Delft University of Technology

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

Cao, Haobing; Zhu, Zhenchang; van Belzen, Jim; Gourgue, Olivier; van de Koppel, Johan; Temmerman, O. Stijn; Herman, Peter M.J.; Zhang, Liquan; Yuan, Lin; Bouma, Tjeerd J.

DOI
10.1002/ecs2.3755

Publication date
2021

Document Version
Final published version

Published in
Ecosphere

Citation (APA)
Cao, H., Zhu, Z., van Belzen, J., Gourgue, O., van de Koppel, J., Temmerman, O. S., Herman, P. M. J., Zhang, L., Yuan, L., & Bouma, T. J. (2021). Salt marsh establishment in poorly consolidated muddy systems: effects of surface drainage, elevation, and plant age. *Ecosphere*, *12*(9), Article e03755. https://doi.org/10.1002/ecs2.3755

Important note
To cite this publication, please use the final published version (if applicable).
Please check the document version above.

Copyright
Other than for strictly personal use, it is not permitted to download, forward or distribute the text or part of it, without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license such as Creative Commons.

Takedown policy
Please contact us and provide details if you believe this document breaches copyrights.
We will remove access to the work immediately and investigate your claim.

This work is downloaded from Delft University of Technology.
For technical reasons the number of authors shown on this cover page is limited to a maximum of 10.

Check for updates

esa ECOSPHERE

COASTAL AND MARINE ECOLOGY

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

Haobing Cao,[1,2,3] Zhenchang Zhu,[4,5] Jim van Belzen,[2] Olivier Gourgue,[6] Johan van de Koppel,[2] O. Stijn Temmerman,[6] Peter M. J. Herman,[7] Liquan Zhang,[1] Lin Yuan,[1,8] and Tjeerd J. Bouma[2,3,9,†]

[1]*State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai 200062 China*
[2]*NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems, Utrecht University, PO Box 140, 4400 AC Yerseke the Netherlands*
[3]*Faculty of Geosciences, Utrecht University, PO Box 80115, Utrecht 3508 TC The Netherlands*
[4]*Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangdong, China*
[5]*Guangdong Provincial Key Laboratory of Water Quality Improvement and Ecological Restoration for Watersheds, Institute of Environmental and Ecological Engineering, Guangdong University of Technology, Guangzhou, China*
[6]*Ecosystem Management Research Group (Ecobe), University of Antwerp, Universiteitsplein 1,2610 Wilrijk, Antwerp, Belgium*
[7]*Hydraulic Engineering Department, Delft University of Technology, Delft, Netherlands*
[8]*Institute of Eco-Chongming, East China Normal University, Shanghai 200062 China*
[9]*University of Applied Sciences, University of Groningen, Vlissingen, the Netherlands*

Citation: Cao, H., Z. Zhu, J. van Belzen, O. Gourgue, J. van de Koppel, O. S. Temmerman, P. M. J. Herman, L. Zhang, L. Yuan, and T. J. Bouma. 2021. Salt marsh establishment in poorly consolidated muddy systems: effects of surface drainage, elevation, and plant age. Ecosphere 12(9):e03755. 10.1002/ecs2.3755

Abstract. Conservation and restoration of salt marsh ecosystems are 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, remain 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 (1) the survival of *Spartina anglica* seedlings from three different age classes: 1-yr, 3-month, and 1-week; and (2) 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-yr, 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.

Key words: establishment; muddy sediment; plant age; relative elevation to mean sea level; salt marsh; surface drainage.

Received 21 April 2021; accepted 3 May 2021. Corresponding Editor: Julie C. Zinnert.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** Tjeerd.Bouma@nioz.nl

Introduction

Conservation and restoration of salt marsh ecosystems are becoming increasingly appreciated because of the many vital ecosystem services they provide (Gedan et al. 2009, Barbier et al. 2011, Shepard et al. 2011, Kirwan and Guntenspergen 2012, Kirwan and Mudd 2012, Burden et al. 2013, Schepers et al. 2017). Yet, the decline and degradation of salt marsh ecosystems continue 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 Herman 2000, Moreno-Mateos et al. 2012, Mossman 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 biogeomorphic 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 (Fagherazzi and Sun 2004, Fagherazzi et al. 2004, 2013, Temmerman et al. 2007, Schwarz et al. 2018). However, as these feedback loops only occur after a critical biomass/density has been exceeded (Bouma et al. 2009*a*), individual marsh propagules such as seedlings or clonal fragments face establishment barriers (Bouma et al. 2009*b*, 2016, Balke et al. 2014, 2016, Hu et al. 2015, Yuan et al. 2020).

The problematic establishment of early-stage establishment on tidal mudflats has both experimentally and theoretically been related to require (1) inundation limits of marsh plants (Wang and Temmerman 2013, Balke et al. 2016, van Belzen et al. 2017) and (2) 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 and Guntenspergen 2012, 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. 1a, 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. 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. 2019, Schwarz et al. 2014). As the tidal area becomes exposed during ebb, water is drained toward 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 and Sun 2004, Fagherazzi et al. 2004). That is, inundation (during flood) and drainage (during ebb) of intertidal areas in general are a complex process that involves not only the water column above the sediment, but may also affect interstitial water and even groundwater exchange (Winterwerp and Kesteren 2004, Perillo et al. 2019). By water recirculation in sediments, drainage may alleviate poor oxygen availability (Rabouille et

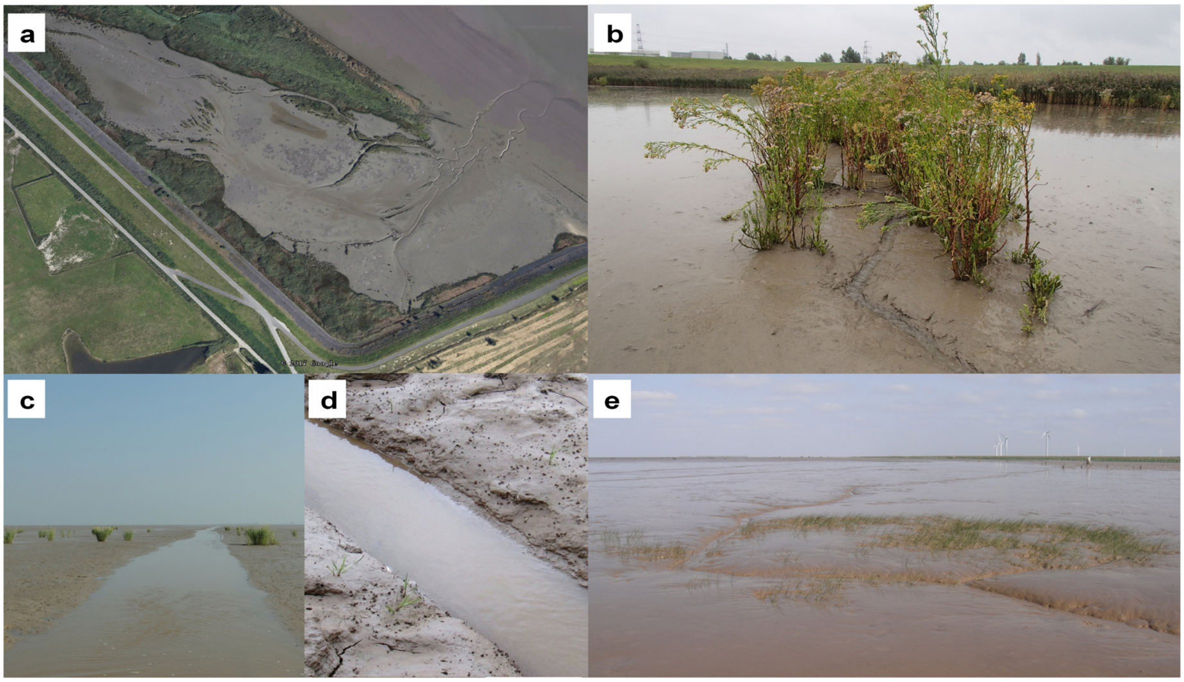

Fig. 1. Empirical observation of channel drainage relief facilitates salt marsh establishment in Paardenschor, Scheldt estuary, Belgium (a and b); and on Chongming Island, Yangtze estuary, China (c; d and e). (a) aerial image showing a large tidal flat that remained unvegetated for several years despite 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.

al. 2003, Fivash et al. 2020) and thereby relieve sulfide toxicity to seedling roots (Redelstein et al. 2018) that lack aerenchyma (Burdick and Mendelssohn 1987, Jung et al. 2008).

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], Padgett and Brown [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 and Kesteren 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 and Kesteren 2004, Hill et al. 2013, Ren and Santamarina 2018, 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 and Ayres 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-yr 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, for example, sustainable coastal defense.

Material and Methods

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. 2a). The estuary is semi-diurnal, with tidal range varies from 440 to 550 cm (Baeyens et al. 1997). 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 Ordnance Level that approximately equal to mean high water level in the Scheldt estuary) (van de Wal et al. 2008).

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 reintroducing tides from the Western Scheldt Estuary (Rijkswaterstaat 2015) (Fig. 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 (van de Lageweg et al. 2019). The elevation of tidal flat in Perkpolder ranged between −80 and+110 cm NAP (compare mean low water at Perkpolder: −2.06 m NAP; mean high water at Perkpolder: +2.56 m NAP), and therefore, the whole area was completely covered by water and completely dried every semi-diurnal tide cycle from the breach (Brunetta et al. 2019, van de Lageweg et al. 2019). The wave actions in Perkpolder were negligible, as it was almost completely surrounded by seawalls (van de Lageweg et al. 2019) (Fig. 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 µm, 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.

Marsh establishment experiment—Mega-Marsh Organs with contrasting surface drainage

Mega-Marsh Organs (MMOs; Fig. 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 (2012), 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. 3 a, 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

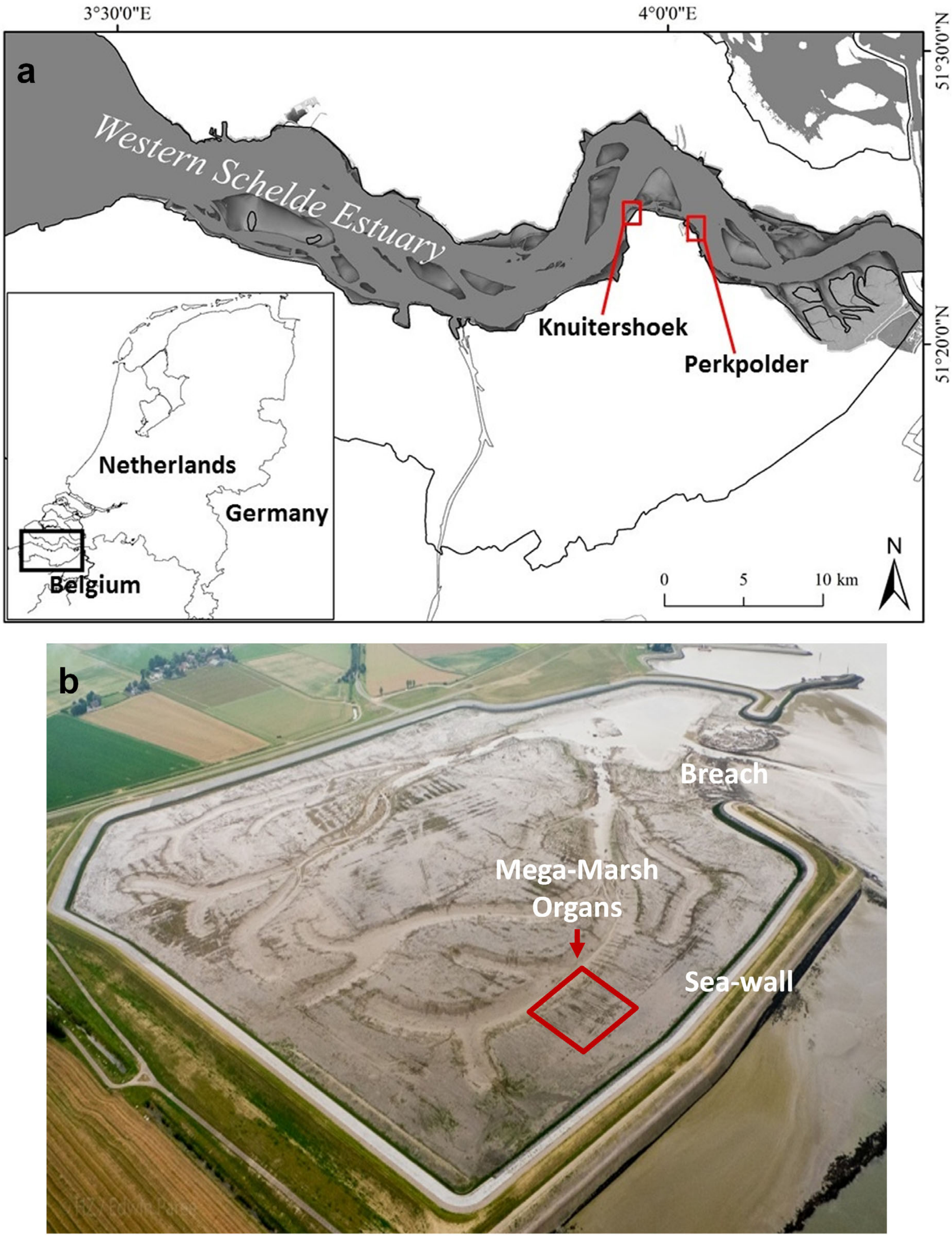

Fig. 2. Study site of present study. (a) Location of Perkpolder; (b) aerial view of Perkpolder (photograph by Edwin Paree and Matthijs Boersema); the red square in (b) show where Mega-Marsh Organs (MMOs) were set up.

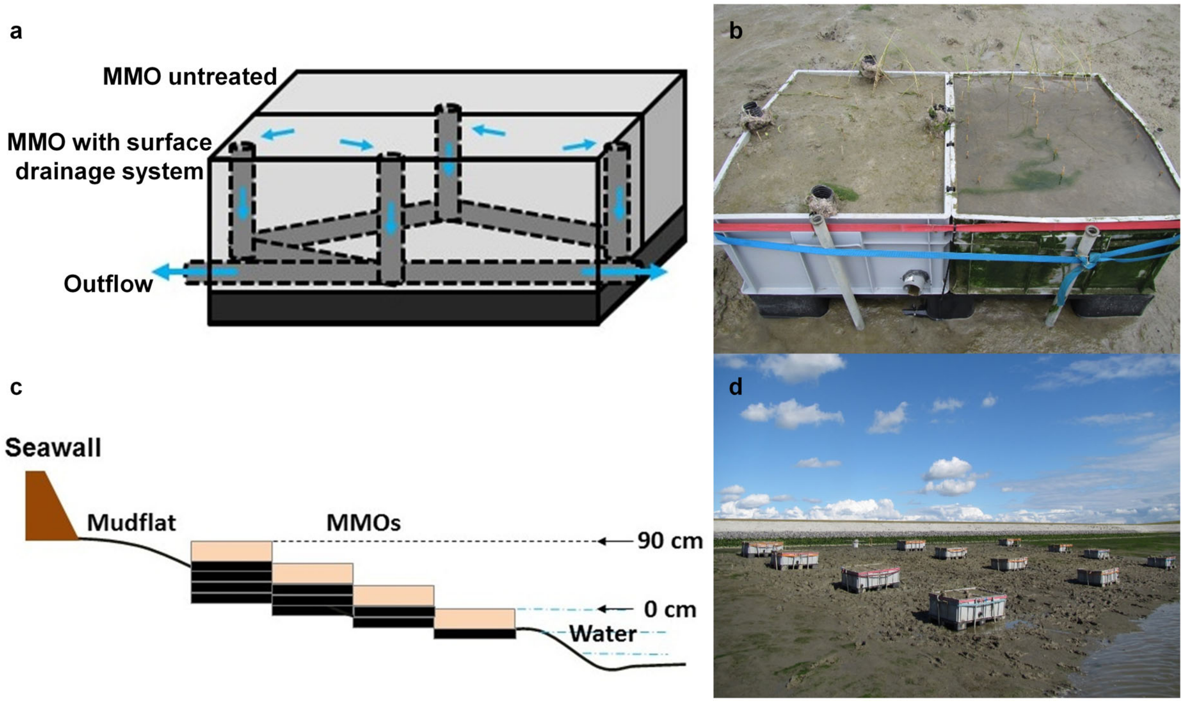

Fig. 3. Schematic diagrams and photographs of the Mega-Marsh Organs (MMO) setups in Perkpolder. (a) each MMO consists of a closed box with a sealed bottom, but in half of them we installed drainage systems (i.e., using standard soil-drainage tubing) going through the muddy sediment and reaching the top 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 to 90 cm NAP (Normal Amsterdam Peil, Dutch Ordnance Level that approximately equal to mean high water level in the Scheldt estuary).

boxes in each MMO with a surface drainage system (Fig. 3a, 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. 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.

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. 3c, 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. 3c, d). The four elevations are 0, 30, 60, and 90 cm leveled to the top of MMO rims respect to NAP (Normal Amsterdam Peil, which is Dutch Ordnance 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 1), respectively, which were measured with one SENSUS

Table 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 Ordnance 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

Ultra device (ReefNet) 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).

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°C during the day and 25°C during the night to speed up germination process, c.f. Cao et al. 2018). To obtain seedlings, *S. anglica* seeds were soaked in nature seawater (32 ppt) in a 4°C refrigerator until germination was performed. Freshwater 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 seawater and freshwater 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 yr 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 laboratory. Care was taken that transplantation into the MMOs always occurred within 12 h. 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-yr 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-week 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. 2015, 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.

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. 2a), where uniform size soil blocks (20 × 20 × 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.

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 h and weighed again to calculate water content and dry bulk density using the following formula:

$$\text{Water content} = (\text{wet sample weight} - \text{dry sample weight}) / \text{wet sample weight}$$

$$\text{Dry Bulk density} = \text{Dry weight of sediment sample} / \text{volume of the sediment sample}$$

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, that is, 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, Chicago, Illinois, USA).

Results

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; $P < 0.05$, Table 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 2). Notably, for 1-yr 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). 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).

Moreover, the overall survival of *S. anglica* seedlings (Fig. 4) was significantly affected by seedling age ($P < 0.001$, Tables 2, 3) and elevation relative to mean sea level ($P < 0.01$, Tables 2, 3). For *S. anglica* seedlings of all elevation differing in age, the survival of both 3-month and 1-yr seedlings were all significantly higher in compared to 1-week seedling (Fig. 4; $P < 0.001$, Table 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 2) to 1-yr seedlings (Exp(B) = 0.095, %95 CI: 0.067–0.135, Table 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

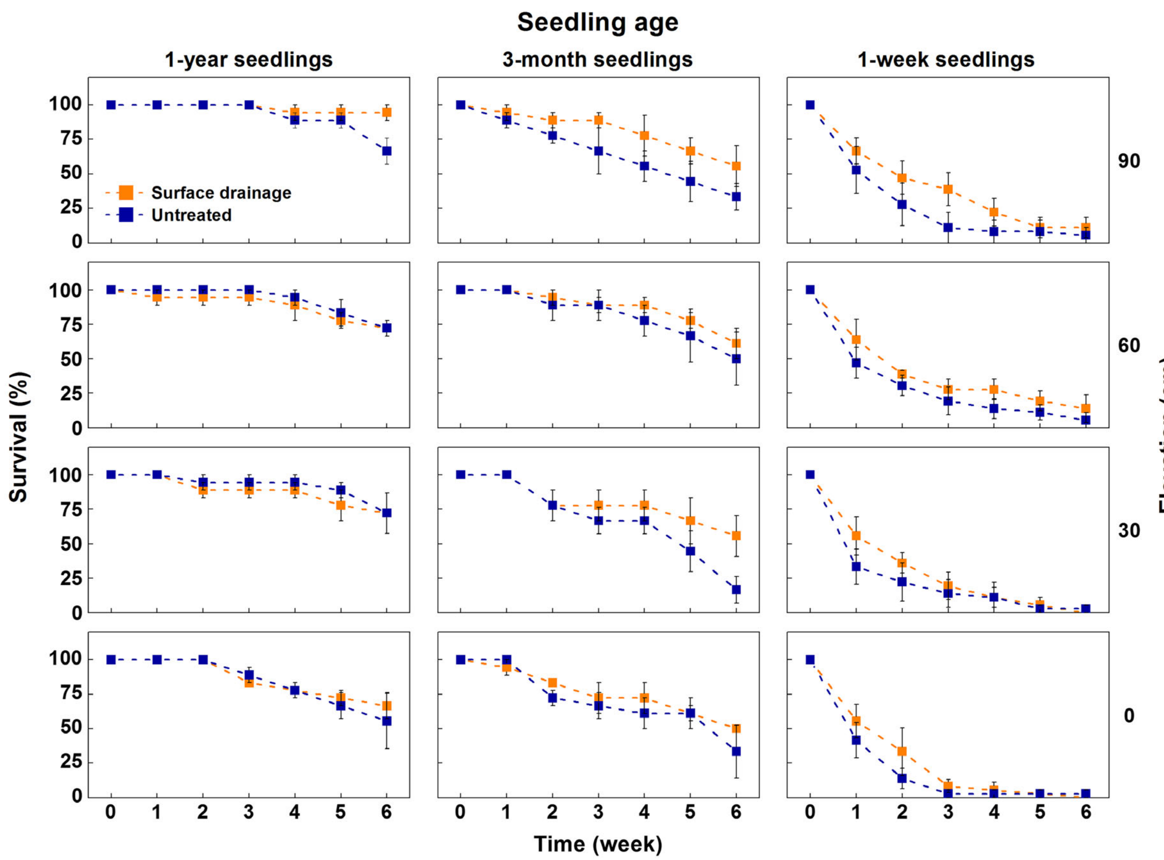

Fig. 4. *Spartina anglica* seedling survival during the 6-week field experiment in Perkpolder in 2016. The overall survival time of seedlings in surface drainage treatment (orange) was significantly higher than in the untreated groups (blue). Increased seedling age and elevation relative to mean sea level (from 0to 90 cm NAP) also facilitated seedling survival (data are presented as mean values + SE).

Table 2. Cox regression results of seedling survival analysis in the 6-week field experiment.

						95% Cl for Exp(B)	
Variable	Subgroups	Wald	df	*P*	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

Notes: Surface drainage treatment, seedling age, and elevation (relative to mean sea level) were set as variables to analysis their overall effects on seedling survival.

† Exp(B) indicated for the ratio of hazard risk relative to the baseline of each variable, that is, 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 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*
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

treatment or elevation (Fig. 4). This meant that the older *S. anglica* seedlings become, the less vulnerable they were to adverse surface-drainage-lacking conditions.

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 Ordnance 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 2) to 90 cm NAP (Exp(B) = 0.65, %95 CI: 0.53–0.92, Table 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 2) was close to which at 90 cm NAP (Exp[B] = 0.65, %95 CI: 0.53–0.92, Table 2). Compare to 0 cm NAP elevation, the overall seedling survival was significantly enhanced both at 60 cm NAP (Fig. 4; $P = 0.003$, Table 2) and 90 cm NAP (Fig. 4; $P = 0.011$, Table 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 3).

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. 5), as no significant effect was found on the survival of tussocks from different surface drainage or elevation treatments ($P > 0.05$, Table 4). Plant height, shoot numbers, and dry biomass of *S. anglica* were reduced as elevation decreased (Fig. 5; $P < 0.01$ for plant height and dry biomass; $P < 0.001$ for shoot numbers, Table 4), with no significant effect of surface drainage treatment or interactive effect of surface drainage and elevation relative to mean sea level (Fig. 5; $P > 0.05$, Table 4). This meant that mature *S. anglica* tussocks survived better than seedlings at lower elevations and poorly surface drained conditions.

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. 6; $P > 0.05$, Table 5). Average water content of sediment from both years was 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 from both 2016 and 2018 that sediment properties were not affected by either surface drainage or elevation (Fig. 6; $P > 0.05$, Table 5), indicating that neither interstitial water drawing, nor sediment compaction was changed by the surface drainage treatment over the course of the experiment.

Discussion

The establishment and persistence of salt marsh are highly relevant for conservation and restoration of coastal salt marsh ecosystems. Yet, our understanding remains limited on the processes controlling salt marsh establishment and

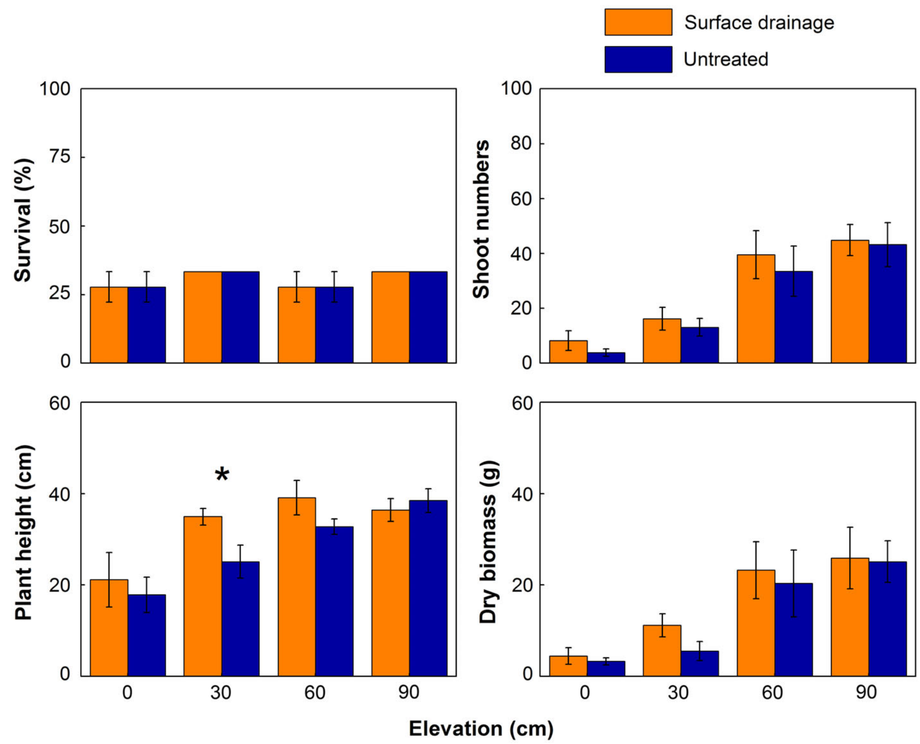

Fig. 5. Regrowth of *Spartina anglica* tussocks at harvest in the field experiment in Perkpolder in 2018. No significant effect was found on the survival of tussocks from different drainage (surface drainage treatment groups in orange, untreated groups in blue) or elevation treatments. Plant height, 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 and 90 cm were not presented because the numbers were same for the replicates (SE = 0). * indicated for significance level <0.05.

Table 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	df	MS	*F*	*P*
Survival	Surface drainage	1	.000	0.000	1.000
	Elevation	3	.006	1.333	0.299
	Surface drainage × Elevation	3	.000	0.000	1.000
Plant height (cm)	Surface drainage	1	113.802	2.822	0.112
	Elevation	3	397.115	9.848	0.001
	Surface drainage × Elevation	3	38.072	0.944	0.443
Shoot numbers	Surface drainage	1	86.260	0.833	0.375
	Elevation	3	1924.927	18.589	0.000
	Surface drainage × Elevation	3	5.038	0.049	0.985
Above-ground dry biomass (g)	Surface drainage	1	41.082	3639	0.436
	Elevation	3	649.023	10.089	0.001
	Surface drainage × Elevation	3	7.189	0.112	0.952

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

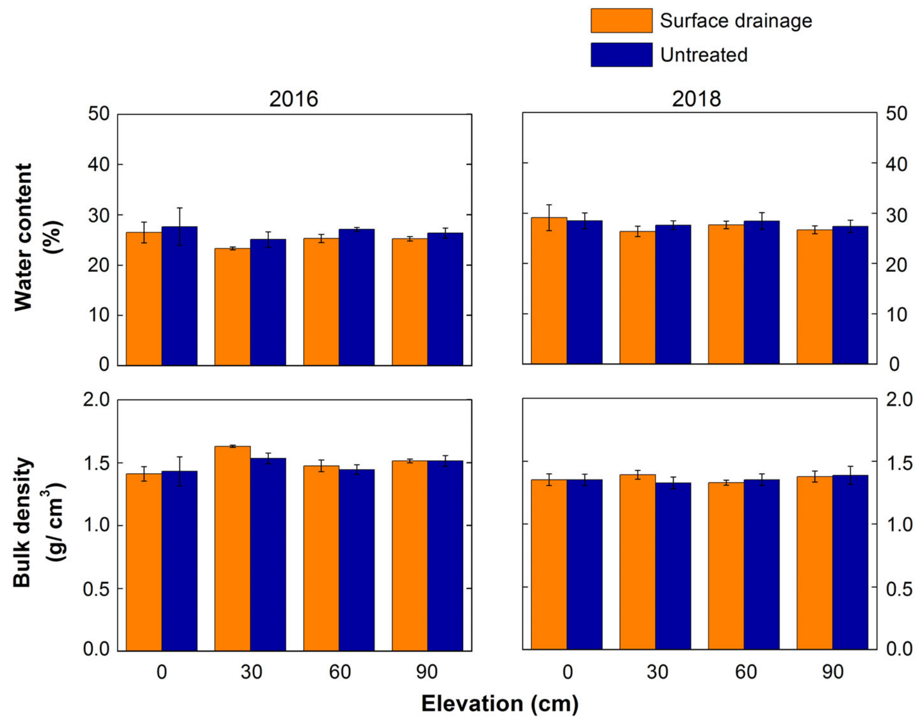

Fig. 6. Sediment water content and bulk density of MMOs in 2016 and 2018. The water content and bulk density from both 2016 and 2018 did not show any significant effect from either drainage (surface drainage treatment groups in orange, untreated groups in blue) or elevation. Data are presented as mean values + SE.

Table 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	df	MS	*F*	*P*
Water content	2016	Surface drainage	1	0.001	1.491	0.240
		Elevation	3	0.001	1.019	0.410
		Surface drainage × Elevation	3	2.250E-5	0.026	0.994
	2018	Surface drainage	1	0.000	0.264	0.614
		Elevation	3	0.000	0.755	0.535
		Surface drainage × Elevation	3	9.463E-5	0.157	0.924
Bulk density	2016	Surface drainage	1	0.004	0.475	0.501
		Elevation	3	0.029	3.256	0.490
		Surface drainage × Elevation	3	0.004	0.434	0.732
	2018	Surface drainage	1	0.000	0.058	0.812
		Elevation	3	0.002	0.283	0.837
		Surface drainage × Elevation	3	0.002	0.347	0.792

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*.

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

In our muddy systems, the removal of the overlying water (Fig. 7) was the most decisive difference between the surface water drained and undrained treatments. Measurements of

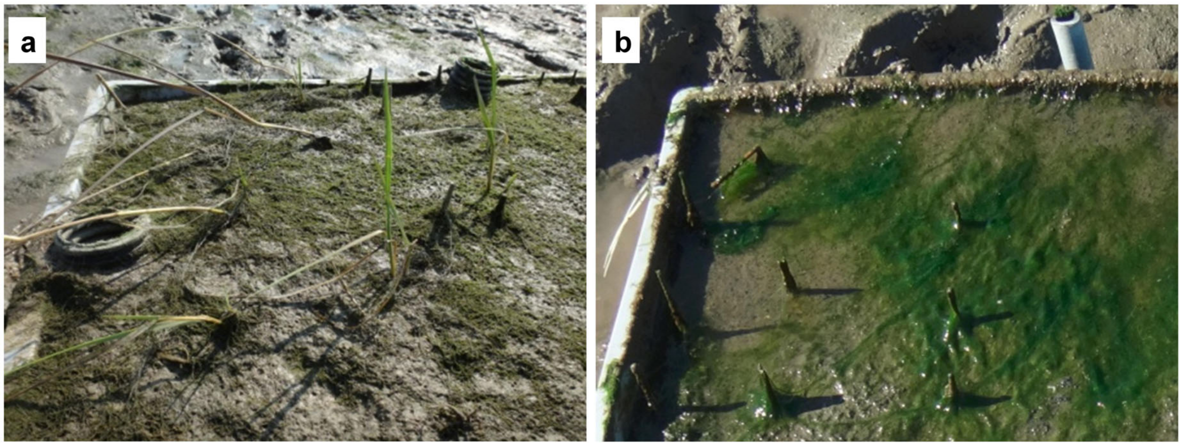

Fig. 7. Close-up view photographs showing seeding establishment in MMOs with surface drainage relief (a) and an overlaying of water in MMOs without surface drainage (b).

sediment water content showed that the water content of these sediments was very high (about 30% by weight, Fig. 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. 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, Padgett and Brown 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 and Kesteren 2004, Ren and Santamarina 2018). 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. 7). Therefore, present study has captured the main effects of surface drainage on marsh establishment in our muddy system.

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. 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 sulfide 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-yr-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. 2007, Kirwan and Guntenspergen 2012, 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 Ordnance 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).

Surface drainage effects as potential drivers for habitat transition in 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. 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. 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. 8a), local-scale surface drainage of the elevated sediment patches may favor early plant establishment via, for example, slight improvement of soil aeration (Crooks et al. 2002, Silvestri et al. 2005), elevated microtopography (Fivash et al. 2020) or by removing of a thin water film (Fig. 7). These established plants may subsequently locally stabilize and trap sediment (Bouma et al. 2009*a*), 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 and Sun 2004, Fagherazzi et al. 2004, 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

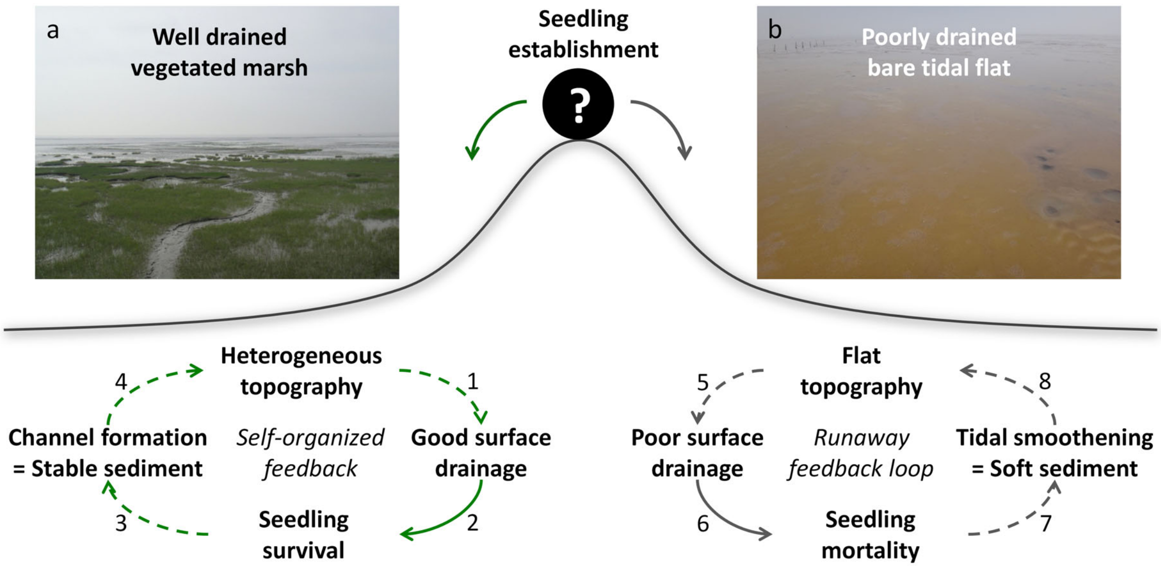

Fig. 8. Conceptual model showing the importance of surface drainage in controlling habitat transition in salt marsh ecosystems. (a) On the left, a heterogeneous topography with good surface drainage (arrow 1; logically assumed) facilitates salt marsh seedling establishment and growth (arrow 2; Crooks et al. 2002; Silvestri et al. 2005; Redelstein et al. 2018; Fivash et al. 2020), which may stabilize and trap sediment (Bouma et al. 2009*a*), stimulate the formation of channels and consequently further improves surface drainage as might occur at channel banks (arrows 3 and 4; Fagherazzi and Sun 2004, Fagherazzi et al. 2004, 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) may lead to 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.

drainage in muddy systems (Fig. 8a). In this way, the presence of good surface drainage may initiate a habitat transition from bare mudflats to vegetated marsh, with positive feedbacks enhancing heterogeneity and self-organized long-term stability (Schwarz et al. 2018).

In contrast, on bare tidal mudflats where heterogeneous microtopography is absent (Fig. 8 b), giving poor drainage conditions, seedling establishment is hampered (this study), most likely due to factors like, for example, 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. 8b). Overall, this feedback loop keeps the tidal flat bare even at elevations where normally establishment of vegetation would be expected. (Fig. 1a; Wang and Temmerman 2013, van Belzen et al. 2017).

Despite that the underlying mechanisms relating microtopography to plant performances remain incomplete from our field study (but see Fivash et al. 2020 for process-based laboratory experiments), present findings and the feedback mechanism schematically described in Fig. 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 mudflats 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-yr 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 (1) 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 and Hesse 2008; and references therein), and (2) for implementing nature-based coastal protection strategies when depending on the creation of new salt marshes (Temmerman et al. 2013, van Slobbe et al. 2013, Temmerman and Kirwan 2015).

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.

Acknowledgments

T. J. Bouma and L. Yuan contributed equally to the work reported here. We thank Daniel Blok, Lennart van IJzerloo, Jeroen van Dalen, and Bert Sinke for their kindly help in setting up the experiment. We also thank Greg Fivash for his help in data processing. This work was supported by the National Key Research and Development Program of China (Grant: 2016YFE0133700); the National Natural Science Foundation of China (Grant: 41876093); the research program BE SAFE, which is financed by the Netherlands Organisation for Scientific Research (NWO) and societal partners (grant # 850.13.011); and the CoE-Perkpolder project, which is financed by RWS and the CoE-Delta technology.

Literature Cited

Adam, P. 2002. Saltmarshes in a time of change. Environmental Conservation 29:39–61.

Baeyens, W., B. van Eck, C. Lambert, R. Wollast, and L. Goeyens. 1997. General description of the Scheldt estuary. Hydrobiologia 366:1–14.

Balke, T., P. M. J. Herman, and T. J. Bouma. 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. Journal of Ecology 102:700–708.

Balke, T., M. Stock, K. Jensen, T. J. Bouma, and M. Kleyer. 2016. A global analysis of the seaward salt marsh extent: the importance of tidal range. Water Resources Research 52:3775–3786.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193.

Bouma, T. J., et al. 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: opportunities & steps to take. Coastal Engineering 87:147–157.

Bouma, T. J., et al. 2016. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics. Limnology and Oceanography 61:2261–2275.

Bouma, T. J., M. Friedrichs, B. K. van Wesenbeeck, S. Temmerman, G. Graf, and P. M. J. Herman. 2009*a*. Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte *Spartina anglica*. Oikos 118(2):260–268.

Bouma, T. J., M. Friedrichs, P. Klaassen, B. K. van Wesenbeeck, F. G. Brun, S. Temmerman, M. M. van Katwijk, G. Graf, and P. M. J. Herman. 2009*b*. Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. Marine Ecology Process Series 388:293–297.

Bouma, T. J., B. B. Koutstaal, M. van Dongen, and K. L. Nielsen. 2001. Coping with low nutrient availability and inundation: root growth responses of three halophytic grass species from different elevations along a flooding gradient. Oecologia 126:472–481.

Broome, S. W., and C. B. Craft. 2000. Tidal salt marsh restoration, creation, and mitigation. Pages 939–959 *in* R. I. Barnhisel, R. G. Darmody, and W. L.

Daniels, editors. Reclamation of drastically disturbed lands. American Society of Agronomy, Madison, Wisconsin, USA.

Bruneta, R., J. S. de de Palva, and P. Ciavola. 2019. Morphological evolution of an intertidal area following a set-back scheme: a case study from the Perkpolder Basin (Netherlands). Frontiers in Earth Science 7:228.

Burden, A., R. A. Garbutt, C. D. Evans, D. L. Jones, and D. M. Cooper. 2013. Carbon sequestration and biogeochemical cycling in a saltmarsh subject to coastal managed realignment. Estuarine Coastal and Shelf Science 120:12–20.

Burdick, D. M., and I. A. Mendelssohn. 1987. Waterlogging responses in dune, swale and marsh populations of *Spartina patens* under field conditions. Oecologia 74:321–329.

Cao, H., Z. Zhu, T. Balke, L. Zhang, and T. J. Bouma. 2018. Effects of sediment disturbance regimes on Spartina seedling establishment: implication for salt marsh creation and restoration. Limnology and Oceanography 63(2):647–659.

Cox, D. R. 1972. Regression models and life tables. Pages 187–220 *in* S. Kotz and N. L. Johnson, editors. Breakthroughs in statistics springer series in statistics (perspectives in statistics). B34. Springer, New York, New York, USA.

Crooks, S., J. Schutten, G. D. Sheern, K. Pye, and A. J. Davy. 2002. Drainage and elevation as factors in the restoration of salt marsh in Britain. Restoration Ecology 10:591–602.

Fagherazzi, S., E. J. Gabet, and D. J. Furbish. 2004. The effect of bidirectional flow on tidal planforms. Earth Surface Processes Landforms 29:295–309.

Fagherazzi, S., and T. Sun. 2004. A stochastic model for the formation of channel networks in tidal marshes. Geophysical Research Letters 31: L21503.

Fagherazzi, S., P. L. Wiberg, S. Temmerman, E. Struyf, Y. Zhao, and P. A. Raymond. 2013. Fluxes of water, sediments, and biogeochemical compounds in salt marshes. Ecological Processes 2(1):3.

Fivash, G., J. van Belzen, R. J. M. Temmink, K. Didderen, W. Lengkeek, T. van der Heide, and T. J. Bouma. 2020. Elevated micro-topography boosts growth rates in *Salicornia procumbens* by amplifying a tidally driven oxygen pump: implications for natural recruitment and restoration. Annals of Botany 125:353–364.

Friess, D. A., K. W. Krauss, E. M. Horstman, T. Balke, T. J. Bouma, D. Galli, and E. L. Webb. 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biological Reviews 87:346–366.

Gedan, K. B., B. R. Silliman, and M. D. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems. Annual Review of Marine Science 1:117–141.

Gray, A. J., D. F. Marshall, and A. F. Raybould. 1991. A century of evolution in *Spartina anglica*. Advances in Ecological Research 21:1–62.

Hill, P. S., J. P. Newgard, B. A. Law, and T. G. Milligan. 2013. Flocculation on a muddy intertidal flat in Willapa Bay, Washington, Part II: observations of suspended particle size in a secondary channel and adjacent flat. Continental shelf research 60S:S145–S156.

Hu, Z., J. van Belzen, D. van der Wal, T. Balke, Z. B. Wang, M. J. F. Stive, and T. J. Bouma. 2015. Windows of opportunity for salt marsh vegetation establishment on bare tidal flats: the importance of temporal and spatial variability in hydrodynamic forcing. Journal of Geophysical Research: Biogeosciences 120(7):1450–1469.

Jung, J., S. C. Lee, and H. K. Choi. 2008. Anatomical patterns of aerenchyma in aquatic and wetland plants. Journal of Plant Biology 51:428–439.

King, G. M., M. J. Klug, R. G. Wiegert, and A. G. Chalmers. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia Salt Marsh. Science 218:61.63.

Kirwan, M. L., and G. R. Guntenspergen. 2012. Feedbacks between inundation, root production, and shoot growth in a rapidly submerging brackish marsh. Journal of Ecology 100:764–770.

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

Kirwan, M. L., and S. M. Mudd. 2012. Response of salt-marsh carbon accumulation to climate change. Nature 489:550–553.

Kuijper, C., R. Steijn, D. Roelvink, T. van der Kaaij, and P. Olijslagers. 2004. Morphological modelling of the Western Scheldt: validation of Delft3D: report. https://puc.overheid.nl/rijkswaterstaat/doc/PUC_114371_31/

Lamers, L. P. M., L. L. Govers, I. C. J. Janssen, J. M. Jeroen, M. E. W. Van der welle, M. M. Van Katwijk, T. Van der Heide, J. G. M. Roelofs, and A. J. P. Smolders. 2013. Sulfide as a soil phytotoxin – a review. Frontiers in Plant Science 4:268.

Linthurst, R. A., and E. D. Seneca. 1980. The effects of standing water and drainage potential on the *Spartina alterniflora* – substrate complex in a North Carolina salt marsh. Estuarine and Coastal Marine Science 11(1):41–52.

Marani, M., A. D'Alpaos, S. Lanzoni, L. Carniello, and A. Rinaldo. 2010. The importance of being coupled:

stable states and catastrophic shifts in tidal biomorphodynamics. Journal of Geophysical Research 115 (F4):F04004.

Marani, M., C. Da Lio, and A. D'Alpaos. 2013. Vegetation engineers marsh morphology through multiple competing stable states. Proceedings of the National Academy of Sciences of the United States of America 110:3259–3263.

Mendelssohn, I. A., and E. D. Seneca. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. Estuarine and Coastal Marine Science 11:27–40.

Moreno-Mateos, D., M. E. Power, F. A. Comin, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. PLoS Biology 10: e1001247.

Morris, J. T. 2007. Estimating net primary production of salt marsh macrophytes. Pages 106–119 *in* T. J. Fahey, and A. K. Knapp, editors. Principles and standards for measuring net primary production in long-term ecological studies. Oxford University Press, Oxford, UK.

Mossman, H. L., A. J. Davy, and A. Grant. 2012. Does managed coastal realignment create saltmarshes with 'equivalent biological characteristics' to natural reference sites? Journal of Applied Ecology 49 (6):1446–1456.

Nehring, S., and K. J. Hesse. 2008. Invasive alien plants in marine protected areas: the *Spartina anglica* affair in the European Wadden Sea. Biological Invasions 10:937–950.

Padgett, D. E., and J. L. Brown. 1999. Effects of drainage and soil organic content on growth of *Spartina alterniflora* (Poaceae) in an artificial salt marsh mesocosm. American Journal of Botany 86:697–702.

Padgett, D. E., C. B. Rogerson, and C. T. Hackney. 1998. Effects of soil drainage on vertical distribution of subsurface tissues in the salt marsh macrophyte *Spartina alterniflora* lois. Wetlands 18(1):35–41.

Perillo, G. M. E., E. Wolanski, R. Donald, and C. Hopkinson. 2019. Geomorphology of tidal courses and depressions. Coastal wetlands (second edition): an integrated ecosystem approach. Elsevier, Amsterdam, The Netherlands.

Rabouille, C., L. Denis, K. Dedieu, G. Stora, B. Lansard, and C. Grenz. 2003. Oxygen demand in coastal marine sediments: comparing in situ microelectrodes and laboratory core incubations. Journal of Experimental Marine Biology and Ecology 285-286:49–69.

Redelstein, R., G. Zote, and T. Balke. 2018. Seedling stability in waterlogged sediments: an experiment with saltmarsh plants. Marine Ecology Progress Series 590:95–108.

Ren, X. W., and J. C. Santamarina. 2018. The hydraulic conductivity of sediments: a pore size perspective. Engineering Geology 233:48–54.

Rijkswaterstaat. 2015. Nieuwe buitendijkse natuur Perkpolder van dichtbij te bewonderen. https://www.rijkswaterstaat.nl/over-ons/nieuws/nieuwsarchief/p2015/12/nieuwe-buitendijkse-natuur-perkpolder-van-dichtbij-te-bewonderen.aspx

Schepers, L., M. Kirwan, G. Guntenspergen, and S. Temmerman. 2017. Spatio-temporal development of vegetation die-off in a submerging coastal marsh. Limnology and Oceanography 62(1):137–150.

Schwarz, C., O. Gourgue, J. van Belzen, Z. Zhu, T. J. Bouma, J. van de Koppel, G. Ruessink, N. Claude, and S. Temmerman. 2018. Self-organization of a biogeomorphic landscape controlled by plant life-history traits. Nature Geoscience 11(9):672–677.

Schwarz, C., Q. H. Ye, D. van der Wal, L. Q. Zhang, T. J. Bouma, T. Ysebaert, and P. M. J. Herman. 2014. Impacts of salt marsh plants on tidal channel initiation and inheritance. Journal of Geophysical Research: Earth Surface 119(2):385–400.

Shepard, C. C., C. M. Crain, and M. W. Beck. 2011. The protective role of coastal marshes: a systematic review and meta-analysis. PLOS ONE 6:e27374.

Shepard, F. P. 1954. Nomenclature based on sand-silt-clay ratios. Journal of Sediment Research 24:151–158.

Silliman, B. R., J. van de Koppel, M. W. McCoy, J. Diller, G. N. Kasozi, K. Earl, P. N. Adams, and A. R. Zimmerman. 2012. Degradation and resilience in Louisiana salt marshes following the BP-Deepwater Horizon oil spill. Proceedings of the National Academy of Sciences of the United States of America 109(28):11234–11239.

Silvestri, S., A. Defina, and M. Marani. 2005. Tidal regime, salinity and salt marsh plant zonation. Estuarine, Coastal and Shelf Science 62(1-2):119–130.

Strong, D. R., and D. R. Ayres. 2013. Ecological and evolutionary misadventures of Spartina. Annual Review of Ecology, Evolution, and Systematics 44:389–410.

Temmerman, S., T. J. Bouma, G. Govers, Z. B. Wang, M. B. De Vries, and P. M. J. Herman. 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh. Journal of Geophysical Research: Earth Surface 110:F04019.

Temmerman, S., T. J. Bouma, J. Van de Koppel, D. Van der Wal, M. B. De Vries, and P. M. J. Herman. 2007.

Vegetation causes channel erosion in a tidal landscape. Geology 35:631–634.
Temmerman, S., and M. L. Kirwan. 2015. Building land with a rising sea. Science 349:588–589.
Temmerman, S., P. Meire, T. J. Bouma, P. M. J. Herman, T. Ysebaert, and H. J. De Vriend. 2013. Ecosystem-based coastal defence in the face of global change. Nature 504:79–83.
Temmerman, S., P. Moonen, J. Schoelynck, G. Govers, and T. J. Bouma. 2012. Impact of vegetation die-off on spatial flow patterns over a tidal marsh. Geophysical Research Letters 39(3):L03406.
van Belzen, J., J. van de Koppel, M. L. Kirwan, D. van de Wal, P. M. J. Herman, V. Dakos, S. Kéfi, M. Scheffer, G. R. Guntenspergen, and T. J. Bouma. 2017. Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. Nature Communication 8:15811.
van de Lageweg, W. I., J. N. S. de Paiva, P. L. M. de Vet, J. J. van der Werf, P. G. B. de Louw, B. Walles, T. J. Bouma, and T. J. W. Ysebaert. 2019. Perkpolder tidal restauration: final report. Center of expertise delta technology, the Netherlands. https://www.zeeweringenwiki.nl/images/a/a4/Perkpolder_Eindrapportage.pdf
van der Wal, D., A. Wielemaker-Van den Dool, and P. M. J. Herman. 2008. Spatial patterns, rates and mechanisms of saltmarsh cycles (Westerschelde, The Netherlands). Estuarine, Coastal and Shelf Science 76(2):357–368.
van Slobbe, E., H. J. de Vriend, S. Aarninkhof, K. Lulofs, M. de Vries, and P. Dircke. 2013. Building with Nature: in search of resilient storm surge protection strategies. Nature Hazards 65(1):947–966.
van Wesenbeeck, B. K., J. van de Koppel, P. M. J. Herman, and T. J. Bouma. 2008. Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems? Oikos 117(1):152–159.
Vandenbruwaene, W., T. J. Bouma, P. Meire, and S. Temmerman. 2013. Bio-geomorphic effects on tidal channel evolution: impact of vegetation establishment and tidal prism change. Earth surface processes and landforms 38:122–132.
Voss, C. M., R. R. Christian, and J. T. Morris. 2013. Marsh macrophyte responses to inundation anticipate impacts of sea-level rise and indicate ongoing drowning of North Carolina marshes. Marine Biology 160:181.
Wang, C., and S. Temmerman. 2013. Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states? An empirical study on intertidal flats and marshes. Journal of Geophysical Research: Earth Surface 118(1):229–240.
Winterwerp, J. C., and W. G. M. van Kesteren. 2004. The nature of cohesive sediment. Introduction to the physics of cohesive sediment in the marine environment. Pages 29–85 *in* Developments in sedimentology. 56. Elsevier, Amsterdam, The Netherlands.
Yuan, L., Y. H. Chen, H. Wang, H. B. Cao, Z. Y. Zhao, C. D. Tang, and L. Q. Zhang. 2020. Windows of opportunity for salt marsh establishment: the importance for salt marsh restoration in the Yangtze Estuary. Ecosphere 11(7):e03180.
Zhu, Z., Z. Yang, and T. J. Bouma. 2020. Biomechanical properties of marsh vegetation in space and time: effects of salinity, inundation and seasonality. Annals of Botany 125:277–290.

Data Availability

Data are available from 4TU.ResearchData: https://doi.org/10.4121/14946021.v1.