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Ecogeomorphic relations between marsh surface elevation and vegetation properties in a temperate multi-species salt marsh

Jean-Philippe Belliard^{1,2}, Stijn Temmerman¹, Marco Toffolon²

¹ University of Antwerp, Ecosystem Management research group, Universiteitsplein 1-c, B-2610 Antwerp, Belgium

² University of Trento, Department of Civil, Environmental and Mechanical Engineering, via Mesiano 77, 38123 Trento, Italy

Abstract

Salt marshes represent a fascinating example of an ecosystem whose dynamic response to climate change is chiefly governed by a two-way bio-physical coupling between marsh ecology and geomorphology. Relationships between vegetation biomass and marsh surface elevation, and between vegetation biomass and its physical properties that influence sedimentation rates, have been progressively formulated in the literature in order to provide mechanistic understandings and mathematical model descriptions of these ecogeomorphic feedbacks. In this study, a field survey was conducted in a temperate salt marsh grown by multiple halophyte species in order to quantify and validate these empirical relationships, yet in a location characterized by different climatic and ecological conditions from the locations where these relationships were initially derived. Regression analysis revealed that vegetation biomass can be expressed as a linearly increasing function of marsh elevation, providing therefore a direct empirical validation for such a

relationship previously reported in the literature and implemented in some ecogeomorphic models. However, previously documented allometric relationships between total standing biomass and vegetation morphometrics—namely stem diameter, stem density and projected plant area per unit volume—were not confirmed by our results, which only showed an allometric scaling for stem height. These results suggest that previously documented formulations of mineral sediment trapping processes modulated by plants, which are partly derived on the basis of these allometric relationships, are not generally validated for multi-species salt marshes. Therefore, existing models that apply these process-based equations to study marsh evolution in a multi-species context may not capture in detail the vegetation-induced geomorphic work.

Keywords:

Biomass - elevation relationship, vegetation morphometrics, ecogeomorphic processes

Introduction

Salt marshes are widely recognized as important environments providing extensive ecosystem services such as flood hazard mitigation (Costanza et al., 2008; Möller et al., 2014; Temmerman and Kirwan, 2015; Temmerman et al., 2013), provision of rare and unique habitats for wildlife (Jones et al., 2011), transformation of nutrients, sequestration of carbon and pollutants; as well as cultural services such as recreation and amenity (Millenium Ecosystem Assessment, 2005; Barbier et al., 2011; Costanza et al., 1997; Spencer and Harvey, 2012). Many of today's marshes have persisted in the stratigraphic record for at least 4000 years (Redfield, 1972). During this period, global sea-level has risen by more than 2 metres (Kemp et al., 2011) and in a recent review, Kirwan et al. (2016) argued that future projections of sea-level rise (SLR) may not constitute a serious threat to many marshes worldwide for the next few decades, as long as sediment availability is sufficient. However, observations of marsh degradation and submergence in places such as coastal Louisiana, USA (Reed, 1995), Chesapeake Bay, USA (Kearney et al., 2002) and the Venice lagoon, Italy (Carniello et al., 2009), indicate that there are limits to marsh adaptability to SLR.

Essential to future assessments of marsh vulnerability are the feedbacks between sedimentation, hydrodynamics and the dynamics of the halophytes living on the marsh surface (D'Alpaos et al., 2016; Elmore et al., 2015; Fagherazzi et al., 2012; Langlely et al., 2009). From a purely physical perspective, mineral deposition on the marsh platform greatly depends on suspended sediment concentrations in the surrounding waters, therefore on the regional availability of sediments (Allen, 2000;

Christiansen et al., 2000; Leonard, 1997). Under conditions of adequate sediment availability, mineral deposition rates are typically highest in low elevation marshes that are inundated for long periods and particularly exposed to sediment settling, and lowest in high elevation marshes that are rarely flooded (Cahoon and Reed, 1995; Marion et al., 2009; Pethick, 1981; Temmerman et al., 2003). Similarly, deposition rates are typically highest when tides and inundation depths are highest (Temmerman et al., 2003). Therefore, sediment availability controlled by hydrodynamic variables such as tidal range and rate of SLR governs the balance between marsh elevation gain and SLR through a feedback between inundation and mineral deposition (French, 2006; Kirwan et al., 2010; Morris et al., 2002).

This fundamental physical feedback is modulated by the presence of the marsh vegetation that attenuates tidal flows and waves within the canopy leading to enhanced settling of mineral sediments, i.e. referred to as particle settling by plant drag (Leonard and Luther, 1995; Leonard and Croft, 2006; Nepf, 1999; Temmerman et al., 2012), and by direct particle capture by plant stems (Leonard and Luther, 1995; Palmer et al., 2004). In addition, vegetation growth directly contributes to marsh surface sedimentation by organic sediment production at both the marsh surface and root zone (Langley et al., 2009; Nyman et al., 2006). A number of researchers have described these ecogeomorphic processes as a function of the physical characteristics of the marsh vegetation such as stem diameter, height, density and projected plant area per unit volume (e.g., Mudd et al., 2010; Nepf, 1999; Palmer et al., 2004; Tanino and Nepf, 2008). These plant morphometrics have been found to depend on the biomass of the marsh vegetation through allometric (power law) relationships following a long record of *Spartina alterniflora* productivity

at North Inlet estuary, South Carolina, USA (Morris and Haskin, 1990; Mudd et al., 2004, 2010). In turn, plant biomass is largely determined by the elevation of the marsh platform relative to sea level (Morris et al., 2002). In particular, research in the *Spartina alterniflora* salt marshes at North Inlet showed that plant productivity depicts a hump-shaped (parabolic) response to marsh surface elevation; aboveground plant biomass reaches its maximal production at an optimal elevation, corresponding to the mean sea level (MSL), and quickly decreases as elevations depart from this optimum (Morris et al., 2002). The resulting quadratic relationship between plant biomass and marsh elevation derived by Morris et al. (2002) partly forms the basis of a number of ecogeomorphic models applied to global studies of marsh evolution (e.g., Belliard et al., 2015, 2016; D'Alpaos et al., 2006, 2007; Kirwan and Murray, 2007; Mariotti and Fagherazzi, 2010; Morris et al., 2002; Mudd et al., 2004, 2009; Zhou et al., 2015)

Yet, this quadratic biomass – elevation relationship may not hold systematically in marshes grown by different halophyte species and/or in different geographic locations. For instance, Kirwan et al. (2012) found biomass production persisting at marsh elevations well above mean high tide, following a decadal measurement of *Spartina Alterniflora* productivity in seven marshes located in Virginia, further north from North Inlet, and which therefore did not give support for a quadratic biomass – elevation relationship. The linear response of *Spartina patens* aboveground biomass to marsh elevation measured in mesocosm experiments within two salt marsh sites located in the Chesapeake Bay tend to demonstrate that this quadratic biomass – elevation relationship may not only be site specific but also species specific (Kirwan and Guntenspergen, 2015). Moreover, field and remotely-sensed observations of

increased plant richness and plant diversity with increasing surface elevation for salt marshes located in the Venice lagoon (Marani et al., 2004; Silvestri et al., 2005) suggest that total plant productivity depicts a linearly increasing response to marsh elevation for marshes grown by a variety of halophyte species. Likewise, Cadol et al. (2014) attributed the observed presence of a two-hump-shaped (bimodal) response of surface elevation change to marsh surface elevation in a freshwater tidal marsh in the Chesapeake Bay to its multi-species community composition. This result suggests that the quadratic biomass - elevation relationship may not persist either across different salinity regimes.

In spite of the significant advances in understanding the implications of marsh surface elevation on ecology, the expected regional and ecological dependences of the biomass – elevation relationship have not been fully tested; further field research should be conducted to quantify and validate such a relationship for salt marshes in different geographic, climatic or ecological settings (Mudd et al., 2004). Surprisingly, few field surveys have addressed this relationship through direct biomass measurements, particularly in European salt marshes (see, e.g., Day Jr et al., 1999), despite their distinct ecology with respect to American marshes where most of the related research has been conducted so far. Here we present a field analysis carried out in a European temperate salt marsh grown by a mixture of halophyte species. This study aims to assess whether surface elevation controls i) patterns of species distribution; and ii) aboveground biomass along an elevation gradient, and if so, what relationship arises; and iii) whether allometric relationships exist between aboveground biomass and vegetation morphometric characteristics, as used in the

formulation of ecogeomorphic processes, so as to fully account for the two-way coupling between marsh ecology (vegetation) and marsh geomorphology (elevation).

Methods

Study site

The field survey was conducted in a salt marsh system right adjacent to the Paulina marsh in the Scheldt estuary, SW Netherlands (Figure 1a).

The study area is dominated by a semi-diurnal macro-tidal regime with a mean tidal range of 3.9 m, and a mean spring and neap tidal range of 4.5 m and 3.0 m, respectively (Vandenbruwaene et al., 2015) . Different stages of geomorphological development and plant succession allow for the distinction of three marsh zones: a high, medium and low marsh zone. The high marsh zone is the oldest and is characterized by a relatively flat topography (Temmerman et al., 2005). Together with the medium marsh zone, it can be intertwined by various tidal creeks of several orders. To the contrary, the younger low marsh zone also called pioneer zone, as being the transition between the salt marsh and the adjacent tidal flat, is gently sloping and is intersected by fewer tidal creeks. The study site depicts a number of halophytic species common to Northwest European salt marshes. The high marsh zone grown by *Elymus athericus* (see Figure 1b), while the medium marsh zone is dominated by *Spartina anglica*, *Aster tripolium* and *Atriplex portulacoides*. A more

patchy vegetation cover of the pioneer *Spartina anglica* (see Figure 1 d) typically characterizes the low pioneer marsh zone.

Sampling methodology

The field campaign took place early September 2013 in order to measure end-of-season biomass as a proxy of annual, aboveground primary production (Silinski et al., under review). Measurements were carried out along a single transect stretching from the marsh seaward edge to its furthest inland side. The location of the transect was determined according to a randomly stratified sampling that attempted to cover the different marsh morphological domains and zonation patterns while following the direction of the topographic slope. Tidal creeks were omitted along the transect as sub-surface soil drainage towards creeks influences soil aeration and therefore plant productivity (Silvestri et al., 2005; Ursino et al., 2004). Similarly, artificial features such as embankments were avoided. In order to cope with the moderate elevation gradient typically characterizing these environments, measurement points along the transect were taken about every 10 cm in elevation with the help of a Real Time Kinematic Global Positioning System (RTK GPS) whose elevation value was referred to the Dutch ordnance datum NAP (which is close to local MSL) with a vertical error +/- 1 cm. At every elevation point, three replicate plots were delimited using quadrats of dimensions 25x25 cm.

Plant species composing the plots were first identified. Their respective percentage cover was then estimated and their relative abundance-dominance score was evaluated according to the Braun-Blanquet method (e.g., Bockelmann et al., 2002;

Silvestri et al., 2005), based on 6 cover classes (<1, 1-5, 5-25, 25-50, 50-75, 75-100%). A species was considered as dominant if it covered > 50% of the plot. Then, all total standing biomass was harvested in the three replicate plots. Biomass samples were stored in a cool chamber and washed in the laboratory. A representative sub-sample of 30 plant individuals was selected from one replicate biomass sample per elevation point to perform direct morphometric measurements of stem diameter (measured at 2 cm from the stem base) and height. Stem density was derived by cross-multiplying the measured sub-sample biomass with known number of plant individuals to the total biomass of the corresponding sample. Projected plant area per unit volume was defined as the product of stem diameter and stem density (Nepf, 1999). Finally, biomass samples were dried in an oven at 70°C for 48 hours until they reached a constant weight, and dry biomass was determined afterwards by weighing.

Statistical analysis

In total, 16 elevation points were measured along the transect (see Figure 1c), which allowed for the extraction of 48 biomass samples. The resulting data set was first explored using descriptive statistics and exploratory graphs including boxplots, bar charts, etc. in order to summarize the main features of the considered variables. Second, correlations between factor and response variables were assessed using Pearson product moment correlation coefficient r (Pearson, 1896), or Spearman's rank correlation coefficient ρ (Spearman, 1904) when the data were not normally distributed. Ordinary Least Square (OLS) regression analyses were subsequently carried out on variables showing high correlation. Regression models were validated

by ensuring that the different assumptions underlying linear regression were satisfied. Normality of the residuals was thus assessed using different normality tests, e.g., Kolmogorov-Smirnov test (Kolmogorov, 1941; Smirnov, 1939), Anderson-Darling test (Anderson and Darling, 1952); heteroscedasticity was evaluated using White test (White, 1980); and the presence of autocorrelation structures was assessed graphically by plotting the residuals versus observation orders. Where necessary, transformation was applied to the data to solve problems of non-normality and heteroscedasticity, and if the assumptions of linear regression were still not met, nonlinear regression models were tested eventually. To test the overall significance of the regression model and its parameters, lack-of-fit sum of square test (F-test) as well as model slope and intercept tests (T-tests) were conducted. Outliers were detected using the Grubbs test (Grubbs, 1950). All statistical tests were carried out with a 95% confidence interval. This statistical analysis was performed using MINITAB v17.

Results

Vegetation species distribution

The topographic profile of the measurement transect, whose planar course is depicted in Figure 1c, is shown in Figure 2. The elevation difference from the seaward to the landward edge of the marsh is 1.5 m. Some contrasting morphologies can be observed. Indeed, the pioneer zone and, to a lesser extent, the lower elevations of the medium marsh zone clearly slope down towards the sea,

although the marsh slope is not gradual and is steepest some distance away from the marsh seaward edge, towards the end of the pioneer zone. To the contrary, the upper elevations of the medium marsh zone and the high marsh zone are rather flat.

In addition, Figure 2 displays the halophytic species identified per elevation point. A total number of 7 species were found along the course of the transect, namely *Spartina anglica* (further referred to by the code Sp), *Aster tripolium* (As), *Suaeda maritima* (Su), *Salicornia europaea* (Sa), *Spergularia marina* (Spe), *Atriplex portulacoides* (At) and *Elymus athericus* (El). Some elevation points are characterized by a monospecific plant cover whereas others, especially in the marsh medium zone, are featured with a multi-species cover. A maximum of four plant species was found at location P11. Looking at the vertical distribution of the observed halophytes, *Spartina anglica* is the only species that occupies the lower marsh domain but appears also to extend well above the pioneer zone at lower abundances and within communities including also other species. On the other hand, some species are present in narrow elevation ranges such as *Elymus athericus* which is solely found in the high marsh zone.

Figure 3 shows the proportion of plant cover as an average of the three replicate plots per elevation point for every identified species. Despite the fact that some elevation points in the medium marsh zone portray a vegetation cover composed of a mixture of several species (e.g., P10 – P14), in reality only *Spartina anglica* and *Aster tripolium* represent the abundant and dominant species compared to the other recorded halophyte species. The results show that the occurrence of some species is dependent on soil elevation, such as for *Elymus athericus* and *Atriplex*

portulacoides. However, the rather uniform distribution of the pioneer *Spartina*
Anglica suggests that such dependence on elevation is weaker for this species. In
fact, its decrease in abundance in the intermediate zone seems to be related to the
increasing abundance of *Aster tripolium* and to a lesser extent *Atriplex portulacoides*
and *Suaeda maritima*, until *Spartina Anglica* disappears where a new zonation
pattern characterized by the nearly exclusive dominance of *Elymus athericus*
establishes in the high marsh zone (i.e., P15 – P16). Particularly, one may discern
that the proportion of *Spartina anglica* is negatively correlated with the proportion of
Aster tripolium ($\rho = -0.54$, significant at $p = 0.034$).

Vegetation biomass distribution

The total standing biomass density (g.m^{-2}) increases with elevation (see Figure 4,
Table S1). The lowest biomass value is indeed measured at the lowest elevation
points (P1 or P2) and the highest value at the highest elevation points (P14 or P16,
depending on the measure of central tendency considered, see Table S1). The data
presentation in Figure 4 emphasizes the presence of three regions that coincides
with the distribution of the halophytes along the measurement transect. A first region
comprises the single species communities situated in the pioneer zone and
colonized by *Spartina anglica* (P1 – P9), for which a gradual increase in biomass
density with marsh surface elevation arises. The second region includes the multi-
species communities located in the medium marsh zone and composed of *Spartina*
anglica and *Aster tripolium* as dominant species (P10 – P13), for which a decrease
in biomass density with marsh surface elevation occurs. Finally, the third region
comprises the higher marsh communities dominated by *Atriplex portulacoides* (P14)

and *Elymus athericus* (P15 – P16), and whose biomass density values depart from those of the two other plant communities. Moreover, the medium and high marsh zones display larger variability in biomass density values both between successive elevation points and between replicate plots for a same elevation point, as opposed to what occurs in the pioneer zone (see measures of variability in Table S1).

OLS regression analyses were subsequently performed to model community-dependent standing biomass density against marsh surface elevation for each of the two largest plant communities (low marsh *Spartina anglica* communities and medium marsh multi-species communities). Residuals of the regression model carried out with the *Spartina anglica* communities were normally distributed (significant at $p > 0.150$), homoscedastic (significant at $p = 0.716$) and uncorrelated. Residuals of the regression model carried out with the multi-species plant communities were normally distributed (significant at $p > 0.150$), homoscedastic (significant at $p = 0.450$) and uncorrelated. Results of these two regression analyses are displayed in Figure 4. The regression lines demonstrate a clear and sudden change from a positive to a negative biomass – elevation relationship as soon as the pioneer *Spartina anglica* co-occurs with the abundant *Aster tripolium* and with sporadic stands of *Suaeda maritima*, at the transition between the low and medium marsh zone.

In order to confront our results with previously reported biomass – elevation relationships, we also investigate the response of the total standing biomass density, i.e., over the whole elevation gradient. Correlation was first tested between total standing biomass density and marsh surface elevation for the entire data set, which appeared to be highly positive ($\rho = 0.861$, significant at $p < 0.001$). This indicates

that the two variables covariate strongly in the same direction. Figure 4 reflects this linear association between biomass and elevation since the plot depicts one main direction. As a result, an OLS regression analysis was performed to model total standing biomass density as a function of marsh elevation. A detected outlying data point (in P10) triggered a positive skewness in the distribution of the residuals of the regression model performed with the response (biomass) and factor (elevation) variables in their respective metric. However, a log transformation of the response variable allowed to correct for the non-normality of the residuals (significant at $p = 0.150$ after data transformation), and thereby validate the regression model; residuals were also homoscedastic (significant at $p = 0.553$) and uncorrelated. Therefore, we performed a new OLS regression using the response variable in its log-transformed state while keeping the factor variable in its original metric. Results of the regression analysis show that the marsh surface elevation is able to explain 71.5% of the variability in total standing biomass density through a linear model (Figure 5). Accordingly, despite variation in plant communities influences the response of biomass density to marsh surface elevation (Figure 4), interestingly a significant biomass – elevation relationship still persists across different community transitions, thereby illustrating the dominant control of marsh elevation in determining plant productivity.

Vegetation biomass - morphometrics relationships

The analysis of the descriptive statistics show that stem height depicts an increasing trend with the total standing biomass density averaged over every elevation point (see Table S2). However, it appears difficult to discern any particular trend between

mean biomass density and the other measured morphometric characteristics. As a next exploratory step, box plots were produced on the direct measurements of stem diameter and stem height against mean biomass density, as displayed in Figure 6, to better visualize possible trends between the variables of interest. Figure 6a notably reveals that stem diameter remains fairly constant with increasing biomass density. Low variation in diameter values occurs for the low marsh *Spartina anglica* communities (P1 – P9) and higher marsh communities dominated by *Elymus athericus* (P15 – P16), compared to the medium marsh multi-species communities. Unlike stem diameter, stem height seems to increase gradually with biomass density all over the measurement transect (Figure 6b), although a higher variation occurs for high biomass densities.

Similarly, we produced scatter plots for every morphometric characteristic against standing biomass density categorized by the plant communities identified along the measurement transect (Figure 7). Although some grouping arise, a large scatter characterizes the distribution of the different community-based vegetation morphometrics, and only a relationship seems to arise between the stem heights of the *Spartina anglica* communities and corresponding biomass densities for which we performed an OLS regression analysis. Residuals of the regression model were normally distributed (significant at $p > 0.150$), homoscedastic (significant at $p = 0.321$) and uncorrelated. Results of the regression analysis are displayed in Figure 7b.

Likewise, we investigated potential relationships between every vegetation morphometrics and standing biomass density across plant community transitions.

Pearson correlation between mean stem height and mean total standing biomass was first carried out, yielding a certain degree of linear association ($r = 0.66$, significant at $p = 0.005$). To the contrary, no correlation arose between mean stem diameter and mean biomass ($r = -0.19$, insignificant at $p = 0.484$). Correlation tests on the median diameter values did not improve the result. Despite a slightly better Pearson score compared to stem diameter, all correlations between mean stem density or mean projected plant area per unit volume and mean biomass density were insignificant at 95% confidence interval.

Based on the correlation results, an OLS regression analysis was therefore performed to model mean stem height as a function of mean biomass density. A detected outlier (in P14) significantly lowers the quality of the applied linear regression model despite its validity regarding the assumptions on residuals as well as on the model parameters and lack-of-fit tests. Attempts to minimize the outlier effect by transforming the original data did not yield any improvement as transformations are used especially to correct for the assumptions underlying linear regression. Alternatively, we opted for a power-law regression model that has shown to improve sensibly the result of the regression. Residuals were normally distributed (significant just on the threshold level of $p = 0.05$ and at $p = 0.070$ using Kolmogorov-Smirnov and Anderson-Darling tests respectively), homoscedastic (significant at $p = 0.615$) and uncorrelated. Results of the regression analysis are displayed in Figure 8.

Stem height therefore shows an allometric scaling with total standing biomass density. The scaling exponent indicates that stem height changes with standing

biomass density to the power of 0.27. This value is less than the expected slope value of 1/3 for any relationship involving a particular length based property to its body mass. Accordingly, plants here are said to show a negative allometry.

Discussion

Role of marsh elevation on patterns of vegetation species distribution

In general, patterns of vegetation species distribution observed in this study qualitatively agree with zonation patterns that are typically found in NW European salt marshes (e.g., Bockelmann et al., 2002; Olff et al., 1997). The exclusive presence of *Spartina anglica* communities in the pioneer zone (P1 – P9), where environmental stress conditions are typically strongest, suggests that *Spartina anglica* is the species with the highest physiological stress tolerance. Furthermore, unlike the other halophyte species, the rather uniform vertical distribution of *Spartina anglica* over a large part of the elevation gradient (see Figure 3) indicates that this species can grow under varying tolerance levels of environmental stress. Moreover, we have seen that the distribution of *Spartina anglica* appears to be particularly conditioned by the presence and density of *Aster tripolium* within the medium marsh multi-species communities (P10 – P13) and the presence of *Elymus athericus* in the high marsh zone (see Figure 3). Therefore, the progressive replacement of the pioneer *Spartina anglica* by successional species in its landward boundary likely results from (1) the specific species tolerance levels to edaphic factors such as soil salinity (Morris, 2000; Phleger, 1971), tidal inundation depth, duration and frequency

(Bockelmann et al., 2002; Morris et al., 2002; Silvestri et al., 2005), soil drainage and oxygen availability (Marani et al., 2006), nutrient availability (Gallagher, 1975), etc., which are all known to be mediated by marsh elevation; and (2) dynamic interactions between species such as competition. It appears that this competition effect becomes stronger with increasing marsh elevation, which may be interpreted as more species become tolerant to less stressful conditions with higher marsh elevation. This key interaction between stress tolerance and competition is common to multi-species salt marshes (Bertness and Ellison, 1987; Olf et al., 1997; Pennings and Callaway, 1992; Silander and Antonovics, 1982).

In the high marsh zone, although the relatively constrained distribution of *Elymus athericus* communities translate a limited physiological tolerance to salinity (Rozema et al., 1985) and waterlogging (Bouma et al., 2001), particularly with respect to *Atriplex portulacoides*, the exclusive dominance of *Elymus athericus* in this zonation pattern also likely results from species competition. Indeed, the rather distinct distributional boundaries between *Elymus athericus* and *Atriplex portulacoides* has been previously demonstrated to be the result of competition between these two species (Bockelmann and Neuhaus, 1999). *Elymus athericus* is known for its high competitive ability (Olf et al., 1997), which can be also appreciated here looking at its high stem height, density and projected plant area per unit volume (see P15 – P16 in Figure 7b, c and d), resulting in dense monospecific stands and therefore leaving little or no space left for other salt marsh macrophytes to develop. Therefore, our observations confirm that the distribution of vegetation zonation along the whole elevation gradient may not only respond to marsh elevation itself, but also to a range

of interacting factors of different nature that are co-varying with elevation
(Bockelmann et al., 2002; Elmore et al., 2015; Kim, 2014).

Role of marsh elevation on plant productivity

Results have revealed the presence of community dependent patterns of biomass density along the elevation gradient. In particular, species community transitions are manifested by distinct changes in the response of biomass density to marsh elevation, such as what occurs between the low marsh *Spartina anglica* communities (P1 – P9) and the medium marsh multi-species communities (P10 – P13). Comparisons between *Aster tripolium* and *Spartina anglica* morphometric characteristics suggest that the former species has a higher average standing biomass density; *Aster tripolium* has a higher averaged stem diameter (Figure 9) and stem height with respect to *Spartina anglica* (each significant at $p < 0.0001$ using Mann-Whitney test). Therefore, the observed decrease in standing biomass density from P10 to P13 may be related to the decline in *Aster tripolium* and the concurrent growth of *Spartina anglica*. In addition, the occurrence of a local biomass density maximum at P10 may result from a combination of two factors. First, changes in community composition at P10, with the encroachment of *Aster tripolium* characterized by its high average biomass, partially contributes to the greater observed biomass density at P10 that clearly departs from P1 to P9 (see Figure 4). Second, the local improved drainage conditions associated with the topographic slope seaward from location P10 (see Figure 2) may expect to favour plant growth and lead to the greater observed standing biomass density at P10 with respect to P11 and the successive plots.

467

468 Regression analysis has also shown the presence of a significant linearly increasing
469 biomass – elevation relationship along the whole elevation gradient, thereby
470 contradicting the well-documented quadratic biomass – elevation relationship
471 derived by Morris et al., (2002) at North Inlet estuary. Salt stress can reduce
472 vegetation productivity in the upper marsh elevations in certain marsh systems
473 where evaporation is important (Pratolongo et al., 2009), such as in North Inlet
474 estuary which is characterized by a sub-tropical climate. To the contrary, we expect
475 that in our study area, salt stress is not significantly increasing with elevation
476 because of the temperate wet climate conditions, where rainfall may even cause a
477 reduction of salt stress with increasing elevation (e.g., Bockelmann and Neuhaus,
478 1999). These different climatic conditions, together with the distinct plant ecology
479 between the two sites (i.e., dominance of one marsh species *Spartina alterniflora* at
480 North Inlet against multiple species in our study site), may explain our different
481 biomass – elevation relationship. The linear increase in total standing biomass as a
482 function of marsh elevation can be explained as follows: in low marsh elevations,
483 relatively severe environmental conditions associated with frequent tidal inundation,
484 soil salinity, soil oxygen limitation, wave action among others, lead to high-level
485 stress and unstable substrate limiting the vegetation only to highly tolerant species,
486 i.e., *Spartina anglica*. In contrary, in high marsh elevations, autogenic vegetation
487 dynamics continuously proceed under the conditions of lower stress levels and
488 stable substrate leading to higher vegetation productivity (Kim, 2012). However,
489 meso-scale topographic changes and associated hydrological conditions can
490 influence vegetation productivity locally (Marani et al., 2006), as in P10.

491

The observed linear increase in biomass density as a function of marsh elevation provides a direct empirical validation for the assumption of linearly increasing biomass – elevation relationship for salt marshes grown by multiple species, as suggested by remote sensing in the literature (e.g. Marani et al., 2004) and parameterized in some ecogeomorphic models of marsh evolution (e.g., Belliard et al., 2015; D’Alpaos et al., 2006, 2007). However, this linear increase in biomass is not associated with an increase in plant diversity, therefore refuting the common assumption that increased diversity is, on average, associated to increased biomass (Tilman, 2000). Indeed, the observed increase in species richness along the low and medium marsh zones is then followed by a progressive decline, eventually returning to a monospecific population at the high marsh zone. The strong physical stress gradient that is expected along such a measurement transect and that greatly affects the biomass distribution may explain the absence of correlation between vegetation biomass and diversity, which to the contrary prevails in ecosystems subject to gentle and slowly-varying environmental stress (e.g., Silvestri et al., 2005). However, additional field measurements should be ideally carried out as the present field survey was only conducted on a single transect, hence only accounting for the vertical biomass distribution and productivity (i.e., within the tidal frame), while a certain degree of horizontal variability may be expected, for example as a consequence of horizontal gradients in soil drainage related to distance from marsh internal creeks. This potential variability is likely reflected in the observed variation in biomass density values between replicate biomass plots for some elevations (see Figure 5 and Table S1).

Implications of relationships between vegetation biomass and morphometric characteristics

The field work analysis has revealed that only total stem height depicts an allometric relationship with total vegetation biomass density (see Figure 9). Yet, the negative allometry indicates that plant biomass is not exclusively materialized by stem height throughout all marsh communities. This observation may be attributed to the variation in species abundance and community composition along the elevation gradient, and which is reflected in the morphometric characteristics. For instance, medium marsh communities are characterized by the highest stem diameter values (due to dominance of *Aster tripolium*, which has typically thick stems), whereas the high marsh communities depict the highest stem density values (due to dominance of *Elymus athericus*, which has typically high stem densities). Therefore, one may expect that plant biomass is also partly explained by stem diameter and stem density for these respective marsh communities. One could also point to non-stem biomass as a possible explanation for this negative allometry, but observed correlation between biomass density and the product of stem height with stem diameter² and stem density ($r = 0.60$, significant at $p < 0.0001$) seems to indicate to the contrary that biomass is primarily found in these plant physical attributes in our study site. On the contrary, total stem diameter does not alone yield any correlation with total plant biomass (see Figure 7a). Here, it is clear that the lack of allometric relationships for the other vegetation morphometric characteristics is explained by the presence of multi-species communities along the elevation gradient with each species having distinct physical attributes. For instance, the large variability in stem diameter data (Figure 7a) is associated with the segregation in diameter values between the

different identified halophytes, as illustrated in Figure 9. Due to their different plant composition and proportion, biomass samples being composed of different plant species thus greatly differ from each other in their stem diameter statistics. Similarly, stem density does not correlate with plant biomass (Figure 7c). As the projected plant area per unit volume is a function of stem diameter and stem density, this morphometric characteristic does not either correlate with plant biomass (see Figure 7d).

The absence of relationships between standing biomass and morphometric characteristics observed in our study site, except for stem height, suggests that previously documented formulations of mineral sediment trapping processes modulated by plants (i.e. direct sediment particle capture and particle settling), and which are partly derived on the basis of these allometric relationships, are not generally valid for multi-species salt marshes. As a consequence, our results reveal that existing models that apply these process-based equations to study marsh evolution in a multi-species context may not capture in detail the relative importance of vegetation-induced sediment trapping in total marsh mineral sedimentation. However, additional field research should be still conducted as our study is only based on measurements that do not capture temporal variability while previous contributions that derived allometric relationships at North Inlet estuary (Morris and Haskin, 1990; Mudd et al., 2004, 2010) were based on an extensive 18-year record of *Spartina alterniflora* growth characteristics.

More research is needed on the mechanistic understandings of belowground organic sediment production, however descriptions of this process express belowground

organic matter as a function of aboveground biomass (Mudd et al., 2004; Randerson, 1979). Specifically, recent formulations relate organic sediment production to belowground biomass which has shown to be linearly increasing with aboveground biomass in specific locations (e.g., Mudd et al., 2009), and thus on marsh elevation (Fagherazzi et al., 2012). As our aboveground biomass – elevation relationship validates the corresponding assumption for multi-species salt marshes that was previously reported in the literature (e.g., Marani et al., 2004), existing models of multi-species salt marsh evolution that incorporate above mentioned formulations of belowground organic sediment production may still provide a simple yet representative description and quantification of the organogenic contribution in total marsh sedimentation.

Conclusions

A field survey was conducted in a temperate multi-species salt marsh in order to quantify and validate previously reported relationships used to describe mechanistically the two-way feedback between marsh elevation and plant productivity, yet in a location with different climatic and ecological settings. These relationships are particularly relevant in the study of salt marsh resilience to sea-level rise.

Results have revealed that total biomass density can be expressed as a linearly increasing function of marsh elevation, thereby providing direct empirical validation for such a relationship previously reported in the literature and implemented in

several ecogeomorphic models applied to the study of salt marsh evolution in a multi-species context. However, regression analyses between vegetation biomass and morphometric characteristics revealed that only stem height shows an allometric scaling with standing biomass density. Absence of significant relationships for other plant morphometrics, including stem diameter, density and projected plant area per unit volume can be attributed to the notable segregation in these physical attributes between the recorded halophytes that ultimately leads to discrepancies for vegetation plots having different plant composition and proportion.

The absence of relationships between standing biomass density and morphometric characteristics, except for stem height, indicates that previously documented formulations of mineral sediment trapping processes modulated by plants, which are partly derived on the basis of these allometric relationships, are not generally validated for multi-species salt marshes. Therefore, our results suggest that existing models may not capture in detail the vegetation-induced geomorphic work in marsh regions colonized by a variety of halophytes, and this should be carefully considered in view of the potential implications in marsh resilience to sea-level rise. Research involving interdisciplinary expertise and linking field observations and laboratory experiments is further encouraged to progress our understanding of the interactions between vegetation and morphology as well as sediment transport, with the ultimate aim to derive globally validated relationships feeding the next generation of ecogeomorphic models of salt marsh evolution.

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Supporting Information

Table S1 Summary of descriptive statistics of plant biomass density per elevation point.

Table S2 Averaged value of vegetation morphometric characteristics.

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Figure underlines

Figure 1 Study area and measurement transect. (a) Location within western Europe; (b) View of the high marsh zone; (c) Aerial view and planar course of the measurement transect; (d) View of the low pioneer marsh zone.

Figure 2 Topographic profile and plant distribution along the measurement transect. Species identified are: *Spartina anglica* (Sp), *Aster tripolium* (As), *Suaeda maritima* (Su), *Salicornia europea* (Sa), *Spergularia marina* (Spe), *Atriplex portulacoides* (At), and *Elymus athericus* (El). MHWL = Mean High Water Level; MHWS = Mean High Water at Spring tides; MHWN = Mean High Water at Neap tides. Note that local MSL is about 0 m NAP.

891 Figure 3 Proportion of plant cover with respect to marsh surface elevation for
892 the different identified halophytic species.

893

894 Figure 4 Scatter plot of total standing biomass density B against marsh
895 elevation z with corresponding community based regression models. *Spartina*
896 *anglica* community regression line has the equation: $B_{sp} = -247 + 648.4z$ with
897 model intercept significant at $p = 0.041$ and slope significant at $p = 0.0001$. F-test on
898 the regression model is significant at $p < 0.0001$. Adjusted $R^2 = 0.733$. Multi-species
899 community regression line has the equation: $B_{multi} = 6685 + 2526z$ with model
900 intercept significant at $p = 0.001$ and slope significant at $p = 0.002$. F-test on the
901 regression model is significant at $p = 0.032$. Adjusted $R^2 = 0.586$.

902

903 Figure 5 Scatter plot of total standing biomass density B against marsh
904 elevation z with the corresponding regression line of equation $\log_{10} B = 2.29 + 0.36z$.
905 Model intercept and slope are both significant at $p < 0.0001$. F-test on the regression
906 model is significant at $p = 0.001$. The adjusted coefficient of determination (R^2) is
907 equal to 0.715.

908

909 Figure 6 Box plots of (a) stem diameter and (b) stem height with respect to the
910 total standing biomass density averaged over every elevation point.

911

912 Figure 7 Scatter plot of stem diameter (a); stem height (b); stem density (c); and
913 projected plant area per unit volume (d) against total standing biomass classified by
914 the plant communities similarly with Figure 4. Regression line is drawn only for the
915 stem height data of the *Spartina anglica* species community, which has the equation

916 $h_s = 0.47B + 22.36$. Model intercept is significant at $p = 0.002$ as well as slope at $p <$
917 0.0001 . F-test on the regression model is significant at $p < 0.0001$. The adjusted
918 coefficient of determination (R^2) is equal to 0.88 . Note that standing biomass and
919 physical attributes data are averaged over the elevation of the corresponding
920 elevation point.

921

922 Figure 8 Scatter plot of stem height h_s against total standing biomass density B
923 with the corresponding regression line of equation $h_s = 0.09B^{0.27}$ and confidence and
924 prediction intervals. The adjusted coefficient of determination (R^2) is equal to 0.53 .
925 Note that the total standing biomass and stem height data are averaged over the
926 elevation of the corresponding elevation point.

927

928 Figure 9 Box plots of stem diameter per identified halophyte species: (Sp)
929 *Spartina anglica*; (As) *Aster tripolium*; (Su) *Suaeda maritima*; (El) *Elymus athericus*;
930 (At) *Atriplex portulacoides*; (Sa) *Salicornia europea*; (Spe) *Spergularia salina*.

931

Figure 1: Study area and measurement transect. (a) Location within western Europe; (b) View of the high marsh zone; (c) Aerial view and planar course of the measurement transect; (d) View of the low pioneer marsh zone.

Figure 2: Topographic profile and plant distribution along the measurement transect. Species identified are: *Spartina anglica* (Sp), *Aster tripolium* (As), *Suaeda maritima* (Su), *Salicornia europea* (Sa), *Spergularia marina* (Spe), *Atriplex portulacoides* (At), and *Elymus athericus* (El). MHWL = Mean High Water Level; MHWS = Mean High Water at Spring tides; MHWN = Mean High Water at Neap tides. Note that local MSL is about 0 m NAP.

Figure 3: Proportion of plant cover with respect to marsh surface elevation for the different identified halophytic species.

Figure 4: Scatter plot of total standing biomass density B against marsh elevation z with corresponding community based regression models. *Spartina anglica* community regression line has the equation: $B_{sp} = -247 + 648.4z$ with model intercept significant at $p = 0.041$ and slope significant at $p = 0.0001$. F-test on the regression model is significant at $p < 0.0001$. Adjusted $R^2 = 0.733$. Multi-species community regression line has the equation: $B_{multi} = 6685 - 2526z$ with model intercept significant at $p = 0.001$ and slope significant at $p = 0.002$. F-test on the regression model is significant at $p = 0.032$. Adjusted $R^2 = 0.586$.

Figure 5: Scatter plot of total standing biomass density B against marsh elevation z with the corresponding regression line of equation $\log_{10} B = 2.29 + 0.36z$. Model intercept and slope are both significant at $p < 0.0001$. F-test on the regression model is significant at $p = 0.001$. The adjusted coefficient of determination (R^2) is equal to 0.715.

Figure 6: Box plots of (a) stem diameter and (b) stem height with respect to the total standing biomass density averaged over every elevation point.

Figure 7: Scatter plot of stem diameter (a); stem height (b); stem density (c); and projected plant area per unit volume (d) against total standing biomass classified by the plant communities similarly with Figure 4. Regression line is drawn only for the stem height data of the *Spartina anglica* species community, which has the equation $h_s = 0.47B + 22.36$. Model intercept is significant at $p = 0.002$ as well as slope at $p < 0.0001$. F-test on the regression model is significant at $p < 0.0001$. The adjusted coefficient of determination (R^2) is equal to 0.88. Note that standing biomass and physical attributes data are averaged over the elevation of the corresponding elevation point.

Figure 8: Scatter plot of stem height h_s against total standing biomass density B with the corresponding regression line of equation $h_s = 0.09B^{0.27}$ and confidence and prediction intervals. The adjusted coefficient of determination (R^2) is equal to 0.53. Note that the total standing biomass and stem height data are averaged over the elevation of the corresponding elevation point.

Figure 9: Box plots of stem diameter per identified halophyte species: (Sp) *Spartina anglica*; (As) *Aster tripolium*; (Su) *Suaeda maritima*; (El) *Elymus athericus*; (At) *Atriplex portulacoides*; (Sa) *Salicornia europea*; (Spe) *Spergularia salina*.

Table S1: Summary of descriptive statistics of plant biomass per elevation point.

Elevation point	Elevation (m NAP)	Plant species	AD scale ¹	Average biomass ² (g.m ⁻²)	Std dev. (g.m ⁻²)	Min. biomass ² (g.m ⁻²)	Median biomass ² (g.m ⁻²)	Max. biomass ² (g.m ⁻²)
P1	1.07	<i>Spartina anglica</i>	5	442.9	121.4	306	485.4	537.4
P2	1.14	<i>Spartina anglica</i>	5	452.9	99.1	369.8	426.4	562.6
P3	1.26	<i>Spartina anglica</i>	5	607.7	31.7	571.2	624	628
P4	1.35	<i>Spartina anglica</i>	5	649.7	181	512	583	854
P5	1.46	<i>Spartina anglica</i>	5	656.3	107.7	535.2	692	741.6
P6	1.58	<i>Spartina anglica</i>	5	804.1	76.9	715.4	844	852.8
P7	1.70	<i>Spartina anglica</i>	5	861.4	212	635	893	1056
P8	1.81	<i>Spartina anglica</i>	5	952.9	109.3	892.8	912.8	1053
P9	1.91	<i>Spartina anglica</i>	5	950.7	87.3	884.2	891	1076.8
P10	1.99	<i>Spartina anglica</i> <i>Aster tripolium</i> <i>Suaeda maritima</i>	5 2 1	1705.1	314	1495	1554	2006
P11	2.09	<i>Aster tripolium</i> <i>Spartina anglica</i> <i>Salicornia europea</i> <i>Suaeda maritima</i>	5 2 1 +	1119.6	214	984	1008	1366
P12	2.19	<i>Spartina anglica</i> <i>Aster tripolium</i> <i>Suaeda maritima</i>	4 3 2	967.0	202	822	881	1197
P13	2.30	<i>Spartina anglica</i> <i>Suaeda maritima</i> <i>Spergularia marina</i>	5 2 +	896.9	62.6	826.6	917.4	946.6
P14	2.40	<i>Atriplex portulacoides</i> <i>Aster tripolium</i> <i>Spartina anglica</i>	4 3 2	1734.5	218	1608	1609	1986
P15	2.49	<i>Elymus athericus</i> <i>Atriplex portulacoides</i>	5 +	1725.4	452	1440	1490	2246
P16	2.57	<i>Elymus athericus</i> <i>Atriplex portulacoides</i>	5 +	1648.1	97.4	1569.2	1618	1757

¹ Braun Blanquet Abundance-Dominance scale : + (< 1% cover and not abundant) ; 1 (< 1% cover); 2 (1 - 5% cover) ; 3 (25 - 50% cover) ; 4 (50 - 75% cover) ; 5 (75 - 100% cover)

²Total standing (live + dead plant material) end-of-season dry biomass (g.m⁻²) averaged over the elevation point.

Table S2: Average value of vegetation morphometric characteristics.

Elevation point	Elevation (m NAP)	Average biomass B ($\text{g}\cdot\text{m}^{-2}$)	Average stem diameter d_s (m)	Average stem height h_s (m)	Average stem density n_s (m^{-2})	Average proj. plant area per unit vol. a_s^3 (m^{-1})
P1	1.07	442.9	0.0039	0.45	505.86	1.97
P2	1.14	452.9	0.0033	0.43	466.13	1.56
P3	1.26	607.7	0.0036	0.50	611.69	2.19
P4	1.35	649.7	0.0043	0.52	608.69	2.59
P5	1.46	656.3	0.0041	0.51	534.36	2/17
P6	1.58	804.1	0.0043	0.56	502.26	2.14
P7	1.70	861.4	0.0037	0.68	487.83	1.83
P8	1.80	952.9	0.0043	0.69	472.83	2.04
P9	1.90	950.7	0.0031	0.63	863.85	2.67
P10	1.99	1705.1	0.0045	0.69	381.72	1.71
P11	2.09	1119.6	0.0072	0.64	261.25	1.87
P12	2.19	967.0	0.0050	0.61	387.21	1.91
P13	2.30	896.9	0.0030	0.58	761.33	2.27
P14	2.40	1734.5	0.0040	0.50	615.26	2.44
P15	2.49	1725.4	0.0019	0.72	1259.24	2.34
P16	2.57	1648.1	0.0020	0.77	1419.55	2.84

³ Projected plant area per unit volume a_s , defined as $a_s = d_s \times n_s$. The projected plant area per unit volume represents the total area of plant material projected orthogonal to the flow direction within a 1 m³ volume (Nepf, 1999; Mudd et al., 2010).