

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

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9 variability, wave attenuation, *Spartina*

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16 **Abstract**

17 Salt marshes attenuate waves and thus have an important function for coastal protection.
18 Biophysical properties of salt-marsh plants play a key role in the process of wave attenuation
19 and can be differentiated by morphological properties such as stem density, vegetation height
20 and aboveground biomass as well as by biomechanical properties related to stem flexibility.
21 Numerical or physical scale models predicting wave attenuation over vegetated surfaces need
22 to include biophysical properties. However, only few studies have quantified morphological
23 and biomechanical properties of salt-marsh plants and fewer have considered seasonal and
24 within-marsh spatial variability of biomechanical properties. The aim of this study was to
25 quantify biophysical properties of the common salt-marsh grasses *Spartina anglica* and *Elymus*
26 *athericus*, including stem flexibility and density as well as aboveground biomass, temporally

27 and spatially. Samples were collected in spring and in summer 2014 at a study site located in
28 the Northern German Wadden Sea. Aboveground biomass was harvested in plots of 50 x 50
29 cm, stem density was determined by counting and flexibility of plant stems was determined
30 with three-point bending tests. Biophysical properties of both species varied significantly
31 between seasons with plant stem stiffness being 5.0 (*S. anglica*) and 2.9 times (*E. athericus*)
32 higher and aboveground biomass being 2.1 (*S. anglica*) and 1.3 times (*E. athericus*) higher in
33 summer than in spring. Small-scale spatial differences for those biophysical plant properties
34 were found for *S. anglica* with plant stem stiffness being 4.0 (spring) and 2.8 times (summer)
35 higher and aboveground biomass being 1.6 (spring) and 1.5 times (summer) higher in a
36 landward than in a seaward-located zone. Small-scale spatial differences of biophysical
37 properties were not found in *E. athericus*. We conclude that variability in biophysical properties
38 should be considered in models and experiments especially for *S. anglica* when predicting and
39 quantifying marsh wave attenuation capacity.

40

41 **Introduction**

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

50 Recent studies have shown that biophysical properties of plants, which can be categorized as
51 morphological (e.g. stem density, vegetation height and aboveground biomass) and

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

67

68 Salt-marsh plants show a wide variability in biophysical properties both within and among
69 species, making their canopies structurally complex (Tempest et al. 2015; Rupprecht et al.
70 2015a). This structural complexity in combination with the unpredictable nature and high
71 variability of hydrodynamic conditions make field measurements of the interaction between
72 vegetation and hydrodynamics extremely challenging. Hence, many studies rely on numerical
73 or physical modelling approaches (Tempest et al. 2015). A high model quality, however, is
74 often hampered by limited data on biophysical properties of salt-marsh vegetation, especially
75 regarding stem flexibility (Tempest et al. 2015). The majority of numerical wave dissipation
76 models capture vegetation effects in a factor that consists of plant stem height, stem density,
77 stem diameter and an empirical bulk drag coefficient C_D . (Mendez and Losada 2004; Paul and

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

84 Morphological properties of salt marsh plants have been examined (e.g. Morris and Haskin
85 1990; Möller and Spencer 2002; Neumeier 2005; Foster-Martinez 2018), however, those
86 concerned with biomechanical properties focused predominantly on freshwater plants
87 (Ostendorp 1995; Coops and van der Velde 1996; Miler et al. 2012; 2014), brackish plants
88 (Heuner et al. 2015; Carus et al. 2016; Silinski et al. 2015; 2018), macroalgae (Harder et al.
89 2006; Paul et al. 2014) or seagrass (Patterson et al. 2001; Fonseca et al. 2007; Luhar and Nepf
90 2011; Paul and Amos 2011). Studies of salt marshes are scarce (but see Rupprecht et al. 2015a).
91 Biomechanical properties of salt-marsh plants are likely to be affected by seasonal climatic
92 variation in temperate zones as previously found for helophytes (Coops and van der Velde
93 1996) or lake and river plants (Miler et al. 2014).

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

101 The aim of this study is to quantify stem flexibility, stem density and aboveground biomass of
102 salt-marsh plants seasonally and spatially between seaward and landward-located zones. Data

103 were collected for two perennial grasses that are widely spread in salt marshes of NW Europe
104 (*Spartina anglica* and *Elymus athericus*) to answer the following questions: (I) how do
105 biophysical properties of the salt-marsh grasses *Spartina anglica* and *Elymus athericus* differ
106 between spring and summer?; and (II) how do biophysical properties of *Spartina anglica* and
107 *Elymus athericus* differ between seaward and landward-located zones?

108 **Methods**

109 **Species**

110 *Spartina anglica*

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

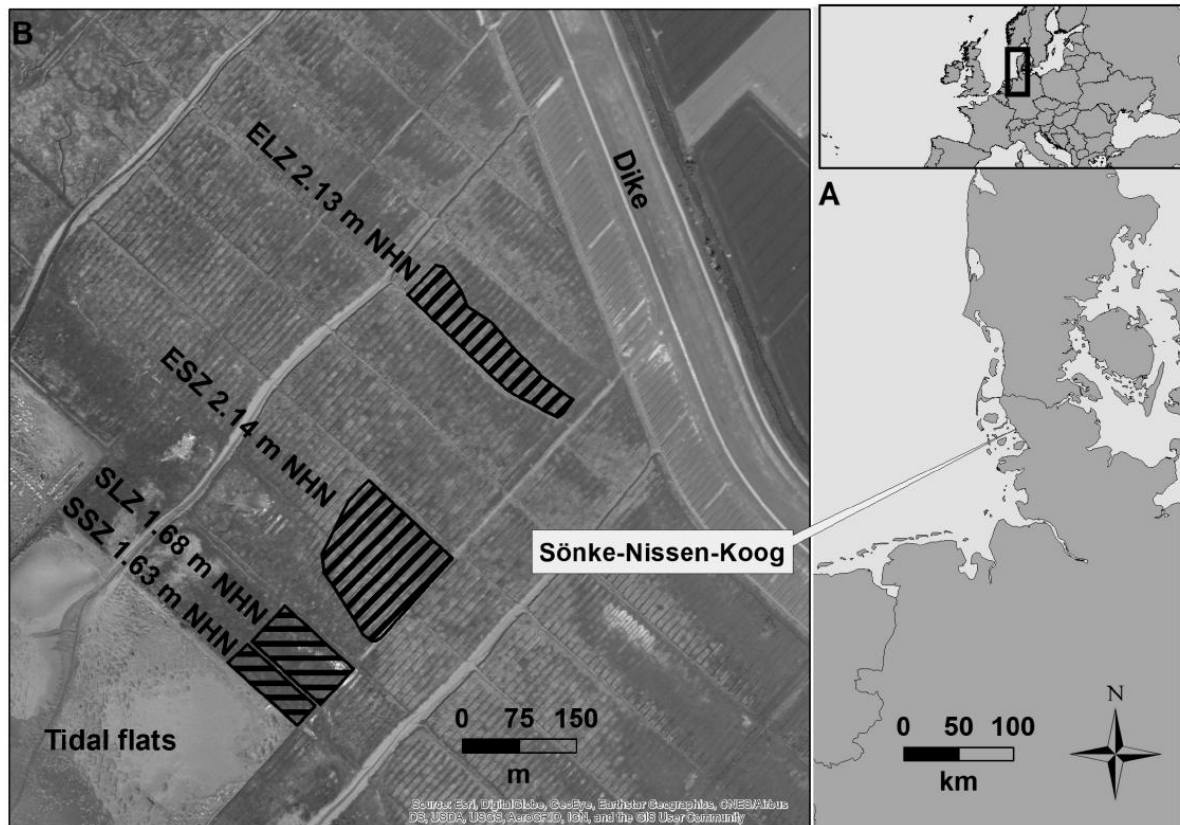
121 *Elymus athericus*

122 The perennial grass *Elymus athericus* (hereafter referred to as *Elymus*) occurs in European salt
123 marshes from Northern Portugal to Southern Denmark and at the southeastern coast of the
124 British Isles (Veeneklaas et al. 2013). *Elymus* is sensitive to grazing and relies on aerated soils
125 (Bockelmann and Neuhaus, 1999). In salt marshes of the Wadden Sea, it forms monospecific
126 dense stands mainly in the high marshes, and it is also increasingly establishing at lower
127 elevations (Bockelmann and Neuhaus 1999; Valéry et al. 2004). In the recent decades,
128 spreading of *Elymus* has been observed, which is caused by the abandonment of grazing, an

129 increasing marsh age and the ability to reproduce by rhizomes, which survive the winter season
130 (Rupprecht et al. 2015b). The shoots die off over the winter season but largely remain withered
131 on the marsh platform.

132 **Study site**

133 Plant samples were obtained from a salt marsh on the mainland coast of Northern Frisia,
134 German Wadden Sea (54.62°N, 8.84°E; Fig. 1 A). The studied salt marsh developed after the
135 embankment of the adjacent Sönke-Nissen-Koog (SNK) polder and subsequent constructions
136 of sedimentation fields in front of the dike (Kunz and Panten 1997; Mueller et al. 2019). As a
137 salt marsh of anthropogenic origin with a thick clayish sediment layer and a regular system of
138 creeks and drainage ditches, it can be considered representative for many salt marshes of North-
139 West Europe. The tidal range is 3.4 m, the mean high tide is +1.59 m NHN (Normalhöhennull,
140 which is comparable to mean sea level). Elevations within the salt marsh range from 0.9 m to
141 2.6 m NHN with a mean elevation of 2 m NHN (Müller et al. 2013b). The marsh stretches from
142 the dike over 700 m to the tidal flats (Fig. 1B) and is predominantly covered by *Elymus* in the
143 high marsh (Mueller et al. 2017) and by *Spartina* in the low marsh (according to own
144 observations and the Trilateral Monitoring and Assessment Program, TMAP; Petersen et al.
145 2013).



146

147 **Fig. 1** A) Location of the study site in the Wadden Sea National Park Schleswig-Holstein at the German
 148 North Sea coast. The black rectangle shows the position of the area in Europe. B) Satellite image of the
 149 study site with the sampling zones. Shown are the seaward and landward located *Elymus* (ESZ, ELZ;
 150 vertically hatched) and *Spartina* (SSZ, SLZ; diagonally hatched) sampling zones with respective mean
 151 elevations above NHN. The map was created using a base map in ArcGIS © Desktop: Release 10, ESRI
 152 2014, Redlands, CA: Environmental Systems Research Institute

153 **Sampling design**

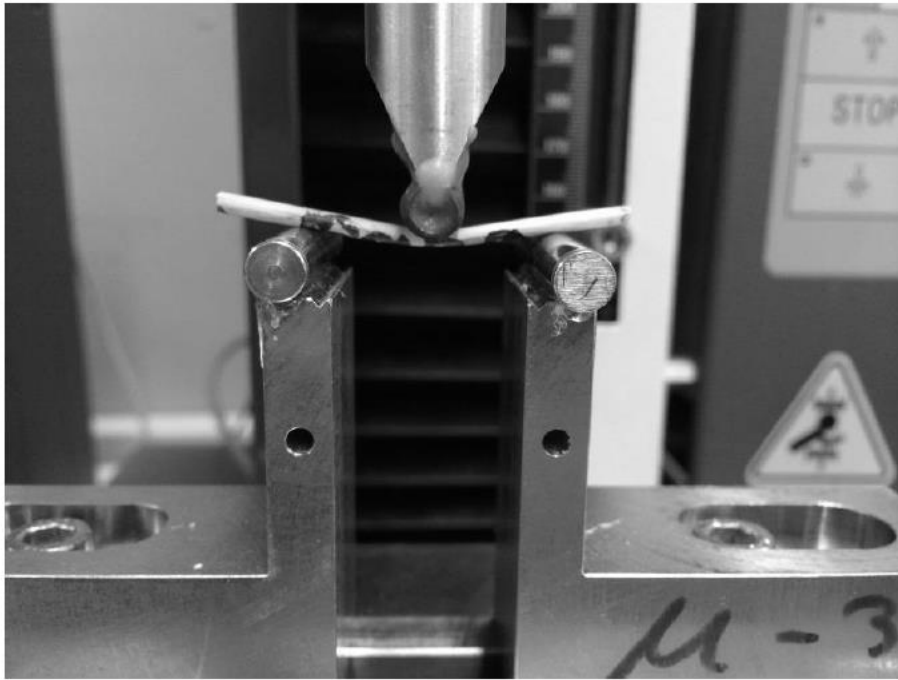
154 Two sampling zones were chosen in the low marsh (dominated by *Spartina*) and in the high
 155 marsh (dominated by *Elymus*). One of the two sampling zones per vegetation type was set closer
 156 to the seaward marsh edge ('seawards'), and one closer to the landward marsh edge
 157 ('landwards'; Figure 1B). The seaward-located *Spartina* zone (hereafter referred to as SSZ;
 158 inundation frequency: 182 times per year; total inundation time: 557.76 hours/year; F. Müller
 159 unpublished data) stretches 40 m perpendicular along the marsh towards the landward-located
 160 zone (hereafter referred to as SLZ; inundation frequency: 156 times per year; total inundation
 161 time: 452.88 hours/year). For *Elymus*, one zone was chosen towards the low marsh (ESZ;
 162 inundation frequency: 23 times per year; total inundation time: 62.64 hours/year) and one zone

163 was chosen closer to the dike (ELZ; inundation frequency: 23 times per year; total inundation
164 time: 64.32 hours/y). An area-based stratified random design was applied with 40 random
165 sampling points (20 points for flexibility measurements; 20 points for aboveground biomass
166 and stem density measurements) generated within each sampling zone of the *Spartina* and
167 *Elymus* vegetation type using a random point tool of QGIS 2.0.1 Dufour (QGIS Development
168 Team 2014). The elevation of each point was assessed using a Trimble LL500 precision laser
169 and a Trimble HL 700 receiver as a levelling instrument (2.0 mm accuracy) and a known closely
170 located benchmark. Data were used to calculate mean elevation per zone (Figure 1B).

171

172 **Measurements of plant stem flexibility**

173 Three-point bending tests were performed to quantify plant stem flexibility under bending
174 forces orthogonal to the plants stem. Plant samples were collected both in mid-March (before
175 the onset of plant growth) and in late August. In the field, samples were excavated as small
176 marsh blocks with a dimension of 10x10x10 cm and were packed in plastic bags to conduct
177 measurements on fresh material. From each marsh block, a single adult and undamaged plant
178 stem was chosen randomly and the stem length up to the inflorescence was measured and
179 divided in four equal parts. A test section was defined as the beginning of the second quarter
180 starting from the bottom end of the stem and was cut out with a razor blade. Test sections were
181 consistently cylindrical. To minimize the effect of shear stress in bending tests, a stem diameter
182 to stem length ratio (here stem length means the horizontal span of the tested stem section
183 between the two metal support bars, see Figure 2) of 1:15 was chosen (see also Miler et al.
184 2012, 2014; Rupprecht et al. 2015a). The bending tests were performed with a Zwick/Roell
185 testing machine (Type 1120.25, Nominal Force: max. 1 kN, using a 10 N load cell; initial load
186 0.01 N; Zwick GmbH & Co. KG, Ulm, Germany).



187

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

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

200 **Biomass and stem density measurements**

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

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

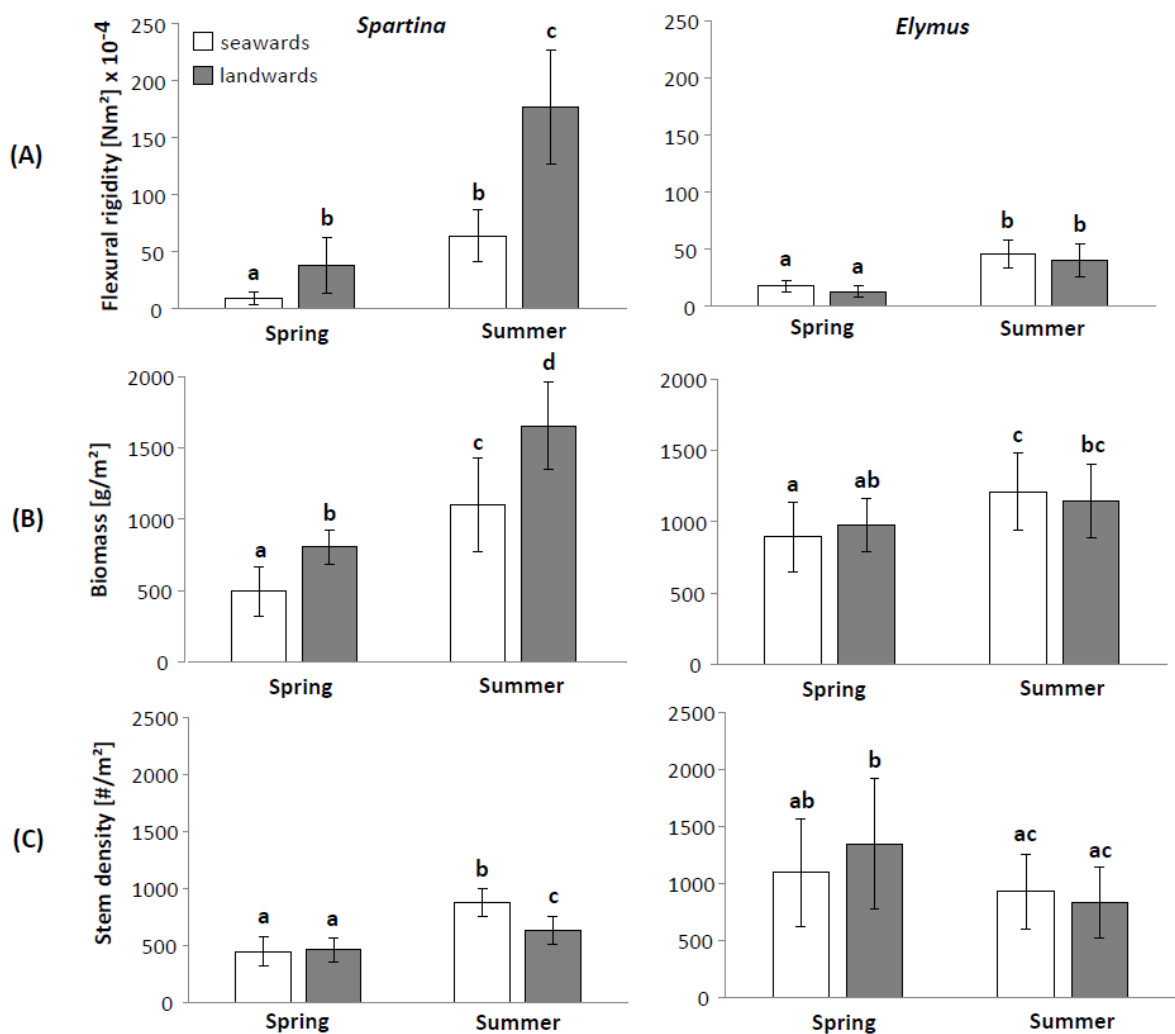
209 **Statistical analysis**

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

219 **Results**

220 **Flexural rigidity**

221 Flexural rigidity of *Spartina* differed significantly between seasons and zones (Fig. 3A; Table
 222 1). However, the interaction between season and zone was also significant. Flexural rigidity
 223 was 5.0 times higher in summer compared to spring. In spring, *Spartina* stems of the SLZ were
 224 4.0 times more rigid compared to the stems of the SSZ. In summer, stems of the SLZ showed a
 225 2.8 times higher value compared to stems of the SSZ.



226

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

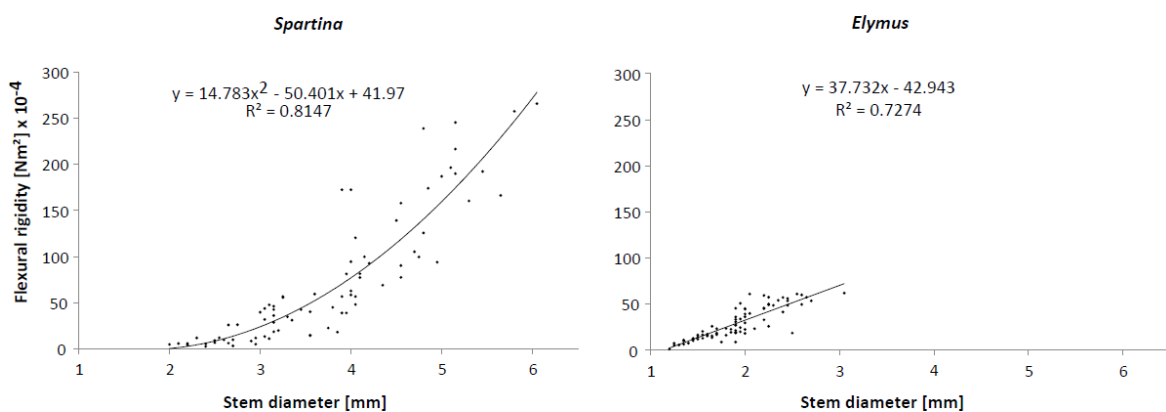
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233 **Table 1** ANOVA table of all biophysical parameters for *Spartina* and *Elymus* in spring and summer
 234 season in the landward and seaward-located zones. Given are F-values and p-values

		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	0.37
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

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

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



252

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

256

257 **Aboveground biomass**

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

264

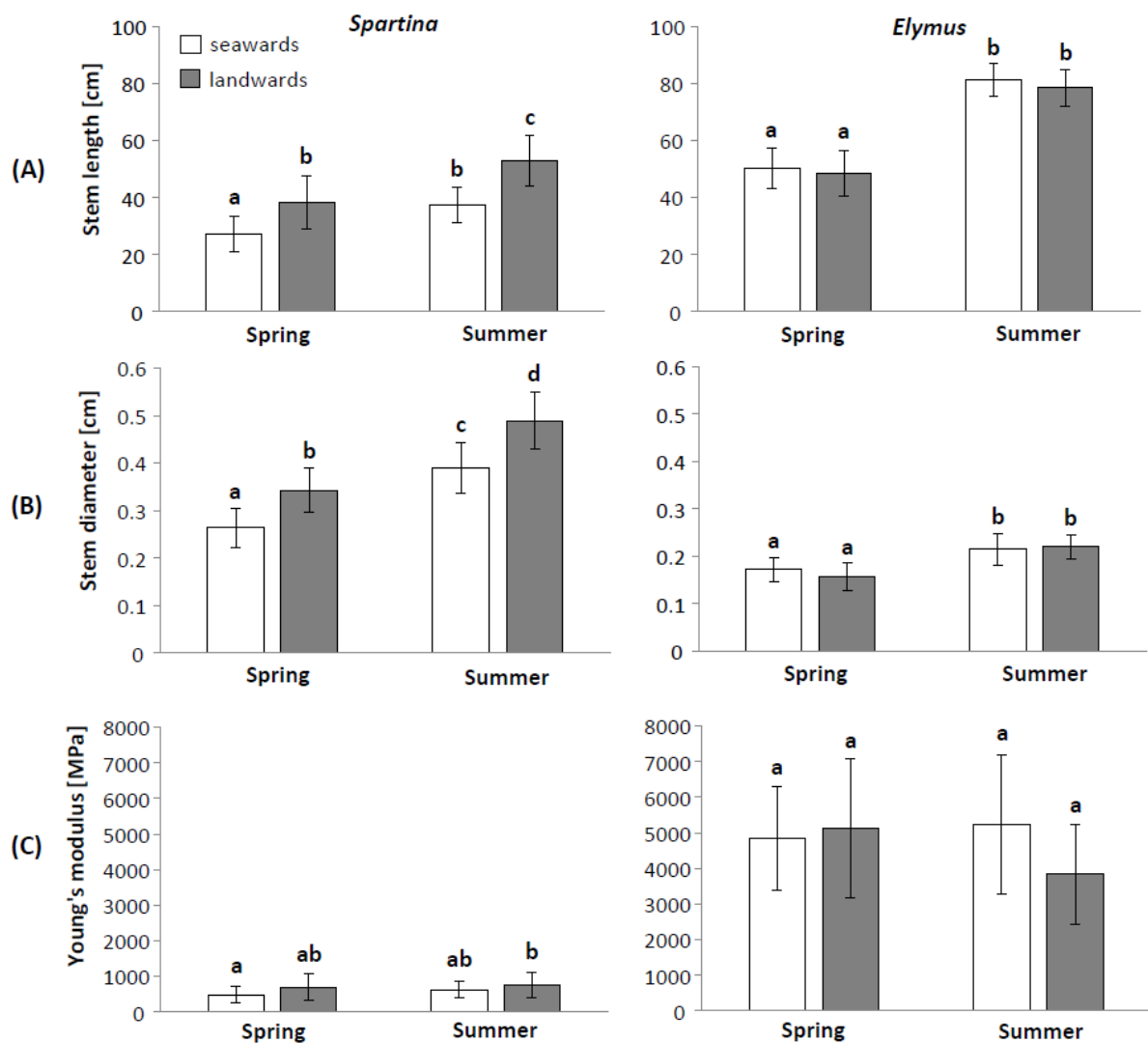
265 **Stem density**

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

272 **Stem length, stem diameter, Young's Modulus**

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

280 compared to the SSZ in either season. No differences for Young's modulus were detected in
 281 *Elymus* stems.



282

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

288

289 Discussion

290 *Stem flexibility*

291 Seasonal variability in stem flexibility was detected for both species with significantly higher
 292 values for flexural rigidity during summer. These results indicate the importance of considering

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

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

312 In contrast, Carus et al. (2016) found the opposite pattern for stems of *Bolboschoenus*
313 *maritimus*, a typical species in the pioneer zone of European freshwater and brackish marshes
314 along shorelines of estuaries where ship and wave induced wave forcing occurs. These findings
315 suggest that species growing under harsh hydrodynamic conditions may develop different
316 biomechanical properties to either minimize physical stress (avoidance strategy; i.e. flexible
317 stems, low flexural rigidity) from waves and currents or to withstand these mechanical forces

318 (tolerance strategy; i.e. stiff stems, high flexural rigidity). Our results show an avoidance
319 strategy of *Spartina* to increasing hydrodynamic forces and drag forces lower in the elevational
320 gradient in salt marshes, as individuals in the SSZ were significantly smaller, thinner and more
321 flexible than in the SLZ in both seasons. These characteristics should minimize the impact of
322 hydrodynamic forces and the risk of plant breakage. However, it may also be possible that stem
323 development in the SSZ is inhibited by constant wave action leading to thinner, smaller and
324 more flexible stems.

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

331 *Biomass*

332 For both *Spartina* and *Elymus*, seasonal differences with higher biomass in summer than in
333 spring were found which can be explained with the breakdown of canopies during the winter
334 season in temperate zones (Bellis and Gaither 1985; Morris and Haskin 1990; Koch et al. 2009).
335 In *Spartina*, we found up to two times higher biomass in summer compared to spring. Seasonal
336 biomass changes in temperate zones have been found to affect wave dissipation in seagrass
337 beds (Chen et al. 2007; Paul and Amos 2011), brackish marshes (Silinski et al. 2018; Schoutens
338 et al. 2019) and salt marshes (Möller and Spencer 2002; Möller 2006). Accordingly, seasonal
339 variability in *Spartina* biomass, as in our study, can be expected to affect wave dissipation
340 capacity of the marsh with a higher contribution of vegetation to wave dissipation in summer
341 than in winter and spring (see Foster-Martinez et al. 2018). *Elymus*, by contrast, shows minor
342 although significant seasonal differences in biomass, which suggests a more continuous

343 contribution of *Elymus* biomass to wave dissipation throughout the year. Overall, wave
344 attenuation and resulting coastal protection should be highest when the biomass of biotic
345 structures is at its maximum (Coops et al. 1996; Chen et al. 2007; Koch et al. 2009).

346

347 Spatial variability in *Spartina* biomass between the SSZ and the SLZ shows the same pattern
348 as for stem flexibility with lower values for the SSZ than the SLZ in both seasons. Coops et al.
349 (1994) found similar results with lower biomass in an exposed site compared to a sheltered site
350 for two helophytes. Furthermore, a biomass decrease downwards an elevational gradient was
351 observed. We assume that higher wave action and higher physiological stress due to salinity
352 and longer inundation time in the SSZ compared to the SLZ explain the significantly lower
353 biomass in *Spartina* (see also Huckle, Potter and Marrs 2000). The lower biomass amounts in
354 the SSZ zone seem to correlate with a decrease in stem diameter and length accompanied by a
355 higher flexibility in this zone compared to the SLZ. Stem length of different *Spartina*
356 populations were studied previously by Gray and Benham (1990), where plants sampled from
357 the pioneer populations had significantly smaller inflorescence sizes and vegetative statures in
358 comparison with plants from higher marsh elevations which is consistent with our results. In
359 contrast to *Spartina*, we found no spatial variability in *Elymus* biomass. This implies a spatially
360 stable contribution of the *Elymus* canopy to wave dissipation.

361

362 *Stem density*

363 Significant seasonal differences in stem density were found for *Spartina* and *Elymus*. *Spartina*
364 stem densities were higher in summer than in spring, whereas *Elymus* showed higher stem
365 densities in spring compared to summer. The high stem densities in *Spartina* during summer
366 correlate with high biomass amounts in summer. This pattern in *Spartina* biomass and stem
367 density confirms results of Hill (1984) and Neumeier (2005). Carus et al. (2016) found lower
368 stem densities at the marsh edge for *B. maritimus*, which underpins the previously discussed

369 strategies of plants in coastal habitats to cope with mechanical stress induced by hydrodynamic
370 forces. In contrast, high stem densities in *Elymus* in spring seem to be negatively correlated
371 with biomass. Similar patterns have been reported by Morris and Haskin (1990) for *Spartina*
372 *alterniflora*. Numerous studies report that variation in plant stem density affects flow velocity
373 and wave dissipation (Bouma et al. 2005; Widdows et al. 2008; Peralta et al. 2008; Anderson
374 and Smith 2014). Paul and Amos (2011) found highest wave dissipation in seagrass beds in
375 summer, when stem density was high. Increasing stem densities in *Spartina* tussocks with
376 decreasing elevations, as found in our study, were previously observed for *Spartina densiflora*
377 and *Spartina anglica* (Nieva et al. 2005; Van Hulzen et al. 2007). Variability in stem density
378 affects hydrodynamic energy within the *Spartina* canopy (Neumeier and Ciavola 2004; Bouma
379 et al. 2005). Van Hulzen et al. (2007) suggest that high stem densities at lower elevations may
380 thus enhance sediment accretion within the canopy. In turn, high accretion rates can enhance
381 growth of *Spartina* (Hemminga et al. 1998), but it is still not resolved which factor induces the
382 increased stem densities at lower elevations (Van Hulzen et al. 2007).

383 *Implications of seasonal and spatial variability in biophysical properties*

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

395 research should provide measurements of biophysical plant properties over the course of the
396 year to get a better overall picture of the change of these properties.
397 Furthermore, spatial variability in biophysical properties within the pioneer and low marsh zone
398 (e.g. lower biomass, lower flexural rigidity but higher stem density in *Spartina* growing at the
399 marsh edge compared to *Spartina* growing more landwards) should be considered and
400 incorporated in models predicting wave attenuation. High marshes by contrast, show spatially
401 more homogenous biophysical properties and can therefore be represented as one coherent
402 zone. When data on stem flexibility are needed, stem diameter can be used as a proxy for
403 flexibility as bending measurements are often time consuming. Whether this is appropriate for
404 other species than *Spartina* and *Elymus* needs to be tested in further studies.

405

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