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Unravelling the controls of lateral expansion and elevation change of pioneer tidal marshes

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Abstract

Many overlapping mechanisms have been proposed to control horizontal seaward expansion of marshes and rates of elevation change that are associated with it. Key questions to resolve are: i) whether simple geomorphological conditions such as elevation are a reliable predictor of marsh expansion rates; ii) whether there are seasonal vegetation-induced effects on elevation change (both, increase and decrease of elevation); and iii) how steep the spatial gradient of elevation change is from the bare tidal flat into the vegetated marsh? These questions have been addressed with a two-scale study approach performed on two contrastingly wave-exposed marshes in the Scheldt Estuary (SW Netherlands and N Belgium) where *Scirpus maritimus* is the dominant pioneer species. On the one hand, we investigated the relations between large-scale, geomorphological parameters (elevation, slope) and clonal marsh expansion rates at both sites. On the other hand, we performed a small-scale monthly field monitoring over two years at the same two marshes where we investigated the relations between spatio-temporal variations in vertical elevation change and spatio-temporal variations in vegetation properties along cross-shore transects. We found that at the sheltered site, clonal expansion rates are almost twice as high as at the exposed site. Furthermore, expansion rates at the sheltered site related well to elevation. At the exposed site, this relation was less strong as wave exposure might cause a dominant disturbance. Moreover, we found clear seasonal elevation change patterns that closely followed the seasonal vegetation cycle, with prevailing increase in elevation in summer when above-ground biomass was maximal and decrease in elevation in winter when plant shoots had largely decayed. Especially at the exposed site, the presence of vegetation has a positive effect on increase in elevation within the marsh. Finally, our results show that clonal marsh expansion succeeded at elevations for which previous studies at the same locations showed that individual shoots could not establish, emphasising the importance of clonal integration for both survival and lateral expansion in disturbance-driven ecosystems.

Keywords: clonal marsh expansion; clonal integration; elevation change; wave exposure

1. Introduction

Tidal marshes provide many ecosystem services, ranging from natural habitat for specialized fauna and flora, to CO₂ sequestration, recreation and coastal protection (e.g. Barbier et al., 2011; Costanza et al., 2014; Möller et al., 2014). Given the increasing worldwide loss of tidal marshes over the last decades (e.g. Barbier et al. 2008; Kirwan and Megonigal, 2013), understanding the mechanisms determining horizontal seaward marsh expansion or landward retreat has gained importance. While vertical evolution of marshes has been well studied and extensively modelled, the mechanisms triggering horizontal expansion or retreat are still poorly understood (see review by e.g. Fagherazzi et al., 2012). For instance, a marsh can be vertically accreting while, at the same time, the marsh edge is horizontally retreating (Van der Wal et al., 2008). This illustrates to what point the two mechanisms – vertical versus horizontal evolution – are not necessarily coupled (Fagherazzi et al., 2013).

Horizontal expansion of marshes onto adjacent bare tidal flats can occur through two different mechanisms. On the one hand (1), individual plants can establish. This can happen when seeds disperse, deposit and germinate, or when pieces of rhizomes that become detached from the marsh settle on the mudflat. Marsh expansion by individual plant establishment typically succeeds in the presence of so-called windows of opportunity (Wiehe, 1935; Mateos-Naranjo et al., 2008; Balke et al., 2011 for mangroves), which are periods without disturbances that are long enough for plants to establish and to outgrow a critical biomass level (i.e. a critical root length) at which they can survive subsequent disturbance events (van Wesenbeeck et al., 2008; Balke et al., 2011, 2013 for mangroves; Hu et al., 2015). Disturbances and environmental stressors potentially limiting successful plant establishment in tidal systems are caused for instance by cyclic tidal inundation, storm surges, currents and waves, and the erosion caused by these water movements. On the other hand (2), the mudflat can also be colonized by lateral clonal propagation of the marsh edge: many perennial marsh plants can reproduce clonally, i.e. produce new shoots from the existing or expanding root system. By lateral below-ground expansion of rhizomes and growth of new above-ground shoots from these rhizomes, the entire marsh edge can advance onto the adjacent tidal flat. These pioneer shoots are connected to the existing marsh through their roots, which has an advantage compared to individually established shoots or seedlings: if they are connected to a sufficiently large patch or marsh they benefit from clonal integration (e.g. Bertness and Hacker, 1994; Amsberry et al., 2000; Burdick and Konisky, 2003). This means that shoots that are clonally connected to each other can

avoid local physical and biological stresses by accessing distant resources. Through clonal integration shoots can then establish and survive in conditions (e.g. critical inundation depth, exposure to waves or currents, sulphide or salinity stress) in which individual shoots or seedlings – which do not benefit from clonal integration – cannot survive.

Colonization of bare intertidal mudflats by either of the two colonization strategies is known to be related to elevation relative to mean sea level or mean high water (MHW) as this is directly related to hydroperiod (e.g. Wiehe, 1935; Burdick and Konisky, 2003; Cox et al., 2003; Mateos-Naranjo et al., 2008; Wang and Temmerman, 2013). Longer hydroperiod linked to lower elevation leads, as direct effect, to higher inundation stress on the plants, and has furthermore indirect consequences such as a longer exposure to wave action or tidal currents. This, in turn, can then lead to higher risks of erosion of the sediment bed and to higher drag forces acting on the plants. These two mechanisms – erosion and drag forces on shoots – can, separately or in combination, potentially prevent plant establishment or provoke uprooting of established plants (e.g. Bouma et al., 2009a; Friess et al., 2012; Balke et al., 2013 for mangroves; Silinski et al., 2015a).

The presence of once established vegetation triggers positive feedbacks between vegetation and increase in elevation: the vegetation will reduce flow velocities and attenuate waves, which promotes increased sedimentation within the vegetation; this enhances surface elevation within the vegetation, which, in turn, creates better growing conditions for the vegetation as it is exposed to less and less tidal inundation, etc. (e.g. Redfield, 1972; Morris et al., 2002; Bouma et al., 2009b; Balke et al., 2014). It is thus generally expected that sedimentation prevails within the marsh due to the flow and wave attenuating effects of the continuous vegetation cover. Furthermore, also the plants themselves can add to an increase in elevation by root production (Morris et al., 2002; Kirwan and Guntenspergen, 2012) and marshes in sediment poor estuaries such as in New England (USA) are known to have grown up with sea-level rise over millennia due to peat accretion, i.e. accretion of (self-produced) organic material (Redfield, 1965; Kirwan and Guntenspergen, 2012). In contrast, these positive feedback mechanisms are absent on the mudflat, except possibly during spring when biofilms can temporarily stabilize the bare sediment (Paterson, 1989; Le Hir et al., 2007; Rietkerk and van de Koppel, 2008; Marani et al., 2010). Over the long term, this would imply that surface elevation increases in the marsh, while only small net surface changes occur on the dynamic mudflat. In certain situations, however, large sediment supply, elevation and local hydrodynamics may

result in higher elevation increase on the low-lying bare tidal flat than within the high-lying vegetated marsh, inundation time being here the driving factor for sedimentation and increase in elevation (e.g. Cahoon et al., 2011).

While establishment of individual plants on bare mudflats has been investigated in a series of flume studies and field experiments (Mateos-Naranjo et al., 2008; van Wesenbeeck et al., 2008; Xiao et al., 2010; Balke et al., 2011 for mangroves; Zhu et al., 2014; Silinski et al., 2015a; 2015b), detailed field studies on horizontal clonal marsh front expansion and its interactions with vertical elevation change in the expanding pioneer marsh zone are still lacking, despite its potential overriding importance for determining the marsh range (Callaghan et al., 2010). The aim of this paper is to elucidate bio-geomorphic processes influencing horizontal seaward expansion and vertical elevation change of pioneer marshes. We study this using the Scheldt Estuary (SW Netherlands and N Belgium) as model, where *Scirpus maritimus* L. Palla is the dominant pioneer species. Three main questions are addressed: (1) can rates of horizontal, seaward clonal expansion of pioneer marshes be explained by simple geomorphological parameters (elevation at the marsh edge, affecting hydroperiod; slope of the mudflat, affecting transformation of approaching waves and hence affecting wave exposure at the marsh edge) be used as proxy for predicting rates of horizontal, seaward clonal marsh expansion; (2) can rates of vertical elevation change within pioneer marshes be explained by temporal (seasonal) variations in plant properties; and (3) how steep is the spatial gradient in rates of vertical elevation change in the transition zone from bare tidal flat to vegetated pioneer marsh? A two-scale study approach was used to answer these questions: on the one hand, we investigated the relations between large-scale, geomorphological parameters and clonal marsh expansion rates at a wave-sheltered and wave-exposed site; on the other hand, we performed small-scale field measurements with a high spatial (meters) and temporal (monthly) resolution on the relations between spatio-temporal variations in vertical elevation change and spatio-temporal variations in vegetation properties (shoot density and height) along cross-shore transects at the same two pioneer marshes.

2. Materials and methods

2.1. Study sites

Two neighbouring marshes were monitored in the brackish part of the macrotidal Scheldt Estuary: the marsh of Rilland (SW Netherlands) and Groot Buitenschoor (N Belgium) (Fig. 1). These two marshes have each an alongshore length of approximately 3.5 km. By choosing these, we followed a disturbance gradient from wave-exposed marshes at the Dutch site (in the following referred to as exposed site) towards more wave-sheltered marshes at the Belgian site (in the following referred to as sheltered site). For example, significant wave heights ($H_{1/3}$) recorded for one location at both sites during the growing season of 2014 were 5.7 cm and 2.8 cm for exposed and sheltered site, respectively, and the mean of the highest percentile ($H_{1/100}$) were 20.3 cm and 9.7 cm (own measurements). These values were calculated for all wave data gathered during tidal inundation at both marsh edges. These differing conditions arise from two compounding effects (Fig. 1c): (1) the wind fetch of dominant south-western winds is shorter at the sheltered site (8 km versus 2 km for exposed and sheltered site, respectively); and (2), a breakwater protects the sheltered site from direct wave impact from both ship and wind waves, while the shipping channel passes very closely by the seaward limit of the tidal flat at the exposed site. Most parts of these marshes are characterized by a gently sloping marsh-mudflat transition zone, indicative of seaward expansion of the marshes. The sediment surface of the sheltered site consists mainly of silty sediment (> 65 % silt in the top 5 cm layer), while the sediment surface of the exposed site is mainly sandy (on average > 85 % sand in the top 5 cm layer). Annual averaged suspended sediment content in the area is 62 ± 4.3 SE mg L⁻¹ (Maris et al., 2013) and the average tidal range is 5 m. At both sites, *Scirpus maritimus* L. Palla is the dominant marsh pioneer. While it has been reported that the marshes in the Scheldt experienced alternating phases of expansion and retreat over the last century (e.g. Cox et al., 2003; Van der Wal et al., 2008), a continuous clonal expansion over large alongshore stretches of the two studied marshes has been observed over the period of 2006-2014 (personal communication by Hug van Beek and own observations since 2010).

2.2. Studied species

Scirpus maritimus L. Palla (also known as *Bolboschoenus maritimus*) is a perennial clonal plant typically growing in the pioneer zones of brackish marshes. It forms dense clonal root-networks through the production of rhizomes and tubers, from which ramets grow. These ramets appear as new shoots in early spring (typically by the end of March in the Scheldt Estuary, personal observation), and can grow to a size of up to 2 m in July and August when they reach the peak of their annual biomass cycle. From September onwards they die back and break off until only dead above-ground ramets of around 20 cm are left in February. The below-ground root system survives the winter and new ramets grow from the tubers with the onset of the next annual growing season. This means that *S. maritimus* shows a marked annual pattern of aboveground biomass production and decay (Charpentier et al., 2012, 2000).

2.3. Large-scale marsh expansion rates

In order to measure the rates of clonal marsh expansion, the position of the entire marsh edges of the wave-exposed and wave-sheltered sites were monitored by the means of a high-precision GPS (real time kinematic GPS, with ± 1 cm accuracy; RTK-GPS in the following) at the end of the growing seasons of 2011 and 2013, i.e. in August and September, respectively. The GPS position was corrected using GSM signals from the SmartNet provider. The GPS coordinates of each measured point along the marsh edge were recorded in the Dutch coordinate system, Rijksdriehoekscoördinaten (RD) and at an alongshore interval of 5 to 10 m. In total, a distance of around 3.5 km per marsh edge was covered. Creeks cutting through the marsh edge were ignored in this approach.

In a GIS (ArcMap 10.1, ESRI), we investigated the relation between marsh expansion rate and potential driving geomorphological variables (elevation at the marsh edge, affecting hydroperiod; slope of the mudflat, affecting transformation of approaching waves and hence affecting wave exposure at the marsh edge). In a first step, we converted the unevenly spaced RTK-GPS marsh edge points of both years into a line each and then the line of the 2013 marsh edge into 1000 evenly spaced points per site (approximately 4 m interval between two successive points at both sites). Of these points, we then selected those at which *S. maritimus* was present from 2011 to 2013 and at which expansion had occurred. This selection left us with 72 % and 79 % of points for the sheltered and exposed site, respectively. We then calculated the

marsh expansion rate that had occurred in each point since 2011 by assessing the shortest distance between the points of 2013 to the marsh edge of 2011. Furthermore, to assess if marsh expansion rates can be derived from elevation at the marsh edge, we interpolated the elevation of the original marsh edge points of 2013 (Kriging-interpolation, 1 m x 1 m) and extracted the interpolated values to the generated equally spaced marsh edge points of 2013 (elevation at marsh edge in the following). Based on a LIDAR-based DEM (with a horizontal resolution of 2 m x 2 m and a vertical error of maximum ± 15 cm; provided by Rijkswaterstaat), we calculated the slope between the marsh edge of 2011 and 1 m below each point along the marsh edge of 2011. The range of 1 m elevation below the marsh edge was chosen given the highest expected waves at the marsh edges of both sites during a normal annual cycle without any major storm events (around 50 cm at the exposed site vs. around 30 cm at the sheltered site, own measurements performed in 2014). From that depth onwards (i.e. around twice the incoming wave height), interference of the sediment surface with the waves can be expected, which might then influence the wave breaking stage and wave energy that reaches the marsh edge. As it turned out in later analyses that large-scale slopes calculated for different distances to the marsh edge (in the order of 50 to 300 m onto the tidal flat) were highly correlated, the fact of having chosen one specific elevation criterion for slope calculation will not affect the outcome of the analysis. The advantage of this approach is the full spatial coverage of both marsh edges and mudflat. However, it needs to be considered that the calculated slopes may include relatively large errors, given the limitation in vertical precision of the LiDAR data.

2.4. Small-scale marsh expansion and elevation changes

We studied the interactions between seasonal variations in above-ground shoot height and density, on the one hand, and elevation changes, on the other hand, at the transition from bare mudflat into an expanding marsh. In 2011, five transects were installed at both the exposed and the sheltered site (Fig. 2). They were initially 8 m long, of which 5 m were in the marsh and 3 m on the mudflat. As the marshes expanded during the monitoring period, we extended them in December 2012 onto the mudflat to a full length of 12 m and 14 m at the exposed and sheltered site, respectively. They were monitored monthly from May 2011 until December 2013, with both February measurements missing due to an ice cover on the sediment surface. For the following analyses, however, only the measurements from October 2011 to

September 2013 were used in order to cover two full annual cycles. Along these transects, Sedimentation-Erosion-Bar (SEB) measurements (Fig. 2a-c) were performed in order to quantify elevation changes in the top 1 m of the soil column along these cross-shore transects (Van Duin et al., 1997; van Wijnen and Bakker, 2001). The SEBs were installed to 1 m depth, perpendicularly to the marsh edge and sediment surface elevation was measured at a 20 cm interval. Accuracy of these measurements is in the order of 1.5 mm (van Wijnen and Bakker, 2001; Nolte et al., 2013). These measurements allowed us to calculate monthly elevation changes along the transects. In order to monitor the seasonal patterns of shoot growth and decay, shoot density was counted on 0.4 m x 0.4 m plots installed at a 2 m interval along the transects within the marsh (Fig. 2c). Height of the 10 highest plants per such plot was measured and the position of the marsh edge along the transects was noted. As trampling would disturb the set-up, the SEBs were approached only by one person and always along the same paths, in order to minimize the soil disturbance close to the SEBs.

For a larger scale elevation change assessment, one additional transect of SEBs at each site was monitored from October 2011 to September 2012 (Fig. 2d): two levels within the marsh and two on the mudflat were monitored at the same moments as the cross-shore transects. The four levels of these SEBs lay at distances of approximately 15 m and 5 m into the marsh and 50 m and 150 m onto the tidal flat, and covered an elevation gradient of around 1 m, reaching from -1.3 m MHW to -0.4 m MHW. Each level along these transects consisted of three replicate SEBs of 2 m length that were installed parallel to the marsh edge and next to each other. Along each of these SEBs, 10 points were measured repeatedly. The average of the monthly elevation changes were calculated per SEB, and then averaged per level.

2.5. Statistical analysis

All statistics were performed in R, version 3.1.1 (R Core Team, 2014).

2.5.1. Large-scale comparison between sites

A t-test was applied to the data gathered from the GIS analysis in order to detect differences between sites in mean expansion rate, mean initial mudflat elevation and mean slope to 1 m below local marsh edge. As no strong deviations from normality were observed upon visual inspection of the residuals and as the number of observations was high (> 700 per site), parametric testing could be applied.

In order to test for relations between marsh expansion rates and both geomorphological parameters (elevation and slope), we first calculated a Pearson's correlation coefficient for expansion rate and each of the two parameters. However, as these data are spatially auto-correlated, we fitted in a next step a multiple linear regression model with expansion rate as dependent variable and slope and elevation, as well as their interaction, as explanatory variables. Models were fitted using the `gls` (general linear model) function of the `nlme`-package (Pinheiro et al., 2014) for both sites separately, taking into account spatial auto-correlation in the form of distance along the marsh edge. Spatial auto-correlation was modelled by an exponential correlation structure. An exponential correlation had produced the lowest AIC values among a wide range of possible correlation structures.

2.5.2. Monthly monitoring

In order to detect differences in elevation changes between marsh and mudflat along the cross-shore SEB transects, linear mixed models were fitted. Elevation change was entered as the dependent variable. Date of the measurements was entered as random intercept. The fixed effects were either site or location along the transects (i.e. mudflat versus marsh). These models were fitted using the `lme` function of the `nlme`-package (Pinheiro et al., 2014).

In order to test for the effect of season on elevation change at each site, we fitted a linear model on the data of each site separately. Elevation change was entered as the dependent variable and season (grouped over both years) as well as location along the transect were entered as independent variables. If the interaction term of season and location was significant, we split the dataset into locations and tested for the effect of season. If the interaction term of season and location was not significant, we removed the interaction term and tested the significance of the main effects of season and location.

3. Results

3.1. Large-scale marsh expansion rates

For the period of August 2011 to September 2013 we find mean expansion rates of 1.67 ± 0.03 SE m y⁻¹ for the sheltered site and of 0.99 ± 0.02 SE m y⁻¹ for the exposed site (Fig. 3). The marsh edges at both sites covered an elevation gradient of around 1 m, from -1.4 m MHW to -0.4 MHW, with an average elevation of -0.92 ± 0.01 SE m MHW and -0.77 ± 0.01 SE m MHW for sheltered and exposed site, respectively. The slope leading to 1 m below the local marsh edge was on average 0.7 ± 0.08 SE % at the sheltered and 0.5 ± 0.07 SE % at the exposed site. The mean of these parameters differed significantly between sites (t-test, $p < 0.001$ for all).

The sheltered site shows a positive correlation between expansion rate and elevation of the mudflat (Pearson's correlation coefficient, $r=0.69$) and a negative correlation between expansion rate and slope ($r=-0.42$) (Fig. 4). At the exposed site, on the other hand, correlations are lower ($r=0.39$ and 0.15 , respectively).

The effects of slope and elevation on expansion rate were modelled using a linear mixed model with expansion rate as dependent variable. In order to correct for spatial auto-correlation we specified an exponential correlation structure. At both sites, the model showed no significant effects of slope. The effect of elevation on marsh expansion rates, in contrast, was significant along both marsh edges, but of better explanatory value at the sheltered site ($R^2=0.15$ and $R^2=0.47$ for exposed and sheltered site, respectively, with $p < 0.001$ for both) (Table 1). The interaction between these terms (elevation*slope) was significant ($p < 0.001$) at the sheltered site, and the overall model resulted in an R^2 of 0.35 (see Table 1). This indicates that the effect of elevation is not uniform across all values of slope.

3.2. Small-scale marsh expansion and elevation changes

Seasonal patterns of elevation change and vegetation growth are shown for two representative transects (out of ten that were monitored in total) for the wave-sheltered and -exposed site (Fig. 5). A clear seasonal vegetation cycle was observed: average shoot heights varied from around 0.2 m just before the onset of the growing season in April (i.e. the heights of the remains of dead stems from the previous year), to

around 1.5 m at the peak of the growing season in August during the monitored period. Shoot density also followed a seasonal pattern with higher densities in summer than in winter, which was, however, not as pronounced as for shoot height. At the sheltered site, rates of elevation change followed well the seasonal vegetation cycle with positive peaks (=increase in elevation) at the onset of the growing season and negative peaks (=decrease of elevation) in winter. At the exposed site, the temporal patterns in elevation change were more variable, i.e. less related to plant properties.

Monthly elevation changes averaged over all transects of each site and over the entire monitoring period were more than ten times higher at the sheltered site than at the exposed site (Table 2), with net increase in elevation dominating the transects. Within the marsh, differences between sites were smaller than over the full transects, the sheltered site exceeding the exposed site only by a factor 3. On the mudflat, differences were bigger, due to a net negative elevation change at the exposed site.

Based on the annual growing cycle of *S. maritimus* (Fig. 5), elevation changes were compared assuming two seasons: the growing season ("summer", April-September) and the season during which *S. maritimus* dies off and decays ("winter", October-March). During winter months, when vegetation decayed and decreased in shoot height and density, elevation change patterns were similar at both sites (Fig. 6). In summer, when vegetation is highest and densest, elevation changes were higher at the sheltered site compared to the exposed site. Furthermore, while elevation changes did not differ significantly between seasons at the exposed site (linear model, $p > 0.05$), the sheltered site shows significantly higher elevation changes in summer (increase in elevation) compared to winter (decrease of elevation) (linear model, $p < 0.001$). On the mudflat of the sheltered site, the differences between winter and summer were significantly more pronounced compared to the seasonal differences in the marsh (linear model, $p < 0.001$). These results suggest that the key determinant for elevation change at the exposed site is the location along the transect (marsh or mudflat), while the key determinant for elevation change at the sheltered site is season (summer or winter). Furthermore, similar elevation changes occur at both sites during the summer seasons of both years. In winter, however, elevation changes differ between the two years (Fig. 6).

Elevation changes grouped by distance classes along the cross-shore transects show clear site effects, with higher rates at the sheltered than at the exposed site over the entire transect (Fig. 6, bottom panel). Over the relatively short distance covered by our transects, elevation changes at the sheltered site increased into both directions with distance from the marsh edge, i.e. both with increasing distance into the vegetated marsh and with increasing distance onto the bare mudflat. In contrast, at the exposed site, slight negative rates (decrease of elevation) prevailed on the mudflat, with a shift towards positive rates (increase in elevation) into the marsh. The large-scale comparison of elevation changes within the marsh and on the mudflat shows no significant differences between marsh and mudflat plots during the winter season at both sites (Fig. 7). In summer, however, the elevation changes within the marsh are significantly higher than on the mudflat. Furthermore, clear seasonal differences appear for the marsh plots at both sites: in summer, when vegetation is highest and densest, elevation increased, while elevation changes varied around zero during the winter season.

4. Discussion

The presence of vegetation usually leads through positive feedbacks to sedimentation within the vegetation (e.g. Sanchez et al., 2001; Bouma et al., 2009; Balke et al., 2014) and thus to increase in sediment surface elevation. In contrast, only small net tendencies in elevation change are usually observed on the bare tidal flat. However, little is known on the steepness of the spatial gradient of elevation change close to the marsh edge, or on the seasonal variability of these small-scale processes, despite its importance for marsh expansion (Callaghan et al., 2010). Moreover, the mechanisms controlling horizontal seaward expansion of tidal marshes through clonal expansion from the marsh edge, and its interactions with vertical elevation change in the expanding pioneer marsh zone is to our knowledge still lacking. In addressing this question we show that i) the horizontal marsh expansion rate at the wave-sheltered site was almost twice as high as at the wave-exposed site, and ii) that elevation at the marsh edge was a better proxy for marsh expansion rates at the sheltered site than at the exposed site, while iii) slope could not be related to the expansion rates found at both sites. The results of the monthly small-scale cross-shore monitoring suggest that the key determinant for elevation change at the exposed site is the location along the transect (vegetated marsh or bare mudflat), while the key determinant for elevation change at the sheltered site is season (summer or winter).

4.1 Elevation and slope as proxies for marsh expansion

Colonization of bare mudflats is typically controlled by elevation relative to MHW. For our study area, Wang and Temmerman (2013) suggested an elevation of around -0.5 m MHW as threshold (within a local tidal range of 5 m) above which a shift from bare mudflat to vegetated marsh becomes likely. In contrast, we find clonal colonization at elevations as low as -1.4 m MHW, and also the average of these elevations lay lower than the reported threshold. These differing elevation thresholds may result from the fact that in the mentioned study, led over a considerably longer timescale (three time steps from 1931 to 2004) and on a bigger area, temporally limited events of large-scale establishment may have played a crucial part. These typically occur rather by seed dispersal and establishment in the presence of a window of opportunity (Wiehe, 1935; Alvarez et al., 2005; Balke et al., 2014) instead of clonal expansion from the marsh edge. The pioneering shoots of a clonally expanding marsh benefit from clonal integration which is why they can resist environmental conditions that may be too extreme for individuals (Bertness and Hacker, 1994; Amsberry et al., 2000; Burdick and Konisky, 2003). This finding is further emphasized by

the fact that clonal marsh expansion occurred successfully at elevations at which colonization of the tidal flat by individual seedlings, shoots and even small patches had failed during the growing season of 2011 (Silinski et al., 2015b).

The fact that elevation was a better predictor for expansion rate at the wave-sheltered site than at the wave-exposed site, relates to the hypothesis that, at the exposed site, the expansion rates may be limited in the first place by waves and that the effect of waves overrules the effect of elevation. At the wave-sheltered location, to the contrary, disturbance through waves may not be a limiting factor for marsh expansion, so that elevation (probably through tidal inundation) was a more important controlling factor for expansion rate.

4.2 Seasonal patterns in elevation change

Given the generally strong positive bio-geomorphic feedback between vegetation and vegetation-induced sedimentation (e.g. Yang, 1998; Mudd et al., 2010; Baustian et al., 2012), the strong seasonal variation of the aboveground biomass of *S. maritimus* was expected to affect elevation change patterns, too: higher standing biomass in summer (obtained through a high and dense marsh canopy, Fig. 5) favours an increase in elevation (e.g. Bouma et al., 2010, 2013; Ysebaert et al., 2011) whereas low standing biomass in winter (obtained through short, leafless and more scattered shoots), combined with local scour at the base of the shoot stems (personal observation in the field and in agreement with flume studies of Bouma et al. 2009), are prone to induce erosion, i.e. decrease of elevation. Furthermore, the production of belowground biomass during the summer months and its partial decay in winter may compound the effect (Kirwan and Guntenspergen, 2012). In accordance to these general expectations, our results revealed relevant temporal and spatial patterns in the marsh-mudflat transition zone. An interesting aspect of the temporal patterns at the sheltered site is the peak in elevation change, both on the tidal flat and in the marsh, at the onset of the growing season, which occurred in both monitored years (Fig. 5). Given that temporal elevation change patterns are similar within the marsh and on the adjacent tidal flat, these peaks cannot be induced by the onset of vegetation growth in April, or changes in vegetation properties in the following months. A possible explanation could be enhanced sediment availability in that period that equally affected elevation change within the marsh and on the tidal flat. Suspended particle matter concentration (SPM), however, do not show any reoccurring peaks in March and April during those two years, nor in spring in general when averaging SPM seasonal data measured close to both field sites over

the last ten years (Maris et al., 2013). Another potential explanation for the elevation change peaks could be the formation of biofilms both in the marsh and on the tidal flat. These biofilms are known to have a stabilizing effect on the sediment surface (e.g. Paterson, 1989; Le Hir et al., 2007; Marani et al., 2010; Paterson, 1989) and are typically found rather on silty than on sandy sediment, i.e. rather at the sheltered than at the exposed site. It has been shown for the Westerscheldt that these biofilms are most abundant in spring and disappear in early summer (De Brouwer et al., 2000; Weerman et al., 2012), which would match our observations. The decline of biofilm and its sediment capturing properties after the spring peak could be related to benthic animals grazing on the benthic biofilm-forming diatoms (Weerman et al., 2012). These explanations remain, however, hypothetical as we cannot base them on own measurements during the monitoring period.

4.3 Spatial patterns in elevation change

It is interesting to note that along the cross-shore transects at the sheltered site, season (summer or winter) mattered more for elevation change than the location along the transect (marsh or mudflat). At the exposed site, in contrast, location mattered more than season, which is also illustrated by the clear shift in both summer seasons from decrease of elevation on the bare mudflat to increase in elevation in the vegetated marsh (Fig. 6). This highlights the wave-attenuating capacities of vegetation and concurring positive elevation change, especially at an exposed marsh (Bouma et al., 2005; Koch et al., 2009; Ysebaert et al., 2011; Möller et al., 2014). The observation that elevation change at the sheltered site in summer did not depend on the location along the transects (marsh versus mudflat) may be a local effect: the elevation changes obtained from the more remote mudflat SEB plots (Fig. 7) revealed a clear contrast between marsh and mudflat plots in summer, with significantly higher positive elevation change within the marsh. This could then further point to specific conditions close to the marsh edge of the sheltered site that favour increase in elevation in summer despite the absence of vegetation. Also here, the presence of biofilms could be a possible explanation for these patterns. These particular conditions at the edge of the sheltered site might then, in turn, affect the expansion rate through the creation of gentler cross-shore slopes.

4.4 Broader temporal context

When considering a longer timescale, our monitoring period, as well as in general the period of 2010-2014, was marked by a clonal expansion of the *S. maritimus*-dominated marsh edge at both sites with only

selective locations of slight marsh retreat (personal observation based on regular field visits in this period). In contrast, considerable horizontal marsh retreat of the pioneer zone in the order of up to several tens of meters had been reported for the period of 1982 to 2004 for the exposed site (Van der Wal et al., 2008). For the sheltered site, it is known that during several years preceding 2004, the *S. maritimus* marsh edge did not move noticeably but expanded since 2006 in the order of locally several meters per year (personal communication Hug van Beek). As marshes are known to alternate between expansion and retreat over time scales in the order of decades (e.g. Allen, 2000; Chauhan, 2009) and based on other long-term studies confirming this alternation for the marshes of the Scheldt Estuary (e.g. Cox et al., 2003; Van der Wal et al., 2008), the momentarily observed prevailing expansion at the two studied sites might be a temporary occurrence. It also needs to be noted that the temporal variability in elevation change observed, both between summer and winter seasons, and between both winter seasons, shows that the temporal scale and the period covered by the monitoring affect the detected elevation change rates and our results need to be interpreted carefully. Furthermore, this also shows that a monitoring campaign of 2 years is actually too short in order to draw definitive conclusions on processes governing these highly dynamic landscapes (Bakker and Olff, 1996).

On a broader scale, our results show that elevation (determining hydroperiod) might be a good indicator for future clonal marsh expansion rates at wave-sheltered sites. At wave-exposed sites, in contrast, the simple effect of hydroperiod might be outplayed by wave-induced disturbance, making predictions of marsh expansion difficult based on elevation alone. Limits to our study might be our simplistic assumption of contrasting wave exposure of both sites as it was based on limited measurements (both in time and in space) and binary definitions of wave exposure ("exposed" versus "sheltered"). Further investigation of wave impact at more locations along both marsh edge stretches and especially at the more exposed site could lead to a better assessment of the wave disturbance. A spatially more differentiated wave exposure gradient might be the missing link for explaining the marsh expansion rates more thoroughly.

5. Conclusions

In the present study, we show that at a wave-sheltered site, a simple morphological parameter such as elevation (determining hydroperiod) correlated well with observed marsh expansion rates and could potentially serve as proxy for predicting (short-term) clonal marsh expansion. At a wave-exposed site, however, this simple parameter could not be reliably correlated to marsh expansion, possibly due to an overruling effect of wave exposure. The seasonality of small-scale cross-shore rates of elevation change demonstrates the importance of marsh vegetation and its wave attenuating capacities at the exposed site: in summer, when *S. maritimus* grows into a tall dense marsh, elevation changes within the marsh were positive (i.e. increase in elevation), while they were slightly negative (i.e. decrease of elevation) on the nearby mudflat. Furthermore, our results show that clonal integration provided by a *S. maritimus* marsh to its pioneering ramets makes colonization of elevations possible at which large-scale colonization by seeds or individual shoots would fail (Silinski et al. 2015b).

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Figure captions

Figure 1: Location of study sites. (a) Position of the Scheldt Estuary in the Dutch-Belgian border region (indicated by the black rectangle). (b) Overview of the Scheldt Estuary downstream of Antwerp up to its mouth near Vlissingen with its tidal flats and marshes. (c) Overview of the location of both studied tidal marshes, Groot Buitenshoor and Rilland, with indication of the breakwater, the shipping channel and fetch length for the dominant SW wind direction.

Figure 2: Sedimentation-Erosion-Bar (SEB) set-up and measurements. (a) Detailed view of the SEB with elevation change between t_x and t_{x+1} . The bar is 2 m long and repeatedly positioned onto the poles that remain in the field and that are assumed to be fixed. Elevation changes compared to a reference moment (e.g. t_x) are assessed by measuring the part of vertically lowered sticks that remains on top of the horizontal bar; (b) Side view of a cross-shore SEB transect. The boxes with dotted outline indicate the position of the bar as it is moved along the transect; (c) Top view of the cross-shore SEB transect. The squares with white dashed outline indicate the location of plant measurements (density and shoot height) next to each SEB pole within the marsh; (d) Top view of the large-scale SEB transect with four levels of three replicate SEB each, i.e. at approximately 15 and 5 m into the marsh and at approximately 50 and 150 m onto the tidal flat.

Figure 3: Expansion rate and geomorphologic parameters. Boxplots of marsh expansion rate (m y^{-1}), elevation at marsh edge (m MHW) and slope to -1 m relative to marsh edge (%) for sheltered and exposed site along the expanding edges of both marshes. The boxes represent the interquartile range of the data and the whiskers delimit 1.5 times the interquartile range. The horizontal line indicates the median. Significance of differences between sites was assessed using a t-test ($p < 0.001 = ***$ for all).

Figure 4: Expansion rate (m y^{-1}) versus elevation at marsh edge (m MHW) and slope towards 1 m below local marsh edge (%) for sheltered and exposed site (left and right column, respectively), along the expanding marsh edges.

Figure 5: Monthly variations in spatially averaged elevation changes (cm month^{-1}) within the marsh (continuous line) and on the mudflat (dashed line), spatially averaged shoot height (cm) and spatially averaged shoot density ($\# \text{ m}^{-2}$) for sheltered and exposed site. The grey vertical rectangles indicate the growing season of *S. maritimus* ("summer", April-September), whereas the white periods indicate the "winter" months (October-March) during which the above-ground shoots decay.

Figure 6: Mean elevation changes ($\pm$ SE cm month⁻¹) per site for the two winter and summer seasons (October-March and April-September, respectively) for the period of 2011-2013 and mean elevation changes ($\pm$ SE cm month⁻¹) per site along the small-scale cross-shore distance gradient from the marsh edge into the marsh and onto the mudflat for the same period. ns = not significant; $p = *** < 0.001 < ** < 0.01 < * < 0.05$ as obtained from a linear mixed model with date as random intercept.

Figure 7: Mean elevation changes ($\pm$ SE cm month⁻¹) per site for the winter and summer season (October-March and April-September, respectively) for the period of 2011-2012 and mean elevation changes ($\pm$ SE cm month⁻¹) per site along a large-scale distance gradient from the marsh edge into the marsh and onto the mudflat for the same period. ns = not significant; $p = *** < 0.001 < ** < 0.01 < * < 0.05$ as obtained from a linear mixed model with date as random intercept.

Tables

Table 1: Results of general linear model analyses with exponential correlation structure correcting for spatial auto-correlation on large-scale relations between marsh expansion rate (dependent variable) and elevation at marsh edge and slope (explanatory variables). Models 1 and 2 explore the effects of initial elevation of the mudflat and of slope to 1 m below the local marsh edge separately, while Model 3 is fitted on both parameters and their interaction term. Cut-off value for significance was at $p=0.05$; ns = not significant.

	Sheltered site		Exposed site	
Model 1	expansion rate = a * elevation + b			
	p	R²	p	R²
elevation	<0.001	0.48	<0.001	0.15
Model 2	expansion rate = a * slope + b			
	p	R²	p	R²
slope	ns	0.18	ns	0.02
Model 3	expansion rate = a * elevation + b * slope + c * elevation * slope + d			
	p	R²	p	R²
elevation*slope	<0.01	0.37	ns	0.17

Table 2: Mean monthly elevation changes ($\pm$ SE cm month⁻¹) along the small-scale cross-shore SEB transects for the 2 year monitoring period (October 2011–September 2013). Averages are given for the full transect extents and for marsh and mudflat separately. The significance of the site effect was calculated using a linear mixed model with date as random intercept.

	mean elevation change		site effect
	($\pm$ SE cm month ⁻¹)		
	sheltered	exposed	p
full transect	0.34 $\pm$ 0.02	0.03 $\pm$ 0.02	<0.001
marsh	0.31 $\pm$ 0.02	0.10 $\pm$ 0.02	<0.001
mudflat	0.41 $\pm$ 0.05	-0.12 $\pm$ 0.04	<0.001

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Highlights

- Higher wave exposure leads to reduced marsh expansion.
- Elevation is a good proxy for marsh expansion rates at sheltered sites.
- Waves might overrule the effects of elevation on marsh expansion at exposed sites.
- At a wave-sheltered site, season (summer/winter) affected elevation change.
- At a wave-exposed site, location (marsh/mudflat) affected elevation change.