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 laboratory experiments, using mesocosms and a 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 cliffs at marsh edges 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.

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; 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; Marani et al. 2013; Corenblit 2018). 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

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et al. 2008; Bouma et al. 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; 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. 2013; Corenblit et al. 2015; Corenblit 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 2018). While pioneer plants may develop plastic responses to abiotic stresses (Puijalon et al. 2011; Silinski et al. 2018; Zhu et al. 2020), ecosystem-engineering plant species tend to attenuate abiotic stresses by modifying their physical environment (Jones et al. 1994; Bouma et al. 2005; Jones 2012). 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. 2005; Bouma et al. 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 (De Rose and Basher 2011), brackish and salt marshes in estuaries and lagoons (Allen 1989; Francalanci et al. 2013; Wang et al. 2017), to seagrass meadows (Twomey et al. 2021) along coastlines. 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 (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; 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 nonvegetated 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 decimeters, 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 the height difference (ΔZ) in the next growing season, i.e., by outgrowth of plants from the cliff top to the initially nonvegetated area in front of the cliff base (Bouma et al. 2016). We presume that the capacity of marsh species to outgrow the height difference (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 nonvegetated 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 species-specific maximal cliff height ($\Delta Z_{\max}$) from which each of these species was able to grow out toward the nonvegetated surface in front of the cliff. We test the hypothesis

that species with smaller clonal step-lengths have higher species-specific maximal cliff height (ΔZ_{max}) values and thus more strongly support the formation and maintenance of cliffs compared with species with larger clonal step-lengths.

Materials and methods

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 $\times$ width $\times$ depth = 70 cm $\times$ 40 cm $\times$ 30 cm) with three kinds of sediment substrates (Supporting Information Table S1) and three species (*S. anglica*, *S. maritimus*, and *P. australis*). The sediments used were sand (D_{50} of 301.01 μm, 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 29.93 μm, silt T_{63} content of 69.03%) (classification cf 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., *S. anglica*, *P. australis*, and *S. maritimus*) for each of the three sediment types (i.e., sand, sandy mud, mud), resulting in a total of 45 mesocosms (Supporting Information Table S1). 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.

At the end of the first mesocosm experiment, we measured the following plant traits in September 2016: plant height (10 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.

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 (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. 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. 1). To mimic a boundary between nonvegetated tidal flat/vegetated marsh with contrasting sediment erodibility for cliff initiation (Bouma et al. 2016), the metal box was divided into two sections (Fig. 1): (i) a sediment section (length of 95 cm) containing nonvegetated tidal flat sediment consisting of noncohesive 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 neighboring 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.

The water level in the flume was maintained at 26 cm (Fig. 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 3 h, to mimic a relatively short event with strong wind-generated near shore waves in the Scheldt estuary (Callaghan et al. 2010; Silinski 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; cf Jonsson 1966; Balke et al. 2011), which corresponds to
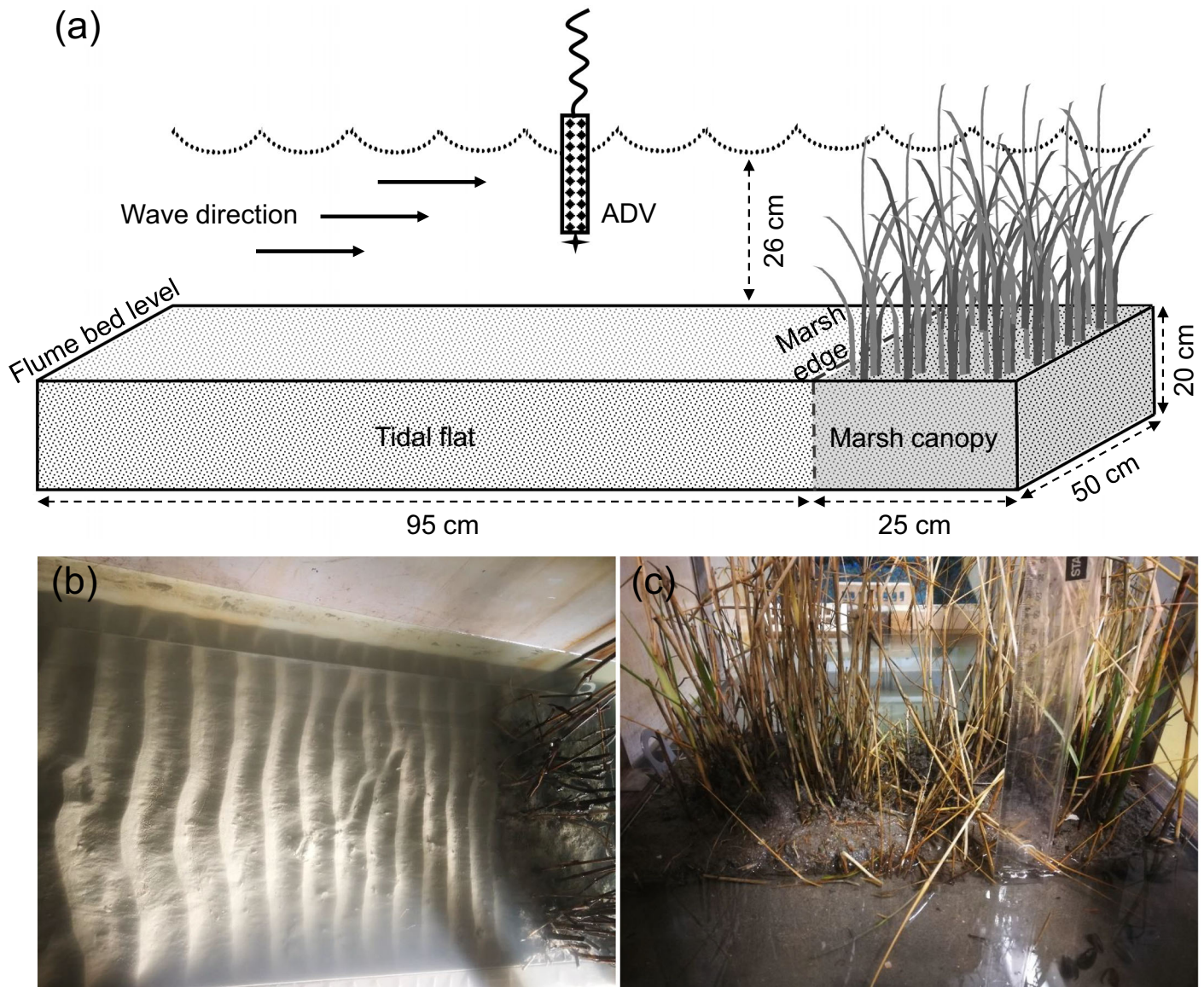
Fig. 1. (a) Schematic sketch of the experimental set up in the test-section of the flume. A nonvegetated tidal flat was placed in front of the marsh edge, and exposed for 3 h to waves (with average period of 1.5 s and height of 10 cm) at a water depth of 26 cm. A slow constant water current of 10 cm s^{-1} was applied to move away any sediment when erosion occurred. Elevation change was measured for 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 close-up view of a marsh edge after 3-h wave run. Measurements are given in cm.

typical bed shear stresses during stormy conditions at natural marsh edges (cf, Callaghan et al. 2010). In addition to the waves, a constant current velocity of 10 cm s^{-1} 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^{-1}; Bouma et al. 2005), 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. 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 method, which consists of manual pin readings of erosion on a space of 50 cm × 25 cm at a resolution of 10 cm × 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.

Mesocosm experiment 2 to quantify species-specific maximal cliff height (ΔZ_{max})

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 species-specific maximal cliff height (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
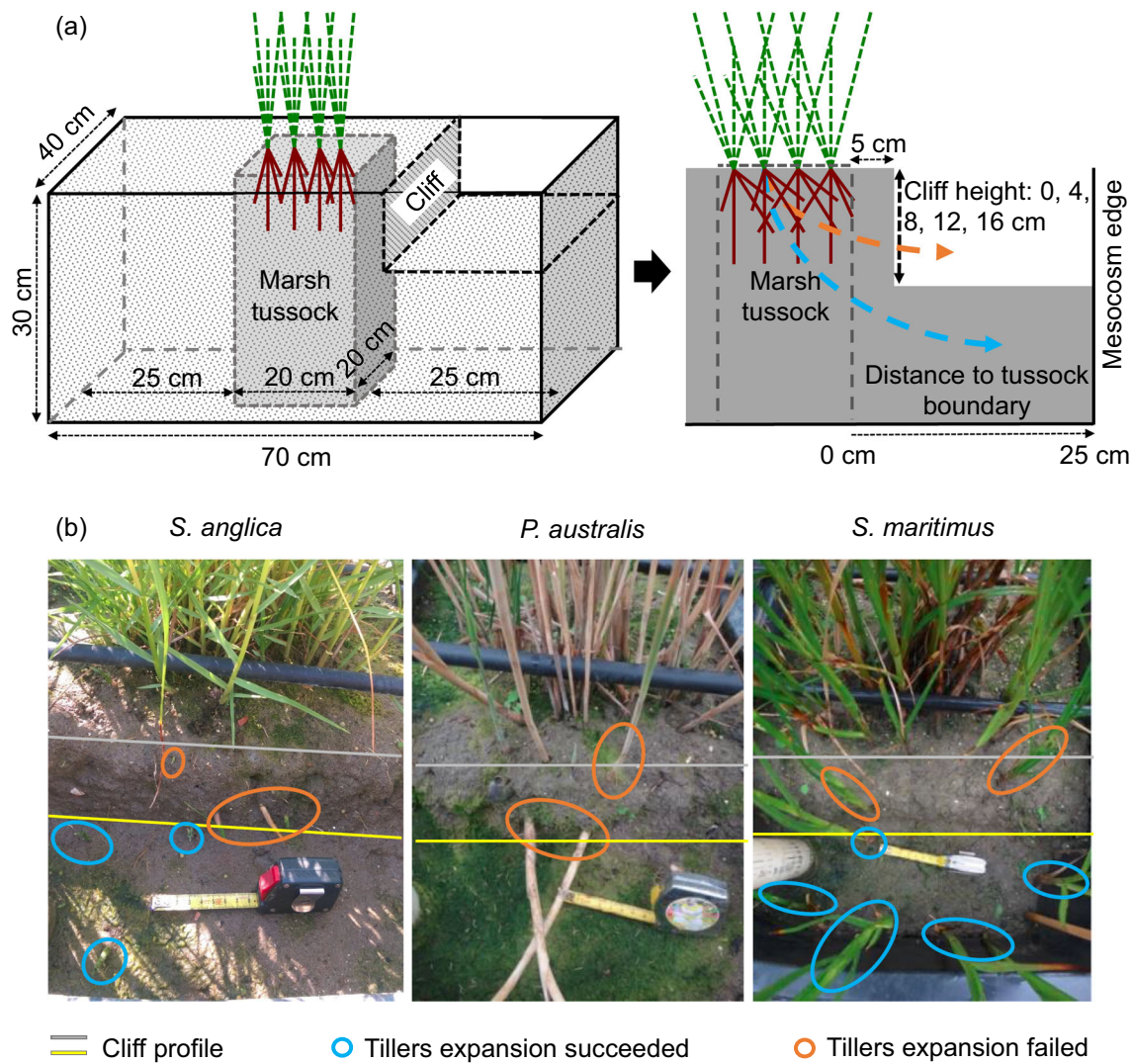
Fig. 2. (a) Schematic sketch of the mesocosm experimental set up and the side view of marsh tussock and cliff front; **(b)** examples taken from the mesocosm experiment 2 showing the growth response at a cliff height of 8 cm for three marsh species (from left to right): *S. anglica*, *P. australis*, and *S. 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) vs. 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 1. Two-way ANOVA results for effects of species and sediment type on marsh plant traits in mesocosm experiment 1.

Response variable	Deviance source	df	Mean Sq	F	p
Plant height (cm)	Species	2	50,834.03	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

a height lower than species-specific maximal cliff height (ΔZ_{max}) would not persist because plants can grow out, while cliffs would only persist if they are higher than species-specific maximal cliff height (ΔZ_{max}). To quantify species-specific maximal cliff height (ΔZ_{max}), cliff-like plateaus were constructed (Fig. 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. 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 (Supporting Information Table S2). All mesocosms were cultivated outdoors for 4 months until September 2016 under the same condition as mentioned above for mesocosm experiment 1.

In order to estimate species-specific maximal cliff height (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 that 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. 2) vs. the tillers that grew out from the vertical cliff surface and hanged in the air (i.e., expansion failed, Fig. 2). The largest cliff height from which tillers were still able to grow out was deemed as species-specific maximal cliff height (ΔZ_{max}).

Statistical analysis

For the mesocosm experiments, two-way ANOVAs were applied to analyze 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) (Supporting Information Table S1), as well as the effects of species and cliff height on these clonal growth traits for all the sandy-mud treatments (Supporting Information Table S2). To compare the clonal architecture of the different treatments in mesocosm experiment 1, we analyzed the statistical distribution (with bin size of 5 cm) of the measured clonal step-lengths of the tillers that grew out from
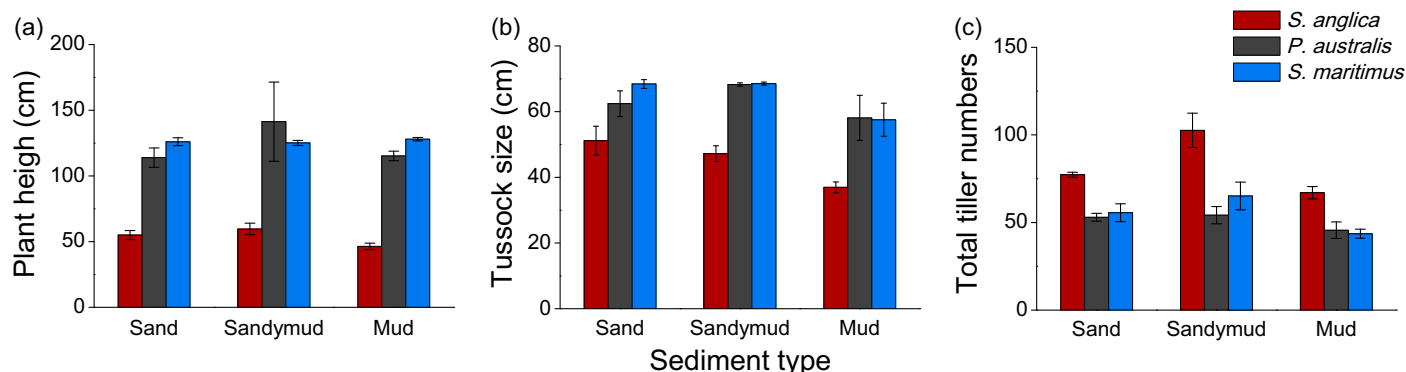
Fig. 3. Plant trait responses found in mesocosm experiment 1 of three marsh species (see Fig. 2 for full names) grown in three contrasting sediment types: Sand, sandy mud, and mud. The response parameters measured were **(a)** plant height (cm), **(b)** tussock size measured as maximum distance between expanded tillers (cm), and **(c)** Total number of tillers per mesocosm of 0.28 m² (70 × 40 cm). See Table 1 for statistical test results.
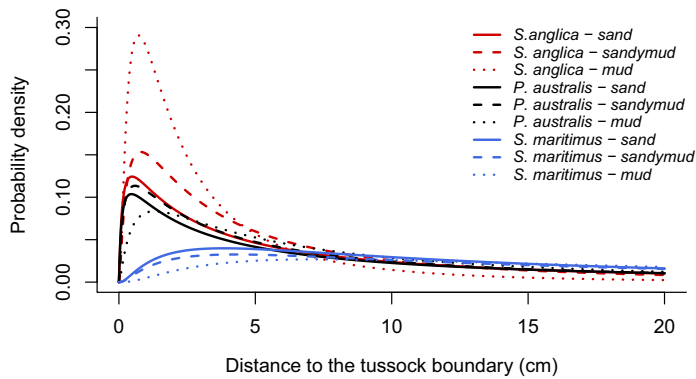
Fig. 4. Relative frequency of clonal expansion distance to the tussock boundary (step-length) found in mesocosm experiment 1 of three marsh species. All marsh species in all sediment types had a log-normal distribution of clonal expansion distances to the original margin of the marsh clumps. Note that tillers growing beyond the 20-cm expansion distance boundary were classified as >20 cm due to limited space in the mesocosms.

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 ≤20 cm 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 ($cm^3\,h^{-1}$) of the nonvegetated 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
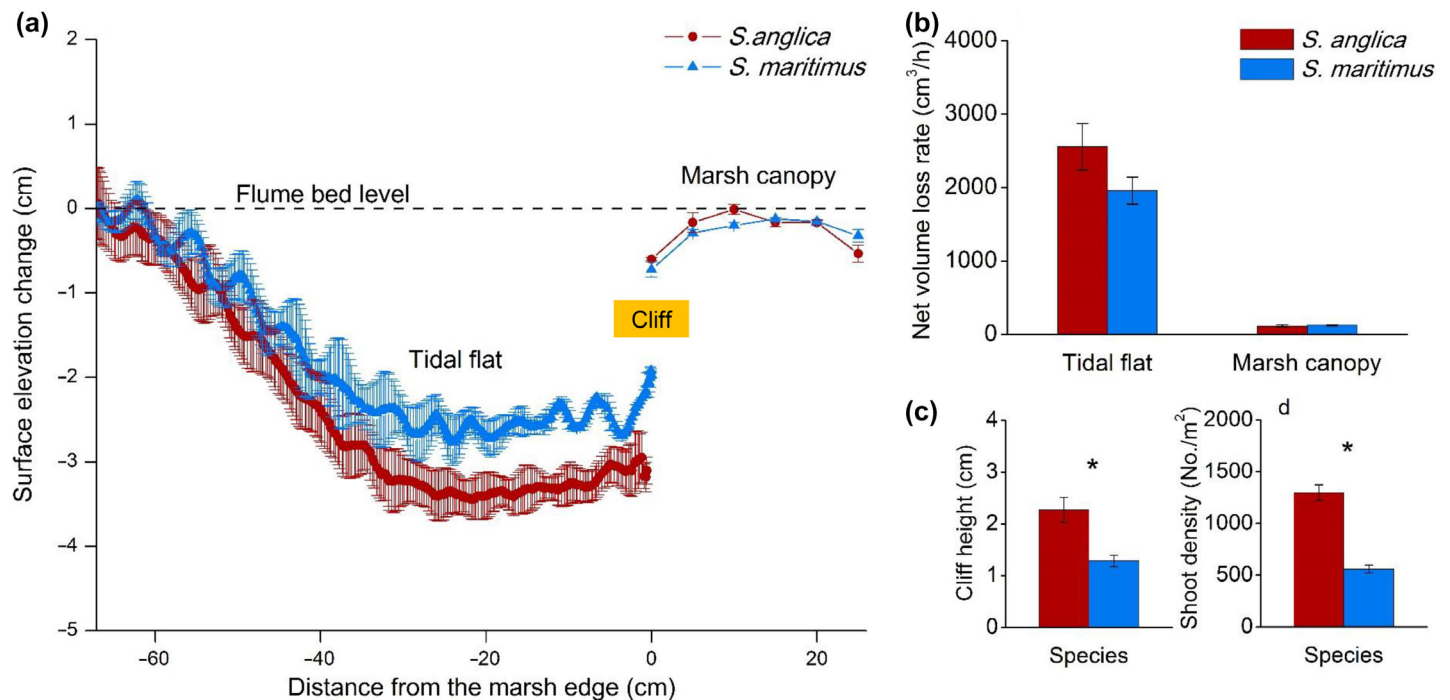
Fig. 5. Measurements taken in flume experiment with two marsh species: **(a)** surface elevation change of the mimicked tidal flat and marsh edge at the end of the flume experiment with deeper cliffs formed at the marsh edge for *S. anglica*, **(b)** net sediment volume loss rate (cm^3/h) of the mimicked tidal flat vs. marsh edge, **(c)** cliff height (cm) adjacent to marsh edges, and **(d)** different shoot densities (No./m^2). * indicates significant differences ($p < 0.05$).

Table 2. Two-way ANOVA results on differences in sediment volume loss rate in the flume experiment between erosion sections (tidal flat vs. marsh canopy) and species.

Deviance source	df	Mean Sq	F	p
Erosion section	1	1.368E7	135.76	<0.001
Species	1	257,983.99	2.56	0.148
Erosion section * species	1	278,750.35	2.77	0.217

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. 2). To compare the outgrowth capacity of different marsh species, we applied a multiple generalized linear model (GLM) to analyze 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.

Results

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 1). *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. 3a,b, *p* < 0.001). Also, *S. anglica* had significantly more tillers than the other two marsh species (Fig. 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.

Sediment type did not affect plant height (Fig. 3a; *p* = 0.33, Table 1) but had a significant effect on both tussock size (*p* < 0.01, Table 1) and total tiller number (*p* < 0.001, Table 1). In comparison to sand and sandy mud, all species in muddy
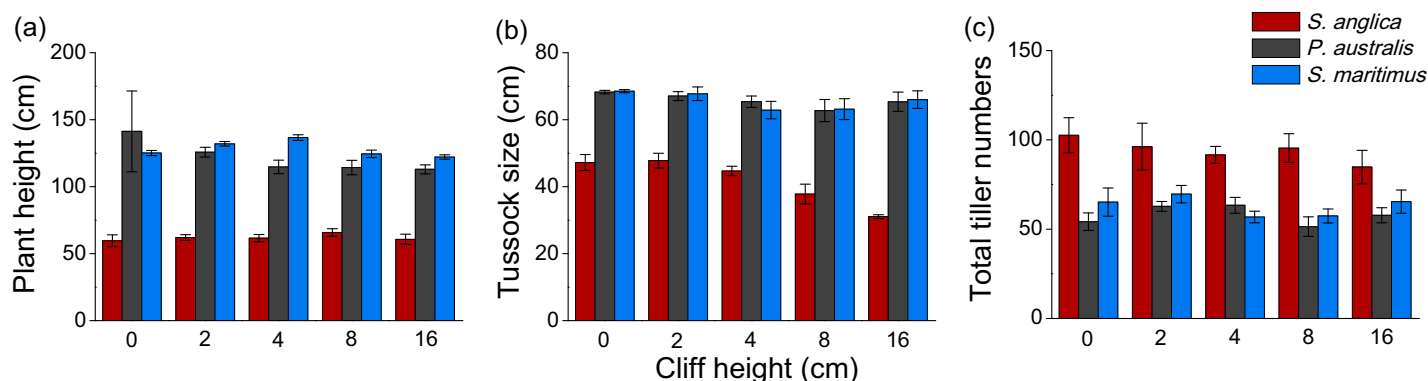
Fig. 6. Plant trait responses of three marsh species found in mesocosm experiment 2 when exposed to different cliff heights: 0, 2, 4, 6, 8 and 16 cm. **(a)** Plant height (cm), **(b)** tussock size, measured as maximum distance between expanded tillers (cm), and **(c)** Total number of tillers per mesocosm of 0.28 m² (70 × 40 cm²). See Table 3 for statistical test results.

Table 3. Two-way ANOVA results on effects of species and cliff height on marsh plant traits in mesocosm experiment 2.

Response variable	Deviance source	df	Mean Sq	F	p
Plant height (cm)	Species	2	66,643.10	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

sediment were observed to have smaller tussock sizes (Fig. 3b, $p < 0.01$) and lower total number of tillers (Fig. 3c; $p < 0.05$ compared with sand, $p < 0.001$ compared with sandy-mud).

When looking at the statistical distribution of the clonal step-lengths (Fig. 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 toward muddy sediments, especially for species with small clonal step-lengths.

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. 5a). We found significant differences ($p < 0.001$, Table 2) 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. 5b,

$p = 0.148$, Table 2). 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. 5a), was significantly higher in the case of *S. anglica* (Fig. 5c; $p < 0.05$, *t*-test). *S. anglica* was also characterized by higher shoot density than *S. maritimus* (Fig. 5d; $p < 0.05$, *t*-test).

Effects of marsh clonal expansion traits on cliff maintenance

In mesocosm experiment 2, we aimed to quantify species-specific maximal cliff height (ΔZ_{max}, the maximum cliff height that a species was able to outgrow) to test whether the maintenance of a cliff at marsh edge 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. 6; $p < 0.001$, Table 3). A significant effect of cliff height was also found on tussock size ($p < 0.001$, Table 3), but not on plant height or total tiller numbers ($p > 0.05$, Table 3). 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. 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).

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. 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. 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. 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.

Discussion

Using marsh cliff-formation as a model system, we examined how species-specific vegetation expansion strategies may
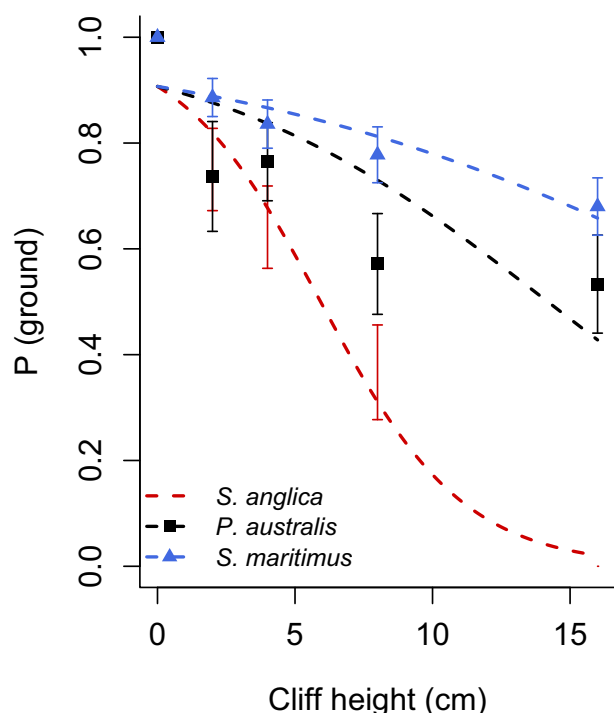
Fig. 7. GLM analysis of the relationship between vegetation expansion successful rate P (fraction of tillers that expanded to the soil ground) of different marsh species against cliff height (cm) in mesocosm experiment 2. Data show mean fraction of tillers in the soil and the standard error of this mean. The curves are the predicted response from logistic regression of the fraction of successfully expanded tillers on the interactions between cliff height and species.

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.

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 toward 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 interparticle 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), 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. 2005; Puijalon et al. 2011; Silinski et al. 2018). With larger step-lengths and sparse patches that allowing more water flow to pass though and over the vegetation canopy (Bouma et al. 2007; Bouma et al. 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). While, 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. 2005; van Hulzen et al. 2007). For example, by having densely growing clonal patches, *S. anglica* plants can optimize sediment trapping efficiency (Bouma et al. 2005, 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.

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 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. 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 are enhanced by a very dense tussock, whereas waves can dissipate more easily in a sparser

vegetation canopy (Bouma et al. 2007; van Wesenbeeck et al. 2008; Bouma et al. 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 (Callaghan 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 species-specific maximal 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. 2005, 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 cannot 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 and Mariotti 2019), wave dynamics (Möller et al. 2014; Leonardi et al. 2018; Finotello et al. 2020), and sea-level rise (Kirwan et al. 2010;

Mariotti et al. 2010; Kirwan and Megonigal 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, 2013; Schwarz et al. 2018).

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 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; Fagherazzi et al. 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. 2015; 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.

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Conflict of Interest
None declared.