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Frontiers in Ecology and Evolution

Published: 08/05/2019

Peer reviewed version

Intraspecific Root Trait Variability Along Environmental Gradients Affects Salt Marsh Resistance to Lateral Erosion

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Keywords: resilience, sediment stability, response-effect framework, functional root traits, environmental gradients, root density, *Spartina anglica*, *Atriplex portulacoides*.

We request that the article will be formatted in British English.
Number of words: 5220
Number of figures: 3

Abstract

Recent studies in salt marshes have demonstrated the role of plant roots in sediment stabilisation, and hence the importance of marshes in providing coastal protection. However, the relative role of root traits and environmental factors in controlling sediment stability, and how intraspecific variability of root traits vary within and among marshes, remain poorly understood. In this study, we investigated which root trait(s) drive sediment stability (resistance to lateral erosion) in two marsh species with an important role in coastal protection (*Spartina anglica* and *Atriplex portulacoides*) and how the environment affects the expression of these traits. We sampled three marshes along salinity gradients in each of two estuaries in Wales (UK), establishing replicate plots in the respective dominant zones of each species. In all plots we sampled abiotic variables (sand, redox potential, pH, salinity) and root traits (root density, specific root density, root volume, root length density); in a subset of these plots (three per species in each marsh) we extracted soil-plant cores and assessed their erosion resistance in a flume. Sediment stability was enhanced by increases in root density and reductions in sand content. Abiotic variables affected root density in different ways depending on species: in *S. anglica*, redox was the only significant factor, with a positive, linear effect on root density; in *A. portulacoides*, redox had a non-linear (U-shaped) effect on root density, while sand had a negative effect. Collectively, these results show that i) intraspecific variability in root density can influence sediment stability in salt marshes, and ii) sediment properties not only influence sediment stability directly, but also indirectly via root density. These results shed light on spatial variability in the stability of salt marshes to lateral erosion and suggest that root density should be incorporated into coastal vegetation monitoring programs as an easy-to-measure root trait that links the environment to sediment stability and hence to the function and services provided by marshes.

1. Introduction

Salt marshes are coastal ecosystems that provide humans with valuable services such as carbon storage, forage for livestock, buffers against eutrophication and coastal protection from storms (Barbier et al., 2008; Möller et al., 2014; Nelson and Zavaleta, 2012; Shepard et al., 2011). Several studies demonstrate the ability of salt marsh vegetation to effectively decrease wave energy and stabilise the shoreline (Bouma et al., 2010, 2009; Möller et al., 2014; Möller and Spencer, 2002; Shepard et al., 2011) indicating that marshes are highly beneficial in terms of coastal protection (Costanza et al., 2008; Foster et al., 2013). At the same time, however, researchers have shown the susceptibility of salt marshes to lateral erosion (Fagherazzi et al., 2013; Leonardi et al., 2016; Marani et al., 2011; Mariotti and Fagherazzi, 2010). An increased understanding of what drives the stability of the sediment in salt marshes is a fundamental requirement to the effective integration of salt marshes into coastal management schemes (Bouma et al., 2014; Feagin et al., 2010).

The capacity of salt marshes to resist lateral erosion has received attention recently, with studies establishing that sediment sand content and plant roots are the main drivers of sediment stability (Feagin et al., 2009; Ford et al., 2016; Wang et al., 2017; Lo et al., 2017). In particular, studies in European marshes have demonstrated that increasing root biomass strongly reduces the negative effect of sand on sediment stability (Ford et al., 2016; Wang et al., 2017). Furthermore, variability in root biomass has been shown to affect sediment stability within *Spartina spp.* (Lo et al., 2017), suggesting that intraspecific variability may play an important role in sediment stabilisation. Yet, little is known about the mechanism by which roots bind the sediment or how the environment drives intraspecific root variability. The response-effect framework of functional traits is a powerful approach for understanding the mechanistic link between the response of organisms to environmental factors and, in turn, the effect on ecosystem functions (Lavorel et al., 2013; Lavorel and Garnier, 2002; Suding et al., 2008). In this framework, variability in environmental factors can modify plant traits (e.g. root length) and, in turn, these changes can affect ecosystem functions (e.g. sediment stability). Thus, understanding the cascade effect from abiotic factors to sediment stability in salt marshes is fundamental to gain insights on marsh lateral resistance to erosion.

In salt marshes, recent studies have investigated only the role of root biomass on sediment stability (Ford et al., 2016; Wang et al., 2017; Lo et al., 2017), while in terrestrial systems wider exploration of a range of traits has shown that root traits underpinning a denser and finer root system reduce soil erosion rates (Baets et al., 2007; Bardgett and van der Putten, 2014; Burylo et al., 2012; De Baets et al., 2006). In particular, studies in terrestrial systems highlight that fine roots are mainly responsible for sediment stabilisation (e.g. Burylo et al., 2012). Furthermore, both work in terrestrial systems and salt marshes has also illustrated the potential for environmental factors to affect root traits that are important for sediment stability. For example, in nutrient poor soils plants invest more biomass in the root system and have higher specific root length (Freschet et al., 2015), which could have a positive effect on soil stability. Similarly, experimental studies in salt marshes have shown that an increasing nutrient load corresponds with a decrease in root biomass and length of first order roots in some species (Bouma et al., 2001; Bouma et al., 2001; Deegan et al., 2012), which could decrease sediment stability. However, in salt marshes it is unknown how root traits, and fine roots in particular, vary along other key environmental gradients and the consequences for sediment stability. Therefore, understanding the effect of the environment on key root traits has the potential to enhance our ability to predict the stability of marshes to lateral erosion.

Salinity, redox potential (a proxy for anoxia in the sediment) and sand content in soils (a proxy for nutrient levels in the sediment) are known to be strong environmental stressors for salt marsh plants (Armstrong et al., 1985; Crain et al., 2004; Olff et al., 1997; Tyler and Zieman, 1999; Watson and Byrne, 2009), yet how variation in these abiotic factors affects root traits in salt marshes remains largely unknown. Plants show a range of morphological and physiological adaptations to cope with these factors (Colmer and Flowers, 2008; Flowers and Colmer, 2008; Naidoo et al., 1992). For instance, plants can produce glands for salt extrusion in high salinity environments (Tabot and Adams, 2014) and aerenchyma and adventitious roots to allow oxygen transport to the root tips in sediment with low redox (Armstrong, 2000; Nishiuchi et al., 2012). Furthermore, the low nutrient status of sandy soils and their mobility could also affect root development (Fourcaud et al., 2008; Freschet et al., 2017; Olff et al., 1997; Schutten et al., 2005; Tyler and Zieman, 1999). Therefore, when environmental conditions are far from a plant's optimum they can directly reduce overall root growth and induce metabolically expensive adaptations that may affect root trait expression (e.g. fewer fine roots) at the intraspecific level. In this way, adaptations to environmental stresses can have detrimental effects on sediment stability.

We investigated how abiotic factors along environmental gradients directly and indirectly affect the stability of saltmarsh sediment through regulating plant root traits. We tested the stability of extracted cores in a flume system and hypothesised first (H1), that root traits associated with a finer root system will be better predictors of sediment stability than other traits (e.g. root density) because they indicate root biomass is more evenly distributed throughout the sediment, which determines that, second (H2), fine roots will be more important for sediment stability than other below-ground compartments (rhizomes, coarse roots). Furthermore, we also considered the effects of sediment properties on erosion and hypothesised (H3) that increasing sand content would reduce sediment stability. Finally, we investigated the potential for environmental factors to indirectly affect sediment stability via their effects on root traits. We hypothesised (H4) that reduced below-ground plant growth and investment in roots would be associated with stressful sediment conditions (e.g., low redox), indirectly reducing sediment stability. We sampled marshes along two estuaries in South Wales (UK) to encompass natural salinity and redox gradients. We focused on *Spartina anglica (C.E. Hubb.)* and *Atriplex portulacoides (L.)* (hereafter *Spartina* and *Atriplex* respectively) because in the UK, both species form large monospecific stands at the marsh edge (*Spartina*) and along marsh creeks (*Atriplex*) (Rodwell, 2000), thus being directly involved in stabilising sediment against lateral erosion. We analysed the two species separately to understand the importance of intraspecific trait variability for sediment stability in salt marshes.

2. Materials and Methods

2.1. Site description

Six salt marshes were selected along a salinity gradient in two estuaries in South Wales (UK), the Loughor and the Taf (Figure 1). These marshes showed some variation in community characteristics, but all shared the common feature of extensive monostands of the two target species. In the Loughor estuary, Pembrey Burrows (PB), Penrhyn Gwyn (PNR), and Loughor (LOG) marshes were situated at the mouth, middle, and head of the estuary, respectively. Pembrey contains several zones, with *Spartina* dominating the pioneer zone and *Atriplex* occupying the low-mid marsh. Penrhyn Gwyn is characterised by the presence of *Spartina* and *Atriplex*, which constitute almost the entire marsh, except for the grazed portion at the landward side; no signs of grazing (browsing marks) were found in the sampling area. Loughor marsh is part of a farm, but no grazing from cattle was observed in the sampled area. *Spartina* dominates the pioneer zone and *Atriplex* is present at the low-mid marsh along the creeks; landward of these zones a mixed community is present.

Laugharne South (LS), Laugharne Castle (LC) and Laugharne North (LN) are the marshes at the mouth, middle, and head of the Taf estuary, respectively. Laugharne South is dominated by *Atriplex* although in the pioneer zone *Spartina* is dominant (with some *Salicornia spp*. and *Suaeda marina*). In Laugharne Castle, *Spartina* is the main species in the pioneer zone with *Atriplex* present in the low-mid marsh, as a small strip of patchy vegetation. Laugharne North is characterised almost entirely by *Atriplex*, with the pioneer zone dominated by *Spartina*.

2.2. Study design

At the end of July 2016, in the areas where *Spartina* and *Atriplex* were dominant we established seven 1m x 1m plots for each species in each salt marsh and recorded GPS positions. Plots were separated by roughly 30 metres, except in the *Spartina* zone in Pembrey where they were 10-15 metres apart due to the limited area covered by this species. Plots were positioned to ensure that only the two targeted species were represented with 100% cover and, thus, excavated roots belonged to the species under study. Thus, for a suite of abiotic and root trait parameters (Appendix I, Table A1) we obtained a total of 42 replicates per species (6 marshes x 7 plots per species). In each marsh and for each species, we collected a core of 16 cm in diameter and 30 cm depth from three of the seven plots for a total of 36 cores. Plots were chosen so as to maximise the distance between cores.

2.3. Root traits

In October 2016, sediment samples of 500 cm^3 volume (5 x 5 cm surface area and 20 cm depth) were collected adjacent to where the core was extracted for root traits measurements. In plots where cores were not collected, we excavated a piece of marsh to simulate the core extraction and collected the sediment sample as described above. Sediment samples were washed over a sieve (mesh size, 1mm) to minimise root loss and roots were collected and divided into rhizome, coarse roots (roots > 1mm in diameter) and a mixture of fine roots (roots < 1 mm in diameter; (Freschet and Roumet, 2017) and dead plant material. Rhizomes and coarse roots were distinguished based on their morphology. Note that, although *Atriplex* is a dicotyledonous with a tap root system lacking true rhizomes, its shoots have a prostrate growth form and are often buried in the sediment, forming adventitious roots. Thus, from a sediment stability perspective these buried shoots would play a similar role as rhizomes and, for ease of discussion, here are grouped in the rhizome category. The fine roots present in the samples were calculated based of the proportion of fine roots present in three subsamples of ~1g fresh material.

Root traits were measured on representative subsamples of rhizome, coarse and fine root sub-samples. We placed the root material into a petri dish, scanned all the material (black and white at 1200 dpi of resolution; Epson Perfection, V550 Photo) and analysed the root length in the scanned images with Rootnav software (Pound et al. 2013). All root and rhizome material was dried at 70°C for 48 hours (Pérez-Harguindeguy et al., 2013) and the total specific root length (SRLt) was measured as the sum of the length of all roots (rhizome, coarse roots, and fine roots) divided by the sum of their dry weight. We used SRLt as a proxy of the investment of the plant in rhizome/coarse roots vs. fine roots (Burylo et al., 2012; Freschet and Roumet, 2017). The diameter of ten roots in each image were measured with ImageJ software (Schindelin et al., 2012) and used to calculate total root volume as $(r2 \cdot \pi) \cdot ERL$, assuming the root is a cylinder; ERL is the estimated length of the entire root system based on the weighted length of scanned roots over the total root weight [(root length/scanned root weight) · total root weight]. Root length density (RLD) and root density (RD) are respectively the length and the weight of the entire root system divided by the 500 m^3 soil volume sampled (Baets et al., 2007; De Baets et al., 2006). Also, we measured root density for rhizomes (RD.R), coarse roots (RD.C), and fine roots (RD.F) as the weight of each root compartment divided by the 500 m3 soil volume.

2.4. Sediment Erosion rate

Cores (36 in total) were collected in the middle of plots according to Ford et al. (2016) at the end of the growing season (late October 2016). We tested the cores in a flume facility at Bangor University using the methods of Ford et al. (2016), except cores were eroded at only one flow strength (146 Pa). Each core was weighed on a scale, eroded for five minutes and weighed again; we repeated this process five times for a total of 30 minutes of erosion for each core (examples of eroded cores in Appendix I, Figure A2). This temporal pattern of erosion and measurement allowed us to detect weight loss of clay cores (*Atriplex*) while avoiding complete erosion of sandy cores (*Spartina*).

2.5. Abiotic variables

We sampled sediment abiotic variables (Appendix I, Table A1) in plots on three spring tides over July-September 2016 to minimise the influence of variation in tide heights and weather, and plot averages were used for analysis. We inserted Macrorhizones (www.rhizosphere.com) at 15 cm depth, extracted the porewater and sampled for salinity and pH (Hanna instrument, HI98129). Redox potential was measured at 5 cm soil depth (Hanna instruments, HI 98120). We sampled for sediment in two of the spring tides, using a 10 cm deep, 2.5 cm diameter core; samples were oven dried for 72 hours at 70°C and consequently we quantified: sediment moisture content, bulk density, and organic matter content (loss on ignition, 18 hours at 440 °C) (Feagin et al., 2009). Combusted sediments were sieved to separate the clay-silt fraction (<53 µm), fine sand (53-250 µm), coarse sand (250-1000 µm) and very coarse sand (>1000 µm) (Denef et al., 2001).

2.6. Statistical analysis

The core erosion data was described by a mixed effects model (Bates, 2010) with time of erosion (mins) both as a fixed explanatory variable and a random effect nested in core; core was a random intercept nested within marsh. This model structure allowed individual cores to vary in their initial mass and erosion rate; it also accounted for the hierarchical nature of the sampling. The response variable (loss of core mass) was log-transformed to account for the non-linear decrease in erosion over time (see example in Appendix I, Figure A2). After fitting the models (one for each species), we extracted the slopes for each core and we used these slopes as a metric of sediment stability (loss of mass/unit of time).

First, a set of a priori mixed-effect models (full models: Appendix I, Table A2) were used to identify root traits that affected sediment stability. Models included parameters for sediment grain size (e.g. sand) and root character (e.g. RLD) because previous studies showed their importance for sediment stabilisation (Ford et al., 2016; Lo et al., 2017; Wang et al., 2017) and marsh as a random factor. Models were ranked with the corrected Akaike Information Criteria (AICc; Akaike, 1973; Burnham et al., 2011) using the R package (Barton, 2016). Second, we designed a set of a priori mixed-effect models (Appendix I, Table A3) using RD, the trait selected in the best model from the previous analysis, to understand which root compartment (Rhizome, Coarse roots, and Fine roots) was more important for sediment stability. Because these models were based on the best model selected in the first part of the analysis, results from this model selection has to be considered more exploratory. Third, a priori mixed-effect models (Appendix I, Table A4) were used to understand the effect of the physical environment on the expression of RD, which was the best-model root trait identified in step 1 for both species. As abiotic predictors we included four well known stressors for salt marsh plants: sand content in the sediment, sediment redox potential, pH, and salinity. Models were designed on expected effects of abiotic variables. We standardised abiotic variables to zero mean and unit variance and fitted these variables as fixed factors and marsh as a random factor. Models were again ranked with AICc and the explanatory power of the best model was evaluated comparing the marginal R^2 (hereafter, mR^2) with the conditional R^2 (hereafter, cR^2). Where necessary, we log transformed the response variable to meet the model assumptions. Quadratic terms were included in candidate models to provide a general and flexible approximation of possible non-linear relationships. Because of great differences in sediment characteristics between the two species (Appendix I, Figure A1), we decided to split the analysis. Plots were generated with the visreg package (Breheny and Burchett, 2013). All the analyses were carried out in R (R core team 2015).

3. Results

3.1. Effect of root traits and sediment grain size on core erosion

The erosion trial was able to account for a high portion of variability in erosion rates in both *Spartina* and *Atriplex* (respectively cR^2: 0.96 and 0.99).

We first examined the role of root traits, alongside sediment properties, in explaining sediment stability. For both species, the best model included sand content and a quadratic effect of root density (RD) (Table 1) (Appendix I, Table A5). In *Spartina*, increasing sand content significantly reduced sediment stability (Table 1, Figure 2a), while RD had a stabilising, though non-linear, effect (Table 1, Figure 2b; model: $mR^2 = 0.72$, $cR^2 = 0.72$). In *Atriplex*, neither sand content nor RD had significant effects on sediment stability (Table 1; Figure 2c, d), consistent with the low explanatory ability of the fixed effects in this model ($mR^2 = 0.18$, $cR^2 = 0.63$). Beyond RD, there was no support for a role of other root traits (e.g., SRLt) in determining sediment stability in either species (Appendix I, Table A5).

We next examined the contributions of different root compartments to sediment stability. In *Spartina*, the best model included sand content and non-linear effects of both rhizomes and coarse roots ($mR^2 = 0.79$, $cR^2 = 0.79$; Figure 2b; Appendix I, Table A6). This model revealed significant effects of sand content and rhizomes, but not of coarse roots (Table 2). The same analysis for *Atriplex* showed that the two best, similarly ranked, models had low explanatory ability and none of the parameters included in these models had significant effects on sediment stability (Table 2; Appendix I, Table A7).

3.2. Effect of the environment on root density

Since RD was the only trait included in the best models explaining sediment stability, we investigated the effect of environmental factors on this trait. (Note that correlations between RD and other root traits are reported in Appendix I, Figure A3). Redox potential and sand content were the main abiotic factors that affected RD, with both retained in the best models, although there were again differences between species (Appendix I, Table A8 and A9). In *Spartina*, there was no significant effect of sand content (Table 3; Figure 3b), while increasing redox values were significantly associated with increased RD (Table 3; Figure 3a). In *Atriplex*, sand content had a significant negative effect, while redox had a non-linear, quadratic, effect (Table 3; Figure 3c,d). In the upper half of the redox range, RD increased with increasing redox; in the lower half of the redox range RD appeared to decrease with increasing redox. However, the scarcity of samples calls for a cautious interpretation of the lower half of the relationship. In both species the marginal R^2 was relatively low with respect to the conditional R^2 (Appendix I, Table A8 and A9), indicating that other factors that vary among marshes are likely to be important for explaining RD variability.

4. Discussion

Our results show that: i) plant roots increased sediment stability (reduced erosion), particularly in the *Spartina* zone; ii) root density (RD) and the fraction of coarse roots/rhizomes – rather than the proportion of fine roots or associated traits, as hypothesised – were responsible for enhanced stability in the *Spartina* zone; and iii) root density was greater in sediment with higher redox potential (both species) and was either lower (*Atriplex*) or unaffected (*Spartina*) in sediment with higher sand content. Collectively, these results deepen our understanding of the consequences and drivers of variability in belowground traits of salt marsh plants.

4.1. Effect of root traits on sediment stability

Salt marsh lateral erosion is a complex phenomenon regulated by different mechanisms. Marsh lateral erosion depends both on blocks failure, where wave action and water pressure lead to cracks in the sediment and/or subsequent fall of entire marsh blocks (Francalanci et al., 2013; Bendoni et al., 2016), and loss of sediment by sediment erosion, where sediment particles detach from the marsh under wave and water flow action (Bouma et al., 2007, 2009, 2010). At the local scale, field and mesocosm experiments showed that sediment particle erosion well correlated with lateral marsh retreat and that root biomass played a key role (Wang et al., 2017). Our study strengthens this case and shows that plant roots can increase sediment stability, contributing to reduction in lateral erosion in salt marshes. In *Spartina*, where evidence of a positive effect of RD was stronger, the non-linear relationship between RD and erosion indicates that small changes in this root trait greatly increase sediment stability until a plateau is reached. This is in accordance with flume studies in terrestrial systems, where roots maximally reduced soil detachment rate at similar values of RD (Baets et al., 2007; De Baets et al., 2006). Interestingly, terrestrial studies look at top soil instead of lateral erosion (e.g. De Beats et al., 2006). Thus, considering that similar RD values lead to comparable erosion reduction in our and their study, suggests that RD effect on sediment erosion is a general mechanism regardless of the flow direction. *Spartina* is a species wide spread worldwide (Adam, 2002) at the edge of the marsh, thus, the stabilising effect of RD in this species further confirms the importance of roots for sediment stabilisation in salt marshes demonstrated recently at intraspecific (Lo et al., 2017), species (Wang et al., 2017) and community (Ford et al., 2016) levels.

Yet, the lack of strong evidence of a sediment stabilising effect of roots in the *Atriplex* zone underlines the context dependency of these processes. Sediment composition might be an important factor explaining this result; when sand content is relatively low, as in the *Atriplex* zone, roots might play a weaker role for sediment stabilisation and sediment cohesiveness is more important (Feagin et al., 2009; Schutten et al., 2005). Indeed, previous studies also showed that root biomass better explained core erosion rates when sand content in the sediment was high (Lo et al., 2017; Ford et al., 2016). In our study, divergent root architecture of the two-focal species (fibrous, rhizomatous root system in *Spartina* versus tap root system in *Atriplex*) may have also contributed to the differences in root effects on sediment stability. Finally, it is possible that cores with low sand content (*Atriplex*) needed a longer period of erosion to show statistically detectable effects of both sand content and RD. More studies are required to fully elucidate the role of roots in sediment stabilisation in salt marshes across diverse sediment types and plant rooting architectures.

Our results further suggest that sediment stability in the sandy *Spartina* zone is mainly determined by coarse roots and rhizomes, rather than by fine roots, as argued in terrestrial studies (Burylo et al., 2012; De Bates et al., 2006). In our study, the primary role of coarse roots/rhizomes is suggested by: i) RD, the trait that we found drove sediment stability, is mainly determined by these compartments ; and ii) rhizomes and coarse roots best explained erosion rates, while fine roots were consistently not included among predictors for sediment stabilisation. Sand content in the *Spartina* zone reached levels (up to 90%) considerably greater than in analogous terrestrial studies (~50%: Vannoppen et al., 2017). Thus, it is possible that coarser roots become more important for sediment stabilisation in environments with high sand content. However, because model selection of the best root compartments involved in sediment stabilisation was more an exploratory analysis and because of methodological differences in defining root classes between our and terrestrial studies, we cannot generalise these results. In our study the root diameter across the entire root system ranged from 0.5 to 3 mm (rhizomes included), which would be considered either as fine roots (Beats et al., 2007) or coarse roots (Burylo et al., 2012) depending on the terrestrial study considered. Future studies should include a wider sand content gradient and range of root diameters to further elucidate the mechanisms involved in sediment stabilisation (e.g. fine vs. coarse roots) thus allowing reconciliation of the apparent discrepancy between salt marshes and terrestrial systems.

4.2. Effect of the environment on root traits and sediment stability

Across the two species, root density showed similarities and differences in its responses to environmental factors, and thus the potential for indirect effect of abiotic factors on sediment stabilisation. First, RD in both species appeared invariant to salinity. This indicates that, while high salinities are known to suppress biomass production in salt marsh plants (Cooper, 1982; Crain et al., 2004; Flowers and Colmer, 2008), these dominant, halophytic, salt marsh plants are able to sustain RD, and therefore associated sediment stabilisation, across sites spanning a range of salinities in our study system. Second, notwithstanding the non-linear pattern in *Atriplex*, both species showed evidence that declining redox, a proxy for low oxygen in the sediment, could suppress RD. This can probably be explained by the metabolic costs associated with mechanisms to cope with low redox (Armstrong 1979; reviewed in Colmer, 2003 and in Nishiuchi et al., 2012). While release of oxygen from plant roots (Pezeshki, 2001) may have contributed to the observed relationships, we assume the direction of causality to flow from the abiotic environment to RD given previous experimental evidence in salt marsh plants that: i) waterlogging can directly reduce growth of salt marsh plants (Bouma et al., 2001; Cooper et al., 1982); and ii) the impact of oxygen release from roots on sediment oxygenation is limited (Koop-Jakobsen et al., 2018). Therefore, factors that influence sediment redox potential, including bioturbation, tidal inundation (and sea-level rise) and livestock grazing, may indirectly affect the stability of salt marsh sediments by altering RD. Third, the species differed in their responses to sand content, and thus nutrient availability. The resistance of RD of *Spartina* to high sand content might be explained by its ability to acquire resources directly from the water column (Bouma et al., 2002), or a greater capacity for compensatory investment in belowground biomass under low soil nutrients, a mechanism known for terrestrial plants (Freschet et al., 2015). *Spartina* therefore sustains an important erosion buffering function even where sand content, and thus the erosion vulnerability of the marsh platform, is at its highest. Indeed, the sandier sites at the mouth of the estuaries (Appendix I, Figure 1) did not erode more quickly than those at the heads. Finally, although we investigated a suite of well-known stressors for plant growth (redox, salinity, sand, and pH), in both species the modest portion of variability accounted for by the best models suggest that other factors may drive RD. For instance, variation in wave exposure that exists within and between marshes might affect plants' investment in roots (Coops et al., 1996). Further developing our understanding of the belowground responses of salt marsh plants to environmental factors will be an important task if the future vulnerability of salt marshes to lateral erosion under climate change are to be predicted.

4.3. Global significance and limitations

Spartina is a pioneer species with a cosmopolitan global distribution (Adam, 2002), thus results of our study highlight the importance of vegetation for reducing lateral erosion in salt marshes. We showed here that marshes with higher sand content in the sediment erode faster, but RD can effectively counteract this negative effect of sand content. Interestingly, despite the differences found here between *Spartina* and *Atriplex*, we showed that RD is a good predictor for sediment stability. Thus, the relatively easy investigation of sediment granulometry and RD among marshes could allow managers to map marshes vulnerability to later erosion. These maps, could also be employed in management schemes for coastal protection and for understanding how climate change would impact marsh survival in the long term. Yet, more studies are need to expand our results to wider abiotic gradients and type of marshes, such as barrier island marshes, microtidal marshes, or marsh zones with mixed vegetation communities. Moreover, we stress here that our study extrapolates from a flume experiment, but marsh lateral erosion is a complex phenomenon. Several factors contribute to marsh lateral erosion, with wind exposure and foreshore morphology acting at large and intermediate scales respectively (Wang et al., 2017). Furthermore, block marsh failure is an important mechanism of marsh retreat (Francalanci et al, 2013; Bendoni et al., 2016), which was beyond the scope of investigation of our study. Although plant roots can play a crucial role in reducing block failure (Bendoni et al., 2016), the role of root density in this regard is yet to be investigated. Overall, future studies should aim at understanding how sediment stabilisation by roots relate to other aspects of marsh erosion (e.g. block failure).

4.4. Conclusion

This study shows roots of saltmarsh plants effectively stabilise sediments against erosion, but that root development varies with environmental context, thus generating spatial variation in erosion protection by plants. By addressing both the response of roots to the environment, and, in turn, the effect of roots on sediment stability (‘response-effect’ approach), we revealed the important role that intraspecific variability plays in marsh resistance to erosion and that environmental factors can propagate torough plant traits to influence salt marsh stability. Surprisingly, we found scarce evidence that fine roots – or associated traits – played an important role in sediment stabilisation. Instead, overall root density, and especially the biomass of rhizomes and coarse roots, drove sediment stability. This suggests that different mechanisms of root-sediment stabilisation might exist depending on sand content, and that, in salt marshes, root density can efficiently capture the role of salt marsh plants for sediment stabilisation. More studies are warranted to elucidate the indirect effect of the environment on salt marsh root traits enabling researchers to better forecast salt marsh stability under future climate change and to inform managers on the effective integration of salt marshes into coastal defence schemes.

5. Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6. Author Contributions

DDB, JG developed the idea and led the writing of the manuscript. DDB performed field work, laboratory work, and data analysis. JG, MF, MR contributed to data analysis. MR contributed to field and laboratory work. MF, SJ, MS, TB, and PN contributed to writing the manuscript. All authors contributed to manuscript revision, read and approved the submitted version.

7. Funding

Funding to support this work was provided by Welsh Government and HEFCW through the Sêr Cymru National Research Network for Low Carbon, Energy and Environment RESILCOAST project.

8. Acknowledgments

Funding to support this work was provided by Welsh Government and HEFCW through the Sêr Cymru National Research Network for Low Carbon, Energy and Environment RESILCOAST project. The authors would like to thank The Wildfowl & Wetlands Trust for access to the Penrhyn Gwyn marsh, Mr C. Delany for access to marshes on the Taf river, and Mr D.A. Roberts for access to the Loughor marsh, and Natural Resources Wales for providing authorisation for sampling. We also thank Tom Fairchild, Kate Davidson, Alizée Mauffrey, Laura Cappelatti, Josh Mutter, Olivia Smith, Ella Milne, Gemma Woodhouse, Livius C. Bozga, and Macarius Howard for practical assistance.

9. Data Availability

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

10. References

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Figures Legends

Figure 1 -The study sites. In panel (A), the circle indicates the location of the sampling areas in UK. Panel (B), shows the area inside the circle from panel a. Marshes sampled are highlighted in black, other marshes in the estuary are shown in dark grey; from the mouth to the head of the estuary, the position of Pembrey (PB), Penrhyn Gwyn (PNR), and Loughour (LOG) marshes in the Loughor estuary (lower side panel) and Laugharne South (LS), Laugharne Castle (LC), and Laugharne North (LN) marshes in the Taf estuary (left side panel).Panel (C), shows the area inside the circle from panel (B). The dark green area represents the *Spartina anglica* zone, light green area represents the *Atriplex portulacoides* zone, white area represents other salt marsh vegetation types; the red ellipses represent areas (~ 200 meters long) were 1x1 meter plots were established.

Figure 2 - Effects of sand content and root content on marsh resistance to erosion (sediment stability represents a change in the slope of sediment loss; more negative values indicates greater sediment loss, g/min) in experimental erosion cores from *Spartina* (A, B) and *Atriplex* (C, D) marshes. In panel b, the insert represents marsh resistance to erosion in experimental erosion cores from *Spartina* when only rhizomes are considered. In panel a and c points indicate partial residuals when root density (RD) was held constant (median). In panels b and d, and the insert in panel b, points indicate partial residuals when Sand was held constant (median).

Figure 3 – The effects of Redox (left panels) and Sand (right panels) on root density in *Spartina* (A, B) and *Atriplex* (C, D). Note: in *Atriplex* the response variable RD has been log transformed to meet model assumptions, but the figures C, D show non-transformed data to allow better comparison between species. Points indicate partial residuals when other abiotic variables are held constant.

Tables

Table 1 - Summary results of mixed-effect models of the effect of sand content and root density (RD) on sediment stability for *Spartina* and *Atriplex*. RD, root density. Sample size: N= 16 in *Spartina* and N=17 in *Atriplex*. The random effect of Marsh has been omitted for clarity.

		Coefficient estimate	Standard error	t value	P	mR^2	cR^2
Spartina anglica							
Sediment stability ~	Sand	-0.0016	0.00022	-4.84	**<0.001**	0.72	0.72
	RD	8.96	2.845	3.15	**0.010**		
	RD^2	-463.3	186.4	2.49	**0.032**		
Atriplex portulacoides							
Sediment stability ~	Sand	-0.00056	0.00032	-1.743	0.105	0.18	0.63
	RD	3.291	3.316	0.992	0.345		
	RD^2	-368.8	438.9	-0.840	0.420		

Table 2 - Summary results of mixed-effect models of the effect of sand and root density (RD) on sediment stability for *Spartina* and *Atriplex*. RD.R, rhizome root density; RD.C, coarse root density; RD.F, fine root density. Sample size: N= 16 in *Spartina* and N=17 in *Atriplex*. The random effect of Marsh has been omitted for clarity.

		Coefficient estimate	Standard error	t value	P	mR^2	cR^2
Spartina anglica							
Sediment stability ~	Sand	-0.0011	0.00002	-5.680	**0.001**	0.79	0.79
	RD.R	16.87	4.345	3.882	**0.005**		
	$RD.R^2$	-944.2	296.3	-3.187	**0.013**		
	RD.C	-13.18	26.13	0.504	0.627		
	$RD.C^2$	-395.4	1802	0.219	0.832		
Atriplex portulacoides							
Sediment stability ~	Sand	0.00076	0.00036	-2.081	0.071	0.23	0.88
	RD.C	-38.21	27.30	-1.399	0.2120		
	$RD.C^2$	50210	54740	0.917	0.3925		
	RD.F	9.265	8.012	1.156	0.2894		
	$RD.F^2$	-983.8	179	-0.550	0.601		
Sediment stability ~	Sand	0.00086	0.00039	-2.203	0.054	0.24	0.77
	RD.R	11.117	5.521	2.023	0.083		
	$RD.R^2$	-2458	1257	-1.956	0.093		
	RD.C	-38.27	45.90	-0.834	0.435		
	$RD.C^2$	44870	79790	0.562	0.594		

Table 3 - Summary table of linear mixed-effect models of the effect of Sand and Redox on Root density (RD) for both *Spartina* and *Atriplex*. Coefficients are standardised. Sample size, N= 40 in *Spartina* and N= 42 in *Atriplex*. The random effect of Marsh has been omitted for clarity.

		Coefficient estimate	Standard error	t value	P	mR^2	cR^2
Spartina anglica							
RD ~	Sand	0.0003	0.0007	0.463	0.646		
	Redox	0.002	0.0008	2.343	**0.025**	0.13	0.61
Atriplex portulacoides							
log(RD) ~	Sand	-0.255	0.117	-2.184	**0.036**		
	Redox	0.423	0.181	2.363	**0.023**		
	$Redox^2$	0.241	0.080	2.998	**0.005**	0.20	0.52