Title: Seasonal and spatial within-marsh differences of biophysical plant properties – Implications for wave attenuation capacity of salt marshes

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Abstract

Salt marshes attenuate waves and thus have an important function for coastal protection. Biophysical properties of salt-marsh plants play a key role in the process of wave attenuation and can be differentiated by morphological properties such as stem density, vegetation height and aboveground biomass as well as by biomechanical properties related to stem flexibility. Numerical or physical scale models predicting wave attenuation over vegetated surfaces need to include biophysical properties. However, only few studies have quantified morphological and biomechanical properties of salt-marsh plants and fewer have considered seasonal and within-marsh spatial variability of biomechanical properties. The aim of this study was to quantify biophysical properties of the common salt-marsh grasses *Spartina anglica* and *Elymus athericus*, including stem flexibility and density as well as aboveground biomass, temporally and spatially. Samples were collected in spring and in summer 2014 at a study site located in the Northern German Wadden Sea. Aboveground biomass was harvested in plots of 50 x 50 cm, stem density was determined by counting and flexibility of plant stems was determined with three-point bending tests. Biophysical properties of both species varied significantly between seasons with plant stem stiffness being 5.0 (*S. anglica*) and 2.9 times (*E. athericus*) higher and aboveground biomass being 2.1 (*S. anglica*) and 1.3 times (*E. athericus*) higher in summer than in spring. Small-scale spatial differences for those biophysical plant properties were found for *S. anglica* with plant stem stiffness being 4.0 (spring) and 2.8 times (summer) higher and aboveground biomass being 1.6 (spring) and 1.5 times (summer) higher in a landward than in a seaward-located zone. Small-scale spatial differences of biophysical properties were not found in *E. athericus*. We conclude that variability in biophysical properties should be considered in models and experiments especially for *S. anglica* when predicting and quantifying marsh wave attenuation capacity.

Introduction

Vegetation plays a vital role in the form, functioning and ecosystem service delivery of coastal salt marshes. Many salt-marsh plants act as ecosystem engineers by modifying their physical environment through the reduction of hydrodynamic energy and the enhancement of sediment deposition (Bouma et al. 2005, 2010; Peralta et al. 2008). If sufficient sediment is deposited, marshes can keep pace vertically with rising sea level (Nolte et al. 2013). This ability implies that vegetated salt-marsh surfaces can be an important component of nature-based coastal protection schemes especially in times of climate change, accelerated sea-level rise and increased storm frequency (Koch et al. 2009; Narayan et al. 2016; Sutton-Grier et al. 2018).

Recent studies have shown that biophysical properties of plants, which can be categorized as morphological (e.g. stem density, vegetation height and aboveground biomass) and biomechanical (e.g. stem flexibility), play a key role in the capacity of marshes to dissipate wave height and energy (Möller et al. 2014; Paul et al. 2016; Rupprecht et al. 2017). Wave dissipation is a combined effect of bottom friction and vegetation, which form an obstruction to wave-induced oscillatory flow. Vegetation induced obstruction depends both on standing biomass or stem density and stem flexibility. Vegetation, in turn, experiences drag and re-orientation by wave forces (Mullarney and Henderson 2010). Flexible plants move with the surrounding water and show an avoidance strategy to minimize the risk of folding and breakage under high drag forces. In contrast, stiff plants maximize the resistance to physical damage (tolerance strategy), thus leading to higher drag forces, higher flow resistance and an increased risk of breakage compared to flexible plants (Coops et al 1994; Puijalon et al. 2011). Apart from stem flexibility, aboveground biomass and stem density also play a crucial role in wave dissipation by vegetation (Bouma et al. 2005, 2010; Widdows et al. 2008; Peralta et al. 2008; Anderson and Smith 2014). For example, species with contrasting biomechanical plant properties can lead to a similar wave dissipation when regarded on a biomass basis (Bouma et al. 2010).

Salt-marsh plants show a wide variability in biophysical properties both within and among species, making their canopies structurally complex (Tempest et al. 2015; Rupprecht et al. 2015a). This structural complexity in combination with the unpredictable nature and high variability of hydrodynamic conditions make field measurements of the interaction between vegetation and hydrodynamics extremely challenging. Hence, many studies rely on numerical or physical modelling approaches (Tempest et al. 2015). A high model quality, however, is often hampered by limited data on biophysical properties of salt-marsh vegetation, especially regarding stem flexibility (Tempest et al. 2015). The majority of numerical wave dissipation models capture vegetation effects in a factor that consists of plant stem height, stem density, stem diameter and an empirical bulk drag coefficient $C_{D.}$ (Mendez and Losada 2004; Paul and

Amos 2011). Physical models often use plant mimics to simulate the effect of vegetation on currents and waves (e.g. Stewart 2006; Anderson and Smith 2014). However, insufficient data on plant biophysical properties lead to problems in reproducing salt-marsh plants realistically by plant mimics (see Anderson and Smith 2014; Tempest et al. 2015). Consequently, it would be valuable to assess the spatial and temporal variation in biophysical properties of salt-marsh species (Rupprecht et al. 2015a).

Morphological properties of salt marsh plants have been examined (e.g. Morris and Haskin 1990; Möller and Spencer 2002; Neumeier 2005; Foster-Martinez 2018), however, those concerned with biomechanical properties focused predominantly on freshwater plants (Ostendorp 1995; Coops and van der Velde 1996; Miler et al. 2012; 2014), brackish plants (Heuner et al. 2015; Carus et al. 2016; Silinski et al. 2015; 2018), macroalgae (Harder et al. 2006; Paul et al. 2014) or seagrass (Patterson et al. 2001; Fonseca et al. 2007; Luhar and Nepf 2011; Paul and Amos 2011). Studies of salt marshes are scarce (but see Rupprecht et al. 2015a). Biomechanical properties of salt-marsh plants are likely to be affected by seasonal climatic variation in temperate zones as previously found for helophytes (Coops and van der Velde 1996) or lake and river plants (Miler et al. 2014).

Recently, the importance of considering seasonal variability in vegetative and biomechanical properties of salt marshes for estimates of wave attenuation over salt marshes was addressed by van Loon-Steensma et al. (2016). In order to generate reliable predictions of the marsh wave attenuation capacity and successfully incorporate marshes in coastal protection schemes, both seasonal and spatial variability in biomechanical and morphological vegetation properties need to be integrated in numerical and physical scale models (van der Meer 2002; Smith, Bryant and Wamsley 2016).

The aim of this study is to quantify stem flexibility, stem density and aboveground biomass of salt-marsh plants seasonally and spatially between seaward and landward-located zones. Data were collected for two perennial grasses that are widely spread in salt marshes of NW Europe (*Spartina anglica* and *Elymus athericus*) to answer the following questions: (I) how do biophysical properties of the salt-marsh grasses *Spartina anglica* and *Elymus athericus* differ between spring and summer?; and (II) how do biophysical properties of *Spartina anglica* and *Elymus athericus* differ between seaward and landward-located zones?

Methods

Species

Spartina anglica

The perennial grass *Spartina anglica* (hereafter referred to as *Spartina*) typically occurs in the salt marsh pioneer zone (below mean high tide level) and the low marsh, where it can form monospecific stands (Nehring and Adsersen 2006). In late fall, shoots die but largely remain as dead vegetation canopies while rhizome development increases (Nehring and Adsersen 2006). Throughout the last century, *Spartina* has spread from the south coast of the UK to salt marshes all over Europe, both naturally and by deliberate transplantations (Gray and Benham 1990; Nehring and Adsersen 2006; Nehring and Hesse 2008). A reason for deliberate transplantations was its function to act as an ecosystem engineer by enhancing sedimentation through dense aboveground canopies and a dense root system (Chung 1993; Bouma et al. 2005, 2010; Van Hulzen et al. 2007).

Elymus athericus

The perennial grass *Elymus athericus* (hereafter referred to as *Elymus*) occurs in European salt marshes from Northern Portugal to Southern Denmark and at the southeastern coast of the British Isles (Veeneklaas et al. 2013). *Elymus* is sensitive to grazing and relies on aerated soils (Bockelmann and Neuhaus, 1999). In salt marshes of the Wadden Sea, it forms monospecific dense stands mainly in the high marshes, and it is also increasingly establishing at lower elevations (Bockelmann and Neuhaus 1999; Valéry et al. 2004). In the recent decades, spreading of *Elymus* has been observed, which is caused by the abandonment of grazing, an increasing marsh age and the ability to reproduce by rhizomes, which survive the winter season (Rupprecht et al. 2015b). The shoots die off over the winter season but largely remain withered on the marsh platform.

Study site

Plant samples were obtained from a salt marsh on the mainland coast of Northern Frisia, German Wadden Sea (54.62°N, 8.84°E; Fig. 1 A). The studied salt marsh developed after the embankment of the adjacent Sönke-Nissen-Koog (SNK) polder and subsequent constructions of sedimentation fields in front of the dike (Kunz and Panten 1997; Mueller et al. 2019). As a salt marsh of anthropogenic origin with a thick clayish sediment layer and a regular system of creeks and drainage ditches, it can be considered representative for many salt marshes of North-West Europe. The tidal range is 3.4 m, the mean high tide is +1.59 m NHN (Normalhöhennull, which is comparable to mean sea level). Elevations within the salt marsh range from 0.9 m to 2.6 m NHN with a mean elevation of 2 m NHN (Müller et al. 2013b). The marsh stretches from the dike over 700 m to the tidal flats (Fig. 1B) and is predominantly covered by *Elymus* in the high marsh (Mueller et al. 2017) and by *Spartina* in the low marsh (according to own observations and the Trilateral Monitoring and Assessment Program, TMAP; Petersen et al. 2013).

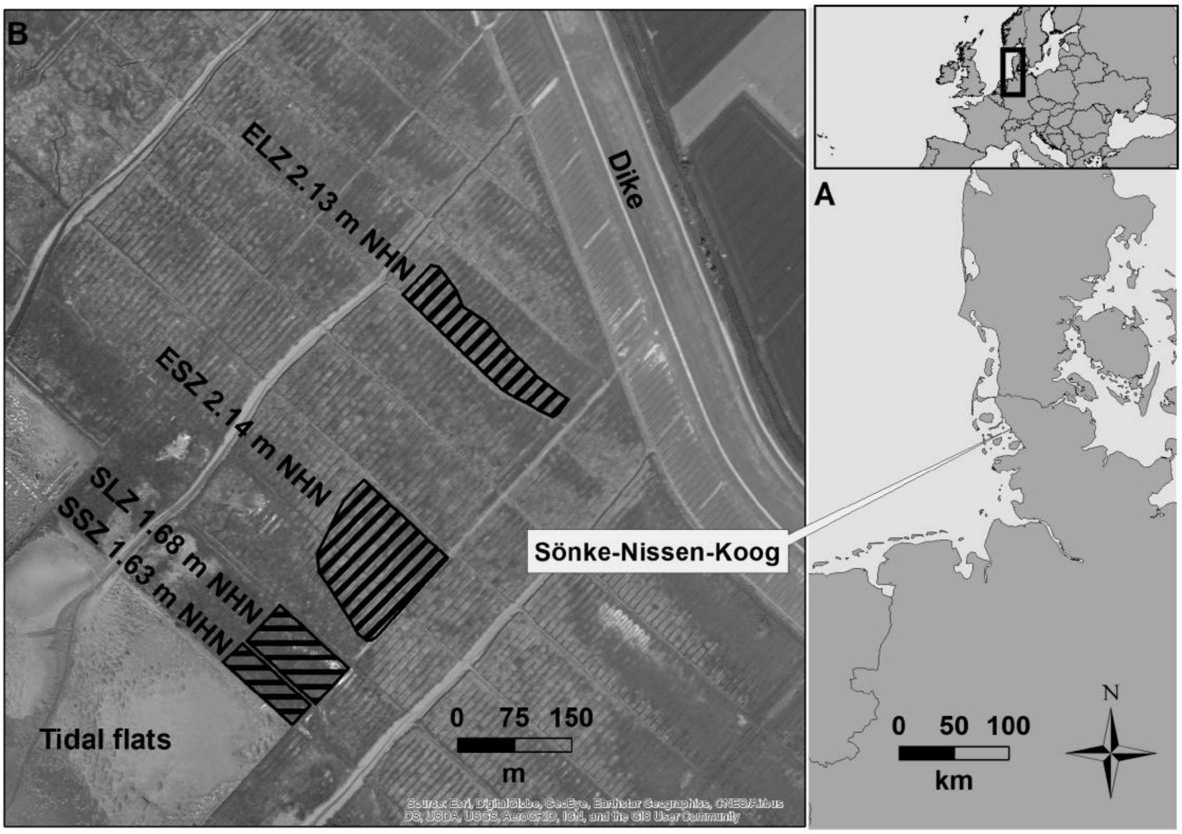

Fig. 1 A) Location of the study site in the Wadden Sea National Park Schleswig-Holstein at the German North Sea coast. The black rectangle shows the position of the area in Europe. B) Satellite image of the study site with the sampling zones. Shown are the seaward and landward located Elymus (ESZ, ELZ; vertically hatched) and Spartina (SSZ, SLZ; diagonally hatched) sampling zones with respective mean elevations above NHN. The map was created using a base map in ArcGIS © Desktop: Release 10, ESRI 2014, Redlands, CA: Environmental Systems Research Institute

Sampling design

Two sampling zones were chosen in the low marsh (dominated by *Spartina*) and in the high marsh (dominated by *Elymus*). One of the two sampling zones per vegetation type was set closer to the seaward marsh edge (‘seawards’), and one closer to the landward marsh edge (‘landwards’; Figure 1B). The seaward-located *Spartina* zone (hereafter referred to as SSZ; inundation frequency: 182 times per year; total inundation time: 557.76 hours/year; F. Müller unpublished data) stretches 40 m perpendicular along the marsh towards the landward-located zone (hereafter referred to as SLZ; inundation frequency: 156 times per year; total inundation time: 452.88 hours/year). For *Elymus*, one zone was chosen towards the low marsh (ESZ; inundation frequency: 23 times per year; total inundation time: 62.64 hours/year) and one zone was chosen closer to the dike (ELZ; inundation frequency: 23 times per year; total inundation time: 64.32 hours/y). An area-based stratified random design was applied with 40 random sampling points (20 points for flexibility measurements; 20 points for aboveground biomass and stem density measurements) generated within each sampling zone of the *Spartina* and *Elymus* vegetation type using a random point tool of QGIS 2.0.1 Dufour (QGIS Development Team 2014). The elevation of each point was assessed using a Trimble LL500 precision laser and a Trimble HL 700 receiver as a levelling instrument (2.0 mm accuracy) and a known closely located benchmark. Data were used to calculate mean elevation per zone (Figure 1B).

Measurements of plant stem flexibility

Three-point bending tests were performed to quantify plant stem flexibility under bending forces orthogonal to the plants stem. Plant samples were collected both in mid-March (before the onset of plant growth) and in late August. In the field, samples were excavated as small marsh blocks with a dimension of 10x10x10 cm and were packed in plastic bags to conduct measurements on fresh material. From each marsh block, a single adult and undamaged plant stem was chosen randomly and the stem length up to the inflorescence was measured and divided in four equal parts. A test section was defined as the beginning of the second quarter starting from the bottom end of the stem and was cut out with a razor blade. Test sections were consistently cylindrical. To minimize the effect of shear stress in bending tests, a stem diameter to stem length ratio (here stem length means the horizontal span of the tested stem section between the two metal support bars, see Figure 2) of 1:15 was chosen (see also Miler et al. 2012, 2014; Rupprecht et al. 2015a). The bending tests were performed with a Zwick/Roell testing machine (Type 1120.25, Nominal Force: max. 1 kN, using a 10 N load cell; initial load 0.01 N; Zwick GmbH & Co. KG, Ulm, Germany).

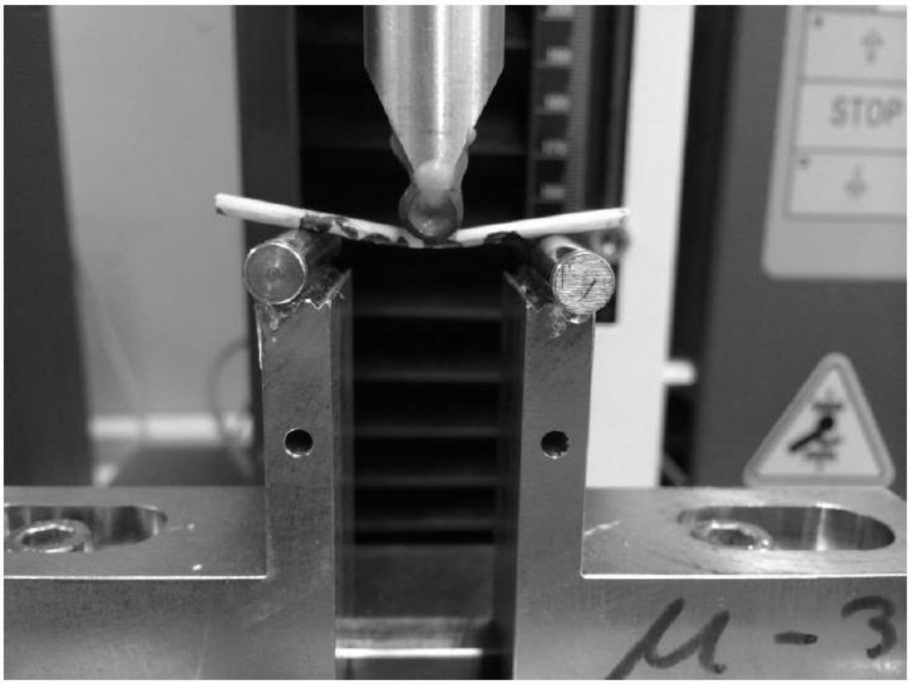

Fig. 2 Three-point bending test with a stem section of Elymus

For the measurements, a metal bar was lowered with a displacement rate of 10 mm min^{-1}. Then, the vertical deflection of the tested stem section and the applied force were recorded (see also Miler et al. 2012, 2014; Rupprecht et al. 2015a; Silinski et al. 2015, 2018). The slope was determined from the most linear part of the force-deflection curve. Furthermore, the diameter and the span of the stem between the two metal support bars were used to determine the following mechanical properties following Rupprecht et al. (2015a): (I) the second moment of area (I given in m^4) which describes the effect of stem morphology (considering stem diameter) on flexibility; (II) the Young's modulus (E given in Pa) which here describes the flexibility of the plant stem tissue without considering stem morphology; (III) the flexural rigidity (EI given in Nm^2) which describes the overall stem flexibility considering stem tissue and morphological parameters. In this study, results on the Young's modulus and flexural rigidity are presented.

Biomass and stem density measurements

Aboveground biomass (hereafter referred to as biomass) was harvested twice in 2014; in early April and in mid-August in order to identify differences in morphological properties between spring and summer. All plants rooting inside a 50x50 cm frame were cut at the soil surface.

Summer sampling was carried out within 1 m distance of the spring plots. Samples were dried for 48 hours at 65 °C to determine the dry biomass. Stem density was measured after the removal of litter by counting only the remaining stems that were still connected to a root. For *Elymus*, stem density was quantified on a 20x20 cm subplot due to large numbers of stems per area.

Statistical analysis

To analyze differences in biophysical parameters between the seasons and zones within one species, two-way analysis of variance (ANOVA) were performed. If necessary, data were log transformed prior to ANOVA to meet normality assumptions and to improve homogeneity of variances. Levene's test was used to test for homogeneity of variances, while Kolmogorov-Smirnov test was used to test the normal distribution of the data. Equal sample sizes assured robustness of parametric testing (McGuinness 2002). As a post-hoc test, Tukey's-HSD (honest significant difference) test was applied to determine pairwise differences. To assess the relationship between plant stem diameter and flexural rigidity, linear and non-linear regressions were used. Statistical analyses were conducted with *STATISTICA 10* (StatSoft Inc.).

Results

Flexural rigidity

Flexural rigidity of *Spartina* differed significantly between seasons and zones (Fig. 3A; Table 1). However, the interaction between season and zone was also significant. Flexural rigidity was 5.0 times higher in summer compared to spring. In spring, *Spartina* stems of the SLZ were 4.0 times more rigid compared to the stems of the SSZ. In summer, stems of the SLZ showed a 2.8 times higher value compared to stems of the SSZ.

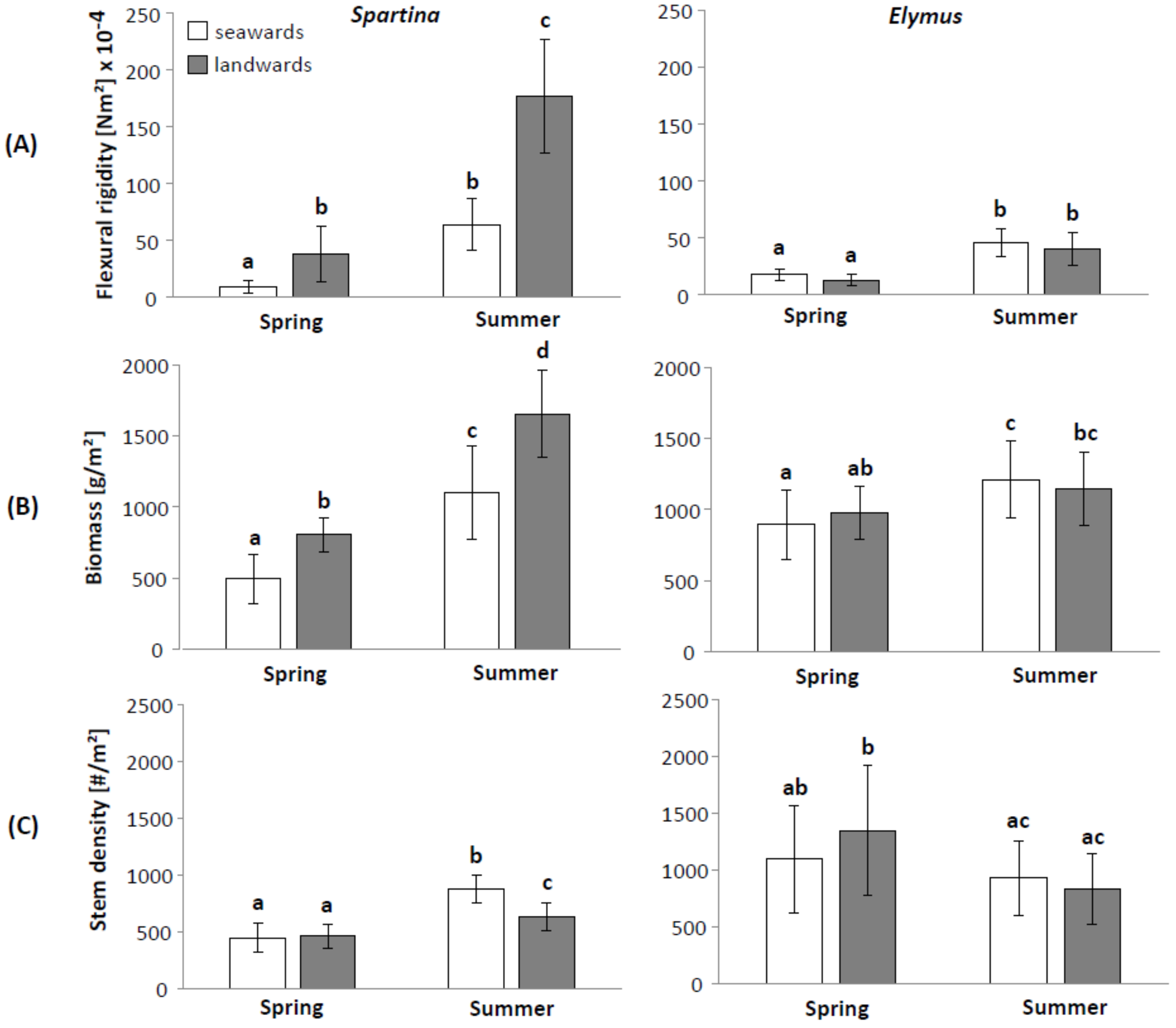

Fig. 3 Flexural rigidity (A), biomass (B) and stem density (C) of *Spartina* and *Elymus* in spring and summer, respectively. Light bars show the zone directed seawards while dark bars show the zone directed landwards. Each bar represents 20 samples. Presented are mean values ± standard deviations. Different lowercase letters indicate significant differences among the zones in both seasons. Interspecific differences have not been assessed

Table 1 ANOVA table of all biophysical parameters for *Spartina* and *Elymus* in spring and summer season in the landward and seaward-located zones. Given are F-values and p-values

		Season		Zone		Season * Zone	
		F	p	F	p	F	p
Flexural rigidity	Spartina	192.39	< 0.0001	103.65	< 0.001	36.50	< 0.0001
	Elymus	145.81	< 0.0001	5.01	< 0.05	0.81	0.78
Biomass	Spartina	163.46	< 0.0001	57.30	< 0.0001	4.33	< 0.05
	Elymus	19.26	< 0.0001	0.02	0.90	1.60	0.21
Stem density	Spartina	120.31	< 0.0001	17.59	< 0.0001	21.58	< 0.0001
	Elymus	11.63	< 0.005	0.61	0.44	3.04	0.08
Stem length	Spartina	48.39	< 0.0001	54.77	< 0.0001	1.40	0.24
	Elymus	380.31	< 0.0001	2.06	0.16	0.08	0.78
Stem diameter	Spartina	136.60	< 0.0001	58.19	< 0.0001	0.81	0.37
	Elymus	65.42	< 0.0001	0.62	0.43	2.42	0.12
Young's modulus	Spartina	2.26	0.14	6.23	< 0.05	0.37	0.54
	Elymus	1.26	0.27	2.07	0.15	4.54	< 0.05

For *Elymus*, flexural rigidity significantly differed between seasons (Fig. 3A; Table 1). Stems were 2.9 times more rigid in summer compared to spring. In both seasons, stems of the ESZ slightly, but not significantly, exceeded the rigidity of stems of the ELZ with a factor of 1.34 in spring and 1.14 in summer.

For *Spartina*, a second order polynomial regression was found to best represent the positive relationship between stem diameter and flexural rigidity. For *Elymus*, we found a linear regression to best represent the positive relationship between stem diameter and flexural rigidity (Fig. 4).

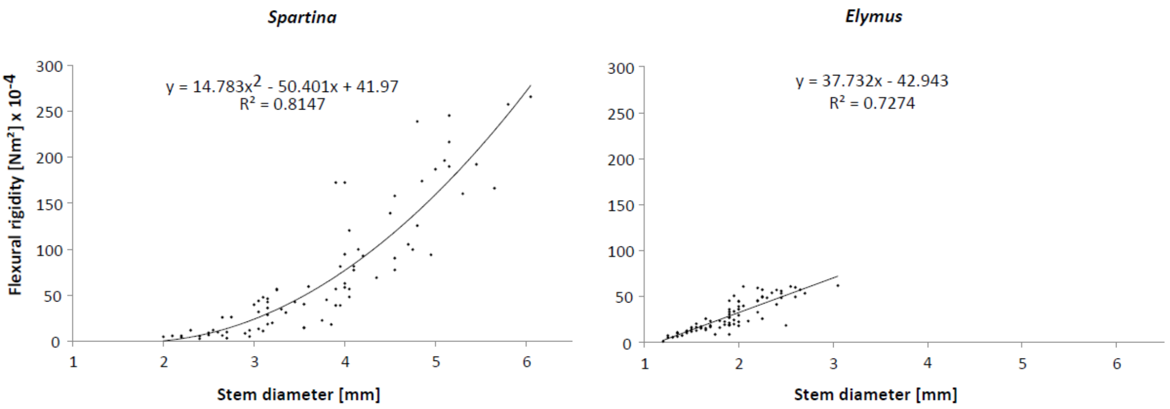

Fig. 4 Best-fit polynomial regression and linear regression between stem diameter and flexural rigidity of *Spartina* and *Elymus* stems of both seasons and zones, respectively. Shown are equations and the coefficients of determination (R^2)

Aboveground biomass

Biomass of *Spartina* differed significantly between spring and summer and between SSZ and SLZ (Fig. 3B; Table 1). Additionally, a significant interaction between season and zone was found. Compared to spring, biomass was 2.1 times higher in summer. SLZ exhibited 1.6 times more biomass compared to SSZ in spring and 1.5 times more biomass in summer. For *Elymus*, significant differences in biomass were only found between the seasons but not between the zones (Fig. 3B; Table 1). *Elymus* biomass was 1.3 times higher in summer compared to spring.

Stem density

Stem density of *Spartina* significantly differed both between seasons and zones (Fig. 3C; Table 1). Furthermore, a significant interaction between season and zone was found. Stem density was 1.7 times higher in summer than in spring. While in spring no difference was detected between the two zones, in summer stem density was 1.4 times higher in SSZ than in SLZ. Stem densities in *Elymus* differed between seasons, but not between zones (Fig. 3C; Table 1). Stem density in spring was 1.4 times greater than in summer.

Stem length, stem diameter, Young’s Modulus

Spartina and *Elymus* stems were significantly longer in summer compared to spring in both zones (Fig. 5; Table 1). Furthermore, *Spartina* stems were significantly longer in the SLZ than in the SSZ in either season, whereas for *Elymus* no spatial differences were detected. Stem diameters show the same pattern with higher values in summer compared to spring for both species, and higher values in the landward zone only for *Spartina*. The least variability between the seasons and zones was detected for Young’s modulus. Here, only *Spartina* stems showed slightly but not significantly higher values in summer compared to spring and in the SLZ compared to the SSZ in either season. No differences for Young's modulus were detected in *Elymus* stems.

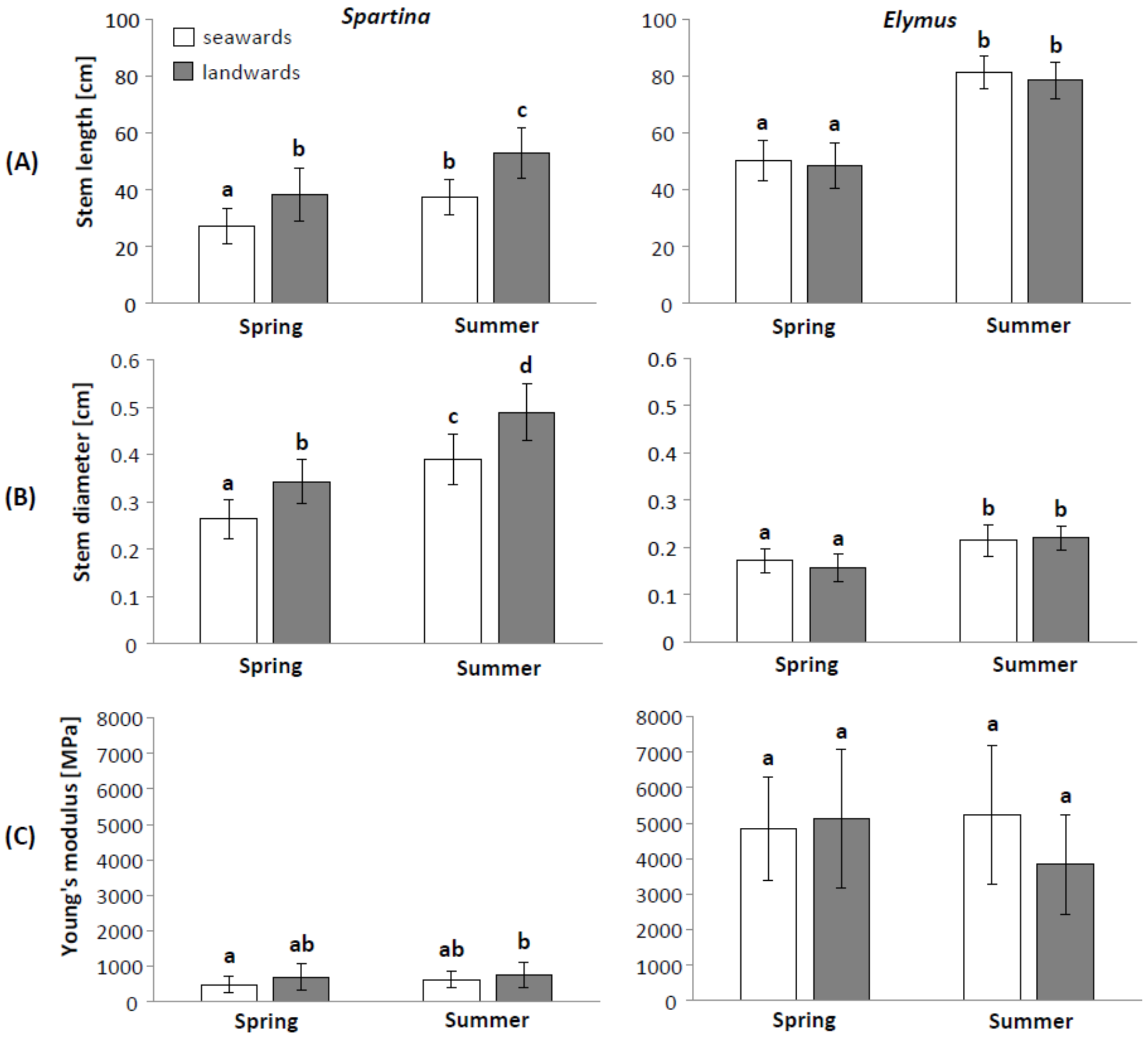

Fig. 5 Young's modulus (A), stem diameter (B) and stem length (C) of *Spartina* and *Elymus* in spring and summer, respectively. Light bars show the zone directed seawards while dark bars show the zone directed landwards. Each bar represents 20 samples. Presented are mean values ± standard deviations. Different lowercase letters indicate significant differences among the zones in both seasons. Interspecific differences have not been assessed

Discussion

Stem flexibility

Seasonal variability in stem flexibility was detected for both species with significantly higher values for flexural rigidity during summer. These results indicate the importance of considering plant morphology (here diameter) when describing plant stem flexibility. According to the regression analyses, more than 70% and 80% (R^2 values) of the variability in stem flexibility was explained by the variability in stem diameter of *Elymus* and *Spartina* stems, respectively. The increase of stem diameter by approximately 30% from spring to summer for both species explains the increase of the flexural rigidity, whereas plant tissue properties (characterized by the Young's modulus) did not vary significantly between spring and summer. As flexible stems avoid high drag forces by reconfiguration and movement with the wave-induced oscillatory flow (Bouma et al. 2005; Paul et al. 2014), the lower resistance of plant stems to wave forces in spring should result in a lower wave dissipation capacity of vegetation compared to summer.

The small-scale spatial differences with smaller diameters and hence higher flexibility of *Spartina* stems in the SSZ, which stretches 40 m from the seaward marsh edge towards the SLZ, can be interpreted as a response to physical stress by higher hydrodynamic forcing close to the seaward marsh edge. Möller and Spencer (2002) found that most wave energy is attenuated in the first 38 m on a vegetated marsh while Silinski et al. (2018) found high wave attenuation rates on a 12 m transect and Ysebeart et al. (2011) for a distance up to 50 m. Similar to our results, Heuner et al. (2015) found a pattern with more flexible plants and lower biomass amounts at the marsh in the Elbe estuary for *Schoenoplectus tabernaemontani*. In accordance, Silinski et al. (2018) found an increase of stiffness in *Bolboschoenus maritimus* stems from the marsh edge towards the higher zones of an elevational gradient.

In contrast, Carus et al. (2016) found the opposite pattern for stems of *Bolboschoenus maritimus*, a typical species in the pioneer zone of European freshwater and brackish marshes along shorelines of estuaries where ship and wave induced wave forcing occurs. These findings suggest that species growing under harsh hydrodynamic conditions may develop different biomechanical properties to either minimize physical stress (avoidance strategy; i.e. flexible stems, low flexural rigidity) from waves and currents or to withstand these mechanical forces (tolerance strategy; i.e. stiff stems, high flexural rigidity). Our results show an avoidance strategy of *Spartina* to increasing hydrodynamic forces and drag forces lower in the elevational gradient in salt marshes, as individuals in the SSZ were significantly smaller, thinner and more flexible than in the SLZ in both seasons. These characteristics should minimize the impact of hydrodynamic forces and the risk of plant breakage. However, it may also be possible that stem development in the SSZ is inhibited by constant wave action leading to thinner, smaller and more flexible stems.

Small-scale spatial variability of stem flexibility in *Elymus* was minor compared to *Spartina*. One reason for that may be that *Elymus* is growing in the high marsh and is exposed to more stable environmental conditions facing wave forcing only during extreme storm surge events. Furthermore, inundation frequency and time in the ESZ were similar to those in the ELZ as the difference in elevation between the two zones was only one centimeter. Therefore, the spatial signal was comparatively low.

Biomass

For both *Spartina* and *Elymus*, seasonal differences with higher biomass in summer than in spring were found which can be explained with the breakdown of canopies during the winter season in temperate zones (Bellis and Gaither 1985; Morris and Haskin 1990; Koch et al. 2009). In *Spartina*, we found up to two times higher biomass in summer compared to spring. Seasonal biomass changes in temperate zones have been found to affect wave dissipation in seagrass beds (Chen et al. 2007; Paul and Amos 2011), brackish marshes (Silinski et al. 2018; Schoutens et al. 2019) and salt marshes (Möller and Spencer 2002; Möller 2006). Accordingly, seasonal variability in *Spartina* biomass, as in our study, can be expected to affect wave dissipation capacity of the marsh with a higher contribution of vegetation to wave dissipation in summer than in winter and spring (see Foster-Martinez et al. 2018). *Elymus*, by contrast, shows minor although significant seasonal differences in biomass, which suggests a more continuous contribution of *Elymus* biomass to wave dissipation throughout the year. Overall, wave attenuation and resulting coastal protection should be highest when the biomass of biotic structures is at its maximum (Coops et al. 1996; Chen et al. 2007; Koch et al. 2009).

Spatial variability in *Spartina* biomass between the SSZ and the SLZ shows the same pattern as for stem flexibility with lower values for the SSZ than the SLZ in both seasons. Coops et al. (1994) found similar results with lower biomass in an exposed site compared to a sheltered site for two helophytes. Furthermore, a biomass decrease downwards an elevational gradient was observed. We assume that higher wave action and higher physiological stress due to salinity and longer inundation time in the SSZ compared to the SLZ explain the significantly lower biomass in *Spartina* (see also Huckle, Potter and Marrs 2000). The lower biomass amounts in the SSZ zone seem to correlate with a decrease in stem diameter and length accompanied by a higher flexibility in this zone compared to the SLZ. Stem length of different *Spartina* populations were studied previously by Gray and Benham (1990), where plants sampled from the pioneer populations had significantly smaller inflorescence sizes and vegetative statures in comparison with plants from higher marsh elevations which is consistent with our results. In contrast to *Spartina*, we found no spatial variability in *Elymus* biomass. This implies a spatially stable contribution of the *Elymus* canopy to wave dissipation.

Stem density

Significant seasonal differences in stem density were found for *Spartina* and *Elymus*. *Spartina* stem densities were higher in summer than in spring, whereas *Elymus* showed higher stem densities in spring compared to summer. The high stem densities in *Spartina* during summer correlate with high biomass amounts in summer. This pattern in *Spartina* biomass and stem density confirms results of Hill (1984) and Neumeier (2005). Carus et al. (2016) found lower stem densities at the marsh edge for *B. maritimus*, which underpins the previously discussed strategies of plants in coastal habitats to cope with mechanical stress induced by hydrodynamic forces. In contrast, high stem densities in *Elymus* in spring seem to be negatively correlated with biomass. Similar patterns have been reported by Morris and Haskin (1990) for *Spartina alterniflora*. Numerous studies report that variation in plant stem density affects flow velocity and wave dissipation (Bouma et al. 2005; Widdows et al. 2008; Peralta et al. 2008; Anderson and Smith 2014). Paul and Amos (2011) found highest wave dissipation in seagrass beds in summer, when stem density was high. Increasing stem densities in *Spartina* tussocks with decreasing elevations, as found in our study, were previously observed for *Spartina densiflora* and *Spartina anglica* (Nieva et al. 2005; Van Hulzen et al. 2007). Variability in stem density affects hydrodynamic energy within the *Spartina* canopy (Neumeier and Ciavola 2004; Bouma et al. 2005). Van Hulzen et al. (2007) suggest that high stem densities at lower elevations may thus enhance sediment accretion within the canopy. In turn, high accretion rates can enhance growth of *Spartina* (Hemminga et al. 1998), but it is still not resolved which factor induces the increased stem densities at lower elevations (Van Hulzen et al. 2007).

Implications of seasonal and spatial variability in biophysical properties

The data presented here show that biophysical properties of salt-marsh plants may differ between seasons and change over small spatial scales, which is probably related to the strength of hydrodynamic forcing, inundation frequency, sedimentation rates and soil properties. Our results support the assumption of seasonal and spatial non-linearity in the delivery of ecosystem services such as coastal protection by vegetation (Koch et al. 2009). This finding has to be taken into account when regarding the coastal protection potential of salt-marsh vegetation. Furthermore, the data provided can be used to incorporate salt-marsh plants, entire canopies and plant surrogates more realistically in numerical and physical models describing the interaction between vegetation and hydrodynamics. Models and flume experiments should incorporate seasonal variability in plant biophysical properties, especially when simulating storm surge conditions that occur in the winter season when vegetation is degenerated. Future research should provide measurements of biophysical plant properties over the course of the year to get a better overall picture of the change of these properties.

Furthermore, spatial variability in biophysical properties within the pioneer and low marsh zone (e.g. lower biomass, lower flexural rigidity but higher stem density in *Spartina* growing at the marsh edge compared to *Spartina* growing more landwards) should be considered and incorporated in models predicting wave attenuation. High marshes by contrast, show spatially more homogenous biophysical properties and can therefore be represented as one coherent zone. When data on stem flexibility are needed, stem diameter can be used as a proxy for flexibility as bending measurements are often time consuming. Whether this is appropriate for other species than *Spartina* and *Elymus* needs to be tested in further studies.

Literature

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