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**Quantifying critical conditions for seaward expansion of tidal marshes:  
a transplantation experiment**

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## ***Abstract***

The alternative stable states theory is increasingly applied to tidal marsh shorelines, where the two opposing stable states – a dense vegetated state on the one hand and a bare tidal flat on the other hand – can coexist in time but differ in space. The shift from the bare to vegetated state by the establishment of individual plants (seedlings, rhizome-grown shoots) on the bare tidal flat is known to be triggered by the occurrence of windows of opportunity. These are periods when species- and life stage-dependent thresholds, such as sediment dynamics or wave impact, are not exceeded. One controlling environmental parameter in intertidal wetlands is elevation, as many important stressors for plants – such as hydroperiod, sediment dynamics and wave properties (wave period and wave height) – are typically correlated to it. Disentangling the respective impact of these correlated stressors remains challenging. In this paper, we present the results of a transplantation experiment where the establishment of three different life stages (seedlings, rhizome-grown shoots and patches) of the brackish pioneer *Scirpus maritimus* was tested over an elevation gradient at two locations of contrasting wave exposure. This gradient reached from the bare tidal flat into the marsh and covered an elevation range at which continuous *S. maritimus*-dominated pioneer marsh is known to occur. We found that erosion stress influences seedling survival on tidal flats while drought stress seems to limit long-term establishment of individual shoots and seedlings in the marsh. Furthermore, survival of transplants was more successful on the tidal flat of the sheltered site compared to the tidal flat of the exposed site whereas survival time within the marsh did not differ between sites. This highlights the attenuation of waves and currents in exposed marshes. However, no long-term establishment occurred on the tidal flat, emphasizing the importance of clonal integration for tidal flat colonization.

## 1. Introduction

Tidal marshes are habitats providing various ecosystem services to coastal and estuarine societies such as enhancing coastal protection through wave attenuation, carbon sequestration and nursery areas for fish (e.g. Barbier et al., 2011; Möller et al., 2014; Temmerman et al., 2013). This is why it is important to preserve and restore them. In this regard, lateral shoreline dynamics (i.e. the processes controlling expansion and contraction of the marshes) are highly relevant. In the past, many studies have been conducted on the risk of vertical drowning of marshes by sea-level rise, but recent studies highlight that many marshes are more vulnerable to lateral erosion (Fagherazzi et al., 2013; Mariotti and Fagherazzi, 2010; van de Koppel et al., 2005). Nevertheless, field studies on the threshold conditions for lateral landward erosion or seaward expansion remain relatively scarce.

In the past decade, the concept of alternative stable states, originally developed to explain drastic shifts in the states of entire ecosystems (Scheffer et al., 2001), has been increasingly applied to tidal marshes (Marani et al., 2010; van Wesenbeeck et al., 2008; Wang and Temmerman, 2013). In these bio-geomorphic environments, two alternative stable states – i.e. continuous marshes or vegetation patches on the one hand, and bare tidal flats on the other hand – may coexist simultaneously. This means that the alternative states are not only distinguished in time, but also in space, with sharp transition zones from high vegetation densities to bare tidal flat (van Wesenbeeck et al., 2008). The temporal shift from one state to the other may either be induced through gradual change of environmental conditions or by episodic events, in both cases causing a critical threshold in environmental conditions to be exceeded (Scheffer et al., 2001; Balke et al. 2014). Those shifts will, over a relatively short time span (months, years), convert bare tidal flat into densely vegetated marsh or vice versa.

The stability of both alternative stable states is the result of positive feedbacks. For example, vegetation that established on a bare tidal flat and passes a critical density or biomass enhances sedimentation and decreases erosion due to its flow-attenuating effect. This will in turn lead to increased elevation, which facilitates further plant establishment and growth and thus sediment trapping (Temmerman et al. 2007; Bouma et al., 2009). Such positive feedbacks will lead to the further development of established vegetation and enhance the long-term stability, as the disturbance threshold required to convert the expanding vegetation back into a low bare tidal flat increases with the amount of sediment trapped. After some time, the disturbance threshold might only be exceeded during extreme events such as during a storm, or through other mechanisms such as cliff erosion. Unvegetated tidal flats, in contrast, are more prone to alternating phases of disturbance and stabilization of the sediment, e.g. through hydrodynamics and bioturbating benthos (van Wesenbeeck et al., 2007), which then hampers vegetation establishment.

Given that the positive feedback loop between vegetation and sediment accretion in marsh formation only works once a critical biomass has been obtained (Bouma et al. 2009), the most important process in colonizing a bare tidal flat is the initial survival success of pioneer plants that are still too small to benefit from such feedback. For most marsh species, colonization can typically occur either through seedlings or through propagules, i.e. parts of rhizomes of various extents that have detached from an existing mature plant or marsh, and from which new shoots can grow. There are many different kinds of regular environmental stressors (e.g. cyclic tidal inundation stress, currents and waves, sediment dynamics) and episodic disturbances (events such as storm surges), which may counteract plant establishment or expansion. Given this, plant establishment can only succeed in periods during which no critical, generally species- and life stage-dependent thresholds of these stressors are exceeded. This concept of requiring short periods with favourable conditions has been introduced as “windows of opportunity” (Balke et al., 2014, 2011; Mateos-Naranjo et al., 2008).

In highly dynamic environments such as the intertidal areas of marshes or mangroves (Dijkema et al., 1990), windows of opportunity result from regular and stochastic variations in hydrodynamic conditions (Balke et al., 2014; Hu et al., 2015). An example of this might be an unusually long windless phase (reducing wave forcing) or the absence of a winter storm in one particular year (absence of an extreme

event that could uproot and wash away freshly established vegetation). Typically a succession of events, such as dispersal followed by a disturbance-free period sufficient in length for germination and establishment (Balke et al., 2014, 2011), is required. An additional constraint is that this succession of events needs to occur in the time of the year during which seeds are available (Zhu et al., 2014).

Different types of thresholds for successful establishment or expansion of marshes have been suggested in previous experimental and modelling studies. Firstly, the plants themselves have specific thresholds, such as (i) a threshold in aboveground biomass of individual plants in order to survive (e.g. Angelini and Silliman, 2012; van Wesenbeeck et al., 2008), but which can differ either due to different life stages (seedlings, shoots) or different sizes of clonal rhizomes (number of shoots) and (ii) the belowground root length of individual plants (Balke et al., 2011). Secondly, the environment can represent abiotic thresholds such as (i) elevation within the tidal frame which determines inundation time (Fagherazzi et al., 2012; Kirwan et al., 2010; Marani et al., 2010; Wang and Temmerman, 2013); (ii) sediment erosion and accretion rates that will highly affect the survival chances of seedlings (Balke et al., 2011); (iii) currents and waves (Callaghan et al., 2010; Hu et al., 2015; Mariotti and Fagherazzi, 2010) as they induce sediment dynamics and mechanical stress that can lead to uprooting or limit growth and, more specifically, (iv) wave period (Silinski et al., 2015). For most perennial marsh plants, colonization of the bare tidal flat by individual seedlings or shoots is complementary to colonization by clonal expansion from the marsh edge. Contrary to the colonization by individuals that need to survive on their own, clonal shoots growing from the marsh edge benefit from clonal integration (Amsberry et al., 2000; Bertness and Hacker, 1994; Burdick and Konisky, 2003). This means that shoots that are clonally connected to each other can alleviate local physical and biochemical stress by accessing distant resources that are redistributed through the clone (Burdick and Konisky, 2003; Charpentier and Stuefer, 1999).

As elevation relative to mean sea level typically combines the effect of a series of environmental variables (such as increasing inundation time and duration of wave exposure with decreasing elevation) the effects of distinct variables are typically tested separately in lab experiments or in numerical models. In nature, however, they overlap and disentangling their respective impacts on plant establishment remains challenging due to their high covariance. Despite these constraints, field experiments offer the opportunity to look at patch-size effects and actual thresholds, which would be impossible or impractical to mimic in the laboratory.

While previous similar studies used *Spartina*-species or *Phragmites australis* (e.g. Amsberry et al., 2000; Burdick and Konisky, 2003; Mateos-Naranjo et al., 2008; van Wesenbeeck et al., 2008), we conducted a full-scale field experiment in the brackish part of the macro-tidal Scheldt Estuary (Belgium and the Netherlands, Fig. 1) with the local dominant pioneer species: *Scirpus maritimus*. Three biomass classes, i.e. life stages (seedlings, individual rhizome-grown shoots and clonal patches), were transplanted to five levels along an elevation gradient from the tidal flat into the pioneer *S. maritimus* marsh zone at two sites of contrasting wave exposure. These levels covered an elevation range at which continuous *S. maritimus*-dominated pioneer marsh existed and expanded at other locations along both marshes. Inundation time and sediment dynamics were monitored in parallel to survival of transplants. We hypothesized a life-stage (or biomass) threshold as well as an elevation threshold for successful establishment. We compared the survival of transplants of *S. maritimus* to the reported survival of *Spartina*-species. Finally, we explored the importance of clonal integration for colonization by *S. maritimus* as clonal marsh expansion had occurred within the range of elevations at which the transplantation experiment was performed.

## 2. Materials and Methods

### 2.1 Site description

We selected two sites along the Scheldt Estuary (Groot Buitenschoor, Belgium (51°21.78' N, 4°14.88 E), and Rilland, The Netherlands (51° 24.05' N, 4° 10.65' E), Fig. 1) where the pioneer marsh zone consists entirely of *Scirpus maritimus* L. Palla. The seaward marsh edge was located at both sites at approximately -0.70 m relative to local mean high water (MHW) at the beginning of the experiment, i.e. in March 2011. The marsh edge is at both locations a gently sloping marsh-mudflat transition zone with slopes of around 3 % (personal observation). The transition from tidal flat (no plants) to dense marsh (> 200 shoots m<sup>-2</sup>) occurs over a distance of a few meters only. No vegetation patches precede the continuous marsh. Elevation along both complete marsh edges (~ 3.5 km each) ranged from around -1.4 m MHW to around -0.2 m MHW. These elevations had been recorded during a high precision GPS survey (real time kinematics GPS, with ± 1 cm accuracy) along both marshes in August 2011, tracing the marsh edge position at intervals of 5 to 10 m. Due to their geographic proximity both marshes have similar tidal influence: they both experience two tidal high waters per day, with an average tidal range of 5.0 m. Spring tides reach up to 0.5 m MHW and neap tides up to -0.6 m MHW. Yearly salinity is 9.2 ppt ± 0.17 SE and suspended sediment content is 0.062 g L<sup>-1</sup> ± 0.0043 SE (Maris et al., 2013). However, the two sites experience contrasting hydrodynamic conditions as the Belgian site is sheltered by a breakwater from ship and wind waves (hereafter referred to as “sheltered site”), whereas the Dutch site is highly exposed through a long wind fetch and the proximity of the shipping channel (hereafter referred to as “exposed site”) (Fig. 1). In the Scheldt, the impact of waves on the tidal flats and marshes can exceed the impact of tidal currents (Callaghan et al., 2010). Waves monitored at the marsh edges of both sites during the growing season of 2014 confirm the contrasting wave exposure of these two marshes: significant wave heights ( $H_{1/3}$ ) were of 2.8 cm and 5.7 cm for sheltered and exposed site, respectively, and the mean of the highest percentile ( $H_{1/100}$ ) was 9.7 cm and 20.3 cm, respectively. These values were calculated for all wave data gathered during tidal inundation at both marsh edges. In this way, wave exposure at the marsh edges as encountered in the course of a tidal cycle was quantified (see 2.6 for methods). Furthermore, silt dominated the top 5 cm sediment layer at the sheltered site (68.1 % ± 3.0 SE) with 8.0 % ± 0.6 SE organic matter contents and 0.73 g cm<sup>-3</sup> ± 0.05 SE dry bulk density, whereas sand dominated at the exposed site (86.8 % ± 1.3 SE) with 1.4 % ± 0.1 SE of organic matter and a dry bulk density of 1.45 g cm<sup>-3</sup> ± 0.01 SE (see 2.4 for methods).

### 2.2 Experimental set-up

At those two selected locations (Fig. 1c), a transect of five levels of elevation was set up (Fig. 2): two levels were within the marsh, at approximately -0.40 and at -0.65 m MHW and three levels were on the tidal flat, at -1.0, -1.30 and -1.60 m MHW. Tidal characteristics were similar for equal levels at both sites and inundation frequency decreased from 100 % at the tidal flat levels to less than 85 % at the highest level (Tab. 1). Each of those levels was divided into three replicate plots. At each plot, we transplanted ten seedlings and eight shoots of *S. maritimus* as well as one vegetation patch of *S. maritimus* shoots taken from the adjacent pioneer marsh zone (approximately 30 x 30 x 30 cm of roots and sediment), i.e. 30 seedlings, 24 shoots and three patches per level. Transplantation to both sites took place within five days at the end of April 2011.

In order to avoid direct competition with established roots and shoots at the plots within the marsh, original marsh vegetation was removed prior to the experiment by digging trenches of 2 m length, 40 cm width and 40 cm depth, spreading root cloth along the bottom and along the walls and refilling these trenches with sediment from the nearby tidal flat.

Water level at both sites was monitored by one pressure sensor per site (Fig. 2, see 2.5 for details).

### 2.3 Plant material

The plant species used in this experiment was *Scirpus maritimus* L. Palla, which is a typical pioneer plant of brackish marshes in European estuaries. It is the dominant plant species at the seaward fringe of both

marshes. It forms monospecific clonal stands with shoot densities of up to 400 stems m<sup>-2</sup> (personal observation). This species grows clonally by producing several underground rhizomes from which new shoots start to grow, hence connecting different shoots to each other (Charpentier and Stuefer, 1999; Charpentier et al., 2000). During the growing season (March-September), tubers are formed which ensure the survival of the clonal, belowground plant in winter, and the regrowth of new shoots in spring, typically by the end of March in the Scheldt Estuary. From September onwards, the aboveground biomass dries and dies off. This species produces vast amounts of viable seeds every autumn and one episodic and local event of natural seedling growth occurred in the period of 2010-2014 at both sites. However, no successful long-term survival was observed in this period. Clonal expansion of the marsh edge, in contrast, was observed over wide stretches of both marshes during that same period (own observations in the field).

### 2.3.1 Seedlings

Seedlings were germinated from seeds that had been collected in the field close to our study sites in September 2009 and stored in wet, cool and dark conditions until February 2011 when germination was initiated. The germinated seedlings were transplanted into sandy Scheldt sediment ( $d_{50}=320\ \mu\text{m}$ ), mixed with osmocote fertilizer, and raised in a mesocosm, where night-day and inundation cycles with brackish water (with a salinity of 6 ppt) were simulated. After two weeks we placed the seedlings in sheltered, outdoor conditions close to the Scheldt and we continued to water them daily with brackish water in order to acclimate them to the field conditions. At transplantation to the field at the end of April 2011, the seedlings had an average size of 22.2 cm  $\pm$  0.2 SE and were selected randomly from the prepared plant material.

### 2.3.2 Shoots

The shoots were grown from tubers extracted from the field end of March 2011 and transplanted into the same natural Scheldt sediment as the seedlings. They were placed next to the seedlings in the sheltered outdoor conditions close to the Scheldt where they were watered with the same brackish water as the seedlings. At transplantation to the field at the end of April 2011, the rhizome-grown shoots had an average size of 36.8 cm  $\pm$  0.6 SE and were selected randomly from the prepared plant material.

### 2.3.3 Patches

The patches of *S. maritimus* were taken from the pioneer zone of the adjacent marsh on the day of transplantation to the field: with a spade we cut blocks of sediment and roots of approximately 30 x 30 x 30 cm out of the marsh and transplanted them directly to the plots. On the day of transplantation, shoot density of the 30 patches was on average 121.5 shoots m<sup>-2</sup>  $\pm$  8.2 SE (i.e. 10.9 shoots per patch  $\pm$  0.7 SE).

### 2.3.4 Transplantation and monitoring

At each level, transplants were planted in three replicate plots in a row parallel to elevation contours (Fig. 2). Each plot consisted of 10 seedlings and 8 shoots transplanted at 10 cm interval, followed by one patch. Given the distance between each transplant, no mutual influence, e.g. through local scour around the stems or through shading, was observed during the experiment. Plant survival and sedimentation were monitored weekly during two months, until early July 2011, then bi-weekly until end of August 2011, and then monthly until the end of November when the experiment ended due to the natural seasonal decay of *S. maritimus*. In order to avoid disturbance of the plots when approaching them during field visit, we followed the same paths at each monitoring date and kept a minimum distance of around 50 cm from the transplants. During the monitoring, each plant and patch was observed individually: survival of each individual transplant (seedling, shoot and patch) was noted and clonally grown shoots counted. Survival could fail either through decay of the aboveground plant material or through uprooting and loss of the entire transplant. Regarding the patches, clonal expansion was monitored by counting the total number of live tillers at each field visit.

## 2.4 Sediment properties and sediment dynamics

For characterizing the field locations (see 2.1), dry bulk density, organic matter content and granulometry of the sediment surface were assessed with three replicate samples for all levels taken in June 2011 (sampled with a Kopecky-Ring (4.6 cm diameter and 5.2 cm height)). In order to determine dry bulk density, the sediment volume was weighed after drying during 72 h at 105 °C. Organic matter content was determined through ashing of the sample at 550 °C during 6 hours. Granulometry was measured with a Mastersizer 2000 (Malvern) after a combined HCl and H<sub>2</sub>O<sub>2</sub> treatment of the sediment samples (main results given in 2.1).

Next to each plot, a Sedimentation-Erosion-Bar (SEB, Cahoon et al., 2002; see Nolte et al., 2013 for review) was installed, i.e. three SEBs per transplantation level (see Fig. 2). They were monitored at the same moments as plant survival. Our SEB consisted of a 2 m long perforated bar that was positioned horizontally onto two vertical 1.5 m long poles of which more than 1 m reached into the ground and that were considered stable. In this way measurements could be repeated at exact same spots. We quantified elevation change with a regular folding ruler at ten points of each 2 m long SEB with an estimated accuracy of ± 1 mm. By using the measure of the day of transplantation as reference, the subsequent measurements showed if net erosion or sedimentation had occurred at the different plots.

## 2.5 Tidal characteristics

The water level was monitored at a frequency of 2 min with one pressure sensor (Cera-diver, Schlumberger) per site that was installed at the lowest level of each site. As these sensors measure total pressure (i.e. water pressure and air pressure), these measurements were corrected for air pressure with data from a pressure sensor that had been positioned on the dike (Baro-diver), measuring simultaneously to the other divers (Fig. 2). Tidal characteristics (inundation frequency, inundation time and depth, dry time) were quantified per level and per considered time step (i.e. once for the entire period, but also for each time period between field measurements) with the Tides-package in R (Cox, 2014). (See Tab. 1 and 2.1 for results.)

## 2.6 Wave measurements

In order to quantify and compare wave exposure of both sites, wave data was collected using submerged stand-alone PDCR 1830 pressure transducers (GE Sensing) at a frequency of 16 Hz. As this data is only used for site description, we show results from data collected at the marsh edges of both sites during the growing season of 2014. Wave data was converted from pressure to surface elevation and subsequently analyzed using a LabView script developed by the Department of Civil Engineering of UGent (Versluys and Troch, 2010). The conversion was performed using linear wave theory, in particular by applying the pressure response factor (Dalrymple and Dean, 1991). The tidal signal was removed from the data by de-trending and de-meaning the wave measurements. Salinity of the water was not accounted for given the high variability of salinity in the brackish part of an estuary in the course of each tide and depending on season. The influence of salinity, i.e. water density, on calculated wave heights is in any case limited to a maximum of 3.5 % (with a water density of 1000 kg m<sup>-3</sup> for fresh water vs. 1026 kg m<sup>-3</sup> for salt water). We then calculated, per site, significant wave height ( $H_{1/3}$ , i.e. the mean of the highest 1/3 of waves recorded) and the mean of the highest percentile as indicator for the maximum wave height for the entire period (see 2.1 for results).

## 2.7 Statistical analysis

All analyses were performed in R, versions 3.1.1 (R Core Team, 2014).

### 2.7.1 Survival analysis

We used the Survival-package from R (Therneau, 2014) in order to fit Cox Proportional-Hazard models (CoxPH) on our dataset. We tested for elevation effect and life stage effect, as well as for site effects (wave-exposed versus -sheltered). Furthermore, we introduced inundation time and elevation change as time-dependent co-variates in order to be able to gain insights into the mechanisms interfering with survival.

First analyses with time-dependent co-variables showed opposing effects along the elevation gradient for tidal flat plots and marsh plots. This is why we recoded the initial elevation variable with five levels into a variable with two levels, “tidal flat” and “marsh”, grouping the three tidal flat levels and the two marsh levels, respectively. We report two different parameters quantifying survival: (1) the hazard ratio that results from the CoxPH analyses indicates hazard of dying relative to a reference group. A hazard ratio < 1 indicates less hazard of dying (= better chances of surviving), a hazard ratio > 1 indicates a higher hazard of dying (= less chances of surviving) than for the reference group. (2) In order to report a parameter that is not dependent on survival of a reference group and that can be better compared between sites, levels and life stages, we estimated the loss rate,  $\epsilon$  (day<sup>-1</sup>), assuming an exponential decay function, as:  $\epsilon = \frac{1}{n} \sum_i^i (\text{survival time})$ . Here,  $\epsilon$  is the relative loss of transplants per day. The smaller the loss rates the longer the survival.

### 2.7.2 Clonal outgrowth

We compared clonal outgrowth as a proxy for plant performance at both sites. For shoots and seedlings, relative clonal outgrowth was assessed by dividing all new, clonally generated shoots of one plot by the initial number of transplants (i.e. per ten seedlings and eight shoots). For patches, relative clonal outgrowth was calculated by dividing the total number of live shoots by the initial number of live shoots per patch. As a summary value for relative clonal outgrowth over time, we used the area under the curve (AUC) that shows relative clonal outgrowth per plot and life stage as function of time: in this way clonal success in terms of number of new shoots (high relative expansion) and in terms of time during which this expansion lasted are considered. AUC values were calculated for each life stage and replicate plot. Differences in AUC between sites were tested for significance with a one-way-ANOVA, both for site overall, and for tidal flat and marsh depending on site. AUC values were calculated using the *pracma*-package in R (Borchers, 2014).

### 2.7.3 Further statistical analyses

Other analyses, e.g. when comparing sedimentation rates between levels, were performed with ANOVAs: one-way-ANOVAs when only site was tested, and two-way-ANOVAs when both, levels and site, were tested.

## 3. Results

### 3.1 Sediment dynamics

Sedimentation dominated within the marsh plots whereas erosion prevailed at the tidal flat plots (Fig. 3). These overall tendencies were, however, variable in time. A two-way-ANOVA showed that there was a significant difference in elevation change between levels ( $p < 0.01$ ), but not between sites ( $p = 0.25$ ).

### 3.2 Survival analysis

#### 3.2.1. Cox Proportional-Hazard Analysis

##### *Survival per life stage*

Median survival time, i.e. the time required until half of the transplants were lost, decreased from 147 to 70 to 35 days for patches, adult rhizome-grown shoots and seedlings, respectively. CoxPH analysis showed that rhizome-grown shoots had a hazard ratio of only 0.22 compared to the seedlings, *ceteris paribus* (i.e. 22 % the hazard of dying of seedlings,  $p < 0.001$ ; Fig. 4). Compared to the patches, on the other hand, rhizome-grown shoots had an increased hazard of dying, with a hazard ratio of 2.6 compared to the patches and seedlings had a hazard ratio of 11.8 compared to the patches ( $p < 0.001$  for both). This indicates a gradient of decreasing survival chances from patches, to rhizome-grown shoots, to seedlings, i.e., a decreasing survival chance with overall size.

##### *Survival per site*

When comparing marsh and tidal flat plots between sites (Fig. 5, 3<sup>rd</sup> column), results for the seedlings and shoots grown from rhizomes showed that survival in the marsh was not site-dependent (no significant site effect for the upper two levels). However, on the tidal flat, significant site effects occurred: seedlings on the exposed tidal flat had a hazard ratio of 0.63 compared to the seedlings on the sheltered tidal flat ( $p < 0.01$ ). For the rhizome-grown shoots, in contrast, the significant site-effect on the tidal flat showed a decreased survival at the exposed site compared to the sheltered site (hazard ratio 1.54,  $p < 0.05$ ). For patches, no significant differences could be detected.

#### *Survival per level*

Survival times for shoots and seedlings were longest on the second highest level, at -0.65 m MHW (hazard ratios of 0.2 to 0.6 compared to the highest level, depending on the subset selected, and with the lowest  $\epsilon$ -values for the respective transect, Tab. 2 and Fig. 5), indicating an optimum for survival for seedlings and rhizome-grown shoots at the second highest level. Patches showed equal chances of survival on the upper three levels, and then an increase in hazard for the lower two tidal flat levels (Fig. 5).

#### *Time-dependent co-variates*

The analysis with time-dependent co-variates was carried out for each observed time step for which the respective sedimentation rates and inundation times have been included in the model. The results show a significant positive correlation between inundation time and hazard for seedlings and patches on the tidal flat, while the correlation is negative for rhizome-grown shoots and seedlings in the marsh (Tab. 3 & Fig. 6). In other words, there is a decrease in survival with increasing inundation time on the tidal flat (i.e. indicative of inundation stress), but an increased survival with inundation time in the marsh (i.e. possibly indicating drought stress). Dry seedlings and shoots had indeed been observed at the marsh plots, especially at the highest level. Regarding elevation change, the only significant correlation was found for seedlings on the tidal flat, with a negative coefficient, indicating that seedlings experienced erosion stress.

#### 3.2.2. Clonal outgrowth

Clonal outgrowth for seedlings was observed, but was very limited in both number and time, given the low survival rate of seedlings (with a maximum of 0.5 new shoots per original seedling for one plot). When comparing sites, levels and grouping for marsh and tidal flats, there were no significant differences in clonal outgrowth (tested with an ANOVA,  $p > 0.05$ ). Similar to the seedlings, patches did not show any significant differences in outgrowth between sites, levels or grouped marsh and tidal flat plots. Rhizome-grown shoots, on the other hand, showed more pronounced clonal outgrowth (Fig. 6 and 7). The maximum clonal outgrowth was of 2.9 new shoots per original shoot for one plot. Differences between sites were not significant. However, when tested for marsh and tidal flats, respectively, significant differences between sites were found for the tidal flat ( $p < 0.05$ ), with significantly more clonal outgrowth at the sheltered site.

## 4. Discussion

In order for establishment of individual plants to succeed, windows of opportunity (Balke et al., 2011; Mateos-Naranjo et al., 2008) are necessary in the form of periods during which species- or life stage-dependent thresholds of abiotic factors are not exceeded during the subsequent phases of colonization (i.e. initial establishment; survival and growth; patch formation). While elevation within the tidal frame is generally acknowledged as a threshold-imposing variable setting a clear limit between (potentially) vegetated and bare areas (Marani *et al.* 2010; Kirwan *et al.* 2010; Fagherazzi *et al.* 2012; Wang & Temmerman 2013), disentangling the underlying controlling factors such as tidal inundation stress and disturbance by waves and sediment dynamics remains challenging (Hu et al., 2015).

The results from our field experiment show that individual seedlings and shoots as well as transplanted patches of *S. maritimus* could not establish in the long-term on the tidal flat at elevations at which continuous marsh vegetation of the same species occurs along the same marsh. We did, however, observe a life stage-dependent increase in survival time. This points to a threshold in biomass beyond which

establishment might have been successful during periods corresponding to a window of opportunity. Furthermore, we see that effects of wave exposure on survival and clonal expansion of transplants might have been negligible within the marsh vegetation, while they might have been important on the tidal flat. With regard to the effects of tidal inundation, our results suggest an inundation stress gradient on the tidal flat but a possible drought stress gradient within the pioneer marsh. Finally, effects of sediment dynamics showed significant erosion stress for seedlings on the tidal flat.

In line with the findings of van Wesenbeeck et al. (2008) for *Spartina anglica*, our results emphasize that establishment chances increase with life stage or biomass, as the patches performed best and the success of seedlings was poorest. Similarly, a size-threshold of patches of *Spartina alterniflora* for recovery and recolonization is known to exist (Angelini and Silliman, 2012). However, as we could not observe any long-term establishment on the tidal flats, the transplants seem to not have exceeded the required species-specific biomass threshold for successful long-term establishment under the prevailing abiotic conditions. This contrasts with other similar transplantation experiments with *Spartina* species, where survival of around 85 % of transplanted seedlings was observed (e.g. Xiao et al., 2010 for *S. alterniflora* tested in the Yangtze estuary). Thresholds for establishment of *S. maritimus* seem to be considerably higher which could be the result of species-specific differences such as rhizome spacing and the annual cycle of massive aboveground biomass decay for *S. maritimus* in winter. Both these characteristics lead to reduced bio-geomorphic feedbacks between vegetation and sedimentation compared to the denser *Spartina* vegetation cover with a less pronounced annual canopy cycle. The fact that *Spartina* species are among the most efficient sediment trappers (e.g. Sanchez et al., 2001 and references therein) generally leads quickly to considerable increase in elevation within a patch, given sufficient sediment supply. Increased surface elevation favours then the production of new clonal modules which was shown to have more influence on survival than changes in inundation stress (Fragoso and Spencer, 2008): the renewal of clonal modules, made possible through sediment deposition, is essential for long-term survival (and expansion) of the clonal plant as they typically do not outlive a two-year period, leading to marsh die-back when renewal is hampered e.g. through prevailing sediment erosion. This effect was shown for *Spartina* (Fragoso and Spencer, 2008) but might also apply for other perennial species such as *S. maritimus*. Given that the latter is a relatively poor sediment trapper, this would then require a relatively big minimum patch size in order to assure sufficient sedimentation and thus long-term survival. This also indicates that in the case of our two study sites, establishment of *S. maritimus* on the bare tidal flat might not be limited by germination or availability of live rhizomes, but by events occurring after initial establishment (Mateos-Naranjo et al., 2008). Furthermore, colonization by seedlings and patch formation are episodic events as they depend on stochastic windows of opportunity which were probably not realized during our experiment (Feist and Simenstad, 2000).

In terms of differing wave exposure between sites, the importance of marsh vegetation in creating a sheltered environment through wave and current attenuation (Möller et al., 2014; Temmerman et al., 2012; Yang et al., 2012) was shown by our results as there was no site effect for either survival or clonal outgrowth of transplants within the marsh. In contrast, on the tidal flat, the differing wave exposure was important for survival as the rhizome-grown shoots had a significantly shorter survival time and were less successful at clonal outgrowth on the tidal flat of the wave-exposed site. That seedlings survived better on the tidal flat of the exposed site might result from the differing sediment properties at both sites: the sandy, well drained sediment of the exposed site might create more favourable conditions for the seedlings than the silty, rather water-logged sediment of the sheltered site. Thus, while wave-exposure should be more favourable for survival at the sheltered site, the local soil conditions might have counteracted this advantage and may have led to a faster die-off.

Inundation stress increases with decreasing elevation on the tidal flat, and our results indicate that it significantly hampers survival. In the marsh, however, it might be drought stress that limits survival of individual shoots and seedlings once inundation frequency falls below a threshold, probably of around 90 % (see Tab. 1). Indeed, dry shoots and seedlings were observed at the marsh plots, which was not the case at the tidal flat plots. This seems odd given the fact that established marsh vegetation does grow and thrive at the exact same spot. However, the established marsh vegetation benefits from clonal integration

(Amsberry et al., 2000; Bertness and Hacker, 1994; Burdick and Konisky, 2003) and probably has deeper roots than the transplanted plants. This implies that the latter are more dependent on local abiotic conditions such as water supply than the neighbouring established marsh vegetation which can also access distant resources (Burdick and Konisky, 2003; Charpentier and Stuefer, 1999), possibly buffering the local effects of drought stress. When looking at survival and clonal expansion per level, we find an optimum at the second highest level (Fig. 5 & 6, Tab. 2). This may result from an overlapping effect of facilitation of survival through the shelter provided by the marsh vegetation on the one hand (making the marsh a safer environment protected from waves, currents and erosion events), and potentially increased drought stress higher up in the marsh on the other hand, leading overall to the most favourable conditions for establishment in the lower part of the marsh.

Regarding erosion stress, sediment dynamics have been suggested to be the bottleneck for seedling establishment (Balke et al., 2013; Han et al., 2012; Hu et al., 2015; Zhu et al., 2014). While Balke et al. (2013) also found a potential negative impact of high accretion on seedling survival, we were only able to prove statistically an impact of erosion, although burial was observed within the marsh. In agreement with the present findings, their results also showed a much more severe impact through erosion than through accretion. As our results show only significant effects for seedlings, this implies further that erosion rates during our observation period reached a life stage-dependent threshold for seedlings on the tidal flat. In contrast, rhizome-grown shoots and patches, which root deeper than seedlings (*c.* 15 cm and 30 cm for shoots and patches, respectively, vs. *c.* 5 cm for seedlings on the day of transplantation, personal observation in the field), did not appear to be significantly influenced by this. This is in agreement with the 'windows of opportunity' concept, which describes that disturbance thresholds gradually increase with plant size (Balke et al., 2014, 2011; Hu et al., 2015). However, we did also observe local scour around transplants of all three life stages that might have had a stronger control on uprooting than large-scale erosion of the tidal flat.

Finally, it is noteworthy that none of our transplants on the tidal flat survived in the long term, meaning that colonization of the tidal flat did not exceed the end of the growing season of 2011. This outcome contrasts with transplantation experiments using species such as *Spartina anglica* or *alterniflora* (e.g. van Wesenbeeck et al., 2008; Xiao et al., 2010) which are generally successful and have high survival rates even for seedlings. In the marsh, we can expect the patches to have survived in the long term, and possibly also certain rhizome-grown shoots. This was not followed up in the following growing season as it had become impossible to distinguish transplants from surrounding marsh vegetation that had grown into our plots despite the root cloth. As loss rate  $\epsilon$  was shown to be life stage-dependent, we can nonetheless presume the existence of biomass thresholds for successful establishment of *S. maritimus* on bare tidal flats. The fact that no transplants survived on the tidal flats in the long term despite the fact that these elevations covered the elevation range at which successful clonal expansion of the marsh was observed, relates to the mechanisms of clonal integration and, possibly, of alternative stable states.

## 5. Conclusions

Our results show that contrary to successful transplantation experiments with other intertidal plant species such as *Spartina anglica*, *S. alterniflora* and *S. densiflora*, biomass thresholds for successful *Scirpus maritimus* establishment seem to be higher and were not reached during the experiment resulting in no survival at the end of the growing season. However, a life stage-dependent increase of survival time from seedlings to patches was observed, which reflect a size dependency of survival thresholds. The actual bottleneck for establishment might not be initial colonization, mimicked by the transplantation, but disturbances and limiting environmental conditions occurring after initial establishment. The effect of clonal integration might be a key parameter in the colonization of tidal flats by *S. maritimus* given that a general clonal expansion of the marsh edge was observed at elevations at which survival of transplants on the tidal flat did not succeed. Furthermore, the sheltering effect of surrounding marsh vegetation compensated the differing exposure of sites as survival and clonal expansion within the marsh did not differ for any of the life stages while significant differences were found on the tidal flat.

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## Tables

**Table 1:** Overview of tidal characteristics along the elevation gradient of the transplantation transects at both sites obtained from continuous water level measurements for the monitoring period (April-November 2011).

Site	Level (m MHW)	Tidal characteristics				
		Inundation frequency (%)	Mean inundation depth (cm)	Mean inundation time (min)	Mean dry time (min)	Maximum dry time (min)
<b>Sheltered</b>	-0.40	84	42	87	635	6782
	-0.65	96	67	124	606	3006
	-1.00	100	99	159	571	1406
	-1.30	100	129	190	539	644
	-1.60	100	159	221	508	589
<b>Exposed</b>	-0.40	83	42	88	637	7478
	-0.65	96	69	126	603	5212
	-1.00	100	99	162	567	1406
	-1.30	100	129	195	535	640
	-1.60	100	159	226	503	600

**Table 2:** Results of Cox Proportional-Hazard Models (hazard ratios, CoxPH) and  $\epsilon$  (day<sup>-1</sup>) on survival of plants per level. The highest level (-0.40 m MHW) represents the base hazard in the models: values < 1 for the other levels indicate decreased hazard (longer survival) at the respective level compared to the reference level while values > 1 indicate enhanced hazard (shorter survival) at the respective level compared to the reference level.  $\epsilon$  indicates average rate of dying per day. p gives level of significance, ns = not significant (p>0.05).

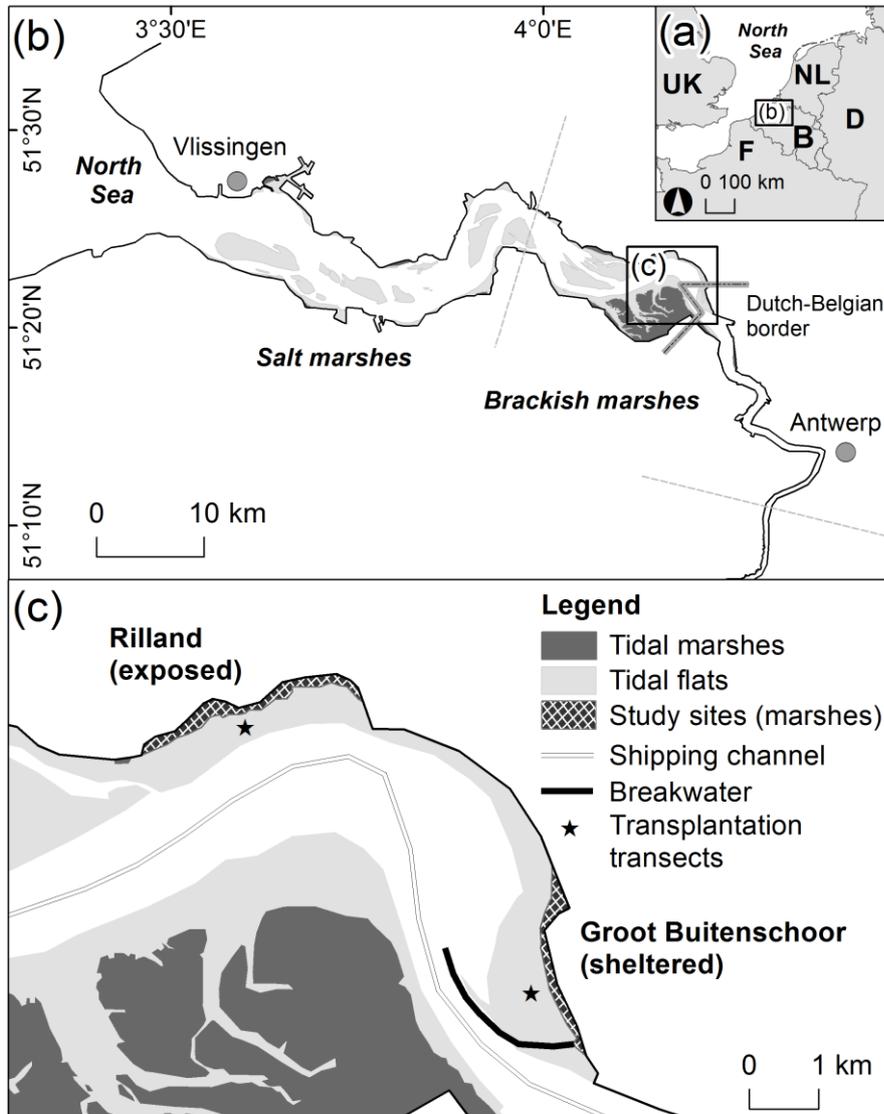
		-0.40 m MHW		-0.65 m MHW		-1.00 m MHW		-1.30 m MHW		-1.60 m MHW	
		CoxPH	$\epsilon$	CoxPH	$\epsilon$	CoxPH	$\epsilon$	CoxPH	$\epsilon$	CoxPH	$\epsilon$
<b>Seedlings</b>	<b>Total</b>	1	0.029	0.58, p<0.01	0.023	ns	0.027	ns	0.034	ns	0.035
	<b>Sheltered</b>	1	0.029	ns	0.023	ns	0.027	2.25, p<0.01	0.044	2.20, p<0.01	0.043
	<b>Exposed</b>	1	0.030	0.42, p<0.01	0.022	0.55, p<0.05	0.026	ns	0.028	ns	0.029
<b>Shoots</b>	<b>Total</b>	1	0.011	0.32, p<0.001	0.007	1.57, p<0.05	0.014	1.66, p<0.05	0.015	2.13, p<0.001	0.018
	<b>Sheltered</b>	1	0.012	0.23, p<0.001	0.007	ns	0.011	ns	0.015	1.79, p=0.05 (ns)	0.018
	<b>Exposed</b>	1	0.010	0.40, p<0.01	0.008	4.65, p<0.001	0.021	2.27, p<0.01	0.016	3.02, p<0.01	0.017
<b>Patches</b>	<b>Total</b>	1	0.006	ns	0.006	ns	0.006	9.55, p<0.01	0.009	6.40, p<0.05	0.009
	<b>Sheltered</b>	1	0.006	ns	0.006	ns	0.007	11.68, p<0.05	0.008	10.47, p<0.05	0.008
	<b>Exposed</b>	1	0.006	ns	0.006	ns	0.006	11.21, p<0.05	0.010	ns	0.010

**Table 3:** Results from the Cox Proportional-Hazard Models with time-dependent co-variables (inundation time and sedimentation rate). *CoxPH* indicates the hazard ratio, *Coeff* indicates if the respective significant correlation is positive (+) or negative (-). *p* gives level of significance, ns = not significant ( $p > 0.05$ ). *Conc.* gives value of concordance of the model, i.e. the part that is explained by our model. Concordance varies from 0 to 1, 0 signifying no explanation and 1 signifying full explanation of observations by the tested model.

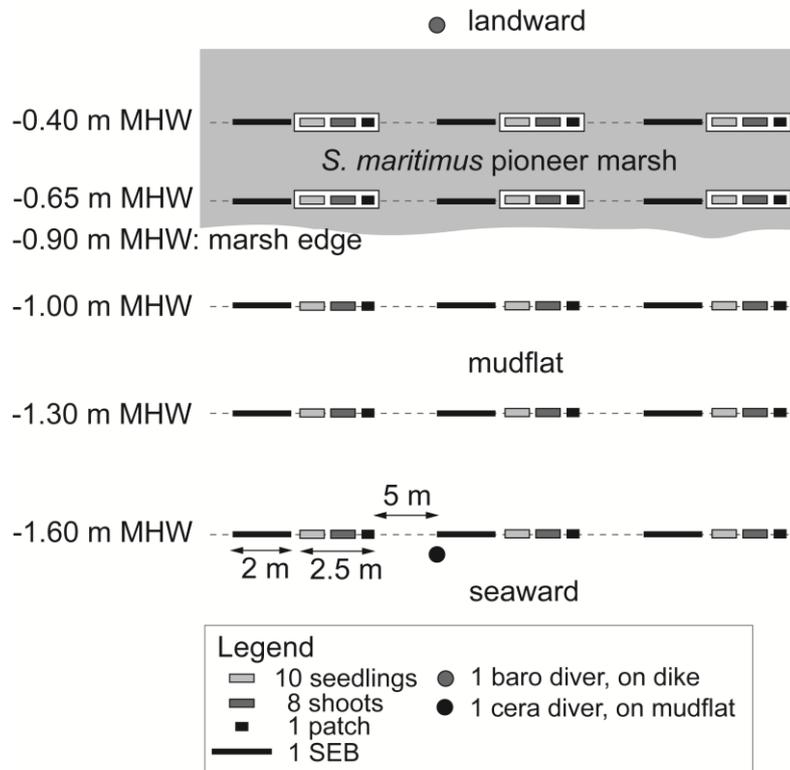
	Marsh			Tidal flat				
	Coeff	CoxPH	p	Conc.	Coeff	CoxPH	p	Conc.
<b>Inundation time</b>								
<b>Seedlings</b>	-	0.99	<0.05	0.57	+	1.01	<0.01	0.60
<b>Shoots</b>	-	0.98	<0.01	0.61			ns	
<b>Patches</b>			ns		+	1.02	<0.05	0.74
<b>Sedimentation rate</b>								
<b>Seedlings</b>			ns		-	0.02	<0.001	0.61
<b>Shoots</b>			ns				ns	
<b>Patches</b>			ns				ns	

## Figures

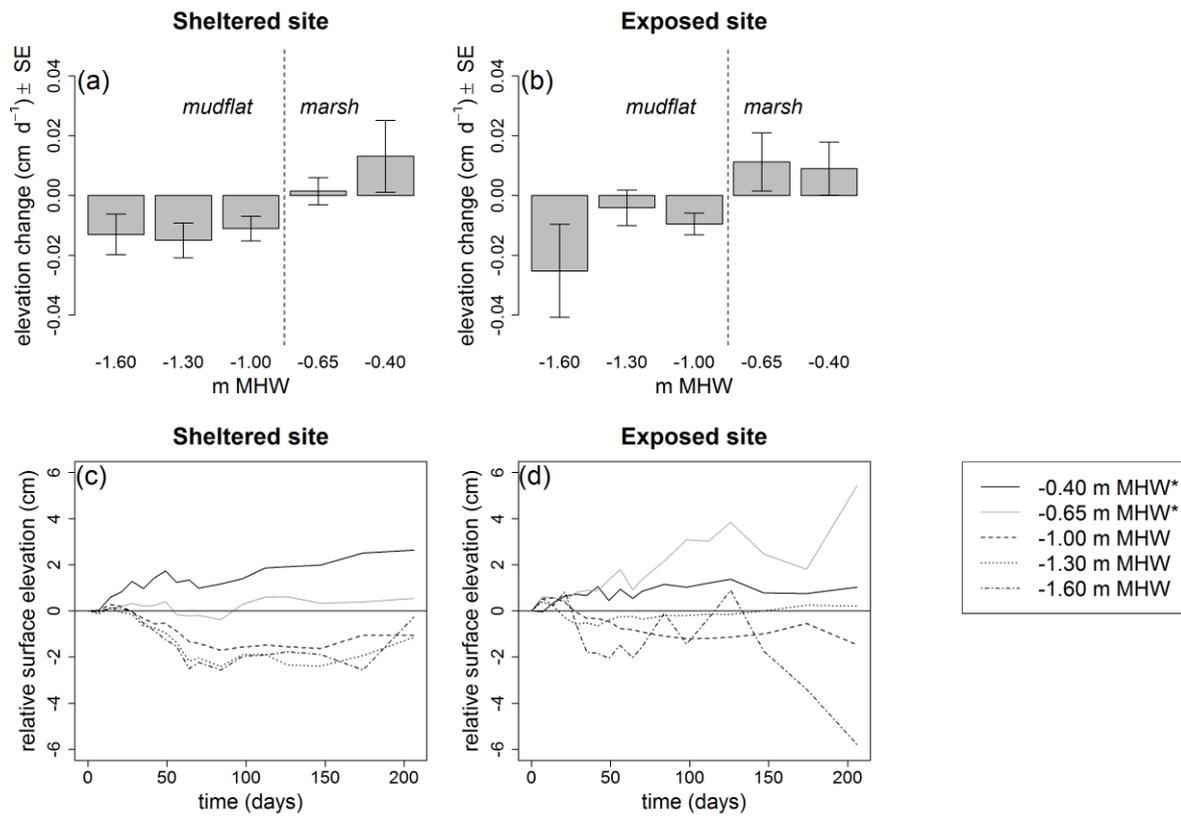
**Figure 1:** (a) Position of the Scheldt Estuary in the Dutch-Belgian border region (indicated by the black square). (b) Overview of the Scheldt Estuary with its tidal flats and marshes downstream of Antwerp to its mouth near Vlissingen. (c) Overview of the location of both transplantation transects (black stars) at both tidal marshes, Groot Buitenschoor and Rilland, with indication of the breakwater and the shipping channel.



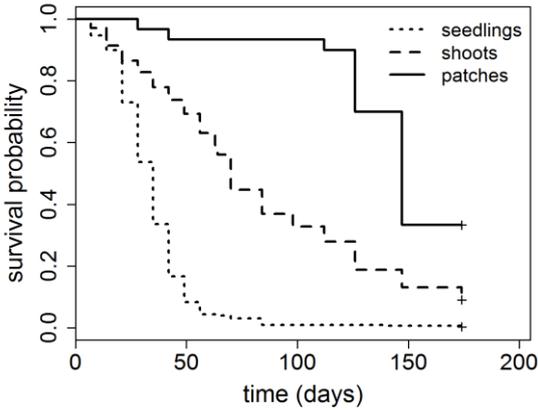
**Figure 2:** Schematic sketch of the experimental set-up. The transplantation was performed at five distinct elevations, of which two were in the marsh vegetation and three on the tidal flat. Three replicate plots were installed per level. Sediment dynamics were monitored with Sedimentation-Erosion-Bars (SEB), water level by a diver on the tidal flat and a baro-diver on the dike for the correction of the atmospheric air pressure.



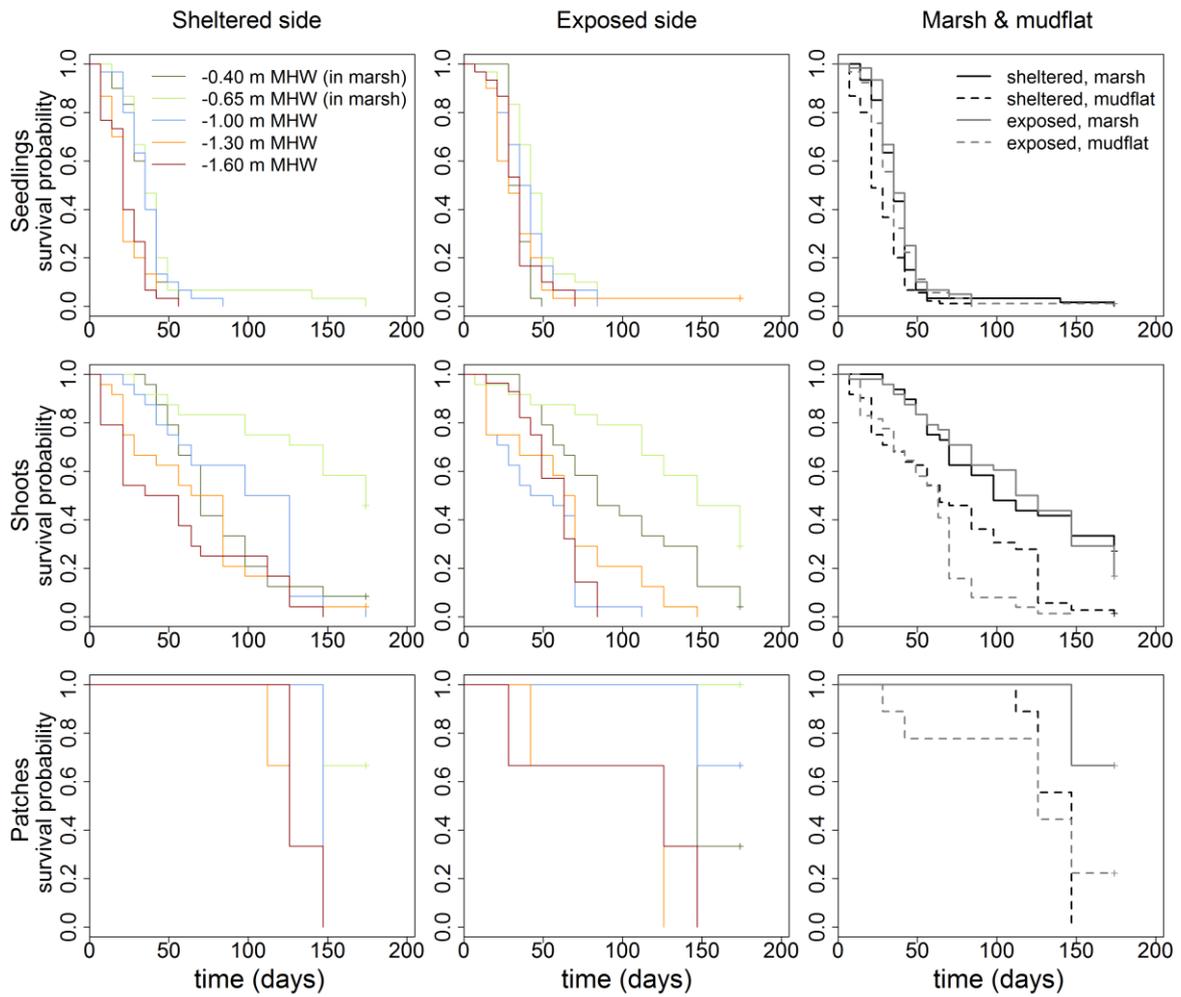
**Figure 3:** Overview of sediment dynamics at the two sites. **(a)** and **(b)**: Mean sedimentation (positive) or erosion (negative) rate  $\pm$  SE per level for sheltered and exposed site, respectively; **(c)** and **(d)**: Net sedimentation (positive) or erosion (negative) per level over time for sheltered and exposed site, respectively.



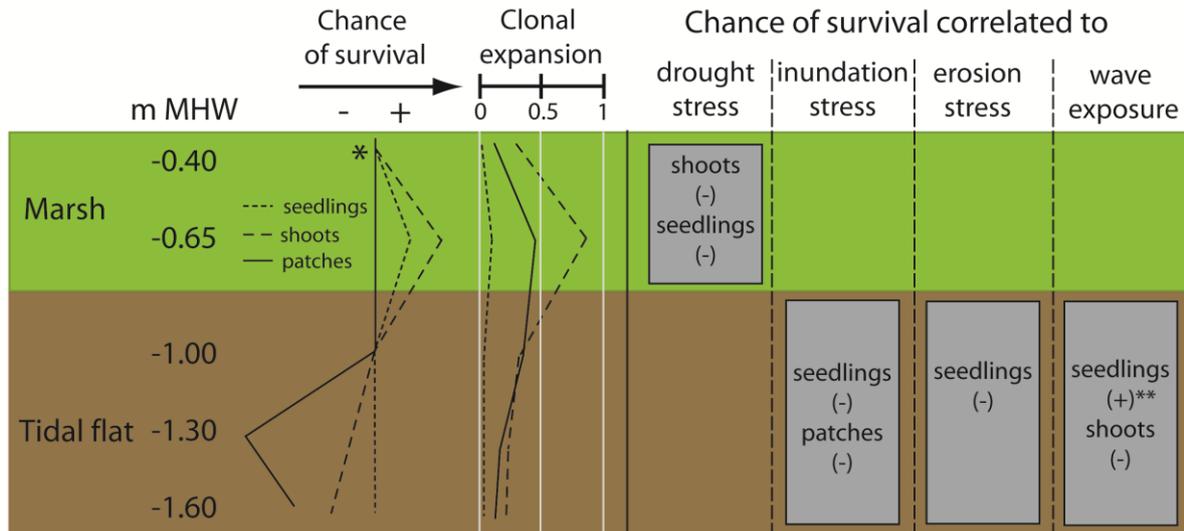
**Figure 4:** Kaplan-Meier-Survival-Curves of the three transplanted life stages, all levels and both sites combined, day 0 being the day of transplantation to the field.



**Figure 5:** Kaplan-Meier-Survival-Curves for the three life stages, divided into both sites (sheltered and exposed) and five levels each (first and second column). The third column shows survival depending on site and environment (tidal flat or marsh) for the three life stages.



**Figure 6:** Conceptual graph of main results. Survival, expressed as the chance of survival relative to the highest level (-0.40 m MHW) for seedlings (dotted line), shoots (dashed line) and patches (continuous line) are indicated per level. Clonal expansion is shown as relative expansion, i.e. clonal reproduction relative to original number of tillers per level. If survival was correlated to (i) drought stress, (ii) inundation stress, (iii) erosion stress and (iv) wave exposure is indicated for marsh vs. tidal flat. Concerned plant life stages are mentioned in the respective boxes. (-) and (+) indicate whether chance of survival increased (+) or decreased (-) in the presence of the stressors.



\* Reference survival: Chance of survival at -0.40 m MHW

\*\* Note that the positive effect of wave exposure on seedling survival might be an artefact due to fast overall seedling die-off (see Discussion).

**Figure 7:** Plots of clonal expansion of the rhizome-grown shoots (new shoots observed on average per original shoot), for both sites (rows) and the five levels (columns). Expansion for each of the three transplantation plots per level is shown by a separate colour. Statistical tests for differences between sites were done based on the surface area calculated under these curves (AUC, see 2.7.2).

