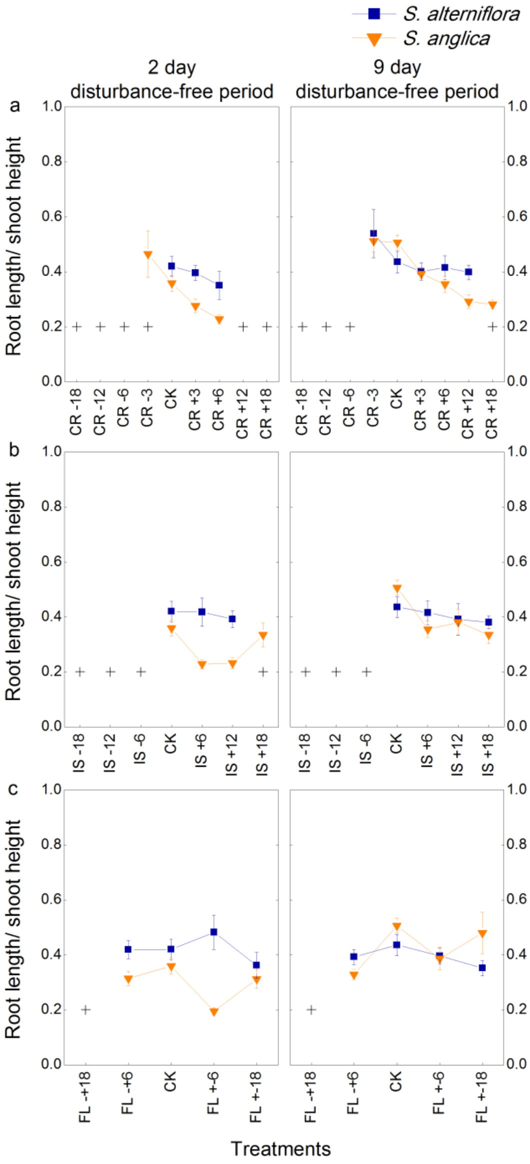

Fig. 2.5. The root/shoot ratio of the surviving seedlings. (a) Constant Rates (CR) treatment groups, (b) Intermittent Supply (IS) treatment groups, and (c) Fluctuant Level (FL) treatment groups. Note that the plus sign indicates treatment groups with less than three surviving seedlings.

Table2.2. 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.	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 days	Species	1	.022
			Treatments	8	.000
		9 days	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 days	Species	1	.008
			Treatments	6	.000
		9 days	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 days	Species	1	.819
			Treatments	4	.000
		9 days	Species	1	.235
			Treatments	4	.000

2.4 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. anglic*a and *S. alterniflora*. Our results indicate the following: (1) erosion strongly hampers seedling establishment, whereas accretion seems favourable 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.

2.4.1 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 hydro-period for successful ecosystem establishment (Balke et al. 2014; Hu et al. 2015b). 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; Balkeet 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; Balkeet 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. 2015b). 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 saltmarshes 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 (Adam2002; 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).

2.4.2 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 focusneeds 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 favourable 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.

2.5 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.

Chapter 3

3. Wave effects on seedling establishment of three pioneer marsh species: survival, morphology and biomechanics

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Abstract

It is important to have an in-depth mechanistic understanding of tidal marsh establishment and dynamics for ensuring the long-term persistence of these valuable ecosystems. As wave forcing may be expected to impact seedling establishment, we studied the effect of water-imposed drag forces on seedling survival, morphology and biomechanics properties of marsh pioneer species that are dominant along the salinity gradient in many areas around the world: *Spartina anglica*(salt to brackish), *Scirpus maritimus*(brackish), and *Phragmites australis* (brackish to fresh). Using a newly developed plant-shaking mesocosm (PSM) that mimicked water-imposed wave drag forces, the effect of wave stress on seedling survival was examined, together with impacts on morphology and biomechanical properties. After seven weeks exposure to wave stress, lowered seedling survival and growth for all species was revealed. Wave treatments enlarged the root/shoot biomass ratio to enhance anchorage and made seedlings more flexible (i.e., reduced flexural rigidity), which might be regarded as a mixed outcome between stress avoidance and stress tolerance strategy. The different biomechanical responses between the three dominant marsh pioneer species, overall, make them less resistant to external stress. Therefore, our results indicate that establishment chances of marshes are reduced if wave energy increases. Despite the different biomechanical response of these three pioneer species to waves, the seedlings of all species were fund to have low resistance to external stresses.

3.1 Introduction

Tidal marsh ecosystems are increasingly valued for their wave attenuation service (Bouma et al. 2005, 2010) even under extreme storm conditions (Möller et al. 2014). In coping with the growing risk of coastal flooding under accelerating sea level (Craft et al. 2008; Lin et al. 2012; Kirwan and Megonigal 2013), conservation and restoration of tidal marshes are now widely appreciated as long-term sustainable protective solutions (Borsje et al. 2011; van Slobbe et al. 2013; Temmerman et al. 2013). Tidal marshes are also valued for many other valuable ecosystem services such as conservation of biodiversity, regulation of nutrients via nutrient cycling, and regulation of climate via organic carbon sequestration (Gedan et al. 2009; Barbier et al. 2011; Burden et al. 2013). Although there is strong evidence that tidal marshes can survive sea level rise due to sediment-trapping plant-growth feedbacks (Kirwan et al. 2013, 2016), over the last decades tidal marshes have rapidly degraded on a global-scale (Silliman et al. 2009; Tonelli et al. 2010; Temmerman et al. 2012). The high value of tidal marshes and the loss of such important ecosystems emphasize the needs to conserve and restore them. The latter requires in-depth understanding of both tidal marsh (re)establishment and lateral expansion under external stressors (Fagherazzi et al. 2013; Bouma et al. 2014; van Belzen et al. 2017; and reference therein).

In many coastal areas around the world, seedling establishment is of particular importance for the (re)colonization of large bare tidal flats. This may be especially important for those erosional marsh edges, where the height of the erosional marsh-cliff may prevent plants growing on top of this cliff, to expand clonally onto the lower tidal flat in front of the cliff. This kind of disconnection between marsh and tidal-flats may be especially important in macro-tidal systems. In these areas, seedling establishment is regarded as the first critical threshold that needs to be surpassed to initiate the transition from a bare mud flat to vegetated state (Wang and Temmerman 2013; Balke et al. 2014; Bouma et al. 2016). Once seedlings have established, further marsh expansion may be expected by lateral clonal growth (van der Wal et al. 2008; Vandenbruwaene et al. 2011). Recent studies have shown that for some species waves may hamper seedling establishment (Silinski et al. 2015, 2016) via wave-induced sediment dynamics (Callaghan et al. 2010; Hu et al. 2015a; Bouma et al. 2016). The direct effect of waves on newly establishing seedlings remains, however, poorly understood. We still lack insight as to whether this may vary among marsh pioneer species that occur along the salinity gradient of estuaries, where wave exposure may also be expected to decrease due to narrowing of the system.

Wave exposure is known to be of critical importance for understanding the long-term marsh development (Callaghan et al. 2010; Fagherazzi et al. 2012; Bouma et al. 2014). For example, recent studies have demonstrated that wave exposure can induce cliff formation at the marsh edge, causing lateral erosion (Callaghan et al. 2010; Marani et al. 2011; Fagherazzi et al. 2013;Wang et al. 2017). In contrast, surprisingly little is known on how wave stress affect tidal marsh plants during the establishment phase. Previous studies indicate that waves can affect individual plants, either directly by drag/pull imposing on the plants (Coops et al. 1991, 1994, 1996a, b; La Nafie et al. 2012, Silinski et al. 2018), or indirectly via sediment scouring around the stems (Bouma et al. 2009a; Silinski et al. 2015). As yet the direct mechanisms that limit or allow marsh establishment are only starting to be quantified by experimental studies (Silinski et al. 2015).

Current knowledge gaps on the direct effects of waves on plants may be partly due to methodological limitations. Studying the interaction between waves and vegetation have conventionally been assessed in wave flumes of different scales (Bouma et al. 2005, 2009b, 2010; Möller et al. 2014; Silinski et al. 2015, 2018). Whereas wave flumes typically provide a perfect method to mimic hydrodynamic conditions, the high construction and operational costs of such infrastructure makes these experiments generally too expensive to do long-term growth experiments or have high numbers of replicates. Long-term studies are commonly carried out in wave tanks (Coops et al. 1996a, b; La Nafie et al. 2012; Wang et al. 2017). in which hydrodynamic conditions are typically less ideal than in flumes, but due to lower costs some level of replication is possible. In this study, we provide an even more simple approach to assess wave effects on plants by designing tidal Plant-Shaking Mesocosms

(PSM). The PSMs mimics wave-induced drag stress on the seedlings, by moving the plants (seedling) back and forth through the water, rather than by moving the water around the plants.

Species-specific insight in the responses of pioneers to enhanced wave climate, is important to inform future restoration projects. As wave exposure may be expected to decrease with salinity, due to the typical narrowing of the estuarine system, species with a higher salt tolerance perhaps be better adapted to wave exposure. The present study aims to extend current knowledge by studying the direct effect of waves stress on the survival, morphology and biomechanical properties of newly establishing seedlings of marsh pioneers, using novel tidal Plant-Shaking Mesocosms. We compare this for three dominant marsh pioneer species that occur along the estuaries with decreasing salinity gradient: *Spartina anglica* (salt to brackish), *Scirpus maritimus* (brackish), and *Phragmites australis* (brackish to fresh).

3.2 Material and methods

3.2.1 Plant material

The seedlings of *S. anglica*, *S. maritimus*, and *P. australis* were obtained from seeds that had been collected from the Scheldt estuary (The Netherlands) in November 2016. Seeds were cool stored in a fridge at 4 ℃ until being germinated in a container with an alternating temperature condition (25 ℃ during the day and 30 ℃ at night to speed up the process, practical choice). Seeds with a visible germ were identified as seedlings suitable for transplantation. All seedlings were prepared one week before transplantation and stored in an incubator with the same germination condition as described above. The plants were regarded to be in the seedling stage during the whole period of the experiment, as they remained short compared to full-grown individuals (longest shoots = 17.7 ± 2.4 cm for *S. anglica*; 34.9 ± 4.3 cm for *S. maritimus*; 44.5 ± 7.2 cm for *P. australis*). For each species, we transplanted 24 seedlings individually to PVC pots (160 mm height × 110 mm inner diameter) by planting them at 1 cm depth of the sediment. The sediment (with an average D50 of 29.93 μm) used was macrobenthos free (by sieving) and selected in a primary test to have a negligible scouring under our experiment conditions.

3.2.2 Experimental design

The experiment was carried out using four tidal mesocosms in a climate room (NIOZ Royal Netherlands Institute for Sea Research, Yerseke, The Netherlands), where light was provided with 12 h d^{-1} (550 μmol m^{-2} s^{-1} PAR), and temperature was controlled at 25℃ during the day and 18℃ during night (for more details see reference within Cao et al. 2018). In each mesocosm, a semi-diurnal 1.5 h inundation regime was mimicked with a mix of fresh water and Scheldt sea water (which gives a salinity of 12.61 ppt). All pots were equally distributed in the four systems with six seedlings of each species per mesocosm, which gives 12 replicate seedlings per species for each treatment. The water depth of all mesocosms was 21 cm from the sediment top during high tide.

Two of the mesocosms were set as controls (C) and the other two were equipped with Plant-Shakers to impose continuous drag forces during mimicked high tide. Each Plant-Shaking Mesocosms (PSM) consists of a piston moved cuboid metal frame with a cribriform bottom that can hold many pots with plants. To simulate a wave like stress (W treatment), the plant-shaker was inserted onto the top tank of a tidal mesocosm. The piston was provided with air pressure that was controlled by a timer, to allow the device to move back and forth during tidal inundation. The distance of the motion was 30 cm in both directions, over a period of 2.6 seconds in the experimental tank, during the semi-diurnal 1.5 h inundation. In this way, we approximated the drag imposed by regular waves with an average frequency of 0.38 Hz. This is to mimic the measured windy weather wave conditions at tidal marshes in the Scheldt estuary (compare ~0.5 Hz that similar to significant wind waves at tidal marsh fronts in the Scheldt estuary field sites, see references within Callaghan et al. 2010;Wang et al. 2017).

3.2.3 Plant morphology and biomechanical properties measuring

The mesocosm experiment lasted for seven weeks, during which seedling health (survived, toppled or dead) and plant height (soil to leaf top) were weekly surveyed. To compare the overall growth rate of seedlings, the plant height change of each week interval was calculated. To test plant stem flexibility under bending forces, as occurs under wave forcing (Rupprecht et al. 2015), all survived seedlings were carefully cleaned from the sediment at the end of the seventh week.

We measured biomechanical traits by three-point bending tests on the 5 cm long basal stem fragments from survived seedlings, using a universal testing machine (Instron 5942, Canton, MA, USA). The tests were performed by applying a constant extension rate to the midpoint of each stem sample on two supports of the testing machine jaw. The following biomechanical traits that related to bending was calculated:

i) the *Yong's modulus* (*E*; KPa) which quantifies the stiffness of the stem that describes how much force needed to bend a stem (higher E value indicates for stiffer stems), is calculated as the slope of the stress-strain curve in the elastic deformation region.

ii) the *second moment of area*(*I*; m^4) that quantifies the distribution of material around the axis of bending (increases with diameter), is calculated using the formula for triangular cross-sections: $I = (bh^3)/36$, in which b and h are the base and height of the cross section.

iii) the *flexural stiffness* (*EI*, $N\ m^{-2}$), which was calculated by multiplying E (the Yong's modulus) and I (the second moment of area) to compare for the overall flexural rigidity of the seedlings (higher EI value indicates for less flexibility of individual plants).

The stem was considered to break or fold when it reaches the maximum bending stress. The *breaking force* (*F*, N) was then calculated to compare the maximum force that samples can withstand before mechanical failure (higher *F* value indicates for more resistance to tensile stress). The breaking force is thus a measurement of external stress that seedling can resist during the establishment phase (Rupprecht et al. 2015; Silinski et al. 2015, 2018; Vuik et al. 2018). Due to mortality, we used five replicates for each species per treatment for the biomechanical test. For calculation, all the stem samples were deemed as circular cross section since hollow stems had not yet developed for all young seedlings in our experiment. Finally, the dry biomass of survived seedlings were measured after oven-drying at 60 °C for 72 hours to compare for the root/shoot ratio of biomass.

3.2.4 Statistics

Seedling survival was analysed with using Kaplan–Meier method applying the log-rank for treatment comparison with seedling toppling and death set as hazard events. Seedling growth rates were calculated by the average plant height change of seven weeks. Two-way ANOVAs were carried out to analyse the effects of wave disturbance and species on the growth rate, root/shoot biomass, and biomechanical parameters. All results were tested in SPSS 18.0 software (SPSS, Chicago, IL, U.S.A.) with a significance level of 5%. Normality and homoscedasticity of the data were tested and these assumptions were passed.

3.3 Results

3.3.1 Seedling survival and growth

In the control groups (C), all seedlings survived (100%) throughout the experiment, regardless of species (Fig. 3.1). However, when subjected to mimicked wave stress (W), the percentage of survived seedlings decreased over time. Kaplan–Meier test showed that wave treatment significantly reduced the overall seedling survival (Fig. 3.1, Table 3.1; $p<0.05$). Although seedlings growth was non-linear in our experiment (Fig. 3.2a), we observed that. for all three pioneer marsh species, the average growth rate that calculated by plant height change (soil to leaf top) by week of seedlings during the seven weeks was also significantly lower under wave treatments as compared to the control groups (Fig. 3.2a, b, Table 3.2; $p < 0.05$). No significant difference regarding survival or growth rate was observed between the three pioneer marsh species (Fig. 3.1, Fig. 3.2a, b). These results identify wave exposure as a common important factor that hampers marsh establishment at the seedling phase.

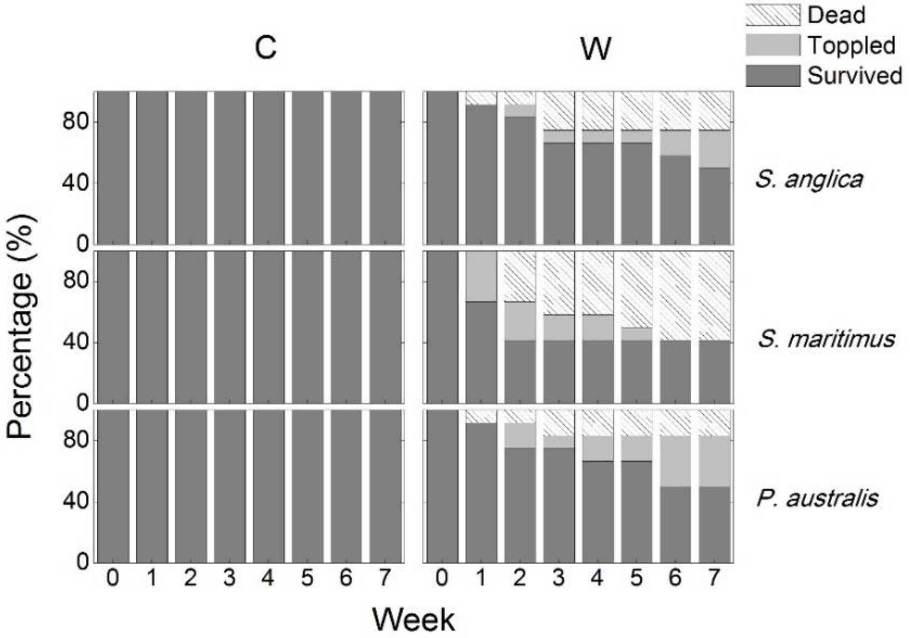

Fig. 3.1. Percentage of survived, toppled, and dead seedlings of three marshes in the mesocosm experiment (C and W indicates for control groups and wave treatment groups separately).

Table 3.1. Results of Kaplan－Meier log-rank test on the effects of wave treatments and species on seedling survival during the course of mesocosm experiment. Both toppling and death of seedlings were set at hazard events during the test.

Variable	χ^2	**d.f.**	***p***
Wave treatment	25.98	1	<0.001
Species	0.32	2	0.85

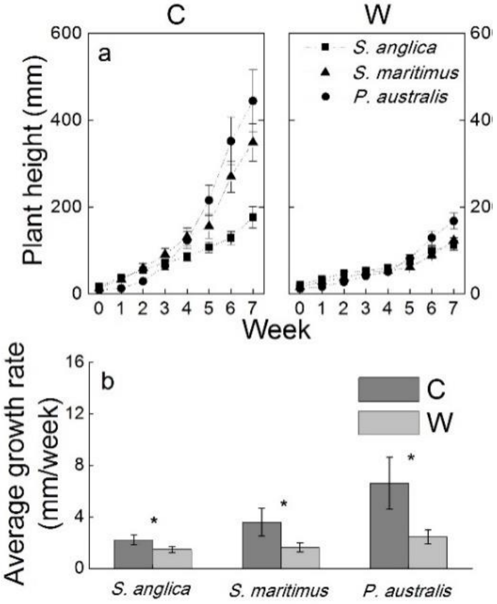

Fig. 3.2. Plant height change and average growth rate over seven weeks of three marsh seedlings (Data are means ± s. e.; C and W indicates for control groups and wave treatment groups separately, * indicates for significance *p*: 0.05 >*).

3.3.2 Seedling biomechanical and morphological traits

When comparing the biomechanical strength of the survived seedlings, two-way ANOVAs shows significant main effects from both wave treatment and species (Table 3.2). Specially, the measurements on Yong's modulus of elasticity (*E*; KPa) indicate that seedlings exposed to the wave treatment are significantly more flexible (i.e., reduced E) (Fig. 3.3a, *p* =0.022 for *S. anglica*, *p* =0.014 for *S. maritimus*, *p* = 0.003 for P. *australis*). A less stiffer stem material together with a reduced second moment of area (*I*, Fig. 3.3b, *p* = 0.01 for *S. anglica*, *p* =0.011 for *S. maritimus*, *p* =0.347 for *P. australis*), lead to significantly decreased overall Flexural stiffness (*EI*) values of seedling stems for all three marsh species in response to wave treatments (Fig. 3.3c, *p* = 0.017 for *S. anglica*, *p* =0.002 for *S. maritimus*, *p* = 0.003 *P. australis*). Consistently, we also observed that the breaking force (*F*) of all three marsh seedlings showed a significant decrease after wave treatments (Fig. 3.3d, *p* =0.041 for *S. anglica*, *p* =0.033 for *S. maritimus*, *p* = 0.008 for *P. australis*). Thus, the overall results of the three point bending test showed that marsh seedlings became more flexible and less resistant to tensile stress after the continuous wave exposure due to different material properties as well as reduced stem diameter.

However, in spite of these general biomechanical trends, the pattern of parameters shifted between marsh species. For example, *S. anglica* seedlings showed the least flexural stiffness (*EI*, Fig. 3.3c) and resistant to tensile stress (*F*, Fig. 3.3d). The biggest stem diameter (*I*, Fig. 3.3b) of *S. maritimus* seedlings leads to the highest mechanical resistance (*F*, Fig. 3.3d). While for *P. australis* seedlings, although the stem diameter (*I*, Fig. 3.3b) is comparable between the control (C) and wave treatment groups (W), the significantly decrease in stem flexibility (*E* and *EI*; Fig. 3.2a, c) still reduced the external stress that they can with stand (Fig. 3.3d).

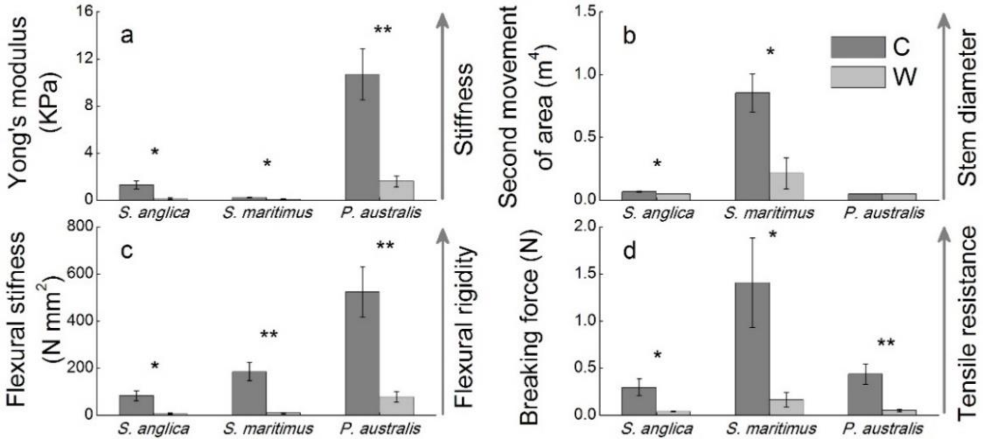

Fig. 3.3 Biomechanical traits of survived seedlings showing more flexibility after the continuous wave exposure: a, Young's modulus; b, Second moment of area; c, Flexural stiffness; and d, Breaking force of three pioneer marsh seedlings (Data are means ± s.e.; C and W indicates for control groups and wave treatment groups separately; * and ** indicates for significance p: 0.5 >* and 0.01 > **).

Measurements of morphological traits at harvest showed that, constant wave exposure also significantly increased the root/shoot biomass ratio of survived seedlings (Fig. 3.4, Table 2, $p< 0.05$). Interestingly, the root/shoot biomass ratio of *S. anglica* seedling was significantly higher than the other two species after wave stress treatment (Fig. 3.4, $p=0.023$ compared to *S. maritimus*; $p=0.016$ compared to *P. australis*).

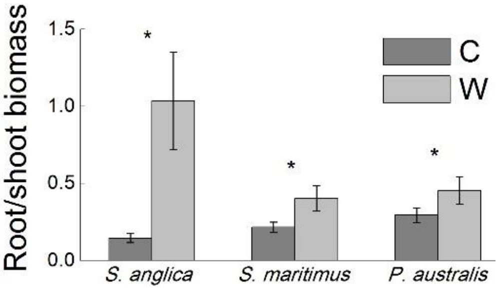

Fig. 3.4 Root/shoot biomass ratio of survived seedlings at harvest showing increased below ground biomass investment after the continuous wave exposure (Data are means ± s.e.; C and W indicates for control groups and wave treatment groups separately; * indicates for significance p: 0.05> *).

Table 3.2. Two-way ANOVAs table of main effects of wave treatment and species and their interactions on the plant traits of seedlings.

Response variable	**Deviance source**	**d. f.**	**Mean Sq**	**F**	***p***
Growth rate (cm/week)	Wave treatment	1	55.2	8.84	0.005
	Species	2	17.1	2.73	0.077
	Wave treatment * Species	2	6.9	1.10	0.341
Yong's modulus (KPa)	Wave treatment	1	86.2	19.67	<0.001
	Species	2	107.8	24.59	<0.001
	Wave treatment * Species	2	59.3	13.52	<0.001
Second moment of area (m^4)	Wave treatment	1	0.35	10.56	0.004
	Species	2	0.76	22.98	<0.001
	Wave treatment * Species	2	0.33	9.93	0.001
Flexural stiffness (N mm^2)	Wave treatment	1	390940	32.56	<0.001
	Species	2	176809	14.73	<0.001
	Wave treatment * Species	2	87799	7.31	0.003
Breaking force (N)	Wave treatment	1	2.83	12.82	0.002
	Species	2	1.11	5.03	0.015
	Wave treatment * Species	2	0.70	3.17	0.061
Root/shoot biomass	Wave treatment	1	1.85	9.84	0.003
	Species	2	0.33	1.78	0.180
	Wave treatment * Species	2	0.69	3.68	0.033

3.4 Discussion

An in-depth understanding of how various physical and biological factors affect tidal marsh establishment thresholds is essential for enabling restoration and sustainable management of these valuable ecosystems (Moreno-Mateos et al. 2012; Bouma et al. 2014). As yet mechanistic studies on the direct effect of waves on the establishment chance and developmental consequence for marsh seedlings are only starting to emerge (see references within Silinski, et al. 2015 for the influence of different wave regimes on the survival chance of *S. maritimus* from different life stages; see references within Rupprecht et al. 2015 for field observation of biophysical properties of NW European salt marshes; but also see references within Zhu et al. 2019 for the effects of salinity, inundation and seasonality on the biomechanical properties of marsh vegetation). The present study for the first time shows the direct effects of wave treatments on the early seedling establishment of three pioneer marsh species, by using tidal Plant-Shaking Mesocosms. We found that wave treatments directly reduced seedling survival, enhanced the root/shoot biomass ratio to enlarge anchorage, and made seedlings more flexible (reduced flexural rigidity). The different biomechanical responses between the three dominant marsh pioneer species: *S. anglica* (salt to brackish), *S. maritimus* (brackish), and *P. australis* (brackish to fresh), overall, make them less resistant to external stress.

3.4.1 The effects of wave stress on seedling establishment and growth

In the present study, our results clearly show for all three pioneer marsh species, that waves are a stress that may create a threshold that directly hampers both seedling establishment and seedling growth. Marsh recovery has been regarded as a critical transition between two alternative stable states (the bare tidal flat state versus the vegetated state; Wang and Termmerman 2013; van Belzen et al. 2017). Present results thus underline the needs for wave-free periods, to provide "Windows of Opportunity" for a marsh to establish (Balke et al. 2014; Bouma et al. 2014). Whereas previous studies related the need for a wave-free period to prevent uprooting due to sediment dynamics (Bouma et al. 2014, 2016; Cao et al. 2018), we show here that there are also direct effects on seedling growth. As the windows of opportunity concept for seedling establishment does require a disturbance-free period for the seedlings to grow large enough to be able to resist hydrodynamic disturbances (e.g., by having longer roots, stronger shoots; with references see Balke et al. 2013 2014; Hu et al. 2015b), a reduced seedling growth implies that marsh establishment could be much more vulnerable to waves than previously anticipated. Moreover, as ship-generated waves and extreme weather events may be expected to increase in the near future (Silinski et al. 2015), wave-free windows of opportunity will become more rare. In these cases, site-specific conditions will have to be taken into account (for example, how much wave stress would be tolerable, or how many windows of opportunity are available) for engineering or management measures that focus on creating mashes by reducing waves on the foreshore.

3.4.2 The response of seedlings in biomechanical traits

Wave-stress induced plasticity can be beneficial to enhance performance of aquatic plants in coping with external forces (Puijalon et al. 2005, 2008, 2011). For example, significant increase in root/shoot biomass ratio indicates an increased investment of seedlings to below ground biomass to reinforce anchorage strength: a 'tolerance strategy' to resist for more drag force. This is in line with more commonly observed anchorage increase under flow in other aquatic plant species, such as *Luronium natans*, *Mentha aquatica*, *Potamogeton coloratus*, and *Sparganium emersum* (Puijalon et al. 2008). Unlike the seedlings in the control group that can tolerate higher breaking force, a decrease in flexural rigidity of seedlings under wave stress enables them to expose less frontal surface areas to incoming waves: an 'avoidance strategy' to experience less drag forces. This supports a well-recognised adaptation of plants to cope with exposure to strong hydrodynamics (see references within Gaylord et al. 2003 for kelp canopies; Bouma et al. 2005 for salt marshes; Bal et al. 2011; Puijalon et al. 2011 for freshwater aquatic plants and La Nafie et al. 2012 for seagrasses). In an earlier study by Silinski et al. (2015), the authors reported that a shift between avoidance and tolerance strategies may occur between life stages within one species. We found that both strategies are, to some extent, adopted particularly during the early seedling phase.

In addition to the above-mentioned similar adjustment in biomechanical trait for all three pioneer marsh seedlings, we also compared inter-specific differences in mechanical characteristics, as they may play a role in the shifts of species along the estuaries with varying wave exposure (Callahan et al. 2010; Wang et al. 2017). For example, the significantly higher root/shoot biomass ratio of *S. anglica* seedlings under wave stress can be expected to enable their establishment at higher hydrodynamic conditions (e.g., higher wind exposure or under sea level rise) than the other two pioneer marsh species. The prominent higher stiffness for *P. australis* seedlings in the control groups might be due to the nodal stabilization in their stems (Spatz et al. 1990). This means that when living in sheltered areas with less oscillating stress, aquatic plants of *P. australis* should be more tolerant to wave attack than the other two species by following a 'tolerance strategy'. Present results extent current knowledge that salinity is an important factor governing spatial species distribution and plant growth (Peinings et al. 2005; Crain et al. 2008), in showing that waves may reduce seedling survival by around 50%. It should be realized that in our experiment, the species were not always grown at their predominant salinity. That is, *S. anglica* was grown at a relatively low salinity whereas *P. australis* was grown at a relatively high salinity compared to their predominant habitat. The latter may have caused a somewhat higher growth rate for *S. anglica* and a somewhat lowered growth rate for *P. australis*, with potential effects on the exact survival percentage. The general trend, that waves hamper seedling survival for pioneer marsh species remains clear. Moreover, recent year-round field observation by Zhu et al. (2019) that salinity did not result in major changes in plant biomechanical properties, suggest that present findings of wave-effects on (biomechanical) plant traits is not strongly affected by using a single salinity.

Our results that *S. anglica* seedling yielded the least flexural rigidity and resistance to tensile stress (in compare to biomechanical properties pattern change for the other two species seedlings) seems controversial to the fact that *S. anglica* is well known for its wave attenuation value with stiff shoots (Bouma et al. 2005). However, considering individual seedlings have been used in the present study and high variability of flexural rigidity of difference life cycles of marsh plants (Rupprecht et al. 2015), the stem biomass of dense mature plants canopies may compensate for the stiffness in wave dissipation (Bouma et al. 2005; Möller et al. 2014; Rupprecht et al. 2015). Therefore, the present finding is in agreement with earlier studies that highlight the importance to consider plant size and morphology in determining plant biomechanical characteristics for their wave attenuation service at different space and time (Niklas 1992; Rupprecht et al. 2015; Silinski et al. 2018; Zhu et al. 2019).

3.4.3 Implications for tidal marsh restoration

In the last decades, physical constrains have been widely recognized to be the overarching control for marsh establishment (Adam 1990; Friess et al. 2012). The mechanisms responsible for determining critical hydrodynamic threshold for marsh establishment and long-term evolution have mainly been elucidated by modelling studies (Mariotti and Fagherazzi 2010). For example, wave stress and the sediment surface erosion they induced are predicted to be the essential processes behind marsh lateral retreating (Callaghan et al. 2010; Tonelli et al. 2010; Marani et al. 2011; Francalanci et al. 2013). Recent experimental studies have extensively looked at the threshold constraints in terms of sediment dynamics (Balke et al. 2014; Bouma et al. 2016; Cao et al. 2018) or elevation related inundation (Wang and Temmerman 2013; van Belzen et al. 2017). In this regard, our results reveal direct wave-stress effects on seedling survival and growth (both restriction and response) and provide a quantitative support for modelling studies to elucidate hydrodynamic driven tidal marsh dynamics. However, wave characteristics (direction, length, height) can vary strongly in space and time (Nielsen 2009). Due to the impact of increasing ship traffic or deeper water levels following sea level rise, we may expect more severe wave forcing in an era of global change (Curtiss et al. 2009;

Houser, 2010). To better understanding the effect of wave stress on vegetation, it is thus also important to quantify the actual wave forcing in the field, and how this changes over time. Such data can then be used to design process-based studies that investigate the effect of waves with varying energy on marsh expansion both by seedling establishment and rhizome expansion (Bouma et al. 2014, 2016; Silinski et al. 2015, 2018).

3.5 Conclusions

Overall, the present study indicates that establishment chances of marshes are reduced if wave energy increases. Despite the different biomechanical response of these three pioneer species, the seedlings of all species have low resistance to external stresses. This type of experimental knowledge is essential to understand the role coastal vegetation plays in mitigating risk and defending coastlines under sea level rise, and to build more reliable process based models as needed to predict the long-term marsh ecosystems dynamics, and evaluate measures for site-specific management and restoration schemes.

Chapter 4

4. Salt marsh establishment in poorly consolidated muddy systems: effects of surface drainage, elevation and plant age

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Abstract

Conservation and restoration of salt marsh ecosystems is becoming increasingly important because of the many ecosystem services they provide. However, the processes controlling salt marsh establishment and persistence, especially on bare tidal flats in muddy areas, remains unclear. As muddy sediments typically experience a restriction of soil drainage, we expect that a surface drainage relief due to a heterogeneity topography, as might occur on the edge of tidal channels, can facilitate the establishment of salt marsh vegetation on muddy tidal flats. By means of a manipulative field experiment, using "Mega-Marsh Organ" mesocosms, we investigated the impact of surface drainage and elevation relative to mean sea-level on *i)* the survival of *Spartina anglica* seedlings from three different age classes: 1-year, 3-month and 1-week; and *ii)* the growth performance of mature *S. anglica* marsh tussocks. *S. anglica* seedling survival, especially in the establishment phase, was positively affected by better surface drainage, increases of seedling age, and higher elevation relative to mean sea-level. That is, the survival rate of *S. anglica* seedlings at the end of 6th week increased from 0% (at surface water undrained, 1-week, 0 cm elevation) to 94.44% (at surface water drained, 1-year, 90 cm elevation). In contrast, surface drainage did not affect the performance of large *S. anglica* marsh tussocks, as only increased elevation relative to mean sea-level was shown to affect *S. anglica* tussock growth in terms of plant height, shoot numbers and dry biomass. Based on our findings, we proposed a conceptual model to understand how surface drainage-driven feedbacks in a heterogeneous topography may be reinforced to induce salt marsh establishment in muddy systems. Further testing of present hypothesized model would be beneficial for insights into salt marsh establishment on tidal mudflats.

4.1 Introduction

Conservation and restoration of salt marsh ecosystems is becoming increasingly appreciated because of the many vital ecosystem services they provide (Gedan et al. 2009; Barbier et al. 2011; Shepard et al. 2011, 2017; Kirwan et al. 2012a, 2012b; Burden et al. 2013). Yet, the decline and degradation of salt marsh ecosystems continues globally, due to the combined threats of sea-level rise and anthropogenic impacts (Silliman et al. 2012; Kirwan and Megonigal 2013; Schepers et al. 2017). Until recently, we still do not sufficiently understand the processes controlling marsh establishment and persistence (Fresiss et al. 2012; Balke et al. 2014, 2016; Bouma et al. 2014, 2016). Especially for poorly consolidated muddy systems, such lack of knowledge has largely hampered a majority of salt marsh restoration schemes in many locations at different scales (Broome and Craft 2000; Mossman et al. 2012; Moreno-Mateos et al. 2012; Bouma et al. 2014).

Salt marshes are complex bio-geomorphic ecosystems occurring in the dynamic intertidal zone, where they are subject to changing environmental conditions (Adam 2002). Salt marshes have been generally suggested to present habitat transition from low-elevation, non-vegetated tidal flats to high-elevation, vegetated marshes (Marani et al. 2010, 2013; Wang and Temmerman 2013; van Belzen et al. 2017). The transition from bare tidal flats to salt marshes is either initiated by seedling establishment or by clonal expansion, possibly after translocation of clonal fragments. The vegetated marsh is stabilized by bio-geomorphic positive feedback loops between vegetation growth, sediment trapping and sediment stabilization (Van Wesenbeeck et al. 2008; Marani et al. 2010; Wang and Temmerman 2013), ultimately also resulting in channel formation (Temmerman et al. 2007; Fagherazzi et al. 2004a, b, 2012; Schwarz et al. 2018). However, as these feedback loops only occur after a critical biomass/density has been exceeded (Bouma et al. 2009a), individual marsh propagules like seedlings or clonal fragments face establishment barriers (Balke et al. 2014, 2016; Hu et al. 2015; Bouma et al. 2009b, 2016; Yuan et al. 2020).

The problematic establishment of early-stage establishment on tidal mudflats has both experimentally and theoretically been related to require *i)* inundation limits of marsh plants (Wang and Temmerman 2013; Balke et al. 2016; van Belzen et al. 2017) and *ii)* episodic occurring Windows of Opportunity with physical calm periods (Balke et al. 2014, Hu et al. 2015, Bouma et al. 2016; Yuan et al. 2020). Although both experimental and theoretical approaches demonstrate that abrupt marsh recovery may occur at an elevation above which marsh vegetation can start to grow (Kirwan et al. 2012a; Voss et al. 2013; van Belzen et al. 2017), haphazard field observations suggest that marsh establishment can be significantly hampered by other factors. That is, in some muddy areas no recovery is observed over prolonged periods, even though their elevations are considered to be sufficiently high for mature marshes to occur. For instance, in Paardenschor (Scheldt estuary, Belgium), a large tidal flat remain unvegetated for several years despite its high elevation and the presence of old marshes in the surroundings (Fig. 4.1a and b). The rare vegetation establishment that does occur in such 'halted' systems, is usually linked to the presence of topography relief at (shallow) tidal channel edges (Fig. 4.1). The latter suggests that besides suitable hydrological inundation regime and calm windows of opportunity, also the presence of topographic heterogeneity to facilitate drainage is needed for early-stage seedlings establishment.

Drainage channels constitute basic pathways for the exchange of water during tidal cycles (Perillo et al. 2009; Schwarz et al. 2014). As the tidal area becomes exposed during ebb, water is drained towards the channels predominantly by surface sheet flow (Fagherazzi et al. 2013). Subsequently, a pressure head develops in the sediments, which depending on the sediment type, may affect soil drainage (Fagherazzi et al. 2004a, b). That is, inundation (during flood) and drainage (during ebb) of intertidal areas in general is a complex process that involves not only the water column above the sediment, but may also affect interstitial water and even groundwater exchange (Winterwerp et al. 2004; Perillo et al. 2009). By water recirculation in sediments, drainage may alleviate poor oxygen availability (Rabouille et al. 2003; Fivash et al. 2020) and thereby relieve sulphide toxicity to seedling roots

(Redelstein et al. 2018) that lack aerenchyma (Burdick and Mendelssohn 1987; Jung et al. 2008).

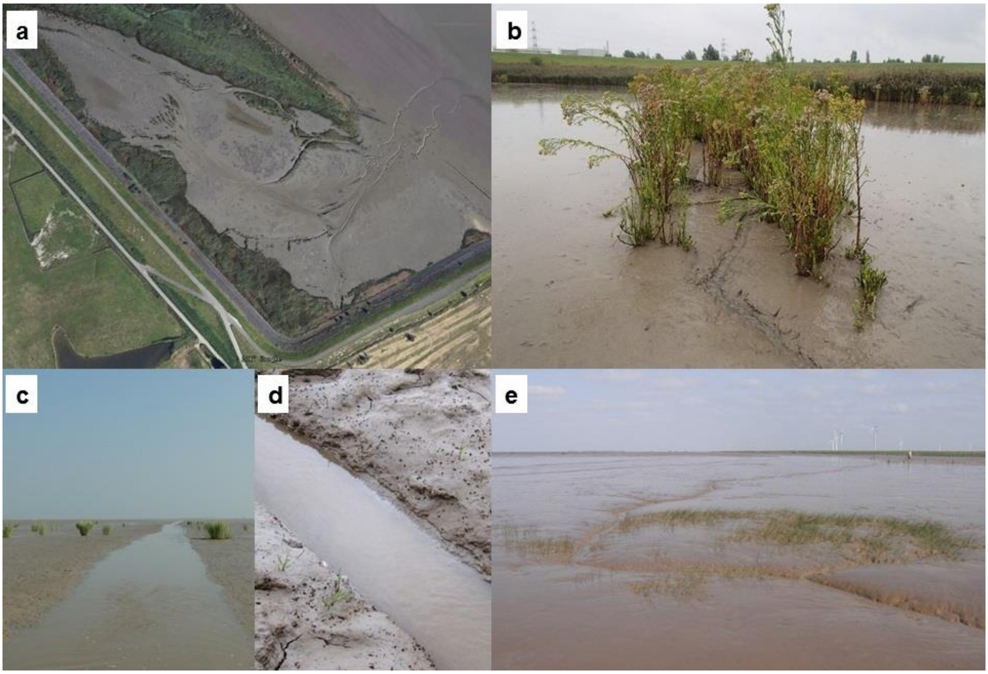

Fig. 4.1. Empirical observation of channel drainage relief facilitates salt marsh establishment in Paardenschor, Scheldt estuary, Belgium (a and b); and on Chongming Island, Yangtze estuary, China (c; d and e). a) aerial image showing a large tidal flat that remained unvegetated for several years despite high elevation and being surrounded by old marshes (Paardenschor; Source: Google Earth, 2017); b) the only fringes of marsh vegetation are distributed alongside tidal channels; c) salt marsh establishment near a channel at a low pioneer tidal flat; d) establishment of seedlings first took place near drainage channels; and e) development of a heterogeneous marsh pattern with drainage channels.

Drainage effects are generally observed in coarse sand or peaty sediments (see e.g., Mendelssohn and Seneca 1980 for peat soil; and Padgett et al. 1998, 1999 in artificial sandy sediments), where hydraulic resistance of the sediment is typically low and capillary forces in the wide pores are restricted, causing interstitial water to drain vertically from the sediment (Winterwerp et al. 2004).

However, vertical drainage is strongly restricted in fine clay (or silt-rich) sediments, and may even not be noticeable at all, because hydraulic conductivity of sediments decreases non-linearly with decreasing particle size, and capillary forces become stronger as pore sizes decrease (Winterwerp et al. 2004; Hill et al., 2013; Ren and Santamarina 2017, and references therein). Therefore, it is necessary to experimentally test if in such muddy systems with poor hydraulic conductivity of the sediment, surface drainage (runoff of an overlaying water), as may occur due to a topography relief, may offer young seedlings an improved establishment chance, while not having a major effect on the performance of larger marsh plants with well-developed aerenchyma.

In this study, we use an experimental approach to test (1) if poor surface drainage, in a theoretically undrainable, recently deposited and poorly consolidated muddy sediment, forms a barrier for initial seedling establishment, while not affecting seedlings at a larger stage, and (2) if the strength of this barrier depends on the level of elevation relative to mean sea-level. We focus on *Spartina anglica*, which is a typical, widely distributed pioneer marsh species (Gray et al. 1991; Strong et al. 2013; Cao et al. 2018). Surface drainage and elevation gradient were manipulated *in situ* by placing a set of field mesocosms, referred to as “Mega-Marsh Organs” (MMOs), with contrasting surface drainage conditions along the elevation gradient of a sheltered tidal flat. By our MMO-designs, we aim to mimic the presence vs. absence of surface water drainage as can be observed at small channel banks in muddy tidal systems. In the first year, seedlings of three successive age classes (i.e. 1-week, 3-month and 1-year seedlings) were transplanted into the MMOs to quantify the effects of surface drainage, seedling age, and elevation relative to mean sea-level on their chances of establishment. In the second year, the MMOs were used to study the growth performance of mature *S. anglica* tussocks. Overall, the present study provides insight in the early establishment processes in salt marshes, thereby supporting the development of measures to enhance successful marsh (re)creation, as needed for e.g. sustainable coastal defence.

4.2 Material and Methods

4.2.1 Study site

Our field experiment was set up at Perkpolder (midpoint: 51°23'27"N, 4° 1'25"E), which is located in the Western Scheldt Estuary in the SW Netherlands (Fig. 4.2a). The estuary is semi-diurnal, with tidal range varies from 440 to 550 cm (Baeyens et al., 1998). Tidal flat of this estuary has a mild bed slop (ca. 3‰), with dominated sediment type of mud (Kuijper et al., 2004). The pioneer vegetation in the estuary consists mainly of common cordgrass, *Spartina. anglica*, which has forming monoculture marshes in the seaward part with elevations ranging from 60 to 200 cm NAP (Normal Amsterdam Peil, which is Dutch Ordance Level that approximately equal to mean high water level in the Scheldet estuary) (van de Wal et al. 2008).

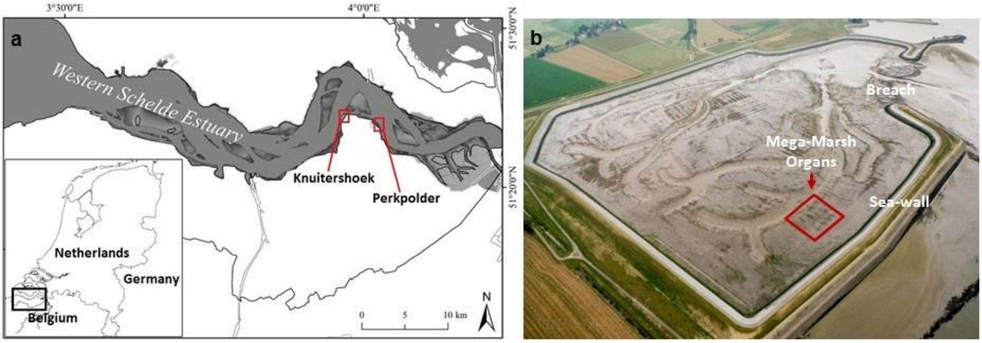

Fig. 4.2.Study site of present study. a) Location of Perkpolder; b) aerial view of Perkpolder (photographed by Edwin Paree and Matthijs Boersema); the red square in b) show where Mega-Marsh Organs (MMOs) were set up.

Perkpolder was formerly embanked agricultural land (polder), which was converted to an intertidal zone in June 2015 for nature restoration purposes, by breaching the dike and re-introducing tides from the Western Scheldt Estuary (Rijkswaterstaat 2015) (Fig. 4.2b). Following the breach, a soft mud layer of around 0.2 to 0.3 m thickness was quickly evolved on top of the highly compacted former agricultural land. After 6-8 months of the breaching, the area stopped morphodynamics and reached equilibrium (Brunetta et al. 2019). Measurements from 2016 to 2018 indicated that the bed-level elevation of tidal flat in Perkpolder had slightly increased to almost nothing (Center of expertise delta technology, 2019). The elevation of tidal flat in Perkpolder ranged between －80 to＋110 cm NAP (compare mean low water at Perkpolder: -2.06 m NAP; mean high water at Perkpolder: +2.56 m NAP), therefore the whole area was completely covered by water and completely dried every semi-diurnal tide cycle from the breach (Center of expertise delta technology, 2019; Brunetta et al. 2019). The wave actions in Perkpolder was negligible, as it was almost completely surrounded by sea-walls (Center of expertise delta technology, 2019) (Fig. 4.2b). As of the end of our experiment (i.e., fall 2018), natural vegetation had still not established on the newly created intertidal flats, and the deposited sediment still consisted of soft, water saturated muddy sediment (with a D_{50} of 27.62 μ m, silt content T_{63} of 62.68 %, classification c.f. Shepard, 1954). Perkpolder was therefore an ideal site for studying the factors affecting survival of *Spartina* seedlings/plants of different ages: surface drainage of a theoretically undrainable, recently deposited and poorly consolidated muddy sediment in interaction with elevation to mean sea-level.

4.2.2 Marsh establishment experiment – Mega Marsh Organs with contrasting surface drainage

Mega-Marsh Organs (MMOs; Fig. 4.3) were used as field mesocosms to study the establishment of seedlings. The original marsh organ concept was introduced by Morris (2007), Kirwan and Guntenspergen (2012a) and Voss et al. (2013), in which narrow PVC pipes with drained bottoms were used to test plant growth response to inundation in relation to sea level. To identify the potential effects of surface drainage on seedling survival, we modified and scaled up the marsh organ to allow for hosting multiple plants and surface drainage treatments in the field. In our experiment, each MMO consisted of two large adjacent boxes (inner dimensions of 75 × 45 × 30 cm each, Fig. 4.3a and b), both with a closed bottom. In simulation of surface drainage in muddy systems (as might occur due to topography relief at channel edges, see introduction), we equipped one of the two boxes in each MMO with a surface drainage system (Fig. 4.3a and b), while left the other one untreated. The surface drainage system consisted of a perforated pipe covered with geotextile (pipe inner diameter of 4.5 cm) at each box side, and that extended to the rim to facilitate dewatering of the surface water film. These pipes were connected at the base of the box to a pipe leaving the box, to allow for free water outflow after tidal inundation (Fig. 4.3a). The geotextile covering the drainage pipes allowed water penetration, while prevented for sediment loss. To avoid sediment clogging the outflow of the drainage pipes, a plastic pallet was placed underneath each MMO to elevate the box bottoms 10 cm higher than the local tidal flat. Given the limited vertical drainage nature of fine muddy sediments in our study, we kept all bottom of the boxes in our MMOs, so as to capture the difference of surface water dewatering via drainage pipes between the two boxes in each MMO.

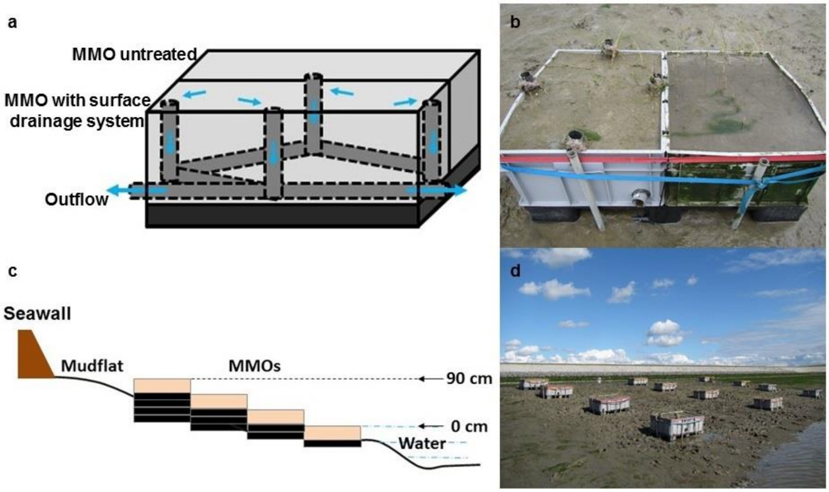

Fig. 4.3. Schematic diagrams and photographs of the Mega-Marsh Organs (MMO) setups in Perkpolder. a) each MMO consists of a closed box with a sealed bottom, but in half of them we installed drainage systems (i.e., using standard soil-drainage tubing) going through the muddy sediment and reaching the top of the sediment so also enabling drainage of surface water; b) an example of MMOs box with and without sediment-surface drainage visible as drainage tubes sticking out of the sediment; c) and d) MMOs setups at from 0 cm to 90 cm NAP (Normal Amsterdam Peil, Dutch Ordance Level that approximately equal to mean high water level in the Scheldt estuary).

Overall, 12 MMOs (i.e., 24 boxes in total, 12 with surface drainage systems and 12 without) were set up on the bare tidal flat in Perkpolder (Fig. 4.3c and d). By using a real-time kinematic global positioning system (RTK-GPS) device, we placed the MMOs at four elevations with three replicate MMOs (3 m interval) per elevation (Fig. 4.3c and d). The four elevations are 0 cm, 30 cm, 60 cm and 90 cm leveled to the top of MMO rims respect to NAP (Normal Amsterdam Peil, which is Dutch Ordance Level that approximately equal to mean high water level in the Scheldet estuary). Inundation time (percent time flooded) of these four elevations during the 2016 experiment period were 56.56%, 49.51%, 45.44% and 41.41% (Table 4.1), respectively, which were measured with one SENSUS Ultra device (ReefNet Inc.) attached to the top rim of a MMO at each elevation. Ten days prior to planting, all boxes were filled with local fine tidal mud (sediment friction see above).

Table 4.1. Mean water depth (in cm) and inundation time (percent time flooded) during 2016 experiment period for the four elevations of the MMOs in respect to NAP (Normal Amsterdam Peil, which is Dutch Ordance Level that approximately equal to mean high water level in the Scheldet estuary).

Elevation of MMOs (cm NAP)	SENSUS Ultra device ID	Mean water depth (cm)	Inundation time (%)
0	SU-12943	76.44	56.56
30	SU-13730	63.88	49.51
60	SU-13699	49.01	45.44
90	SU-12955	37.88	41.41

4.2.3 Marsh establishment experiment – seedlings of different ages

To investigate the influence of drainage in relation to elevation on seedling survival for different age classes, we manipulated a seedling establishment experiment in the growth season of 2016. Seedlings of *S. anglica*, which is a dominant pioneer species in this part of the estuary, were germinated in a climate chamber with an alternating temperature condition (30℃ during the day and 25℃ during the night to speed up germination process, c.f. Cao et al. 2018). To obtain seedlings, *S. anglica* seeds were soaked in nature sea water (32 ppt) in a 4 ℃ refrigerator until germination was performed. Fresh water was then used to accelerate germination and to avoid seedlings drying out. All seeds with a visible sprout were identified as seedlings. Seedlings were transplanted to a tray filled with sandy mud in a climate room and watered regularly with a mix of sea water and fresh water until they were transplanted into the MMOs in the field. To be able to compare seedlings of different age classes, three batches of seedlings were germinated, so that they were 1-week, 3-months and 1-year of age at the moment of transplantation.

Before transplanting into the MMOs, seedlings were carefully washed out from the sediments in which they had been grown in the lab. Care was taken that transplantation into the MMOs always occurred within 12 hours. The roots of all seedlings were planted at the depth of 1 cm in the sediment. In order to address the importance of seedling age, we used six replicates for the 1-year seedlings, six replicates for the 3-month seedlings and 12 replicates for the 1-week seedlings within every experimental treatment group (24 seedlings in total each box). The experiment was set up on July 2016 and lasted for six weeks, during which surface drainage treated MMOs were checked regularly in avoidance of sediment blocking. As we did not want to disturb the survival conditions for the vulnerable seedlings in the MMOs by other measurements, only the survival of seedlings was recorded every week over a six weeks period. A 6-week period was chosen as experimental time frame, as initial survival was the most important component for seedling establishment (Balke et al. 2014, 2016; Hu et al. 2014; Cao et al. 2018). The age effects on seedling survival were accounted for by planting seedlings of different age classes, which allows comparing all age classes under similar growing conditions.

4.2.4 Marsh establishment experiment – mature marsh plants

To compare the potential effects of surface drainage and elevation relative to mean sea-level on mature marsh plants, we carried out a follow-up tussock transplant experiment using the same MMOs. On April 2018, *S. anglica* tussock transplants were extracted from an existing monoculture marsh from Knuitershoek (close to Perkpolder, Fig. 4.2a), where uniform size soil blocks (20 x 20 x 30 cm) were collected by cutting of all above ground vegetation. The tussock transplants were then placed in the above mentioned 12 MMOs in Perkpolder (i.e., 12 treated surface drainage and 12 untreated) with two plant donor soil blocks diagonally embedded in each box in avoidance of limitations of expansion space. Regrowth of each tussock was quantified by clipping all above ground vegetation as close to the sediment surface as possible at harvest in October 2018. When no above ground biomass was present at this time, the tussock was deemed as establishment failure. After measuring above ground vegetation height and recording shoot numbers of each tussock, all the collected plant material was dried at 60 °C in an oven to a constant weight for measuring dry biomass.

4.2.5 Marsh establishment experiment – Sediment properties

To compare the sediment properties (in terms of water content and bulk density) between the surface drained and untreated MMOs, we sampled three replicate sediment cores with a syringe (inner diameter = 2.8 cm, depth= 3 cm) on the top of sediment in each box of the MMOs at the end of the seedling establishment in 2016 and the mature marsh establishment in 2018. In total, we collected three replicates per elevation from each MMO box for both marsh seedling (2016) and mature marsh (2018) establishment experiments. Each sediment sample was stored in a container and weighed for wet weight. All sediment samples were then freeze dried for 72 hours and weighed again to calculate water content and dry bulk density using the following formula:

Water content = (wet sample weight - dry sample weight) / wet sample weight

Dry Bulk density= Dry weight of sediment sample / volume of the sediment sample

4.2.6 Statistical analysis

Cox regression analysis (Cox 1972) was used to investigate the main effects of each variable (i.e., surface drainage, seedling age and elevation relative to mean sea-level) upon the survival time of seedlings. For which, the death of a seedling was considered as a hazard event during analysis. During the Cox regression, the hazard ratio Exp(B) of each variable was calculated relative to its baseline of each variable, i.e., no surface drainage, 1-week seedling age, and 0 cm elevation relative to mean sea-level separately, applying a confidence interval of 95%. In general, the Exp(B) was interpreted as a relative risk of the treatment group compared to the baseline (control or placebo group), which was calculated as the ratio of hazards between individuals whose values of hazard differ by one unit when all other covariates were held constant (Cox 1972). Three-way ANOVAs were also applied to test the interaction effects of surface drainage, seedling age, elevation relative to mean sea-level upon the survival time of seedlings. Two-way ANOVAs were used to test the effect of surface drainage treatment and elevation relative to mean sea-level on tussock survival, plant height, shoot numbers, dry biomass and sediment properties. The significance level of 5 % was used for all analyses. All analyses were performed with SPSS 18.0 software (SPSS Inc., Chicago, IL, USA).

4.3 Results

4.3.1 Seedlings establishment

Both Cox regression and three-way ANOVAs results revealed that the surface drainage treatment significantly affected *S. anglica* seedling survival during the 6-week experiment with the poorly consolidated mud of Perkpolder (Fig. 4.4; $p < 0.05$, Table 4.2). Compared to the groups that untreated with surface drainage, surface drainage treatment reduced the hazard ratio (relative to baseline of surface drainage untreated groups) to (Exp(B)=0.721 (%95 CI: 0.591-0.880, Table 4.2). Notably, for 1-year seedlings at 90 cm elevation, there was significant more ($p = 0.036$, t-test) seedling survived (94%±6%) at week 6 in MMOs that were treated with surface drainage as compared with 67% ±9% where it was not (Fig. 4.4). For 3-month seedlings at 30 cm elevation, the survival rate at week 6 was 72.2%±15% in MMOs with surface drainage, which was significantly higher ($p = 0.014$, t-test) than the seedling survival rate 17%±9% in MMOs untreated with surface drainage at the same elevation (Fig. 4.4).

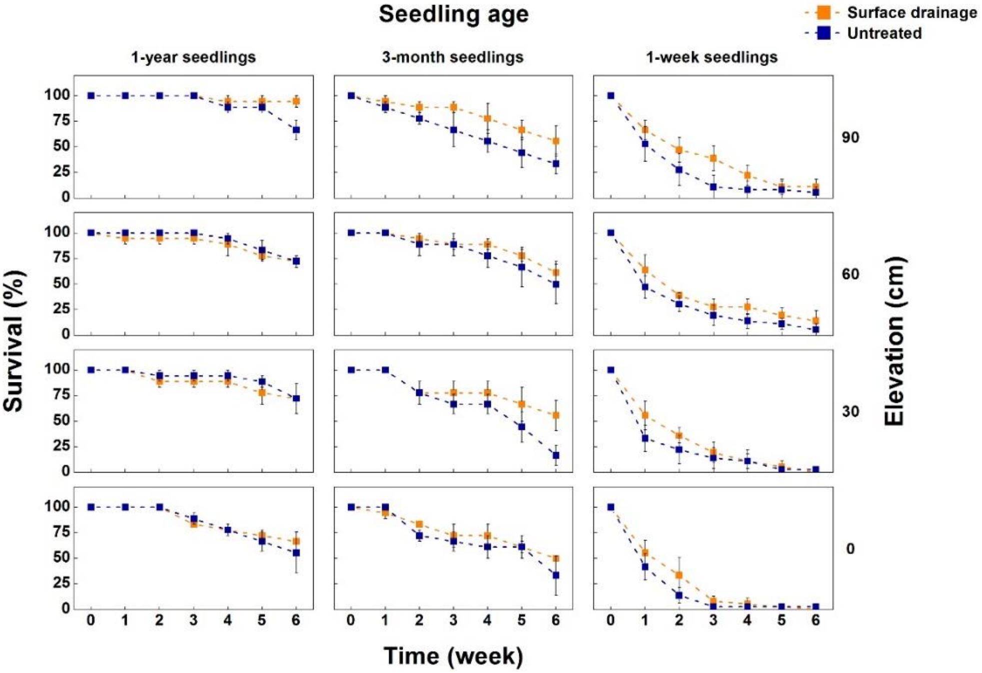

Fig. 4.4. *S. anglica* seedling survival during the 6-week field experiment in Perkpolder in 2016. The overall survival time of seedlings in surface drainage treatment was significantly higher than in the untreated groups (blue). Increased seedling age and elevation relative to mean sea-level (from 0cm to 90cm NAP) also facilitated seedling survival (data are presented as mean values + SE).

Moreover, the overall survival of *S anglica* seedlings (Fig. 4.4) was significantly affected by seedling age ($p < 0.001$, Table 4.2 and 4.3) and elevation relative to mean sea-level ($p < 0.01$, Table 4.2 and 4.3). For *S. anglica* seedlings of all elevation differing in age, the survival of both 3-month and 1-year seedlings were all significantly higher in compared to 1-week seedling (Fig. 4.4; $p < 0.001$, Table 4.2), with a decrease of hazard ratio (relative to baseline group of 1-week seedlings) as seedling age increases: from 3-month seedlings (Exp(B)=0.230, %95 CI: 0.177-0.299, Table 4.2) to 1-year seedlings (Exp(B)=0.095, %95 CI: 0.067-0.135, Table 4.2). The steepest decrease in *S. anglica* seedling survival has been found directly after transplanting (i.e., from week 1 to week 2) for the 1-week old seedlings, regardless of drainage treatment or elevation (Fig. 4.4). This meant that the older *S. anglica* seedlings become, the less vulnerable they were to adverse surface-drainage-lacking conditions.

Table 4.2. Cox regression results of seedling survival analysis in the 6-week field experiment. Surface drainage treatment, seedling age and elevation (relative to mean sea-level) were set as variables to analysis their overall effects on seedling survival.

Variable	**Subgroups**	**Wald**	**df**	***p* value**	**Exp(B)***	**95% Cl for Exp(B)**	
						Lower	**Upper**
Surface drainage		10.354	1	0.001			
	Treated	10.354	1	0.001	0.721	0.591	0.880
Seedling age		238.439	2	0.000			
	1-year	174.167	1	0.000	0.095	0.067	0.135
	1-month	120.111	1	0.000	0.230	0.177	0.299
Elevation		11.667	3	0.009			
	90 cm	6.524	1	0.011	0.648	0.525	0.919
	60 cm	9.096	1	0.003	0.695	0.489	0.859
	30 cm	1.018	1	0.313	0.869	0.662	1.141

*Exp(B) indicated for the ratio of hazard risk relative to the baseline of each variable, i.e. untreated with surface drainage, 1-week seedling age, and 0 cm elevation in this case. The 95% confidence interval was also presented right to Exp(B). In general, the Exp(B) was interpreted as the relative risk of the treatment group compared to the baseline (control or placebo group), which was calculated as the ratio of hazards between individuals whose values of hazard differ by one unit when all other covariates are held constant (Cox 1972).

Table 4.3. Three-way ANOVAs table show effects of surface drainage treatment, seedling age, and elevation (relative to mean sea-level) and their interactions on the survival of seedlings.

Deviance Source	**df**	**Mean Sq**	**F**	***p*-value.**
Surface drainage	1	23.003	8.335	0.004
Seedling age	2	949.107	343.896	0.000
Elevation	3	10.857	3.934	0.009
Surface drainage*seedling age	2	5.232	1.896	0.151
Surface drainage*elevation	3	1.671	0.606	0.612
Seedling age*elevation	6	2.051	0.743	0.615
Surface drainage*seedling age*elevation	6	0.431	0.156	0.988

For *S. anglica* seedlings of all ages differing in elevation, Cox regression showed that the hazard ratio relative to the baseline of 0 cm NAP (Normal Amsterdam Peil, which is Dutch Ordance Level that approximately equal to mean high water level in the Scheldet estuary) diminished when the elevation increased from 30 cm NAP (Exp(B)= 0.87, %95 CI: 0.66-1.14 Table 4.2) to 90 cm NAP (Exp(B)= 0.65, %95 CI: 0.53-0.92, Table 4.2). It was noted that the hazard ratio (relative to 0 cm elevation) at 60 cm NAP (Exp(B)= 0.70, %95 CI: 0.49-0.90, Table 4.2) was close to which at 90 cm NAP (see above). Compare to 0 cm NAP elevation, the overall seedling survival was significantly enhanced both at 60 cm NAP (Fig. 4.4; $p = 0.003$, Table 4.2) and 90 cm NAP (Fig. 4.4; $p = 0.011$, Table 4.2). This indicated that the survival of seedling was significantly enhanced when the elevation increased to above 60 cm NAP. However, three-way ANOVAs did not show interactive effects of surface drainage, seedling age and elevation relative to mean sea-level on the overall survival time of *S. anglica* seedlings (Table 4.3).

4.3.2 Mature marsh plants

In contrast with the seedling results, for mature *S. anglica* tussocks, survival was similar among the surface drainage and elevation treatments (Fig. 4.5), as no significant effect was found on the survival of tussocks from different surface drainage or elevation treatments ($p > 0.05$, Table 4.4). Plant height, shoot numbers and dry biomass of *S. anglica* were reduced as elevation decreased (Fig. 4.5; $p < 0.01$ for plant height and dry biomass; $p < 0.001$ for shoot numbers, Table 4.4), with no significant effect of surface drainage treatment or interactive effect of surface drainage and elevation relative to mean sea-level (Fig. 4.5; $p > 0.05$, Table 4.4). This meant that mature *S. anglica* tussocks survived better than seedlings at lower elevations and poorly surface drained conditions.

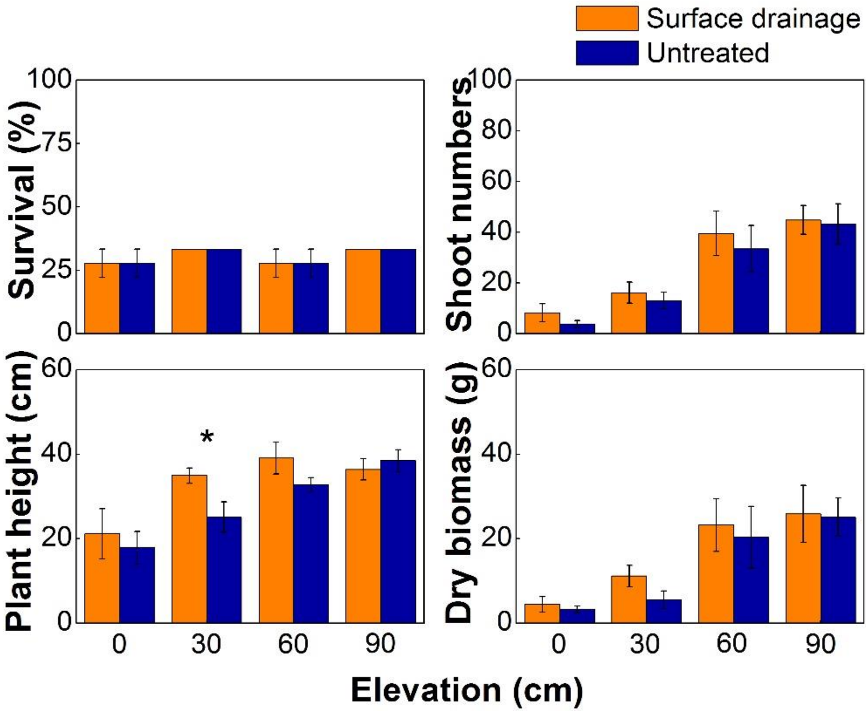

Fig. 4.5. Regrowth of S. anglica tussocks at harvest in the field experiment in Perkpolder in 2018. No significant effect was found on the survival of tussocks from different drainage or elevation treatments. Plant height, shoot numbers and dry biomass were only affected by elevation relative to mean sea-level (data are presented as mean values + SE). Error bars for the survival at 30 cm and 90 cm were not presented because the numbers were same for the replicates (SE=0). * indicated for significance level <0.05.

Table 4.4. Two-way ANOVAs table show effects of surface drainage and elevation (relative to mean sea-level) and their interactions on the tussock regrowth traits.

Response Variable	**Deviance Source**	**d.f.**	**Mean Sq**	**F**	***p*-value**
Survival	Surface drainage	1	.000	.000	1.000
	Elevation	3	.006	1.333	.299
	Surface drainage*Elevation	3	.000	.000	1.000
Plant height (cm)	Elevation	1	113.802	2.822	.112
	Surface	3	397.115	9.848	.001
	drainage*Elevation	3	38.072	.944	.443
Shoot numbers	Surface drainage	1	86.260	.833	.375
	Elevation	3	1924.927	18.589	.000
	Surface drainage*Elevation	3	5.038	.049	.985
Above ground dry biomass (g)	Surface drainage	1	41.082	3639	.436
	Elevation	3	649.023	10.089	0.001
	Surface drainage*Elevation	3	7.189	.112	.952

4.3.3 Sediment properties

We did not observe any effect of surface drainage on the sediment properties in our MMOs. The water content of sediment from the MMOs in both 2016 and 2018 did not show any significant effect from either drainage or elevation (Fig. 4.6; $p > 0.05$, Table 4.5). Average water content of sediment from both years were around 26%, regardless of surface drainage or not. For example, in 2016, for surface drainage treated MMOs, the water content of sediment ranged from 24% ± 1% at 30 cm NAP to 26% ± 1% at 0 cm NAP; and for the MMOs untreated with surface drainage, the water content of sediment ranged from 25% ± 1% at 30 cm NAP to 27% ± 4% at 0 cm NAP; in 2018, for surface drainage treated MMOs, the water content of sediment ranged from 26% ± 1% at 30 cm NAP to 29% ± 2% at 0 cm NAP; and for the MMOs untreated with surface drainage, the water content of sediment ranged from 27%±3% at 90 cm NAP to 28%± 2% at 0 cm NAP. This was confirmed by the dry bulk density data form both 2016 and 2018 that sediment properties was not affected by either surface drainage or elevation (Fig. 4.6; $p > 0.05$, Table 4.5), indicating that neither interstitial water drawing, nor sediment compaction was changed by the surface drainage treatment over the course of the experiment.

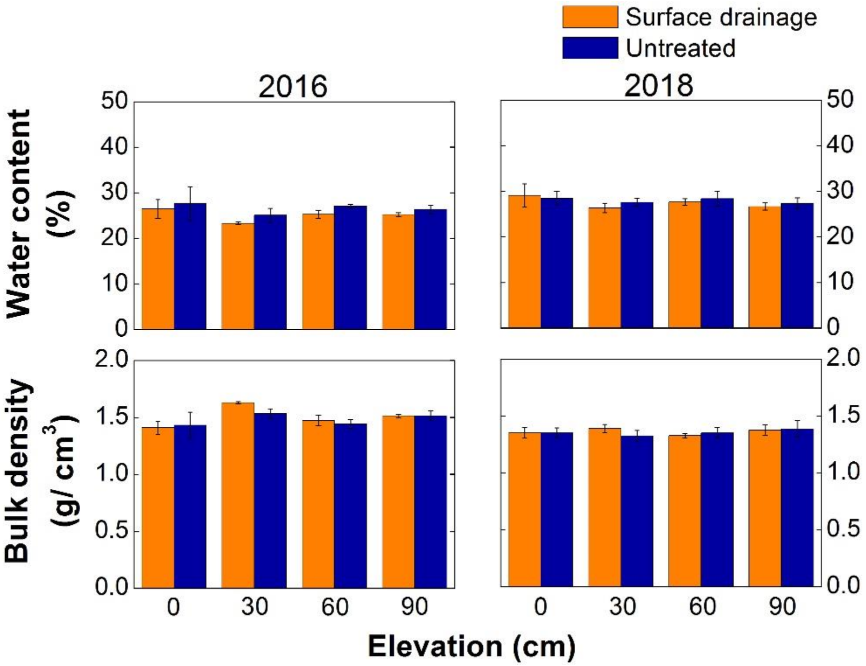

Fig. 4.6. Sediment water content and bulk density of MMOs in 2016 and 2018. The water content and bulk density from both 2016 and 2018 did not show any significant effect from either drainage or elevation (data are presented as mean values + SE).

Table 4.5. Two-way ANOVAs table show effects of surface drainage and elevation (relative to mean sea-level) and their interactions on the sediment properties.

Response Variable	Year	Deviance Source	d. f.	Mean Sq	F	*p*-value
Water content	2016	Surface drainage	1	0.001	1.491	.240
		Elevation	3	.001	1.019	.410
		Surface drainage*Elevation	3	2.250E-5	.026	.994
	2018	Surface drainage	1	.000	.264	.614
		Elevation	3	.000	.755	.535
		Surface drainage*Elevation	3	9.463E-5	.157	.924
Bulk density	2016	Surface drainage	1	.004	.475	.501
		Elevation	3	.029	3.256	.490
		Surface drainage*Elevation	3	.004	.434	.732
	2018	Surface drainage	1	.000	.058	.812
		Elevation	3	.002	.283	.837
		Surface drainage*Elevation	3	.002	.347	.792

4.4 Discussion

The establishment and persistence of salt marsh is highly relevant for conservation and restoration of coastal salt marsh ecosystems. Yet, our understanding remains limited on the processes controlling salt marsh establishment and persistence, especially on bare tidal flats in muddy areas. As muddy sediments typically experience a restriction of vertical soil drainage, we expect that a surface drainage as might occur due to a topography relief on the edge of tidal channels, can facilitate the establishment of salt marsh vegetation on muddy tidal flats. Using well designed MMOs with surface drainage systems to mimic surface water dewatering, we experimentally showcased for a poorly consolidated muddy system, a positive effect of surface drainage on the initial seedling establishment of the widely-distributed pioneer salt marsh species *S. anglica*.

4.4.1 Surface drainage in poorly consolidated muddy systems and its effects on marsh establishment

In our muddy systems, the removal of the overlying water (Fig. 4.7) was the most decisive difference between the surface water drained and undrained treatments. Measurements of sediment water content showed that the water content of these sediments was very high (about 30% by weight, Fig. 4.6) and did not change between surface drainage treated and untreated MMOs when measured during ebb. There was also no evidence for increased compaction (higher dry bulk density) of the sediment over the course of the experiment (Fig. 4.6). Both observations were in accordance with theoretical expectations that such fine muddy soil cannot lose much interstitial water during a single ebb tide (see references in introduction). This makes present study starkly contrast to earlier works on drainage effects on salt marshes in systems with relatively coarse sediments (for salt marshes in peaty soils see Mendelssohn and Seneca 1980; for salt marshes in sandy soil see Padgett et al. 1998, 1999; Redelstein et al. 2018) that have a high hydraulic conductivity and therefore can reduce water saturation as a consequence of vertical draining of sediment. The grain size (with a D_{50} of 27.62 μm, silt content T_{63} of 62.68 %) of the sediment in our system was too fine, and the hydraulic conductivity consequently too low, to allow for substantial drainage of interstitial water from the sediment during the low water period (Winterwerp et al. 2004; Ren and Santamarina 2017). The only difference between the surface drainage treated and untreated experiments that was clear from visual inspections, was the absence of a thin layer of overlying water on top of the sediment during ebb (Fig. 4.7). Therefore, present study have captured the main effects of surface drainage on marsh establishment in our muddy system.

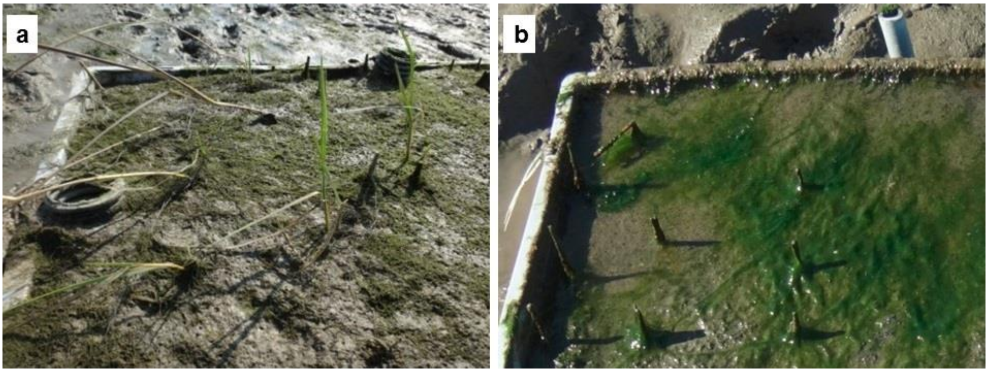

Fig. 4.7. Close up view photographs showing seeding establishment in MMOs with surface drainage relief (a), and an overlaying of water in MMOs without surface drainage (b).

Our experimental results indicate that the removal of surface water can indeed improve the survival of *S. anglica* seedlings in muddy systems, with additional facilitation effects from an increase of seedling age, and a higher elevation relative to mean sea-level. The facilitative effect of surface water drainage on seedling establishment could be benefited from the alleviation of anoxic conditions in low-elevation inundated soils (Rabouille et al. 2003; Fivash et al., 2020), where oxygen availability typically restricted for young seedling with reduced rooting under increased inundation (King et al. 1982; Bouma et al. 2001; Redelstein et al. 2018). Although our soil sampling method made it unable for us to distinguish oxygen content within the soil profile, the most shallow sediment layer in which the youngest 1-week old seedlings were planted (top 1 cm layer), was expected to be more oxygenated after surface drainage (Fig. 4.7) that allows for soil top layer aeration (i.e., for Redox potential at different sediment depth in mesocosms and field see Redelstein et al. 2018, for soil oxygen decline profile during tidal cycle see Fivash et al. 2020). Such aerobic alleviation can prevent directly toxicity to seedlings from microbial sulphide formation in anoxic sediments (Linthurst and Seneca 1980; Lamers et al. 2013). In contrast, the effect of surface drainage was much less expressed or even absent in larger 1-year old seedlings and well-established mature plants. The latter might be explained by the presence of well developed aerenchyma in both roots and shoots, by which they could transport oxygen into soil, to terrestrialize inundation stress (Burdick and Mendelssohn 1987; Jung et al. 2008). The overall effects make that drainage of a thin surface water layer benefit for oxygen supply to the growth of especially young seedlings, while not affecting larger plants (Bouma et al. 2001; Redelstein et al. 2018).

A strength of present in situ study was that we included an elevation gradient in our experiment settings, revealed that decreased elevation (=increased inundation time) increased the hazard ratio for seedling survival and reduced tussock growth. Since increase of inundation would lead to decreased marsh production at suboptimal elevations (Morris et al. 2002; Kirwan and Guntenspergen 2012a; Voss et al. 2013), our results indicated that the absolute elevation of our study site relative to mean sea-level is below optimal for *S. anglica* establishment. *S. anglica* seedling survival was found to be significantly enhanced for elevations above 60 cm NAP (Normal Amsterdam Peil, which is Dutch Ordance Level that approximately equal to mean high water level in the Scheldet estuary). In fact, this matches well with field observations that dominate *S. anglica* monocultures in the Scheldt estuary generally occur with elevations ranging from 60 to 200 cm NAP at the seaward part (van de Wal et al. 2008). At lower elevations, however, our experiments revealed that surface drainage could substantially enhance *S. anglica* seedling survival. Hence, present findings suggest that, for primary establishment of young *S. angica* seedlings on mudflats, insufficient surface drainage could be a major factor besides inundation that prevent marsh from extending to lower levels (Voss et al. 2013).

4.4.2 Surface drainage as potential drivers for habitat transition of salt marshes

The present experimental results confirmed the low establishment probability of seedlings in the poorly drained, fine sediments that generally have a high water content. Although the addition of surface drainage treatment did improve the survival of *S. anglica* seedlings, the overall survival remained low, and moreover the surface drainage treatment affected only the overlying water but not the water draining of the sediment matrix. At the same time, however, the overall results suggest that the addition of surface drainage that affected the runoff of overlying water, did improve the survival of *S. anglica* seedlings and on low elevations. This is consistent with field observations showing that sparse vegetation recruitment in these habitats occurs at the banks of the shallow channels developing in the soft mudflat (Fig. 4.1). Thus, in these muddy systems, the only possibility to transit habitat from the bare mudflat to the vegetated marsh seems to be mediated by physical processes leaded by topography relief of surface drainage as channel presents (Temmerman et al. 2007, Vandenbruwaene et al. 2013; Wang and Temmerman 2013). Therefore, the results of the present study indicate that surface drainage plays an important role as a driving mechanism for the habitat transition between non-vegetated tidal flats and vegetated marshes.

Based on our findings and the relevant literature, we propose a conceptual model (Fig. 4.8) to show how surface drainage may drive habitat transition in salt marsh ecosystems: On a heterogeneous marsh platform that with good surface drainage due to topographic elevation differences (Fig 4.8a), local-scale surface drainage of the elevated sediment patches, may favor early plant establishment via e.g. slight improvement of soil aeration (Crooks et al. 2002; Silvestri et al. 2005), elevated microtopgraphy (Fivash et al., 2020) or by removing of a thin water film (Figure 7, this study). These established plants may subsequently locally stabilize and trap sediment (Bouma et al. 2009a), thereby gradually concentrating the tidal flow in between vegetation patches. This may lead to the initiation of channel incision in between vegetation patches (Temmerman et al. 2005). Thus, the heterogeneous topography is strengthened with the establishment and growth of vegetation enhancing channel formation (Fagherazzi et al. 2004a, b, 2013; Temmerman et al. 2005, 2007; Vandenbruwaene et al. 2013), which further stimulates surface drainage through the channels. As such, this development of surface drainage could further facilitate seedling establishment, resulting in a positive feedback loop between plant establishment and surface drainage in muddy systems (Fig. 4.8a). In this way, the presence of good surface drainage may initiate a habitat transition from bare mud flats to vegetated marsh, with positive feedbacks enhancing heterogeneity and self-organized long-term stability (Schwarz et al. 2018).

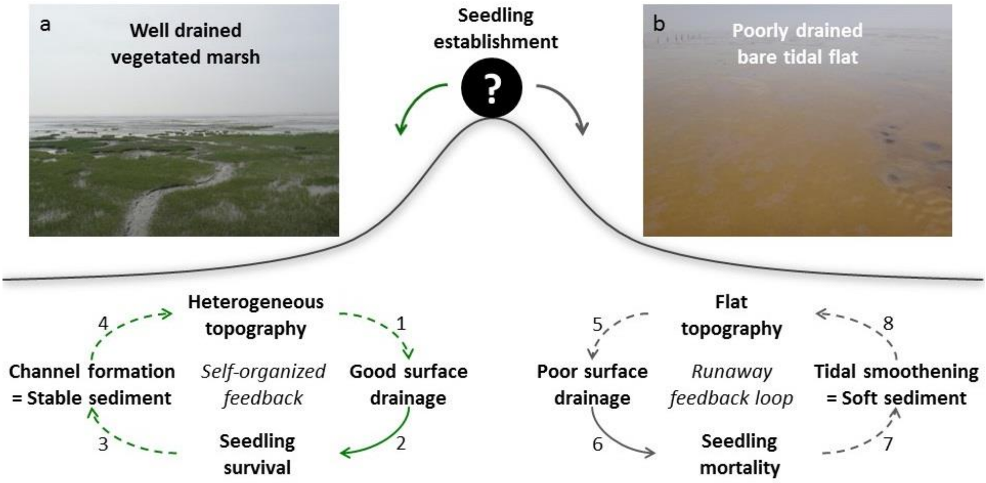

Fig. 4.8. Conceptual model showing the importance of surface drainage in controlling habitat transition in salt marsh ecosystems. a, On the left, a heterogeneous topography with good surface drainage (arrow 1; logically assumed) facilitates salt marsh seedling establishment and growth (arrow 2; Crooks et al. 2002; Silvestri et al. 2005; Redelstein et al. 2018; Fivash et al. 2020; and this study), which may stabilize and trap sediment (Bouma et al. 2009a), stimulate the formation of channels and consequently further improves surface drainage as might occur at channel banks (arrows 3 and 4; Fagherazzi et al. 2004a, b, 2013;Temmerman et al. 2005, 2007; Vandenbruwaene et al. 2013), resulting in self-organized feedbacks. b, On the right, a flat topography with poorly surface drained mudflat (arrow 5; logically assumed) hampers seedling establishment (arrow 6; Redelstein et al. 2018; Fivash et al. 2020; and this study) may leads to a soft sediment and flat topography due to tidal smoothening (arrows 7 and 8; Temmerman et al. 2007, 2012); this induces a runaway feedback loop that keeps the tidal flat bare.

In contrast, on bare tidal mud flats where heterogeneous microtopography is absent (Fig. 4.8b), giving poor drainage conditions, seedling establishment is hampered (this study), most likely due to factors like e.g. a thin water film limiting oxygen penetration (Fivash et al. 2020) in the top soil and/or low sediment stability (Redelstein et al. 2018). Seedling mortality prevents vegetation-induced topography heterogeneity and ultimately channel formation, thereby facilitating the persistent smoothening of the mud flat surface by daily tides (Temmerman et al. 2007, 2012; Vandenbruwaene et al. 2013). This keeps sediment on bare tidal flats smooth and soft, favoring the development into a homogeneous intertidal platform with waterlogged sediments (Temmerman et al. 2007) (Fig. 4.8b). Overall, this feedback loop keeps the tidal flat bare even at elevations where normally establishment of vegetation would be expected. (Fig. 4.1a; Wang and Temmerman 2013; van Belzen et al. 2017).

Despite that the underlying mechanisms relating microtopography to plant performances remain incomplete form our field study (but see Fivash et al. 2020 for process-based lab experiments), present findings and the feedback mechanism schematically described in Fig. 4.8 have important implications for management options in muddy systems. For example, creating artificial surface drainage relief to facilitate natural seedling recruitment or planting of older and larger transplant units could both be an efficient management strategy to facilitate marsh restoration on tidal mud flats at suboptimal elevations. For low elevations tidal mudflats that young salt marsh seedlings cannot successfully establish, restoration might be achieved via adopting larger seedlings (e.g. 1-year seedlings in the present study). More importantly, the size of the system to be restored should guide which way to go. Given that clonal expansion is much slower than expansion via seedling recruitment (Yuan et al. 2020; Zhu et al. 2020), large systems should aim at facilitating natural seedling recruitment by creating topographic heterogeneity, whereas small systems may benefit from planting. Further testing of present hypothesized model would be beneficial both for i) identifying those conditions where *Spartina* species are more or less likely to appear as invasive species, which is a major problem at many locations around the world (Nehring et al. 2008; and references therein), and ii) for implementing nature-based coastal protection strategies when depending on the creation of new salt marshes (Temmerman et al. 2013, 2015; van Slobbe et al. 2013).

4.5 Conclusion

The present study highlights the importance of surface drainage in assisting salt marsh seedling establishment in muddy mineral systems that have a poor hydraulic conductance. Based on our experimental results, we proposed a conceptual model for further studies to understand how surface drainage-driven feedbacks may be reinforced to induce salt marsh establishment. Future research should explicitly account for surface drainage related when aiming to understand salt marsh establishment on especially muddy tidal flats. The findings that seedling perform better on more heterogeneous topographies while large planting units are not sensitive to this, should be used to optimize salt marsh (re)creation designs in order to improve the outcomes in muddy systems.

Chapter 5

5. Plant traits determining biogeomorphic landscape dynamics: a study on clonal expansion strategies driving cliff formation at marsh edges

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Abstract

Despite the well-recognized importance of plant traits for biogeomorphic development of landscapes, our understanding remains limited of how species-specific plant traits respond to and serve as drivers for the sedimentary dynamics within a biogeomorphic landscape. By manipulating a series of lab experiments, using mesocosms and flume, we examined how species-specific differences in expansion strategy, i.e. clonal step-length of laterally expanding tillers, both respond to sediment type and drive cliff formation and persistence. We compared three marsh species, with contrasting clonal expansion traits, that are dominant in many estuaries worldwide: *Spartina anglica*, *Scirpus maritimus*, and *Phragmites australis*. Our results revealed that *S. anglica* tussocks tend to have high shoot density due to a short clonal expansion step-length, whereas *S. maritimus* tussocks were much more diffuse and tend to have a longer clonal expansion step-length. *P. australis* showed intermediate traits. Clonal expansion step-length did show within-species variation in response to sediment texture, but species-specific differences remained the most important. Species with smaller clonal step-lengths, such as *S. anglica* in this study, are more likely to induce cliffs at the marsh edge by driving formation of larger cliff heights and also having lower capacity to grow out from cliffs. Our findings thus illustrate how dynamic landscape features like marsh-edge cliffs depend on the clonal expansion traits of the dominant species. This enhances current understanding of the formation and development of marsh edges, and is instructive for understanding the role of species-specific traits in driving distinct biogeomorphic landscape dynamics.

5.1 Introduction

Biogeomorphic ecosystems are among the most dynamic environments on Earth, which are wide-spread that include tidal marshes, mangroves, seagrass meadows, coastal dunes, river deltas, river beds and floodplains (Corenblit et al. 2011, 2015 Reijers et al. 2019). These ecosystems have to cope with regularly occurring physical disturbances and extreme events, such as floods, tides, water currents, waves and storms (Naiman et al. 2008; Balke et al. 2014; Corenblit et al. 2015; Walcker et al. 2015). When adapting to stressful environments, organisms may adopt particular strategies that enhance their fitness by modifying abiotic constraints (Jones et al. 1997; Steiger and Corenblit 2012; Bouma et al. 2013).

In typical biogeomorphic ecosystems, such as fluvial and coastal ecosystems, plant species strongly influence geomorphic processes and may produce species-specific signatures in the organization and development of landforms and landscape features (Corenblit et al. 2011, 2018; Marani et al. 2013). In some cases, plants may impose scale-dependent feedbacks, meaning that they induce different landform changes close by and farther away from plant patches (van Wesenbeeck et al. 2008; Bouma et al. 2009, 2013; Schwarz et al. 2018) and thereby induce the formation of self-organized biogeomorphic landscapes (for tidal marshes see D'Alpaos et al. 2007; Temmerman et al. 2007 and van de Koppel et al. 2012; for aquatic river systems see Schoelynck et al. 2011). The strength of such scale-dependent feedbacks can be species-specific and relate to the morphological traits, growth strategies and life history traits of the species (Bouma et al. 2005a, 2013; Corenblit et al. 2015a, 2018). For example, plant species with fast and spatially extensive colonization strategies produce spatially homogenous geomorphic landscapes in stark contrast to slow and patchy colonization strategies that facilitate formation of geomorphologically heterogeneous patterns (Temmerman et al. 2007; Schwarz et al. 2018).

Despite growing understanding of the role of biogeomorphic feedbacks in landscape formation and evolution, much remains unknown about how species-specific plant traits influence the formation and evolution of biogeomorphic landscapes (Bouma et al. 2013; Corenblit et al. 2018). Whereas pioneer plants may develop plastic responses to abiotic stresses (Puijalon et al. 2011; Silinski et al. 2015, 2018; Zhu et al. 2020), ecosystem-engineering plant species tend to attenuate abiotic stresses by modifying their physical environment (Jones et al. 1994, 1997, 2012; Bouma et al. 2005a; van Hulzen et al. 2007). However, ecosystem-engineering plants can also show plasticity in their ability to modify stress levels (Crain and Bertness 2006). This has been demonstrated in studies on marsh-forming *Spartina* spp., in which clear trade-offs were found in the morphology of plants between clonal-shoot architecture (e.g., shoot density, stiffness, expansion rate) and habitat-modification capacity (e.g., sediment trapping) along a gradient of sediment type (van Hulzen et al. 2007; Schwarz et al. 2018). As different species with contrasting traits and potentially different levels of plasticity may be found in relatively similar physical environments (e.g. see Bouma et al. 2005a, 2013), we use marsh plant species with contrasting traits growing at the edge of estuarine tidal marshes as a model system to study how species-specific differences in expansion strategy can depend on the sedimentary environment as well as drive cliff formation and persistence.

Cliffs associated with vegetation edges and ranging in height from a few centimeters to meters are frequently occurring landforms feature in biogeomorphic landscapes, ranging from freshwater marshes along the banks of rivers and lakes, brackish and salt marshes in estuaries and lagoons, to seagrass meadows along coastlines (Allen 1989; De Rose and Basher 2011; Francalanci et al. 2013; Wang et al. 2017). In many of these areas, cliffs present at vegetation edges are laterally retreating through cliff erosion processes, leading to loss of the vegetated marsh area is lost predominantly by lateral retreat of cliff marsh edges (Marani et al. 2011; Mariotti and Fagherazzi 2013; Huff et al. 2019; Finotello et al. 2020). Once a pronounced cliff has formed at a vegetated marsh edge, the strong topographic and vegetation discontinuity at the bare sediment/vegetation boundary often leads to a shift from lateral marsh expansion to lateral marsh erosion (Mariotti and Fagherazzi 2010; Bendoni et al. 2016; Bouma et al. 2016). As marsh erosion may lead to loss of valuable ecosystem services (Barbier et al. 2011), mechanistic insights into the initial formation and subsequent maintenance of marsh cliffs are highly relevant (Marani et al. 2011; Fagherazzi et al. 2013; Bouma et al. 2016; Leonardi et al. 2018).

In tidal marshes, as plant roots add cohesive strength to sediment beds, this often results in differences in cohesive strength between non-vegetated tidal flats and adjacent vegetated marsh areas (van Eerdt 1985; Deegan et al. 2012; Fagherazzi et al. 2013). The onset of a cliff can result then from a small height difference (ΔZ) of only a few centimeters to decimetres, when vertical erosion of the tidal flat surface during storms is stronger than vertical erosion of the vegetated marsh surface (Bouma et al. 2016; Leonardi et al. 2018). This height difference will develop into a larger cliff if the marsh plants cannot outgrow ΔZ in the next growing season, i.e. by outgrowth of plants from the cliff top to the initially non-vegetated area in front of the cliff base (Bouma et al. 2016). We presume that the capacity of marsh species to outgrow ΔZ, and thereby prevent maintenance of a retreating cliff, is related to the clonal step-length. Clonal step-length is defined here as the horizontal distance between laterally expanding clonal tillers to the original tussock boundary, and is thus a measure of plant clonal expansion capacity. At the same time, the tiller density of vegetation may also affect the degree of cliff initiation strength at the vegetation edge. We hypothesize that denser vegetation, due to a smaller clonal step-length, is likely to induce larger differences in vertical erosion between vegetated and adjacent non-vegetated surfaces, and hence result in formation of higher cliffs.

To assess the role of species-specific plant traits in cliff formation and maintenance, we carried out a series of mesocosm experiments on three dominant marsh species with contrasting clonal expansion traits, which can be found under relatively similar hydrodynamic conditions in many estuarine areas: *Spartina anglica* (salt to brackish), *Scirpus maritimus* (brackish), and *Phragmites australis* (brackish to fresh). First, we measured the variability in clonal step-length in response to different sediment types both within and between the studied species. Second, we assessed the effect of species-specific variation in plant traits on cliff formation by carrying out a simplified flume experiment that compared the marsh species with the greatest contrast in clonal traits (*S. anglica* vs. *S. maritimus*) to determine if higher cliffs at marsh edges are induced by species with a smaller clonal step-length and higher tiller density. Third, we evaluated the impact of species-specific clonal expansion traits on the maintenance of cliffs by quantifying the maximum value of the cliff height (ΔZ_{max}) from which each of these species was able to grow out towards the non-vegetated surface in front of the cliff. We test the hypothesis that species with smaller clonal step-lengths have higher ΔZ_{max} values and thus more strongly support the formation and maintenance of cliffs compared with species with larger clonal step-lengths.

5.2 Materials and methods

5.2.1 Mesocosm experiment 1 to quantify plasticity of clonal step-length

In order to find out if there are differences in the clonal expansion traits of species in different sediment types, we first carried out a mesocosm experiment in a batch of plastic boxes (inner dimensions: length × width × depth = 70 cm × 40 cm × 30 cm) with three kinds of sediment substrates (Table 5.1) and three species (*S. anglica*, *S. maritimus* and *P. australis*). The sediments used were sand (D_{50} of 301.01μm, silt T_{63} content of 0%), sandy mud (D_{50} of 143.64 μm, silt T_{63} content of 42.34%) and mud (D_{50} of 29.93μm, silt T_{63} content of 69.03%) (classification c.f. Shepard 1954) in order to mimic the variation found in the field under different hydrodynamic exposure conditions (Herman et al. 2001; Winterwerp and van Kesteren 2004; van Hulzen et al. 2007).

In May 2016, patches of *S. anglica*, *S. maritimus* and *P. australis* with attached sediment were collected from monoculture communities of each species in a tidal marsh area near Rilland-Bath in the Western Scheldt estuary, the Netherlands. Cuboid-shaped metal frames (height = 30 cm, length = width = 20 cm) were used to extract equal-sized blocks of sediment and to protect the below-ground plant material during transportation. Each sample was transplanted individually to a mesocosm on the day of collection. During transplantation, plant-sediment samples were set level with the sediment top in the mesocosm boxes with all above ground part been carefully clipped. In each mesocosm, one plant-sediment sample was positioned at the center of the 70-cm-long box making up the mesocosm, allowing for 25 cm of space on each side from the original tussock boundary to the sides of the box in the longitudinal direction. In total, we set up five replicates per three plant species (i.e. *Spartina anglica*, *Phragmites australis*, and *Scirpus maritimus*) for each of the three sediment types (sand, sandy mud, mud), resulting in a total of 45 mesocosms (Table 5.1). All mesocosms with plants were cultivated under the same conditions: outdoors in an open area at the Royal Netherlands Institute for Sea Research (NIOZ) in Yerseke, the Netherlands, for one growing season (May – September 2016), exposed to natural temperature and light conditions, irrigated with a surplus of tap water (twice a day), and equipped with a drainage pipe each mesocosm to avoid water-logging.

Table 5.1 Treatment details in mesocosm experiment 1 to quantify clonal step-length

Sediment type	Species	Cliff height (cm)	No. of replicates.
Sand	*S. anglica*	0	5
	S. maritimus	0	5
	P. australis	0	5
Sandy-mud	*S. anglica*	0	5
	S. maritimus	0	5
	P. australis	0	5
Mud	*S. anglica*	0	5
	S. maritimus	0	5
	P. australis	0	5

At the end of the first mesocosm experiment, we measured the following plant traits in September 2016: plant height (ten random shoots), maximum tussock size (distance between the two furthest shoots in the longitudinal direction, i.e. parallel to the 70-cm box sides), and shoot density (total shoot numbers in each mesocosm). To compare the potential species-specific clonal expansion strategies in different sediment types, the clonal expansion step-lengths (*S*, cm) of tillers were estimated by measuring the distance of tillers to the original tussock boundary in the longitudinal direction.

5.2.2 Flume experiment to determine if compact vegetation growth induces higher cliffs

To investigate how different plant traits affect cliff formation, *S. anglica* (dense vegetation type with shorter clonal step-length) and *S. maritimus* (sparse vegetation type with larger clonal step-length) tussocks from the first mesocosm experiment were maintained under the same conditions until winter 2017. The flume experiment was conducted under winter conditions as this is the period when wave activity is the most intense in the Scheldt estuary, and waves are well-known driving forces for erosion, cliff formation and cliff retreat at marsh edges (Marani et al. 2011; Mariotti et al. 2010; Leonardi et al. 2018; Huff et al. 2019). The wave flume experiment was conducted in an oval-shaped racetrack flume (length of 17.5 m, width of 0.6 m) with a deeper test section (Fig. 5.1, for more details see Bouma et al. 2009) at NIOZ, Yerseke, the Netherlands. During the experiment, a standard-sized metal box (length of 120 cm, width of 50 cm, depth of 20 cm) was inserted in the test section to allow for a flat basin that was level with the flume bed (Fig. 5.1). To mimic a boundary between non-vegetated tidal flat/vegetated marsh with contrasting sediment erodibility for cliff initiation (Bouma et al. 2016), the metal box was divided into two sections (Fig. 5.1): *i)* a sediment section (length of 95 cm) containing non-vegetated tidal flat sediment consisting of non-cohesive sand (dredged from the Scheldt estuary; D_{50} of 277.28 μm; critical shear strength of 0.17 N m^{-2}, measured by an Eijkelkamp Agrisearch shear vane testing device), directly followed by *ii)* a vegetated marsh edge (length of 25 cm) consisting of two neighbouring marsh tussocks that were carefully set to be level with the flume bed sediment (D_{50} of 105.72 μm; critical shear strength of 0.50 N m^{-2}, measured by the same shear vane testing device). To examine the potential effects of contrasting plant traits on cliff formation, all above-ground shoots were kept intact when transplanted to the flume. We conducted three replicate tests for both *S. anglica* (dense vegetation type) and *S. maritimus* (sparse vegetation type) using identical wave treatments as described below.

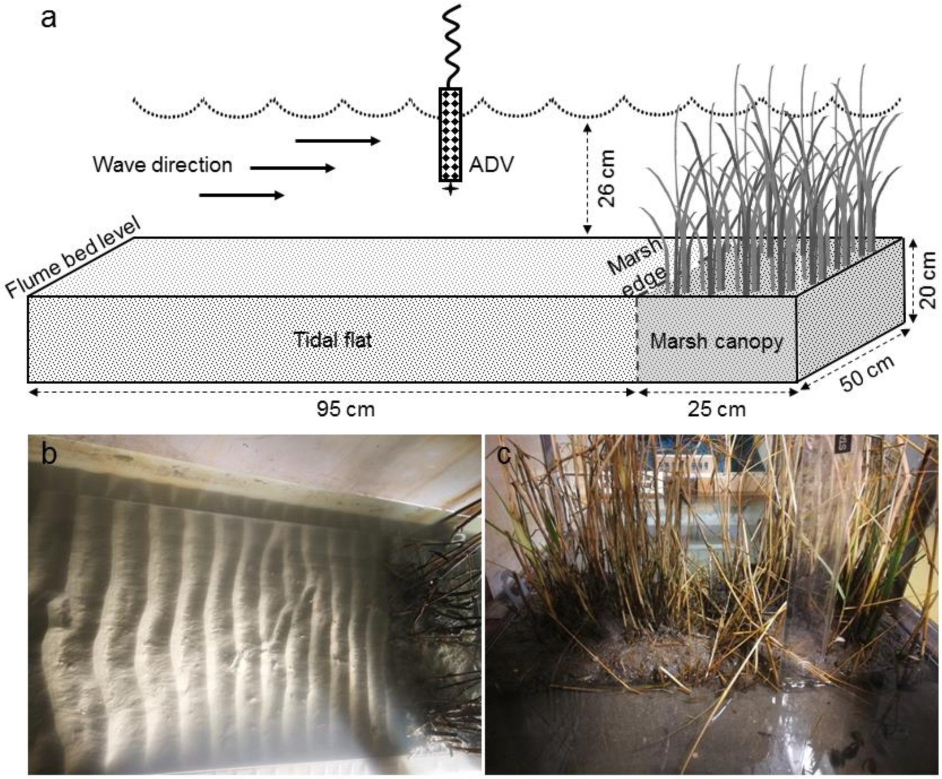

Fig. 5.1. (a) Schematic sketch of the experimental set up in the test-section of the flume. A non-vegetated tidal flat was placed in front of the marsh edge, and exposed for three hours to waves (with average period of 1.5 s and height of 10 cm) at a water depth of 26 cm. A slow constant water current of 10 cm/s was applied to move away any sediment when erosion occurred. Elevation change was measured of the mimicked tidal flat after wave exposure using an ADV (Vectrino); (b) An example photography for the top view of the flume test-section; and (c) A closeup view of a marsh edge after three hours wave run. Measurements are given in cm.

The water level in the flume was maintained at 26 cm (Fig. 5.1a), using natural sea water from the Eastern Scheldt estuary with an average salinity of 31 ppt. Regular waves in the flume were produced by a wave paddle that was controlled by an actuating piston with a spiral arm. The speed of the spiral arm was set at 2000 RPH and run for three hours, to mimic a relatively short event with strong wind-generated near shore waves in the Scheldt estuary (Callaghan et al. 2010; Silinsiki et al. 2015; Wang et al. 2017). This wave paddle setting resulted in waves with an average period of 1.5 s, maximum height of 10 cm, and peak bed shear stress of 0.46 N m^{-2} (calculated from wave properties; c.f. Jonsson et al. 1966; Balke et al. 2011), which corresponds to typical bed shear stresses during stormy conditions at natural marsh edges (c.f. Callaghan et al. 2010). In addition to the waves, a constant current velocity of 10 cm/s was applied during the whole experiment. This velocity is much lower than peak tidal currents in marsh vegetation under field conditions (around 30 cm/s; Bouma et al. 2005b), but is applied in our experiment to export suspended sediment eroded by the waves. At the end of the test section, a semi-permeable cushion barrier was used to minimize wave reflection.

To measure the erosion at the mimicked marsh edge, as a proxy for cliff formation, the surface elevation of sediment after wave exposure was measured in a spatial grid using an ADV (Nortek Vectrino, Fig. 5.1a), which can measure the vertical distance to the sediment surface. The ADV was mounted on a robot arm, which allows for an automatic scan of a space of 67 cm × 44 cm on the unvegetated part of the box at a resolution of 2 cm × 2 cm grid with a vertical accuracy in the order of 0.1 mm. Due to the technical constraints of the ADV, the surface elevation within the vegetated part was measured manually using the sedimentation erosion bar (SEB) method, which consists of manual pin readings of erosion on a space of 50 cm × 25 cm at a resolution of 10 cm x 5 cm grid and with a vertical accuracy in the order of 1 mm (Nolte et al. 2013). The shoot density (number of shoots per surface area) was recorded for each experiment by counting the shoots.

5.2.3 Mesocosm experiment 2 to quantify maximum cliff height (ΔZmax)

To compare the capacity of specific marsh species to grow out from the top of cliffs to the bare sediment in front of cliffs, and how this outgrowth capacity varies in relation to cliff height, we carried out a second mesocosm experiment simultaneously with the first mesocosm experiment. We defined ΔZ_{max}, i.e. the maximum cliff height from which a species is able to grow out, as a proxy for the species' effects on cliff persistence: cliffs with a height lower than ΔZ_{max} would not persist because plants can grow out, while cliffs would only persist if they are higher than ΔZ_{max}. To quantify ΔZ_{max}. Cliff-like plateaus were constructed (Fig. 5.2) within the same type and size of boxes as used in mesocosm experiment 1. For sediment, we used sandy-mud (D_{50} of 143.64 μm, silt T_{63} content of 42.34%) that was stable enough to maintain a range of contrasting cliff heights: 0, 2, 4, 8, 16 cm. All mesocosms with substrate were prepared before plant samples were transplanted. Plant tussocks of *S. anglica*, *S. maritimus* and *P. australis* were collected during the same time as those for mesocosm experiment 1 using the same protocol (see above).

For mesocosms with a cliff treatment, each cliff profile was constructed 20 cm from the box edge and 5 cm from the plant clump (Fig. 5.2a). Different cliff heights were maintained throughout the experimental period at 0, 2, 4, 8, 16 cm. In total, 75 mesocosms were set up, allowing for 3 species × 5 cliff heights × 5 replicates per treatment (Table 5.2). All mesocosms were cultivated outdoors for four months until September 2016 under the same condition as mentioned above for mesocosm experiment 1.

In order to estimate ΔZ_{max}, we quantified the lateral expansion of tillers in front of the cliff at harvest. Among these, we recorded separately the number of tillers grew through the soil and emerged from the lower horizontal sediment surface in front of the cliff (i.e., expansion succeeded to the lower-lying tidal flat, Fig. 5.2) versus the tillers that grew out from the vertical cliff surface and hanging in the air (i.e., expansion failed, Fig. 5.2). The largest cliff height from which tillers were still able to grow out was deemed as ΔZ_{max}.

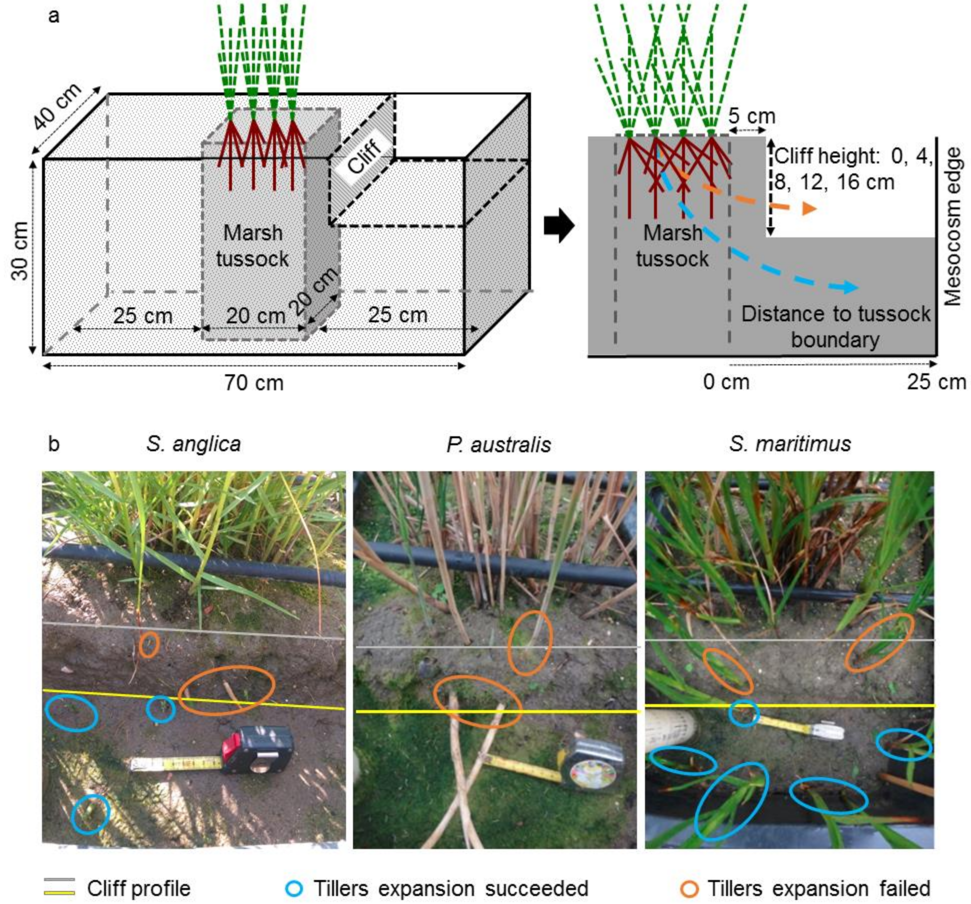

Fig. 5.2. (a) Schematic sketch of the mesocosm experimental set up and the side view of marsh tussock and cliff front; (b) Examples taken from the mesocosm experiment 2 showing the growth response at a cliff height of 8 cm for three marsh species (from left to right): *Spartina anglica*, *Phragmites australis*, and *Scirpus maritimus*. To compare the outgrow capacity of the marsh plants, tillers that had expanded past the cliff front were recorded and separated into tillers that had succeeded in expanding into the lower-lying bare sediment (blue circles) versus tillers that had failed to grow into the lower-lying sediment surface, and hence had ended up free-hanging in the air (orange circles). Note that all above ground part of the original tussocks had been carefully clipped during transplantation. Measurements are given in cm.

Table 5.2. Treatment details in mesocosm experiment 2 to quantify maximum cliff height (ΔZ_{max})

Cliff height (cm)	Species	Sediment type	No. of replicates.
0*	*S. anglica*	Sandy-mud	5
	S. maritimus	Sandy-mud	5
	P. australis	Sandy-mud	5
2	*S. anglica*	Sandy-mud	5
	S. maritimus	Sandy-mud	5
	P. australis	Sandy-mud	5
4	*S. anglica*	Sandy-mud	5
	S. maritimus	Sandy-mud	5
	P. australis	Sandy-mud	5
8	*S. anglica*	Sandy-mud	5
	S. maritimus	Sandy-mud	5
	P. australis	Sandy-mud	5
16	*S. anglica*	Sandy-mud	5
	S. maritimus	Sandy-mud	5
	P. australis	Sandy-mud	5

*Note the overlapping design in that the 0-cm cliff height treatment is the same group of mesocosms under sandy-mud treatment in Table 5.1.

5.2.4 Statistics

For the mesocosm experiments, two-way ANOVAs were applied to analyse the effects of species and sediment type on clonal growth traits in terms of plant height, tussock size, and total tiller numbers for all data resulting from mesocosm experiment 1 (see above) (Table 5.1), as well as the effects of species and cliff height on these clonal growth traits for all the sandy-mud treatments (Table 5.2). To compare the clonal architecture of the different treatments in mesocosm experiment 1, we analysed the statistical distribution (with bin size of 5 cm) of the measured clonal step-lengths of the tillers that grew out from the margin of the marsh clumps. However, growth of the vegetation was faster than originally anticipated. Many shoots had grown into the last 5 cm adjacent to the box edge (note the maximum of 25 cm of space for each side from the original tussock boundary in the longitudinal direction of 70-cm-long box sides). Presumably, the rhizomes that could not grow out any further had generated shoots in this limited space. Therefore, we considered all tillers that had grown beyond the 20-cm expansion distance boundary as shoots that would have grown over considerably longer distances than actually observed, and classified them as 'censored' observations. The R package "fitdistrplus" (Delignette-Muller and Dutang 2015) was applied to examine the possible distribution. We used the actual observed measurement data for all individuals growing at a distance of ≤20cm from the tussock, while classifying the other observations as ">20 cm". The following distributions were fitted to the data: log-normal, normal, exponential, cauchy, gamma, and logistic weibull. Based on the Akaike's information criterion (AIC), the log-normal distribution was consistently chosen as the best-fitting distribution in all cases.

To compare the potential differences in cliff-formation capacity at the marsh edge in the flume experiment, we calculated the average net sediment volume loss rate (cm^3/ h) of the non-vegetated tidal flat section and the vegetated marsh section by multiplying the average vertical surface elevation change and surface area of each section and dividing it by the time the flume experiment had been run (i.e. three hours). The cliff height at the marsh edge was estimated as the maximal height difference measured when approaching the vegetated area from the bare area. Two-way ANOVAs were used to test the effects of species (*S. anglica* vs. *S. maritimus*) and erosion section (tidal flat vs. marsh edge) on sediment volume loss rate. Student's t-tests were used to compare cliff height and shoot density at the marsh edge for different species.

The outgrowing capacity to the cliff front of different species in mesocosm experiment 2 was evaluated by calculating the successful expansion rate as the percentage of tillers that had expanded into the mud flat in front of the cliff divided by the total number of shoots reaching the cliff side (i.e. in front of the cliff + penetrating the vertical cliff profile, see Fig. 5.2). To compare the outgrowth capacity of different marsh species, we applied a multiple generalized linear model (GLM) to analyse the relationship between the successful expansion rate of different marsh species and cliff height. All analyses were done in R (https://www.r-project.org) using a significance level of 0.05.

5.3 Results

5.3.1 Species-dependent clonal expansion traits in response to different sediment types

In mesocosm experiment 1, for all sediment types, our results showed that plant height, tussock size and total number of tillers were significantly affected by marsh species ($p < 0.001$, Table 5.3). *S. anglica* tussocks were observed to be significantly shorter and smaller in size than those of *S. maritimus* and *P. australis* at the end of the mesocosm experiment (Fig. 5.3a and b, $p < 0.001$). Also, *S. anglica* had significantly more tillers than the other two marsh species (Fig. 5.3c, $p< 0.001$). This shows that *S. anglica* tussocks grew to be significantly denser than those of sparser-growing *S. maritimus* and *P. australis*, regardless of the sediment types in which they had been grown.

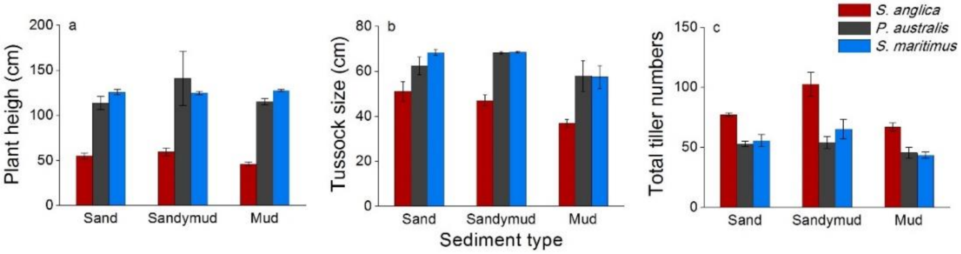

Fig. 5.3. Plant trait responses found in mesocosm experiment 1 of three marsh species (see Fig. 2 for full names) grown in three contrasting sediment types: sand, sandy mud and mud. The response parameters measured were (a) Plant height (cm), (b) tussock size measured as maximum distance between expanded tillers (cm), and (c) Total number of tillers per mesocosm of 0.28 m2 (70 × 40 cm). See Table 5.3 for statistical test results.

Sediment type did not affect plant height (Fig. 5.3a; $p = 0.33$, Table 5.3) but had a significant effect on both tussock size ($p < 0.01$, Table 5.3) and total tiller number ($p < 0.001$, Table 5.3). In comparison to sand and sandy mud, all species in muddy sediment were observed to have smaller tussock sizes (Fig. 5.3b, $p < 0.01$) and lower total number of tillers (Fig. 5.3c; $p < 0.05$ compared with sand, $p < 0.001$ compared with sandy-mud).

Table 5.3 Two-way ANOVA results for effects of species and sediment type on marsh plant traits in mesocosm experiment 1

Response variable	**Deviance source**	**d.f.**	**Mean Sq**	**F**	***p***
Plant height (cm)	Species	2	50834.03	44.46	<0.001
	Sediment type	2	1290.53	1.13	0.33
	Species* Sediment type	4	782.56	0.68	0.61
Tussock size (cm)	Species	2	1479.09	21.85	<0.001
	Sediment type	2	445.12	6.57	<0.01
	Species * Sediment type	4	37.82	0.56	0.69
Total tiller numbers	Species	2	3650.58	24.13	<0.001
	Sediment type	2	1645.44	10.88	<0.001
	Species * Sediment type	4	260.98	1.73	0.17

When looking at the statistical distribution of the clonal step-lengths (Fig. 5.4), we found that all three species in all sediments have log-normal distributions of step-lengths (only in the case of *S. anglica* there is some systematic deviation of the data). Notably, *S. anglica* had the shortest clonal step-lengths and the largest differences in step-length distribution between sediments. *S. maritimus* had the longest clonal step-lengths and smallest variation in distribution between sediments. *P. australis* showed intermediate results. This means that lateral salt marsh expansion is diminished towards muddy sediments, especially for species with small clonal step-lengths.

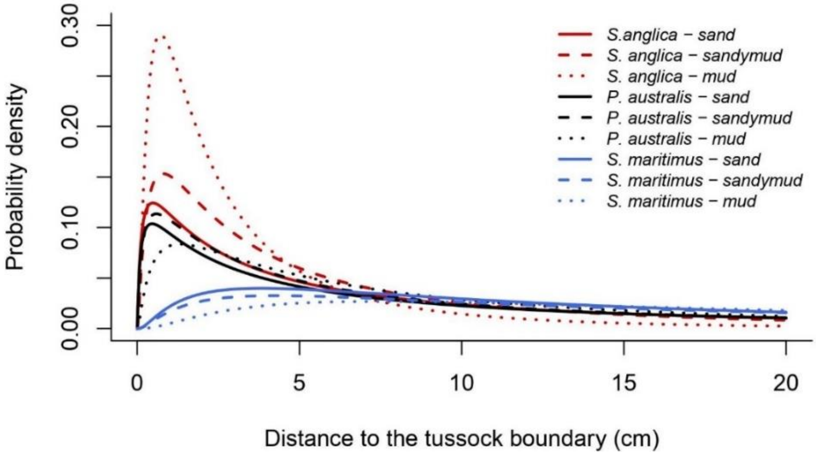

Fig. 5.4. Relative frequency of clonal expansion distance to the tussock boundary (step-length) found in mesocosm experiment 1 of three marsh species. All marsh species in all sediment types had a log-normal distribution of clonal expansion distances to the original margin of the marsh clumps. Note that tillers growing beyond the 20-cm expansion distance boundary were classified as >20cm due to limited space in the mesocosms.

5.3.2 Effects of marsh clonal expansion traits on cliff formation

In the flume experiment, we observed that the tidal flat section was not eroded homogeneously. A scouring cliff developed on the tidal flat section, with the maximum depth observed at the marsh edge (Fig. 5.5a). We found significant differences ($p < 0.001$, Table 5.4) in the net sediment volume loss rate between the bare tidal flat and vegetated marsh canopy, but not between species *S. anglica* and *S. maritimus* (Fig. 5.5b, $p = 0.148$, Table 5.4). This demonstrates that cliff formation can be initiated at the transitions between bare and vegetated areas with contrasting erodibility of the sediment bed. Although the average net sediment volume loss rate on the mimicked tidal flat in front of the *S. anglica* marsh canopy was only slightly higher than that in front of the *S. maritimus* marsh canopy, we found that the cliff at the marsh edge (Fig. 5.5a),was significantly higher in the case of *S. anglica* (Fig. 5.5c; $p < 0.05$, t-test). *S. anglica* was also characterized by higher shoot density than *S. maritimus* (Fig. 5.5d; $p < 0.05$, t-test).

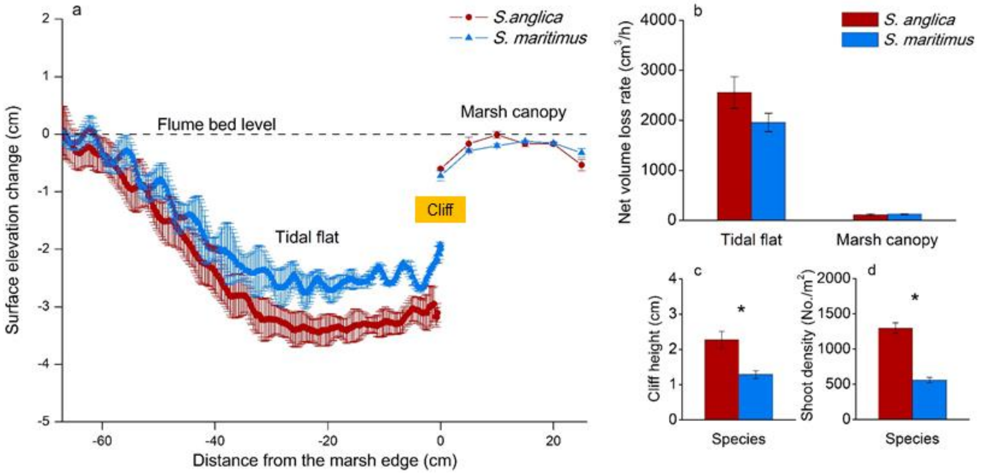

Fig. 5.5. Measurements taken in flume experiment with two marsh species: (a) surface elevation change of the mimicked tidal flat and marsh edge at the end of the flume experiment with deeper cliffs formed at the marsh edge for *S. anglica*, (b) net sediment volume loss rate (cm3/h) of the mimicked tidal flat versus marsh edge, (c) cliff height (cm) adjacent to marsh edges, and (d) different shoot densities (No./m2). * indicates significant differences ($p < 0.05$).

Table 5.4. Two-way ANOVA results on differences in net sediment volume loss rate in the flume experiment between erosion sections (tidal flat vs. marsh canopy) and species

Deviance Source	d. f.	Mean Sq	F	*p*
Erosion section	1	1.368E7	135.76	< 0.001
Species	1	257983.99	2.56	0.148
Erosion section * Species	1	278750.35	2.77	0.217

5.3.3 Effects of marsh clonal expansion traits on cliff maintenance

In mesocosm experiment 2, we aimed to quantify ΔZ_{max} (the maximum cliff height that a species was able to outgrow) to test whether the maintenance of a marsh-edge cliff depends on the clonal expansion traits of species. When comparing basic plant traits at different cliff heights, significant species effects were still found on plant height, tussock size and total tiller numbers (Fig. 5.6; $p < 0.001$, Table 5.5). A significant effect of cliff height was also found on tussock size ($p < 0.001$, Table 5.5), but not on plant height or total tiller numbers ($p > 0.05$, Table 5.5). We found that the tussock size of *S. anglica* under the treatment of a 16-cm-high cliff was significantly smaller than that under all other cliff height treatments (Fig. 5.6b; $p = 0.019$ compared to 0 cm treatment, $p = 0.002$ compared to 2 cm treatment, $p = 0.002$ compared to 4 cm treatment, $p = 0.013$ compared to 8 cm treatment).

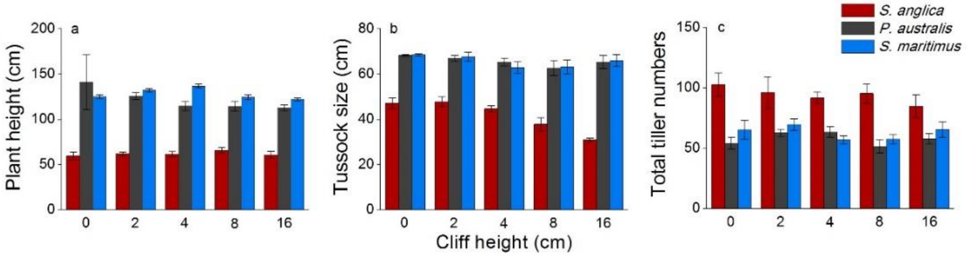

Fig. 5.6. Plant trait responses of three marsh species found in mesocosm experiment 2 when exposed to different cliff heights: 0, 2, 4, 6, 8 and 16 cm. (a) Plant height (cm), (b) tussock size, measured as maximum distance between expanded tillers (cm), and (c) Total number of tillers per mesocosm of 0.28 m2 (70 × 40 cm2). See Table 5.5 for statistical test results.

Table 5.5 Two-way ANOVA results on effects of species and cliff height on marsh plant traits in mesocosm experiment 2

Response variable	**Deviance source**	**d.f.**	**Mean Sq**	**F**	***p***
Plant height (cm)	Species	2	66643.10	93.97	<0.001
	Cliff height	4	480.70	0.68	0.61
	Species*Cliff height	8	694.07	0.98	0.46
Tussock size (cm)	Species	2	4762.89	192.81	<0.001
	Cliff height	4	168.31	6.81	<0.001
	Species * Cliff height	8	69.55	2.816	0.010
Total tiller numbers	Species	2	9518.55	40.38	<0.001
	Cliff height	4	164.13	0.70	0.60
	Species * Cliff height	8	167.83	0.71	0.68

When looking at the vegetation expansion success (fraction of tillers that expanded to the soil ground) in front of the cliff, GLM analysis indicated that this changes with cliff height but in different ways for the three species (Fig. 5.7). Logistic models were used to test the effects of species, cliff height and their interactions as independent variables. The model with a common intercept and a species-dependent slope provided the most parsimonious fit, as judged by the AIC criterion. We found a strong decrease in outgrowing capacity from species with longer clonal step-lengths to those with shorter clonal step-lengths (i.e. in decreasing order: *S. maritimus*, *P. australis*, *S. anglica*; Fig. 5.7). The highest cliff height that *S. anglica* marsh tussocks were able to outgrow was 8 cm, while *P. australis* and *S. maritimus* tussocks could still successfully expand to the area in front of 16-cm-high cliffs, which was the maximum height applied in our experiments (Fig. 5.7). These results mean that species-specific expansion strategies, in terms of clonal step-length, indeed affected the outgrowing capacity of plants at marsh-edge cliffs.

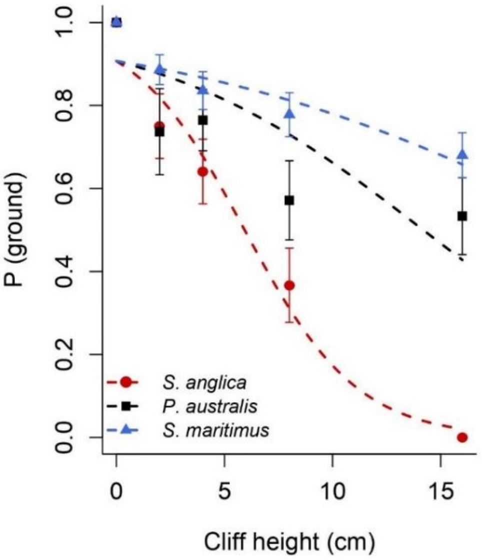

Fig. 5.7. Generalized liner model (GLM) analysis of the relationship between vegetation expansion successful rate P (fraction of tillers that expanded to the soil ground) of different marsh species against cliff height (cm) in mesocosm experiment 2. Data show mean fraction of tillers in the soil and the standard error of this mean. The curves are the predicted response from logistic regression of the fraction of successfully expanded tillers on the interactions between cliff height and species.

5.4 Discussion

Using marsh cliff-formation as a model system, we examined how species-specific vegetation expansion strategies may drive biogeomorphic landscape dynamics. We found that with a shorter clonal step-length, marsh species increased the degree of cliff formation at the vegetation edge due to having a higher shoot density. At the same time, a shorter clonal step-length also reduced the capacity of a plant species to grow out from a cliff, and hence increased the probability of cliff maintenance. Overall, species with shorter clonal step-lengths are more likely to form and maintain cliffs at transitions from vegetated to bare surfaces in biogeomorphic landscapes.

5.4.1 Species-specific clonal-expansion strategies and their response to sediment types

In the present study, we found that marsh clonal expansion, in terms of tussock size and tiller numbers, diminished towards muddier sediments. Clonal expansion step-length of marsh species decreased as well, especially for *S. anglica* which presented a notable increasing frequency of shorter step-lengths from sand to mud substrates. This could be a direct mechanistic effect of sediment on plants. Due to the strong inter-particle attraction force in cohesive sediment (Winterwerp and van Kesteren 2004), well-drained and compacted muddy soils, as may occur in our mesocosms in which hydrodynamic forces were not include, are generally highly resistant to penetration compared to poorly drained muds. *S. anglica* tillers may tend to penetrate the muddy sediment at shorter intervals (i.e. shorter step-length, as shown in this study) and therefore producing a higher shoot density (van Hulzen et al. 2007; and this study). However, indirect causal relations between sediment composition and plant growth are also possible. In general field conditions that sediment properties of tidal marshes are inherently affected by hydrodynamics along a stress gradient of tidal action (Winterwerp and van Kesteren 2004; Bouma et al. 2007). The gradient from sand to mud indicates a gradient from hydrodynamically more exposed to sheltered conditions (Herman et al. 2001; Defew et al. 2002; van Hulzen et al. 2007). In response to such gradient of mechanical stress to the plants (e.g. drag force from the water flow acting on the plants; Puijalon et al. 2011; Steiger and Corenblit 2012; Silinski et al. 2015, 2018), there may be intraspecific variations in plant traits due to differences in rougher hydrodynamic areas with sandy soils compared to gentler habitats with muddy sediment (van Hulzen et al. 2007;Bouma et al. 2013; Schwarz et al. 2018).

Within-species variations in clonal expansion were negligible in comparison with the contrasting clonal architecture of the three marsh species studied. *S. anglica* tussocks tend to have denser patches of shoots with short expansion step-lengths. *S. maritimus* tussocks are more diffuse and tend to expand with larger step-lengths. *P. australis* seems to present an intermediate strategy. These results suggest that marsh species have trade-offs that may either distribute less dense but longer tillers (*S. maritimus* and *P. australis*) to maximizing expansion rates, or distribute biomass and energy over denser but shorter tillers (*S. anglica*) to optimizing self-facilitation. Such trade-offs are related to different options of stress-avoidance or stress-tolerance strategy in fluvial and coastal ecosystems (Bouma et al. 2005a; Puijalon et al. 2011; Silinski et al. 2015, 2018; Zhu et al. 2020). With larger step-lengths and sparse patches that allowing more water flow to pass though and over the vegetation canopy (Bouma et al. 2007, 2013), *S. maritimus* could be a more hydrodynamic stress-avoiding species in sandy habitats where flow velocity and wave energy are relatively high (Defew et al. 2002; van Hulzen et al. 2007). Whereas, for autogenic ecosystem-engineer species *S. anglica*, which has shortest stems (Zhu et al 2020; and this study) and lowest stem stiffness (Zhu et al. 2020), its clone has to tolerate wave energy with dense tillers (short step-lengths) as a whole to be able to modify habitat sufficiently (Bouma et al. 2005a; van Hulzen et al. 2007). For example, by having densely growing clonal patches, *S. anglica* plants can optimize sediment trapping efficiency (Bouma et al. 2005a, 2007), and thereby alleviate local anoxic conditions in muddy habitat via elevated topography and channel formation (Schwarz et al. 2018; Fivash et al. 2020). These enhanced drainage patterns in *S. anglica* marshes may further promote sediment compaction on the marsh platform and further limit clonal expansion, resulting in its typical patchy landscape.

5.4.2 Influence of species-specific clonal traits on cliff formation and maintenance

By comparing cliff formation capacity of marsh species with contrasting clonal traits at a marsh edge, our flume experiment showed that densely growing *S. anglica* plants are more likely to induce higher cliffs at marsh edges than more sparsely growing *S. maritimus*. First, our results suggest that the different erodibility at the bare tidal flat/ vegetation transition zone can indeed cause cliff formation. While sediment type and its consolidation are the primary variables that affect sediment erodibility (Allen et al. 1989, 2002; Feagin et al. 2009; Wang et al. 2017), the general presence of a plant canopy may additionally influence sediment stability via above-ground hydrodynamic attenuation (Mudd et al. 2010; Bouma et al. 2005a, 2009; Möller et al. 2014) and below-ground sediment binding (van Eerdt 1985; Deegan et al. 2012). The abrupt change of sediment erodibility at the tidal flat/marsh transition zone can create a local height difference that may subsequently be reinforced by wave impact and erosion on the incipient cliff face (Feagin et al. 2009; Mariotti and Fagherazzi 2010; Bouma et al. 2016).

Second, although our limited scale of marsh tussocks did not allow us to simulate the generally elongated marsh edge at the landscape scale, our flume experiment results suggest that marsh plants may induce cliff formation by blocking the flow and inducing scouring in front of the vegetation, which leads to spatially concentrated patterns of erosion. Local intensification and reflection of wave is enhanced by a very dense tussock, whereas waves can dissipate more easily in a sparser vegetation canopy (van Wesenbeeck et al. 2008; Bouma et al. 2007, 2013). Such scale-dependent feedbacks concentrate wave erosion in the unvegetated area in front of the marsh edge leading to the development of vertical scarps in tidal landscapes (Mariotti and Fagherazzi 2010; Fagherazzi et al. 2012). This effect was indeed strongest in the case of

S. anglica with a dense tussock, which formed a higher cliff at the marsh edge than the more sparse *S. maritimus* tussock. The absence of vegetation-related wave attenuation in front of cliffs will make the marsh edge more vulnerable to wave impacts (Callahan et al. 2010; Möller et al. 2014; Wang et al. 2017) and increasingly sensitive to cliff-retreat processes (Bendoni et al. 2016; Valentine and Mariotti 2019; Finotello et al. 2020).

Last, we observed that the capacity of marshes to grow out over an initially forming cliff is determined by the species-specific plant traits of clonal step-length. The lack of ability to outgrow a higher cliff height (ΔZ_{max}) at the marsh edge makes *S. anglica* especially prone to encourage cliff formation and further cliff growth. *P. australis* and especially *S. maritimus* are better at growing over initially forming cliffs, while also being less likely to cause initial formation of high cliffs. Even though dense *S. anglica* tussocks are well-adapted to stressful conditions (e.g. by enhancing sediment accretion via wave attenuation, Bouma et al. 2005a 2007; Möller et al. 2014; promoting drainage and alleviating anoxia stress, Schwarz et al. 2018; Fivash et al. 2020), they are also more liable to be negatively impacted by cliff formation, as denser tussocks can cause higher cliffs that their tillers with short step-lengths can not successfully grow out (as show in flume experiment and mesocosm experiment 2). This finding is in good agreement with observations that regeneration of the vegetation removed by progressing cliff erosion in *S. anglica* marshes will not primarily take place by the plants growing over the cliffs, but by new recruitment of vegetation patches in front of existing cliffs (see model simulations e.g. van de Koppel et al. 2005; Mariotti and Fagherazzi 2010; Fagherazzi et al., 2012; see observations e.g. van der Wal et al. 2008; Bouma et al. 2016). Although we have only adopted one sediment type to investigate the outgrowing capacity of different species (mesocosm experiment 2), it is also of note that the effect of sediment properties in affecting marsh outgrowing capacity (mesocosm experiment 1) is also expected to impact cliff formation capacity in different systems.

This present study emphasizes the role of species-specific plant traits like clonal strategies in driving the formation and maintenance of cliffs at marsh edges. Even though cliff erosion at marsh edges is a complex geotechnical problem that depends on many critical extrinsic factors like sediment type (Allen 1989; Feagin et al. 2009), wind exposure (Marani et al. 2011; Wang et al. 2017; Valentine et al. 2019), wave dynamics (Callaghan et al. 2010; Möller et al. 2014; Leonardi et al. 2018; Finotello et al. 2020), and sea-level rise (Mariotti et al. 2010; Kirwan et al. 2010, 2013), intrinsic characteristics of marshes that autonomously drive cliff retreat have also been recognized (van de Koppel et al. 2005; Mariotti and Fagherazzi 2013; Wang et al. 2017). The importance of intrinsic mechanisms is supported by our findings in that plant traits determined the height of initially forming cliffs, as well as the likelihood of these initial cliffs to be overgrown and rendered inactive by the vegetation. The combined impacts of both extrinsic and intrinsic factors will shape marsh boundary dynamics and steer the long-term evolution of coastal areas at landscape scales (Mariotti and Fagherazzi 2010; Wang et al. 2017; Schwarz et al. 2018).

5.4.3 Research implications

The formation of a cliff generally acts as a tipping point, causing a state shift in marshes from lateral expansion to erosion (van de Koppel et al. 2005; Scheffer et al. 2009; Bouma et al. 2016). The present species-specific data can be used in models for predicting how critical transitions in ecosystems depend on the characteristics of dominant species. Such relationships can further be used for understanding the dynamics of marsh ecosystems under sea-level rise (Fagherazzi et al. 2012, 2013; Kirwan and Megonigal 2013) or storm conditions (Mariotti et al., 2010; Möller et al., 2014; Leonardi et al. 2018). Species-specific plant traits that determine the formation and maintenance of cliffs can be expected to modify landscape evolution trajectory, and ultimately determine the total aerial extent of marsh ecosystems along coastlines (Marani et al. 2011; Mariotti and Fagherazzi 2013; Huff et al. 2019). The mechanisms of cliff formation at marsh edges, as well as their long-term dynamics, could be investigated with models and comparative field studies across systems with very different dominant species.

The contrasting clonal strategies of different marsh species and their cliff-forming capacity adds to our growing understanding that variation in plant traits can lead to different colonization traits over space and result in distinct landscape-shaping abilities (Corenblit et al. 2015a, 2018; Schwarz et al. 2018; Reijers et al. 2019). Further exploration of these relationships will not only improve our understanding of natural processes, but may also prove essential in predicting how ecosystems can cope with anthropogenically induced stress at local and global scales.

5.5 Conclusion

The relationship between plant traits and their geomorphic environment are highly intertwined in the long-term evolution of biogeomorphic ecosystems. Using pioneer marsh edge as a model system, we examined clonal expansion traits of pioneer marsh plant assemblages in response to different sediment types. The species-specific expansion strategy of clonal step length is revealed to affect landscape evolution both in the capacity of plants to outgrow a cliffed marsh edge, and in cliff formation capacity at marsh edges. Present findings are essential for understanding the overall resilience of marsh ecosystems, and are instructive for understanding species-specific traits in driving distinct biogeomorphic landscapes evolution on the Earth surface.

Chapter 6

General discussion

6.1 Tidal marsh cyclic dynamic mechanisms

In the face of a changing climate, tidal marsh ecosystems are increasingly valued for their sustainable coastal defense functions. Although strong evidence exists that tidal marshes can vertically keep pace with sea level rise (Kirwan et al. 2009, 2013, 2016), the long-term persistence of marsh ecosystems may also be threatened by global change stressors (Zhu et al. 2019). Laterally, the extent of tidal marshes is highly dynamic with alternating phases of expansion and retreat over time and space (Yapp et al. 1917; Adam 2002; van der Wal et al. 2004, 2008; van de Koppel et al. 2005; Bouma et al. 2016). As a consequence of two-way interactions between biological and physical processes (van de Koppel et al. 2005; Mariotti and Fagherazzi 2010), the cyclic marsh dynamics may not always be apparent and typically present one of the alternative phases with a discontinuity at the bare flat / pioneer vegetation boundary (Callaghan et al. 2010; Mariotti and Fagherazzi 2010). In-depth mechanistic insights into the actual processes that drive these dynamics and in their critical transitions is essential for understanding long-term tidal marsh evolution in a changing climate (Bouma et al. 2016).

6.1.1 Critical factors in tidal marsh establishment

It is important to identify critical factors in tidal marsh establishment processes , as these processes control the transition from bare tidal flat to vegetated state (Marani et al. 2010, 2013; Wang and Temmerman 2013; van Belzen et al. 2017). However, the establishment of marshes on the tidal flat is often problematic due to disturbance by abiotic conditions (Schwarz et al. 2011; Friess et al. 2012). For example, the lack of sediment stability under wave stress can be one of the main factors in the primary marsh establishment phase

(Bouma et al. 2014; and references therein). By quantifying the effects of sediment regimes on seedling establishment (Chapter 2), this study found that marsh seedlings are more sensitive to erosion than accretion, and are less sensitive to gradual sediment disturbance than to abrupt changes. Similarly, by quantifying the effects of wave stress on marsh seedling establishment of three pioneer marsh species that dominate along a salinity gradient of an estuary (Chapter 3), this study found evidence for direct effects from wave stress on early marsh establishment. Gaining such quantitative insights is important, as global accretion/erosion regimes vary greatly among coastal areas (Temmerman et al. 2012), and climate change is expected to induce more extreme disturbance events with higher wave pressure during the establishment period (Mariotti and Fagherazzi 2010, 2013; Silinski et al. 2015).

Moreover, this study found that seedling survival, especially in the earliest phase, was positively affected by the presence of (channel-related) surface drainage relief (Chapter 4). This was examined in a poorly consolidated muddy system, where the effect may be most expressed. Fine-grained sediments cannot lose much interstitial water during a single ebb tide (Winterwerp et al. 2004) and are expected to remain fully water-saturated. At the same time, field observations show that vegetation establishment in these ecosystems is sparse, but when it does occur it is usually linked to the presence of shallow tidal channel reliefs. The results of this experimental study suggest that the only possibility to transit from the bare to the vegetated state in poorly consolidated muddy system is mediated by physical processes leading to the formation of shallow surface drainage reliefs (Temmerman et al 2007 Vandenbruwaene et al. 2013; Wang and Temmerman 2013). Therefore, in addition to previous studies that mainly focused on how plants contribute to channel formation or evolution (Temmerman et al 2007, Vandenbruwaene et al. 2013; Schwarz et al. 2018), this study shows how topographic heterogeneity and channel formation may facilitate initial marsh establishment by surface drainage.

By studying the establishment of marsh seedlings under different disturbance-free periods in both laboratory (Chapter 2) and field (Chapter 4) experiments, this study confirmed that a longer disturbance-free period can strongly enhance seedling survival. It also contributes to their resistance to later extreme disturbances. These findings offer quantitative support to the prevalent "Windows of Opportunity" concept, which highlights the requirement of having a disturbance-free hydroperiod for seedlings to establish successfully (Balke et al. 2014; Hu et al. 2015b). Given increasing frequency and intensity of flooding risks, even longer disturbance-free periods might be needed particularly for seedling establishment of pioneer species that are among the first plants that will have to cope with the rising sea level (Andersen et al. 2011).

6.1.2 Critical factors in tidal marsh erosion

The vital ecosystem function of tidal marshes for coastal protection depends on the width of the marsh landscape (Koch et al. 2009; Fagherazzi et al. 2012; Bouma et al. 2014; Zhu et al. 2019). However, the retreat of cliffs at the marsh edge has led to recent marsh loss in many coastal areas and lagoons across the world (van der Wal and Pye 2004; Gedan et al. 2009; Mariotti and Fagherazzi 2010; Marani et al. 2011). Identifying the locations where cliff erosion starts is essential for understanding the long-term stability of tidal marshes (Fagherazzi et al. 2013; Bouma et al. 2014, 2016; Wang et al. 2017).

A large number of experimental and modelling studies have provided considerable advances in identifying and quantifying both extrinsic (e.g., wind waves) and intrinsic factors (e.g., sediment properties, the presence of vegetation) involved in marsh-cliff retreat mechanisms (Feagin et al. 2009; Fagherazzi et al. 2012; Francalanci et al. 2013; Lo et al. 2017; Wang et al. 2017). However, very few studies so far have focussed on the initial processes causing the onset of cliff formation and subsequent marsh erosion (Bouma et al. 2014, 2016). Therefore, this study has taken a step back and looked at the cliff initiation process. That can be the actual tipping point that transforms marsh expansion to lateral erosion, eventually leading to a long-term state shift from vegetated marsh to bare tidal flat (van de Koppel et al. 2005; Scheffer 2009).

By means of mesocosm and flume experiments under controlled conditions, this study investigated the effects of both physical (sediment properties) and biological (vegetation) factors on the cliff formation process at the marsh edge (Chapter 5). The present findings confirm that when erosion of the tidal flat during storms is stronger than erosion of the vegetated marsh, a difference in elevation arises that can develop into a cliff, if the marsh plants cannot outgrow the height difference in the next growing season (Bouma et al. 2016, and Chapter 5). In addition, the presence of vegetation at the marsh edge may enhance the neighbouring erosion process by deflecting waves and currents. Both the outgrowing of initial cliffs and the deflection of waves and currents are dependent on the species-specific clonal growth strategy, reflected in in rhizomal step length, shoot density, stem diameter and stem stiffness. These traits have important effects on the biogeomorphic landscape evolution at marsh edges (Chapter 5).

6.2 Species-specific plant traits for biogeomorphic landscape evolution

Tidal marshes are typical biogeomorphic ecosystems that are among the most dynamic environments on the Earth's surface (Corenblit et al. 2011, 2014, 2015a, b). In such ecosystems, plants are particularly influential on the landscape development. As species differ in their essential traits for this interaction, species-specific signatures in the organization and development of the landscape features may become visible (Corenblit et al. 2011, 2018; Schwarz et al. 2018).

By comparing the response of different species, with different traits, to the afore-mentioned critical factors, this study identified species-specific strategies in life-history that are important for establishment and erosion processes in the tidal marsh. For instance, this study found inter-specific differences in mechanical response to wave stress (Chapter 3) and clonal growth strategy (Chapter 5) of marsh species that dominate along a salinity gradient. Whilst *S. anglica* seedlings tend to have a significantly higher root/shoot biomass ratio under wave stress than *S. maritimus* and *P. australis*, the clonal expansion step length of mature *S. anglica* is the smallest of the three species, leading to denser tussocks. These traits facilitate *S. anglica* seedlings to establish at higher hydrodynamic stress (e.g. higher wind exposure) than the other two pioneer marsh species. The dense mature *S. anglica* tussocks at the marsh edge may thus present higher engineer capacity in inducing self-organized heterogeneity landscapes (van Wesenbeeck et al. 2008; Bouma et al. 2009a; Schwarz et al. 2018).

Plasticity in growth form and adapted species-specific growth strategy traits can be beneficial to enhance the performance of aquatic pioneer plants in coping with external forces (Puijalon et al. 2005, 2008 2011). Although many pioneer species share equivalent responses in their morphology, physiology and phenology (e.g. the clonal growth form), optimization of plant traits to stressful physical conditions does not necessarily result in convergence, as different options of resistance and/or resilience mechanisms remain open (Bouma et al. 2005a, 2013; Stallins 2005; Corenblit et al. 2015a).

The three species used in the present study (Chapter 3 and Chapter 5) shift dominance as pioneers in a gradient from high to low salinity: *Spartina anglica* (salt to brackish), *Scirpus maritimus* (brackish), *Phragmites australis* (brackish to fresh). Presumably, this gradient is also reflected in the physical stress from currents and waves, which decrease as one goes landwards in estuaries. Of the three species, *S. anglica* that is less stiff and occurs in dense patches with a small clonal step length (Chapter 5), presents the strongest avoidance of stress (Chapter 3). It diverts physical stress outside of its hummocks by the dense growth, while bending to strong waves and currents where this is not sufficient. The stiffer species (*S. maritimus* and *P. australis*) have sparser clones with larger clonal step length (Chapter 5) and thicker stems, presumably capable of tolerating the (generally lower) physical stress at the places where they occur.

Taking together that *S. anglica* seedlings require a shorter disturbance-free period than *S. alterniflora* seedlings in dynamic sedimentary conditions (Chapter 3), and that self-organized heterogeneous landscapes with channel drainage relief can facilitate early seedling establishment (Chapter 4), this may help to understand the highly successful distribution of *S. anglica* marsh landscapes worldwide (Watson 2008).

However, as shown by our experiments, the different strategies also imply different biogeomorphic feedbacks, such as the likelihood of cliff formation (Chapter 5), that might co-determine the selective conditions for the species (Odling-Smee et al. 2003; Davies and Gibling 2013; Corenblit et al. 2015a).

6.3 Implications for coastal ecosystem restoration under global change

A prominent objective of studies of tidal marsh dynamics is to use mechanistic understanding in tidal marsh restoration designs. This may facilitate nature-based solutions in coastal defense schemes under global change. However, restoration of tidal marshes is never easy due to the overarching control of physical constraints on marsh establishment (Adam 2002; Friess et al. 2012). The most obvious first requirement for tidal marsh presence is that the conditions should allow them to establish and persist (Bouma et al. 2014). That fundamental restriction limits the spatial extent of sites suitable for this type of nature-based defense.

The present study shows that the primary establishment of tidal marshes benefits from small to moderate disturbance of the sediment (Chapter 2), lower wave stress (Chapter 3), better surface drainage relief (Chapter 4), as well as sufficiently long disturbance-free periods (Chapter 2, 3 and 4). Therefore, tidal marsh restoration projects should, at least temporarily, create a favourable environment with suitable sedimentary and hydrodynamic conditions. Addition of small topographic irregularities to increase surface drainage may be needed to facilitate the primary establishment of young marsh seedlings. This can be achieved by integrating of ecological knowledge into engineering measures (Bouma et al. 2014). For example, one can provide offshore barriers or dredging-derived sediment slurry additions to create sedimentation fields with low wave exposure (Chapter 2 and 3). Specifying broader tolerances in vertical elevation to contractors preparing a managed realignment area for marsh creation, may create enough drainage for plant establishment (Chapter 4). Nevertheless, one should avoid the tendency to find a general handbook for tidal marsh restoration worldwide. Species-specific plant traits and location-specific sediment properties (Chapter 5) preclude such an approach, and argue for a tailor-made design taking due consideration of these effects.

6.4 Conclusion and implication for future research

Tidal marshes are valuable ecosystems, with their coastal protection function depending on the marsh stability. Marsh ecosystems vary over space and time, as marshes are highly dynamic with alternations between expansion and retreat phases at the tidal flat/marsh boundary. Therefore, in the aim to enhance the current mechanistic understanding of marsh ecosystem dynamics in a changing climate, this thesis has taken pioneer tidal marshes as focal systems. It examined critical factors and processes for marsh establishment and marsh erosion. This study indicates that, in addition to the effects of critical abiotic factors (e.g., sediment dynamics, wave stress, surface drainage relief) in determining marsh establishment at energetic coastal areas, species-specific traits (e.g. clonal step length, root and shoot characteristics) of dominant species may at the local scale dictate the style of cliff formation at marsh edges and modify their long-term lateral dynamics. These findings are essential for understanding the overall resilience of marsh ecosystems under the threat of sea level rise.

Future research should take these mechanisms of marsh dynamics in consideration, in both empirical and modelling studies that aim at quantifing ecosystem dynamics against a background of large scale sea level rise. The critical factors for the dynamics of pioneer marshes, demonstrated in this thesis, can help to improve experimental design as well as modelling, leading to better representation of long-term dynamics.

Given increasing threats of global and regional change, there is a need to go beyond the level of single ecosystems to obtain a more comprehensive insight into the fundamental mechanisms of biogeomorphic processes on the earth surface. For example, comparative studies on ecosystems along coastlines with different dominant species provide a promising way forward that contributes to a more holistic understanding the dynamics of ecosystems at different spatial and temporal scales. To achieve this, an interdisciplinary perspective and methodology are required to link physical and biological processes in understanding the general change in coastal areas with differing background stresses.

The practical application of integrating insights of ecosystem dynamics in coastal defence designs, is another important aspect that needs to be addressed. Until recently, successful ecosystem-based coastal defence schemes were scarce globally. The actual protective value of existing projects is primarily limited by a lack of perspective on long-term persistence under extreme conditions. The implementation of fundamental knowledge in methods, tools and management decisions, will contribute to more cost-effective solutions and novel governance in the sustainable use of coastal ecosystems. For this aim, joint efforts are required by both ecologists and engineers to innovate tailor-made designs for different coastal ecosystems, in order to optimize their coastal defense services in a changing climate with a large degree of uncertainty.

Summary

Tidal marshes often present cyclic dynamics, with alternating phases of expansion and lateral retreat. Marsh seedling establishment is a primary condition for marsh colonization and expansion. Successful establishment is often episodic due to bio-physical thresholds, as expressed in the ‘Windows of Opportunity’ concept. Identifying critical factors and understanding how they enable or hamper seedling establishment, is highly relevant for coastal management and restoration schemes.

This study quantified the effects of critical factors in tidal marsh establishment processes. Firstly, by exposing marsh seedlings to different disturbances in terms of sedimentation regime and wave exposure, this study found that these disturbances affect seedling establishment both directly and via bio-morphological adjustments (Chapter 2 and 3). Secondly, channel related drainage relief was found to facilitate seedling survival, especially in the early phase of marsh establishment in muddy systems (Chapter 4). Thirdly, by using marsh seedlings with different disturbance-free periods in both laboratory and field experiments, this study confirmed that a longer disturbance-free period can strongly enhance seedling survival as well as their resistance to later extreme disturbances (Chapter 2 and 4).

The erosion of tidal marshes often leads to the development of a cliff at the boundary between tidal flat and marsh. The formation of a cliff shifts marsh development from a phase of lateral expansion to a retreating phase, as a result of the interdependent feedbacks between marsh vegetation and external forcing. This thesis investigated the tipping point conditions of cliff formation at marsh edges with different marsh species. The clonal growth of vegetation at marsh edges was found to respond to different sediment types and to affect the cliff formation processes. Species-specific clonal growth strategies in step length have important effects on initiating cliffs, lateral retreat and thus landscape dynamics at marsh edges (Chapter 5).

In summary, this study provides mechanistic insight into the primary expansion (i.e., seedling establishment) of tidal marshes under a variety of

critical forcing factors, as well as insight in the factors contributing to cliff formation and the onset of lateral retreat. It highlights the variability in relevant species-specific responses, as well as the importance of location-dependent factors. These results add quantitative support to models predicting the critical transitions in marsh dynamics, both marsh expansion and marsh retreat. The findings of this study are instructive for marsh restoration and nature based coastal defense schemes. While they contribute to understanding the overall stability of marsh ecosystems in the face of global change, they also highlight the need for tailor-made solutions for the application of nature-based solutions at particular locations.

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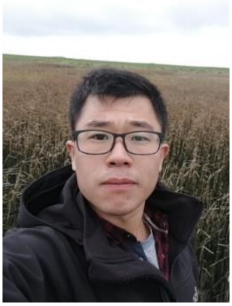
Biography



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