

Morphological Variation and Habitat Modification are Strongly Correlated for the Autogenic Ecosystem Engineer *Spartina anglica* (Common Cordgrass)

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ABSTRACT: We explored to what extent morphological variation and habitat modification are correlated for an autogenic ecosystem engineer, which is an organism that modifies its habitat via its own physical structures. The intertidal salt marsh species *Spartina anglica* is well known for its capacity to enhance sediment accretion within its canopy by reducing hydrodynamic energy. Sediment accretion is favorable to *Spartina*, as it reduces inundation stress, enhances soil drainage, and enhances nutrient availability. Shoot density and clonal architecture showed a large variation that was strongly correlated with the marsh elevation and sediment type. This correlation showed that at the lowest elevations at the muddy site, *Spartina* tussocks had the highest shoot density, which is known to be favorable for sediment accretion by reduction of hydrodynamic energy. There was also a strong positive correlation between the amount of sediment that accumulated within a tussock and gully formation around that *Spartina* tussock. The tussocks at the lowest elevations at the muddy site had the lowest lateral tussock growth. At the highest elevations at the sandy site, stem densities were lower and there was a relatively high rate of clonal expansion and marsh formation. At this location, we also observed tussock mortality due to erosion of several of these openly structured tussocks. Based on the observed correlations, we hypothesize that the morphology of *Spartina* represents trade-offs between the capacity to maximize habitat modification through sediment trapping by having a high shoot density versus the capacity to maximize clonal expansion by spreading shoots widely and the capacity of maximal clonal expansion by spreading shoots widely versus the risk of tussock mortality due to insufficient modification of the habitat that makes the tussock vulnerable to erosion. Our results indicated that morphological variation and habitat modification are strongly correlated for the autogenic ecosystem engineer *S. anglica*.

Introduction

Ecosystem engineering has been defined as the direct or indirect physical or chemical modification of the abiotic environment (Jones et al. 1994). By altering the abiotic environment, ecosystem engineers can attenuate abiotic stresses that might especially be beneficial as an adaptation to stressful environments (Jones et al. 1997). As a result of the habitat modification, ecosystem engineers can affect biodiversity significantly (Bertness and Callaway 1994; Bruno and Kennedy 2000; Wright et al. 2002; Castilla et al. 2004). Ecosystem engineers are called autogenic if the habitat modification depends on the interaction between their physical structures and the abiotic environment (e.g., trees in a forest) and allogenic if they modify the environment via an activity (e.g., dam building beavers). Ecosystem engineering may be a by-product caused by the engineers' physical structures or behavior (i.e., often referred to as accidental), but may as well be an adaptation that is the result of natural selection. In case of the latter, the modified environment can

be regarded as an extended phenotype that contributes to the fitness of the ecosystem engineer (Dawkins 1982, 2004; Wright and Jones 2006). Interpreting ecosystem engineering in a proper evolutionary context is complicated and is only recently gaining attention (Day et al. 2003; Odling-Smee et al. 2003; Bouma et al. 2005b; Wright and Jones 2006). In stressful and heterogeneous environments where organisms depend on ecosystem engineering to survive or expand their habitat, morphological variation may be crucial for species to maintain their ecosystem-engineering capacity. The latter is especially true for autogenic engineers with a sessile growth form, as they modify the habitat with their own physical structures and are not able to move. The importance of morphological variation for a species in its autogenic ecosystem engineering capacity has not yet been assessed.

Salt marshes offer an ideal model system to investigate various aspects of autogenic ecosystem engineering by sessile organisms. Salt marshes are characterized by a limited number of plant species that are distributed along an elevation gradient (Adam 1990), which is also a stress gradient due to tidal action and its effects on soil properties (Adam

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1990; Hacker and Bertness 1999; Bouma et al. 2001, 2007). The lowest vegetation zone is inhabited by ecosystem engineers that modify the harsh environmental conditions by aerating the anoxic sediment (Arenovski and Howes 1992; Pezeshki and DeLaune 1993; Holmer et al. 2002), reducing hydrodynamic energy (Leonard and Luther 1995; Bouma et al. 2005a), or increasing the elevation via enhanced sediment accretion (Castellanos et al. 1994; Sanchez et al. 2001). The most dominant ecosystem engineer at the lower zone of most North European salt marshes is *Spartina anglica*. In contrast to various North American marshes (Redfield 1972), many European marshes have relatively high sediment accretion rates within their canopy, making it the main process that increases elevational height (Allen 2000). We focus in this study on autogenic ecosystem engineering in the form of enhanced sediment accretion in sessile *S. anglica* tussocks.

Enhanced sediment accretion within *Spartina* canopies (Castellanos et al. 1994; Sanchez et al. 2001) is the result of decreased current velocity inside the canopy (Leonard and Luther 1995; Bouma et al. 2007). Over time the centrifugally expanding *Spartina* tussocks become raised compared to their surroundings, with the oldest center part being highest (Castellanos et al. 1994; Sanchez et al. 2001). Neighboring tussocks can eventually coalesce and form a continuous sward (Ranwell 1967; Allen 2000). Enhanced sediment accretion within the *Spartina* canopy has a positive effect on plant growth through enhanced nutrient availability (Hemminga et al. 1998) and reduced tidal inundation (Miller et al. 2001). Variation in shoot morphology and clonal architecture that would maximize the sediment trapping capacity in different hydrodynamic and sedimentary environments would be beneficial to *Spartina*. There may be a trade-off related to a shoot morphology and clonal architecture that maximizes sediment accretion rates. Whereas a dome shaped tussock benefits plant growth by reducing the inundation period, enhancing nutrient availability (Hemminga et al. 1998) and improving sediment drainage, a pronounced dome shape may enhance current velocity around the tussock, which may induce erosion. Such erosion may be expected to limit lateral expansion (Van de Koppel et al. 2005). These plant-environment interactions make *S. anglica* an interesting model system to test to what extent variation in shoot morphology and clonal architecture contributes to local ecosystem engineering capacity. As a first step we assessed if the autogenic ecosystem engineer *S. anglica* has variation in shoot morphology and clonal architecture and if such variation is correlated with variation in the abiotic environment, especially for those abiotic parameters

that are typically expected to be influenced by ecosystem engineering by *Spartina* (e.g., sediment accretion). To address these two questions, we compared *Spartina* tussocks at two contrasting sites in the Scheldt estuary, in the southwest Netherlands.

Methods

SITE DESCRIPTION

Research was carried out at a recently formed marsh at a flat Platen van Valkenisse that started to develop around 1980 in the eutrophic Westerschelde estuary in the southwest of the Netherlands. The water at that location is brackish ($\pm 0.5\%$ seawater). Measurements were done at a sandy site and muddy site of the flat. The average elevation of the sandy site was about 1 m higher compared to that of the muddy site. As grain size is indicative for the local hydrodynamics (Herman et al. 2001), the flow velocity at the sandy site was presumably high relative to that at the muddy site.

SHOOT CHARACTERISTICS

From May to August 1999 shoot growth was measured once a month. At both the muddy and sandy sites, at the border and center of four large tussocks (4–6 m diam) and within two small tussocks (1–2 m diam), the length of 30 randomly selected shoots was measured from the surface to the youngest expanded leaf using a ruler.

In October 1999 aboveground biomass was harvested for analysis at 10 large (4–6 m diam) and 10 small (1–2 m diam) randomly chosen tussocks at both the muddy and sandy sites. Harvest was done within 0.25×0.25 m quadrats that were equally divided (10 for large and 4 for small tussocks) along a single transect per tussock. These transects were oriented perpendicularly to the shoreline (northeast-southwest) and crossing the top center of a tussock. Elevation also was measured within the center of each quadrant using a theodolite. Stem, leaf, and spike dry weights were determined after drying at 70°C for 3 d. Leaf carbon and nitrogen content was analyzed with a Carlo Erba element analyzer NA-1500. The nitrogen content of the youngest full-grown leaves were used as an indicator for the nitrogen availability (Silliman and Zieman 2001), which is a function of both the nitrogen concentration in the sediment and stress factors like soil anaerobics (Bradley and Morris 1990).

TUSOCK CHARACTERISTICS

In the summer of 1997 at the muddy and sandy sites, 21 and 20 tussocks, respectively, were marked. Lateral tussock growth (clonal expansion) and

erosion or sedimentation was measured at the north, south, east, and west (NSEW) border of all 41 marked tussocks. Early December 1997 at each of the four sides two 0.5-m long PVC pipes were placed 0.4 m deep into the soil (i.e., 0.1 m above the soil) and at 0.3 m distance of each other just in front of the canopy in such a way that no shoots occurred outside the imaginary straight line between these pipes. Between a set of pipes a lath was placed and the distance between the lath and the nearest shoot was measured. Repeated measurements in July and October 1998 allowed calculation of lateral tussock expansion. To quantify sedimentation or erosion between July and October 1998, the height of each pipe above the lath was measured. The elevation of the tussock at its four (NSEW) flanks also was determined at 0.5 m inside the tussock relative to the elevation 1.5 m outside the tussock taking the imaginary line between each set of PVC pipes as the tussock border.

In August 2003 gully depth was quantified around tussocks at both the muddy and sandy sites. Sixteen tussocks were measured at the muddy site and 7 at the sandy site. Elevation was determined (Trimble LL 1,500 laser system) at the canopy border and at 0.5, 1.0, and 1.5 m outside the tussock. To investigate the relation between gully depth, enhanced sediment accretion and tussock surface, the maximum elevation of each tussock and the longest and shortest tussock diam were measured. Basal elevation of tussocks was calculated as the average of the left and right flanks of a tussock faced in seaward direction. Total accretion of tussocks was calculated as the difference between elevation at the highest point and basal elevation of a tussock.

SEDIMENT CHARACTERISTICS

During the growing season of 1999 a time series of monthly soil measurements was done at the sandy and muddy sites on 4 large tussocks and 2 small tussocks that were randomly selected at each site. The large tussocks were 4 to 6 m in diam, while for the small tussocks the diam varied between 1 and 2 m. These were the same tussocks at which shoot length was measured. Soil samples of 30 cm depth were taken at the center of each tussock and at large tussocks at 50 cm distance from the outer border towards the tussock center. All analyses were done at three depth intervals: 0–10, 10–20, and 20–30 cm. We measured particle size within tussocks using soil samples taken in June 1999. At both the sandy and muddy sites, 2 nearby unvegetated sites served as controls.

For the calculation of the time-integrated sedimentation, we used elevation measurements that were done at plots along transects across tussocks in October 1999 as described above. Time integrated

sedimentation of tussock top centers was calculated by subtracting the relative elevation of the lowest plot from that of the highest plot within each transect. Soil particle distribution was analyzed with a Malvern particle analyzer.

STATISTICS

Linear correlation analyses were used to examine the relationships between tussock dynamics (shoot density, standing biomass, lateral tussock growth, tussock high center accretion, tussock surface area, tussock border sedimentation dynamics [sedimentation or erosion]) and basal tussock elevation relative to mean high water. Correlation analyses were also performed between average shoot parameters (average shoot, stem, and leaf dry mass) and shoot density. For grain size an analysis of variance (ANOVA) was carried out for main effects of site (sandy versus muddy), tussock surface (small versus large), and position within the tussock (border versus center). For shoot density, shoot weight (October 1999), and shoot length (August 1999; other months were omitted) main effects and their interactions were analyzed in addition to the previously mentioned variables. Post hoc analyses were done using Fisher (LSD) test (5% significance level). Differences of carbon:nitrogen ratio means between the sandy and muddy sites were tested using a *t*-test. For all analyses STATISICA software (StatSoft Inc., Tulsa, Oklahoma) was used.

Results

SHOOT CHARACTERISTICS WITHIN TUSOCKS

Plant morphology showed large differences that were strongly correlated with site (sandy or muddy) and position along the elevation gradient (Fig. 1). Shoot density increased with decreasing elevation ($p < 0.0001$), which explained 48% of the variability of shoot density along the elevation gradient. Analyzing the muddy and sandy sites separately showed a similar significant increase of shoot density with decreasing elevation at the muddy site ($R^2 = 0.50$, $p < 0.01$), but this was not the case at the sandy site ($R^2 = 0.03$, $p = 0.47$). Shoot density within tussocks was significantly higher (ANOVA, $p < 0.001$) at the muddy site (304–3,584 shoots m^{-2}) compared to the sandy site (16–2,416 shoots m^{-2}). The range of relative variation in shoot density within tussocks, expressed as the coefficient of variation (standard deviation/mean $\times 100$), was higher at the sandy site (10–116%) compared to the muddy site (12–53%). Despite differences found in shoot density, shoot length in August showed no significant differences between muddy and sandy sites ($p = 0.18$), small and large tussocks ($p = 0.51$), and the center and border of large tussocks ($p = 0.25$).

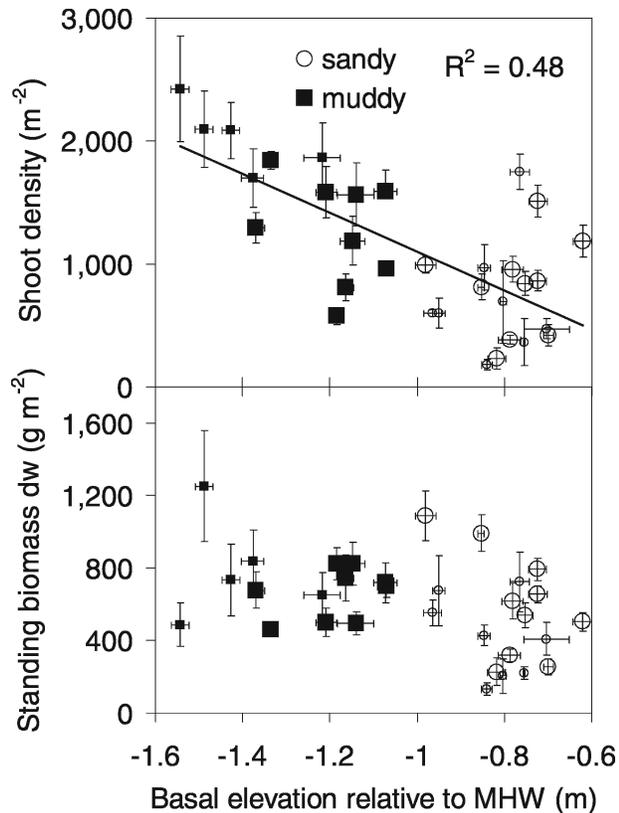


Fig. 1. Mean density and mean dry weight of shoots of small and large individual tussocks (small and large symbols) as a function of elevation relative to mean high water (MHW) at the muddy and sandy sites. Error bars represent ± 1 SE.

Standing biomass was slightly but significantly higher at the muddy site compared to the sandy site (ANOVA, $p < 0.001$). No correlation was found between elevation and the standing biomass per unit surface area (Fig. 1). This indicates that there must be changes in clonal growth and investment in individual shoots across the elevation gradient. We found that the leaf weight per stem was negatively and exponentially related to shoot density ($R^2 = 0.49$, $p < 0.0001$), whereas the mean weight of the stem was not affected ($R^2 = 0.004$; data not shown). Investment in individual stems appeared to be relatively constant across environmental gradients, while investment in leaf weight per stem seemed to depend on shoot density and increased with increasing elevation.

Average nitrogen percentage of youngest full grown leaves was 1.76 ± 0.54 at the muddy site and 2.04 ± 0.35 at the sandy site, while the difference in the carbon:nitrogen ratio between sites was small but significant (24.4 ± 5.6 at the muddy site versus 22.0 ± 3.7 at the sandy site; t -test, $df = 107$, $p < 0.05$) and showed no relation to elevation.

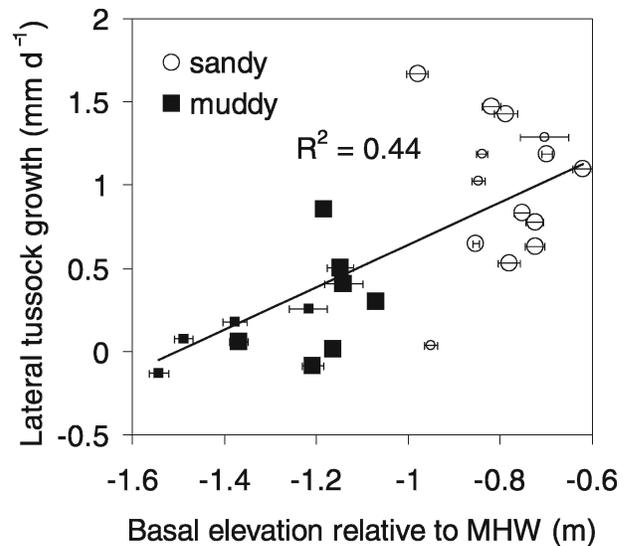


Fig. 2. Tussock expansion as a function of elevation relative to mean high water (MHW) at the muddy and sandy sites. Lateral tussock growth is an average of tussock expansion in four wind directions during 324 days from the beginning of December 1997 until the end of October 1999. Error bars represent ± 1 SE.

ECOSYSTEM ENGINEERING CHARACTERISTICS OF TUSOCKS

Morphological parameters like shoot density may be expected to strongly affect the ecosystem engineering capacity of *Spartina*. While lateral tussock growth increased with increasing elevation ($R^2 = 0.44$, $p < 0.0005$; Fig. 2), we observed a negative correlation between lateral tussock growth and shoot density ($R^2 = 0.45$, $p < 0.0005$), independent of site properties like sediment type (combining Figs. 1 and 2). Between December 1997 and October 1999, highest lateral tussock growth, averaged over north, south, east, and west directions, was found at the sandy site where it ranged between 0.039 and 1.7 mm d^{-1} . At the muddy site it ranged between -0.13 and 0.86 mm d^{-1} , with negative values indicating lateral tussock erosion. The tussocks with the highest shoot densities (i.e., the smallest tussocks at the low end of the muddy site; Fig. 1) were also the tussocks that had the most lateral erosion on the sides of the tussock (Fig. 2).

At the muddy site, a positive linear relation was found between basal elevation and the total, time integrated, sediment accretion ($R^2 = 0.51$, $p < 0.005$; Fig. 3), and a positive exponential relation was found between basal elevation and the overall tussock surface area ($R^2 = 0.38$, $p < 0.05$). A higher basal elevation and a larger tussock surface area are both indicative for an older age of a tussock. These positive relations may suggest that tussock growth at the muddy site is more or less continuous over time, although the variation in overall accretion and

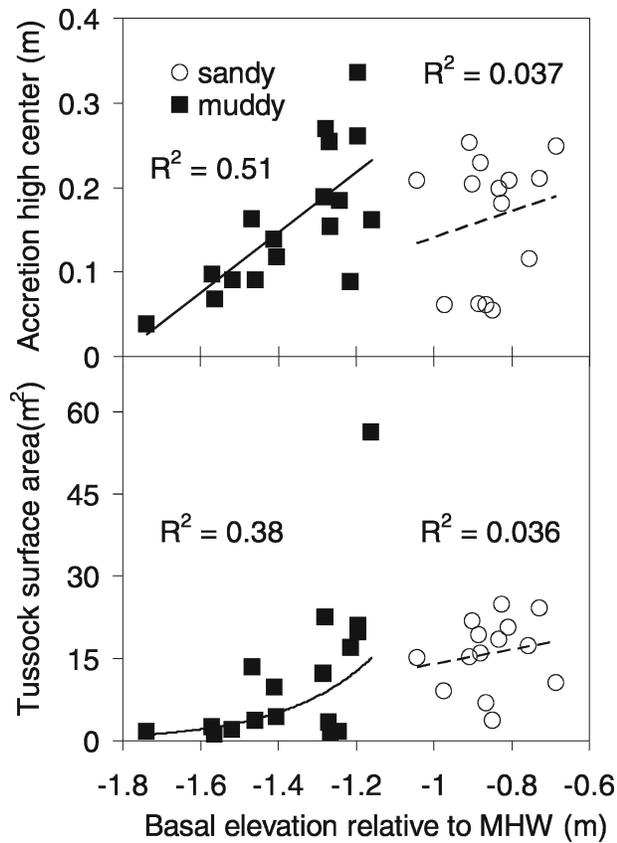


Fig. 3. Relation between relative elevation of the highest point of a tussock (= time integrated accretion) and tussock surface as a function of the elevation relative to mean high water (MHW) of tussock surrounding (basal elevation) for the muddy and sandy sites.

tussock surface area increased with basal elevation. In contrast to the muddy site, no significant relations were found between basal elevation and overall accretion (linear: $R^2 = 0.037$, $p = 0.51$) or tussock surface area (linear: $R^2 = 0.036$, $p = 0.52$) at the relatively elevated sandy site. The lack of a relation was due to large variation in overall accretion and tussock surface area. This may suggest that tussock growth at the sandy site is less continuous than at the muddy site, which may hint at more variable conditions at the sandy site.

Ecosystem engineering by *Spartina* in the form of enhanced sediment accretion within a tussock caused in some of the tussocks a negative feedback effect in the form of gully formation next to the tussocks (Fig. 4). The presence of sedimentation or erosion (i.e., gully formation) at the tussock border was for an important part related to position at the elevation gradient. That is, over a 224-d period between December 1997 and July 1998 a positive relation was found between net sedimentation-erosion rate (average of borders at four wind

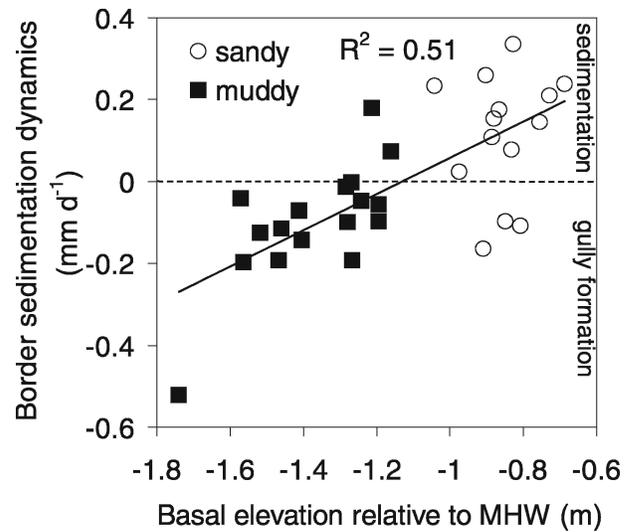


Fig. 4. Tussock border sedimentation or erosion rates (averages over time and borders at four wind directions) of individual tussocks as a function of basal elevation relative to mean high water (MHW) at the muddy and sandy sites. Measurements were done covering a period of 224 days between December 1997 and July 1998.

directions) and basal elevation ($R^2 = 0.51$, $p < 0.0001$). The gullies at the muddy site were always filled with water and ranged from 0.003 to 0.37 m depth, while at the sandy site there were just slight depressions ranging from 0.006 to 0.057 m depth (Fig. 5). At the muddy site, gully depths were positively related to the total, time integrated, sediment accretion of the tussock top ($R^2 = 0.55$, $p < 0.005$), while this relation was not present at the sandy site ($R^2 = 0.14$, $p = 0.41$).

Chances for the complete disappearance of tussocks due to lateral erosion were found to be strongly site specific. As sediment type is indicative for local hydrodynamics, the results at the sandy versus muddy sites are indicative for hydrodynamically more exposed versus sheltered conditions. In May 2003 at the muddy site, 1 out of 20 tussocks that were marked in 1997 had totally disappeared, while at the sandy site 13 out of 21 marked tussocks had disappeared. This total erosion of tussocks occurred solely at tussocks located closest to the seaward edge of the vegetation. At the sandy site, the remaining marked tussocks had grown together and became part of a growing *Spartina* marsh. At the muddy site no marsh formation had occurred and tussocks had just slightly expanded during the measurement period.

SEDIMENT PARTICLE SIZE

Since particle size is indicative for the hydrodynamics at a site and the particle size within a tussock for the modification of those hydrodynamics by

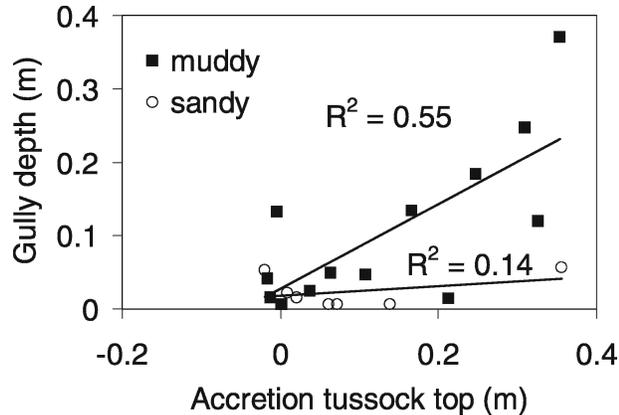


Fig. 5. Gully depth in seaward direction of each tussock as a function of total accretion of the highest tussock center at the muddy and sandy sites. Gully depth was calculated as the elevation at 150 cm distance minus the elevation measured at a 50 cm distance from the tussock border outside each tussock.

Spartina, a more detailed analysis was done on site-specific particle distributions in relation to vegetation occurrence and shoot density. The particle distribution differed significantly between the sandy and muddy sites for all fractions except the largest (250–500 μm ; ANOVA, $df = 1$, $p < 0.05$). There was an overall trend towards finer sediments at large tussocks compared to control sites, with the trend being much more pronounced at the muddy site (Fisher LSD, all silt fractions, $0.03 < p < 0.31$) than at the sandy site (Fisher LSD, all silt fractions, $0.12 < p < 0.74$; Fig. 6), although no significant differences were detected except for 63- μm silt at the muddy site (Fisher LSD, $p < 0.05$). At the muddy site a higher silt fraction ($< 50 \mu\text{m}$) was found at the center of large tussocks compared to the border and control sites (Fisher LSD, $p < 0.05$). This trend became more pronounced towards more shallow soil depths, with increasing age of the tussock (Fig. 6). At both the sandy and muddy sites medium grain size increased with soil depth within both *Spartina* tussocks and control sites. Our results clearly indicate that the presence of *Spartina* canopy induced the accretion of finer sediment types.

Discussion

S. anglica is an autogenic ecosystem engineer that increases sediment accretion (Castellanos et al. 1994; Sanchez et al. 2001; Bouma et al. 2007), which is known to have a positive effect on plant growth by reducing inundation periods, reducing hydrodynamic forces, enhancing drainage, and enhancing the nutrient availability (Castellanos et al. 1994; Hemminga et al. 1998; Bruno 2000; Miller et al. 2001). Using *S. anglica* as an example, we assessed to what extent an autogenic ecosystem

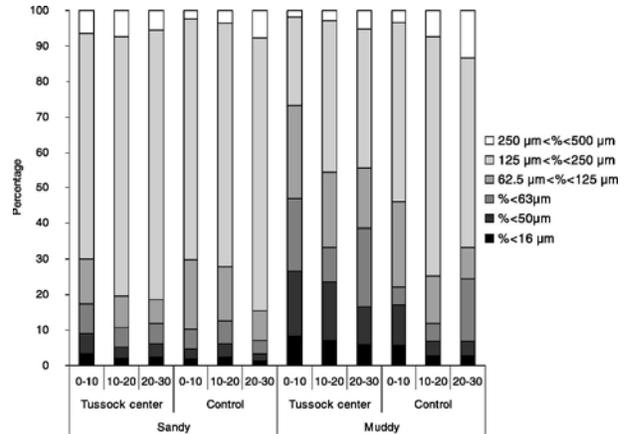


Fig. 6. Distribution of the relative percentage of size classes of grain size within three different depth intervals (0–10, 10–20 and 20–30 cm depth) of large tussock centers and unvegetated control sites at the sandy and muddy sites.

engineer is morphologically variable and if such variation is correlated with variation in the abiotic environment, especially for those abiotic parameters that are typically expected to be influenced by ecosystem engineering.

We found *S. anglica* to have a high variability in tussock morphology. Shoot density was shown to strongly increase with decreasing elevation, similar to patterns reported for the also highly invasive species *Spartina densiflora* (Nieva et al. 2005). Variation in shoot density is known to strongly affect hydrodynamic energy within *Spartina* canopies, as was shown by Gleason et al. (1979; 27–108 shoots m^{-2}), Leonard and Luther (1995; 180 and 360 shoots m^{-2}), Neumeier and Ciavola (2004; 2340–3030 shoots m^{-2}), Widdows and Brinsley (2002; 0–1850 shoots m^{-2}), and Bouma et al. (2005b; 225–2400 shoots m^{-2}). The high shoot densities that were found at low elevation may enhance sediment accretion within the canopy by reduction of hydrodynamic energy. Beside the potential to enhance sedimentation, a dense canopy has also been shown to decrease resuspension and erosion of bed sediment within its vegetation (Gleason et al. 1979). At the large marsh scale, it has been shown that sediment accretion strongly depends on inundation time, causing sediment accretion rates to decrease with increasing elevation (Temmerman et al. 2003). We expect that at the small scale of individual *Spartina* tussocks, the presence of a high shoot density to be most important for the sediment dynamics. From hydrodynamic studies, it is well known that it takes some distance to reduce hydrodynamic energy by flow deflection, and that this distance is affected by shoot density (Nepf 1999; Bouma et al. 2007). The most

direct indications for enhanced sediment accretion in the *Spartina* tussocks we studied is the finer grain size at more shallow depths within tussocks and the elevated accretion height of the tussock center (Fig. 3). Our correlative analyses do not allow us to relate shoot density directly to sediment accretion rates.

Our study cannot resolve which factor induces the increased shoot density with decreasing elevation. The fact that a similar relationship between shoot density and elevation was found by Nieva et al. (2005), but with a sediment texture distribution that was opposite to the one at our study site, suggests that factors other than sediment type control shoot density in *Spartina*. Inundation duration and covarying edaphic factors that are increasingly constraining plant growth with decreasing elevation (Mendelssohn and Morris 2000) are likely candidates to play a role in inducing a compact clonal growth form at low elevation. We expect the inundation period to be the most likely factor to explain the increasing shoot density with decreasing elevation, but are not aware of a study that quantifies such a response. Photoperiod was found to affect the allocation pattern in *Spartina alterniflora* seedlings (Seneca and Blum 1984). In this study it was shown that a relative short photoperiod (9 h high intensity light period) resulted in a three times higher rhizome production within 17 wk compared to a relatively long photoperiod (an extra 3 h low light intensity period) over a temperature range from 18°C to 30°C. The effect of inundation period on photoperiod might stimulate a similar response on clonal growth in *Spartina*.

Shoot length and the investment in individual stems were independent of tussock location. In vascular plants a high shoot density can lead to stem elongation and a reduction in leaf area due to shading and changes in the red:far red ratio, but it can also lead to a reduced investment in support structures as a result of the relief of mechanical stress (Niklas 1992). Shoot density was shown to hardly affect the length and strength of *Spartina* stems (Harley and Bertness 1996). This might be because clonal plants are often able to control shoot density to optimize light capture (Hutchings 1979). For the closely related *S. alterniflora* it has been well established that height is mainly a function of nitrogen availability and that genetic variability also plays a role (Anderson and Treshow 1980). The eutrophic nature of the Scheldt estuary (Bouma et al. 2002; Soetaert et al. 2006) and the overall relatively high leaf-nitrogen levels in plants growing in this estuary (Ornes and Kaplan 1989; Bouma et al. 2001) may explain why no differences were found in average shoot length. The stiff stems enable *Spartina* to withstand hydrodynamic forces

related to tidal inundation (Bouma et al. 2007) and at the same time enhance sedimentation by attenuating hydrodynamic energy from currents (Leonard and Luther 1995; Leonard et al. 2002) or waves (Bouma et al. 2005b). Regarding the importance of the mechanical strength of stems in *Spartina* for both withstanding hydrodynamic forces and its ecosystem engineering capability, it may be speculated that there has been selection towards a relatively high investment in stem structure. It cannot be excluded that *Spartina's* stem stiffness is not a true adaptation to withstanding hydrodynamic forces, but an exaptation (i.e., a trait whose current function is not the function performed while it evolved under earlier pressures of natural selection, sensu Gould and Vrba 1982).

The present study also revealed a strong positive correlation between the amount of sediment that has accumulated within a tussock and gully formation around that *Spartina* tussock (Fig. 5). As gully formation is caused by flow deflection from within a canopy to around a tussock (Bouma et al. 2007), gully formation may be expected to be most pronounced in those tussocks that have the highest canopy densities. This was supported by our results indicating that gully formation was pronounced at the low marsh border (Fig. 4) where the highest canopy densities were found (Fig. 1). Once a gully is formed, it may be expected to have a negative effect on lateral expansion of a tussock. Combining our observations on gully formation with the negative relation between shoot density and lateral clonal expansion, as can be derived by combining Figs. 1 and 2, may suggest that there could be a trade-off related to the morphology of the autogenic ecosystem engineer *Spartina*. There could be a trade-off between the maximization of the ecosystem engineering capacity in the sense of enhancing sediment trapping by having a high shoot density that reduces hydrodynamic energy (Gleason et al. 1979; Leonard and Luther 1995) versus the capacity to maximize clonal expansion by spreading shoots widely and having a sparse vegetation, which also reduces the risk of reduction of lateral growth due to gully formation.

At the higher sandy site with relatively high flow velocity (Herman et al. 2001), there was a strongly enhanced risk of total erosion of the tussock. The relatively open tussock structure with a low shoot density is likely to have contributed to this effect. The relatively low stability of sandy sediments compared to more muddy sediments (Defew et al. 2002) also will probably have played an important role. The present finding that the tussocks with the highest lateral expansion are also the tussocks that have the highest mortality may suggest that there could be a second trade-off related to morphology

of the autogenic ecosystem engineer *Spartina*. This second trade-off would exist between the capacity of maximal clonal expansion by spreading shoots widely versus the risk of tussock mortality due to insufficient modification of the habitat, which makes the tussock vulnerable for erosion. Regarding the higher stability of muddy sediments than sandy sediments (Defew et al. 2002), this second trade-off is expected to be less important on the more cohesive muddy sediments. The benefits related to rapid lateral expansion also seemed high, in that only at the sandy site, the surviving tussocks were able to form a marsh by coalescence.

We showed that *S. anglica* has considerable morphological variation in both clonal and shoot architecture, and that this variation was strongly correlated to the position along the elevation gradient. We also observed that the tussocks with these contrasting canopies had strongly different characteristics. Regarding the correlative nature of our study, we cannot draw conclusions on the causal nature underlying the observed correlations, but based on our correlations, we were able to hypothesize two possible trade-offs related to the morphology of the autogenic ecosystem engineer *Spartina*. Experimental testing of these hypotheses may shed light on the importance of morphological variation for a species its autogenic ecosystem-engineering capacity. A long tradition of experiments have shown that studying trade-offs offers an important way to learn more about the possible adaptive nature of a certain morphology or behavior (Grime 1977, 1988; Tilman 1988; Stearns 1989; Grime and Mackey 2002). Cost-benefit analyses of ecosystem engineering may offer a first simple approach towards enhancing our understanding of the adaptive nature of ecosystem engineering (Bouma et al. 2007), which is a topic that recently is gaining strong attention (Day et al. 2003; Odling-Smee et al. 2003; Bouma et al. 2007). An in-depth understanding of the ecosystem engineering mechanisms by *S. anglica* is particularly important for understanding the rapid spreading of this highly invasive species in some parts of the world (Hacker et al. 2001), especially because invading engineers often induce cascading effects on the diversity of an entire ecosystem (Crooks 2002).

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