1	Vegetation-wave interactions in salt marshes under storm surge
2	conditions
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4	Rupprecht F ^{1*} , Möller I ^{2,3} , Paul M ^{4,8} , Kudella M ⁴ , Spencer T ² , van Wesenbeeck BK ^{5,6} , Wolters G ⁵ , Jensen
5	K ¹ , Bouma TJ ⁷ , Miranda-Lange M ⁴ & Schimmels S ⁴ .
6	
7	¹ Applied Plant Ecology, Biocenter Klein Flottbek, University of Hamburg, Ohnhorststr. 18, 22609
8	Hamburg, Germany
9	² Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing
10	Place, Cambridge CB2 3EN, UK
11	³ Fitzwilliam College, Storey's Way, Cambridge CB3 0DG, UK
12	⁴ Forschungszentrum Küste (FZK), Merkurstr. 11, 30419 Hannover, Germany
13	⁵ Deltares, Boussinesqweg 1, 2629 HV Delft, Netherlands
14	⁶ Department of Hydraulic Engineering, Delft University of Technology, P.O. Box 5048, 2600 GA Delft,
15	The Netherlands
16	
17	⁷ Yerseke Spatial Ecology, Netherlands Institute for Sea Research (NIOZ), Korringaweg 7, 4401 NT,
18	Yerseke, Netherlands
19	8 present address: Environmental Systems Analysis, Institute of Geoecology, Technische
20	Universität Braunschweig, Langer Kamp 19c, 38106 Braunschweig, Germany
21	
22	
23 24 25	[*] Corresponding author. E-mail address: franziska.rupprecht@uni-hamburg.de, Phone: +49 (0)40-42816-272
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Highlights

42	-	Salt marsh vegetation can reduce near-bed orbital velocities during storm surges
43	-	Vegetation effect on orbital velocities varies with biophysical properties
44	-	Flexible low-growing plant canopies show high resilience to storm surge conditions
45	-	More rigid and tall grasses experience stem folding and breakage
46	-	The contribution of vegetation to wave dissipation is plant species specific

48 Abstract

49 Vegetation-wave interactions are critical in determining the capacity of coastal salt marshes to 50 reduce wave energy (wave dissipation), enhance sedimentation and protect the shoreline from 51 erosion. While vegetation-induced wave dissipation is increasingly recognized in low wave energy 52 environments, little is known about: i) the effect of vegetation on wave dissipation during storms 53 when wave heights and water levels are highest; and ii) the ability of different plant species to 54 dissipate waves and to maintain their integrity under storm surge conditions. Experiments 55 undertaken in one of the world's largest wave flumes allowed, for the first time, the study of 56 vegetation-wave interactions at near-field scale, under wave heights ranging from 0.1 - 0.9 m (corresponding to orbital velocities of 2 - 91 cm s⁻¹) and water depths up to 2 m, in canopies of two 57 58 typical NW European salt marsh grasses: Puccinellia maritima (Puccinellia) and Elymus athericus 59 (Elymus). Results indicate that plant flexibility and height, as well as wave conditions and water depth, 60 play an important role in determining how salt marsh vegetation interacts with waves. Under 61 medium conditions (orbital velocity 42 – 63 cm s⁻¹), the effect of *Puccinellia* and *Elymus* on wave 62 orbital velocities varied with water depth and wave period. Under high water levels (2 m) and long 63 wave periods (4.1 s), within the flexible, low-growing Puccinellia canopy orbital velocity was reduced by 35% while in the more rigid, tall Elymus canopy deflection and folding of stems occurred and no 64 65 significant effect on orbital velocity was found. Under low water levels (1 m) and short wave periods 66 (2.9 s) by contrast, Elymus reduced near-bed velocity more than Puccinellia. Under high orbital 67 velocities (\geq 74 cms⁻¹), flattening of the canopy and an increase of orbital velocity was observed for 68 both *Puccinellia* and *Elymus*. Stem folding and breakage in *Elymus* at a threshold orbital velocity \geq 42 69 cm s⁻¹ coincided with a levelling-off in the marsh wave dissipation capacity, while *Puccinellia* survived 70 even extreme wave forces without physical damage. These findings suggest a species-specific control 71 of wave dissipation by salt marshes which can potentially inform predictions of the wave dissipation 72 capacity of marshes and their resilience to storm surge conditions.

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Key words: Wave dissipation; Flow reduction; Coastal wetlands; Biophysical plant properties; Plant
 breakage; Vegetation resilience; Wave flume experiment

77 **1. Introduction**

78

The interaction of vegetation with currents and waves affects a wide range of ecosystem functions of coastal salt marshes including the reduction of hydrodynamic energy, sediment deposition and erosion and carbon storage (Duarte et al., 2013; McLeod et al., 2011; Möller et al., 1999; Temmerman et al., 2005).

83 Most knowledge on flow dynamics in and around salt marsh canopies has been acquired under 84 average hydrodynamic conditions. Field studies have shown a reduction of both unidirectional and 85 wave-induced oscillatory flow within plant canopies that can lead to a decline in bed shear stress and erosion and promote sedimentation (Leonard and Croft 2006; Neumeier and Amos 2006a; Neumeier 86 87 and Amos 2006b; Peralta and others 2008). Flume and numerical modelling studies have highlighted 88 the importance of plant posture and motion as a mechanism for the vegetation-mediated reduction 89 of water velocity and hydrodynamic energy (Bouma and others 2005; Dijkstra and Uittenbogaard 90 2010; Luhar and Nepf 2011; Luhar and Nepf 2016; Mullarney and Henderson 2010). When waves 91 advance over a vegetated marsh surface, and water depths are low enough to allow wave-induced 92 oscillatory flow to penetrate into the canopy layer, vegetation interacts with this flow and provides 93 flow resistance. In return, the vegetation experiences drag and re-orientation by wave forces 94 (Mullarney and Henderson 2010). The drag caused by plants causes a reduction of wave orbital 95 velocities and thus wave height and energy (wave dissipation).

96 Knowledge of this wave dissipation function has generated high interest in the use of vegetated 97 ecosystems, such as salt marshes, as a cost-effective element of coastal protection schemes. 98 Furthermore, the ability of marshes to track rising water levels as a result of the positive feedbacks 99 between vegetation growth and marsh accretion suggests sustainable protection under accelerated 100 sea level rise (Kirwan and others 2016). However few empirical observations of vegetation-wave 101 interactions exist, especially during storm surges when water levels and waves are highest and large 102 amounts of sediments are mobilized (Cahoon 2006; Stumpf 1983; Turner and others 2006). I Hence it 103 is not clear how canopies of different salt marsh plants vary in their ability to reduce wave orbital 104 velocities and thus in their contribution to wave dissipation and erosion protection.

Detailed insights into vegetation-wave interactions are of major importance for salt marsh conservation and management aiming to maximize the sea defence value of marshes as well as for the generation of reliable predictions of the marsh wave dissipation capacity and marsh resilience to storm events. Only with this knowledge will it be possible to successfully incorporate marshes into coastal defense schemes (Anderson and Smith 2014; Bouma and others 2014; Möller and others 2014).

111 Vegetation-wave interactions, and the resulting wave dissipation, are a function of biophysical 112 plant properties such as flexibility, density, biomass and height as well as hydrodynamic conditions 113 such as incident wave height, wave period and water depth (Anderson and others 2011; Paul and 114 others 2016).

Plant flexibility determines how much, and in what way, plants move and hence the magnitude
of drag forces experienced (Luhar and Nepf 2016; Mullarney and Henderson 2010; Paul and others
2016). Under wave forcing two types of plant movement need to be distinguished:

118 Swaying is an oscillatory plant movement throughout the wave cycle with symmetric bending in 119 the both directions of water flow under wave motion. Whip-like movement is characterized by a fast 120 flipping over from a short backward bending of the plants, to an extended 'forward' bending and 121 wide stem extension in the dominant direction of wave-induced oscillatory flow (in general the 122 direction of wave travel). The latter motion results in flattening of the canopy, a loss of flow 123 resistance and high orbital velocity for part of the wave cycle. A transition from swaying to whip-like 124 movement can occur for a species when wave height and energy increases, with the point of 125 transition depending on the stiffness of the plant and the ratio of plant height to wave orbital 126 excursion (Manca 2010; Paul and others 2012).

127 Numerical models simulating the motion of flexible aquatic vegetation under wave orbital 128 velocities use primarily two dimensionless parameters to describe plant movement and predict drag 129 forces acting on vegetation: (i) the Cauchy number, Ca, which represents the ratio of the 130 hydrodynamic forcing to the restoring force due to plant stiffness; and (ii) the ratio of plant height to 131 wave orbital excursion, L (Luhar and Nepf 2016). A value of Ca < 1 implies an upright plant posture 132 under wave-induced oscillatory flow, as hydrodynamic forces are much smaller than the restoring 133 force due to stiffness. When Ca > 1, plants start to bend with increasing values of Ca indicating a 134 decrease of flow resistance and drag acting on vegetation due to increasing plant bending under 135 wave forces. For L > 1, a swaying plant movement with moderate bending angles can be assumed. When L < 1, the high orbital velocities are expected to cause an extended 'forward' bending and a 136 137 flattening of the canopy and low flow resistance for part of the wave cycle (Luhar and Nepf 2016), i.e. 138 a plant behaviour typically occurring under a whip like canopy movement. For flexible aquatic 139 vegetation the buoyancy parameter B, representing the ratio of restoring forces due to buoyancy and 140 stiffness, also affects plant bending (Luhar and Nepf 2011). However, B can be neglected in the case 141 of the terrestrial salt marsh plants that exhibit high stiffness compared to seagrasses or macroalgae 142 (Rupprecht et al., 2015a).

Salt marsh plants show a wide variability of stem flexibility, both between different species and the different stem parts of specimens of one species. Little is known on how this variability affects vegetation-wave interactions (Rupprecht and others 2015a). Previous studies on plants of tidal

146 marshes (Bouma and others 2005; Heuner and others 2015; Silinski and others 2015) but also on 147 freshwater macrophytes (Aberle and Jarvela 2013; Robionek and others 2015; Sand-Jensen 2003) 148 and macroalgae (Gaylord and Denny 1997; Stewart 2006) have shown that drag experienced by 149 plants under hydrodynamic forcing is inversely related to their flexibility. Flexible plants show an avoidance strategy and minimize the risk of folding and breakage through reconfiguration; stiff plants 150 151 by contrast maximize the resistance to physical damage (tolerance strategy) but may break if 152 hydrodynamic forces increase beyond a critical level (Heuner and others 2015; Puijalon and others 153 2011; Silinski and others 2015). For plants characterized byswaying movement, a positive correlation 154 between stem stiffness and vegetation-induced wave dissipation has been observed (Bouma and 155 others 2005). When comparing two salt marsh grasses with different stem flexibility and stem 156 density, Bouma et al. (2010) found that an increase in stem density and biomass can counteract the 157 reduced wave dissipation capacity of flexible plants.

Apart from stem flexibility, density and biomass, the wave dissipation capacity of salt marsh canopies is affected by the ratio of water depth to canopy height (submergence ratio) (Möller and others 1997; Möller and others 1999; Yang and others 2012). The effectiveness of vegetation in dissipating waves has been shown to increase with the percentage of the water column that it occupies, i.e. with decreasing submergence ratio (Augustin et al., 2009; Paul et al., 2012).

163 Beyond a critical combination of orbital velocities and water depth, changes in type and 164 magnitude of vegetation-wave interactions are likely to result in a significant alteration of 165 vegetation-induced wave dissipation. The existence of hydrodynamic thresholds determining the 166 transition from wave regimes with vegetation-induced wave modification and wave dissipation to 167 those regimes characterized by a flexing, folding or breakage of plants under wave orbital velocities 168 and a decline in vegetation-induced wave dissipation has been suggested by various authors (Gedan 169 et al., 2011; Koch et al., 2009; Möller et al., 1999; Yang et al., 2012), but remains to be demonstrated. 170 This is because the quantification of such hydrodynamic thresholds either by field studies, flume experiments or by numerical modelling is extremely challenging. Field studies suffer from the 171 172 unpredictable nature and high temporal variability of wave conditions and difficulties in deploying 173 instrumentation under higher energy wave events. Laboratory flume studies offer controlled wave 174 conditions, but are often hampered by limits to the water depths and waves that can be generated. It 175 has proved difficult to build realistic small-scale physical models of vegetated surfaces (Fonseca and 176 Cahalan 1992; Mendez and Losada 2004).

177 Numerical models of wave dissipation can simulate a wide range of wave conditions (Mendez 178 and Losada 2004; Riffe et al., 2011) but in the absence of suitably representative flume or field 179 calibration data suffer from the difficulty of realistically representing vegetation as well as its effect 180 on wave orbital velocities.

181 In this paper we report results from a unique experiment on wave dissipation over coastal salt 182 marshes conducted in one of the world's largest wave flumes at a near field scale (for details see 183 Möller et al., 2014). We analyzed vegetation-wave interactions in canopies of two salt marsh grasses, 184 the low growing and flexible *Puccinellia maritima* and the tall, less flexible *Elymus athericus*, over a 185 wide range of wave conditions and corresponding orbital velocities to answer the following questions: 186

(1) How do plant canopies of different biophysical properties (flexible and low-growing vs.

stiff and tall) affect wave orbital velocities under rising wave energy and water depths?

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- 189

(2) Does physical damage to vegetation under increasing wave energy differ between flexible,
low-growing canopies and stiff, tall canopies? If so – is there a threshold in orbital velocity

- 192 beyond which differences in plant susceptibility to folding and breakage become apparent?
- 193

194 **2. Methods**

195 **2.1 Study species and biophysical properties**

We investigated two grasses commonly occurring in NW European salt marshes, *Puccinellia maritima* (Hudson) Parl. and *Elymus athericus L.*; hereafter referred to as *Puccinellia* and *Elymus*(Fig. 1). *Puccinellia* is typical of marshes at low to mid elevations in the tidal frame and characteristic of earlyto mid-successional stages of salt marsh vegetation development. Where sandy soils are present, it can also be found in the lower-lying pioneer zone. *Puccinellia* is also a characteristic species of grazed salt marshes, as the species is tolerant to trampling, biomass loss and waterlogging and can reproduce by clonal growth.

203 In contrast to Puccinellia, Elymus needs aerated soils and is sensitive to grazing. In many salt marshes 204 of NW Europe, it forms monospecific dense stands in the high marshes and represents a late-205 successional stage of salt marsh vegetation. In recent decades, Elymus has rapidly colonized 206 mainland salt marshes along the North Sea coast and the Atlantic coast where it can be found not 207 only in the high marsh but also in mid and sometimes low marshes (Bockelmann and Neuhaus 1999; 208 Valéry et al., 2004). The expansion of *Elymus* has been related to the abandonment of grazing, high 209 vertical accretion rates and marsh age as well as the species ability to reproduce clonally by rhizomes 210 (Rupprecht et al., 2015b; Veeneklaas et al., 2013).

Puccinellia and *Elymus* differ with respect to their biophysical properties, such as plant stem
 flexibility, stem density and stem height, which have relevance for flow and wave dissipation.
 Puccinellia canopies are characterized by a high stem flexibility, high stem density and low canopy

height (around 0.2 m, Table 1). Canopies of *Elymus* show a low stem flexibility and stem density and a
canopy height (around 0.8 m) that is four times greater than that of *Puccinellia* (Table 1). Previous
measurements of stem flexibility in salt marsh grasses have shown that variation of stem flexibility
between the bottom (more rigid) and the middle and top (more flexible) stem parts of *Elymus* is
much higher than in *Puccinellia* (Rupprecht et al., 2015a).

As measures of stem flexibility, the Young's bending modulus and flexural rigidity of *Puccinellia* and *Elymus* stems were determined of 17 and 18 samples, respectively, using a three-point-bending test (for methodology see Rupprecht et al. (2015a)). Prior to performing the tests, stem length up to the onset of the youngest leaf was measured and stems were divided into three equal parts (bottom, middle, top). The test section was cut from the middle of each part of the stem.

Stem height was measured with a folding rule for 30 randomly chosen stems. Stem density of *Elymus* was measured by counting the number of stems in 15 quadrats of a size of 20 x 20 cm randomly distributed across the vegetated test section in the flume. For *Puccinellia*, the very high stem density (N/m² >1000) and the low stem diameter meant that a quantitative assessment of stem density was not feasible in the framework of the present study.

229 We compared biophysical properties of the *Puccinellia* and the *Elymus* canopy between the flume 230 test section and the field site from where the salt marsh for the flume experiment was excavated 231 (see also section 2.2). No statistical difference was found in the Young's bending modulus; t-test; p >232 0.05. However flexural rigidity of *Puccinellia* and *Elymus* stems was significantly lower in the flume 233 than in the field (t-test; p < 0.01). This indicates that stems of *Puccinellia* and *Elymus* in the flume 234 were more flexible than stems at the field site, when accounting for varying stem diameter. The 235 lower nutrient supply and less mechanical stress experienced during the one year storage period of 236 the vegetation prior to the start of the experiment (for detailed information see Möller et al., 2014), 237 as compared to the regular flood of in situ marshes, may explain these differences.

238 Stem height of *Puccinellia* was significantly higher in the flume than in the field (t-test; p < 0.05). 239 For *Elymus,* no significant differences of stem height and stem density were found between the 240 flume and the field site (t-test; p > 0.05).

241 #Figure 1

242 #Table 1

243

244 2.2 Experimental set-up

The study was carried out in conjunction with an experiment on wave dissipation over natural
salt marsh transplants under storm surge conditions (Möller et al., 2014). This experiment was
conducted in the 5 m wide, 7 m deep and approx. 310 m long Large Wave Flume (GWK) of the
Forschungszentrum Küste (FZK) in Hannover, Germany and lasted 17 days (15 – 31 October 2013). . A

detailed description of the excavation of the salt marsh and its installation within the flume, the
experimental set-up and the employed instrumentation to measure wave dissipation is given in
Möller et al. (2014).

252 An elevated vegetated test section of 40 m length was constructed approx. 115 m from the wave 253 paddle on top of a 1.2 m high sand base covered by a geotextile layer. This was necessary to ensure 254 sufficient water depth at the wave paddle to generate the desired waves and to allow waves to fully 255 develop before reaching the vegetated test section. At the front and rear end of the vegetated test 256 section a concrete berm, followed by a slope of 1:10 was built to allow the waves to shoal and/or 257 break, as would be the case in a natural shallow water marsh setting (Fig. 2 a). Wave breaking at the 258 1:6 asphalt slope at the end of the flume minimized wave reflection and active wave absorption of 259 the wave maker.

The vegetated test section consisted of a coherent patchwork of marsh blocks, each with a size of approximately 0.8 x 1.2 x 0.3 m. The blocks were vegetated with either *Puccinellia*, *Elymus* or the herbaceous forb *Atriplex prostrata*.

263 An underwater observation window in the flume wall 6 meters from the start of the vegetated 264 test section allowed the video capture of individual Elymus and Puccinellia movement during the 265 experiment. Four marsh blocks with Puccinellia and four marsh blocks with Elymus were deployed 266 next to each other in front of this window covering an area of 4 m² respectively. Two 2D-267 Electromagnetic current meters (EMCMs) were positioned on both sides of the underwater 268 observation window approximately 15 cm above the bed, one in the canopy of Puccinellia and one in 269 the canopy of *Elymus* (Fig. 2b). During wave tests, the EMCMs recorded wave orbital velocities with a 270 frequency of 100 Hz and a precision of \pm 10 cm s⁻¹. In the immediate vicinity of the EMCMs, water 271 pressure oscillation was recorded with a PTX1830 pressure wave gauge at the same sampling 272 frequency as the EMCMs (100 Hz).

273 The marsh canopy was submerged for 2 - 3 days at a time for wave tests. After each two day 274 period of submergence the vegetation was exposed for at least 12 hours to allow plants regular gas 275 exchange. As wave dissipation can be induced through both wave-plant and wave-sediment bottom 276 interactions, a number of tests were conducted with initially intact and then removed (mowed) 277 vegetation (height of remaining plant stems after mowing approx. 2 - 3 cm). This enabled us to 278 quantify the effect of vegetation on the observed wave dissipation. During the course of the 279 experiment the entire vegetated test section was illuminated for the benefit of the plants by a total 280 of 60 lamps (GE 750W 400V PSL or equivalent) mounted along the upper margins of the flume.

281 #Fig. 2

282 #Table 2

283

284 **2.3 Experimental programme**

Eight wave heights (H; 1 – 0.9 m, seven wave periods (T; 1.5 – 6.2 s) and two different water depths (h; 1 m and 2 m) were simulated to analyze vegetation-wave interactions in canopies of *Puccinellia* and *Elymus* (Table 2). For each hydrodynamic condition tested, regular non-breaking waves ($96 \le N \le$ 148) were generated (Table 2).

289 In order to quantify the wave energy and the drag imparted by wave orbital velocities on the 290 vegetation, as well as the vegetation response to hydrodynamic forcing, we calculated for each test the wave energy flux per meter crest length (P, equation 3) and the peak orbital velocity in direction 291 292 of wave travel 15 cm above the bed (matching the height at which orbital velocities were recorded 293 within plant canopies) according to linear wave theory (U_{predf} , equation 5). The Cauchy number (Ca, 294 equation 6) and the ratio of plant stem height to wave orbital excursion (L, equation 7) were 295 calculated according to the formula proposed in Luhar and Nepf (2016). Both P and Umax pred were 296 determined from wave parameters recorded by the wave gauge set deployed immediately in front of 297 the vegetated test section (Fig. 1a). The first 11 fully developed waves were found to be entirely 298 unaffected by reflection from the flume rear end and were used to determine average wave height 299 (H, from min-max water surface elevations) and period (T, from zero-upcrossing points).

300 The following formulae were used to calculate $U_{max pred}$ (m s⁻¹), P (kW m⁻¹), Ca and L:

301

$$302 P = C_g E [Eq. 1]$$

303 in which

$$304 \qquad C_g = \frac{1}{2} \left[1 + \frac{4\pi h/L_{wave}}{\sinh(\frac{4\pi h}{L_{wave}})} \right] \frac{L_{wave}}{T}$$
[Eq. 2]

305
$$E_{wave} = \frac{1}{8}\rho g H^2$$
 [Eq. 3]

306 and

307
$$L_{wave} = \frac{gT^2}{2\pi} tanh\left(\frac{2\pi h}{L_{wave}}\right)$$

$$H\pi$$
[Eq. 4]

308
$$U_{peak f pred} = \frac{\frac{1}{T}}{sinh(2\pi \frac{h}{L_{wave}})}$$
 [Eq. 5]

$$309 \quad Ca = \frac{\rho dU_{peak f \, pred}^2 l^3}{El}$$
[Eq. 6]

310 in which

311
$$I = \frac{\pi d^4}{64}$$

312 and

313
$$E = \frac{E_b I}{I} = \frac{4 \, s^3 F}{3D\pi d^4}$$
 [Eq. 7]

314
$$L = \frac{l}{A}$$
 [Eq. 8]
315 in which
316 $A = \frac{U_{peak f pred}}{\omega}$ [Eq. 9]
317 and
318 $\omega = \frac{2\pi}{\pi}$ [Eq. 10]

$$318 \qquad \omega = \frac{2\pi}{T}$$
[Eq. 1]

where C_g = group wave celerity (m s⁻¹), E_{wave} = wave energy (J m⁻²), H = wave height (m), T= wave period (s), L_{wave} = wave length (m), h = water depth (m), A = wave orbital excursion (m), ω = angular frequency (rad s⁻¹), ρ = water density (1.02 kg m⁻³), g = acceleration by gravity (m³ (kg s)⁻¹), I = second moment of area (m), d = plant stem diameter (m), I = plant stem height (m), E_b = Young's bending modulus (Pa). D = vertical deflection of the stem (m), F = force orthogonal to the plant stem (N) and s= horizontal span of the plant stem (m) in the three-point bending tests used to measure E_b (see Rupprecht et al., 2015a).

327

Conditions with $U_{peakfpred} \le 32 \text{ cm s}^{-1}$ (corresponding to $P \le 0.48 \text{ kW m}^{-1}$) are referred to as 'low orbital velocity'; $42 \le U_{peakfpred} \le 63 \text{ cm s}^{-1}$ (corresponding to $0.47 \le P \le 1.36 \text{ kW m}^{-1}$) as 'medium orbital velocity' and $U_{peakfpred} \ge 74 \text{ kW cm s}^{-1}$ (corresponding to $0.65 \le P \le 3.39 \text{ kW m}^{-1}$) as 'high orbital velocity' (Table 2, Fig. 4 a). Conditions with values of $U_{peakfpred}$ and P between these classes were not covered during the experiments.

333

2.4 Videography and analysis of plant movement

Video cameras were installed behind the lateral observation window 6 m from the front of the vegetated test section (Fig. 2). These cameras recorded the movement of *Puccinellia* and *Elymus* at bed level simultaneously to the records of wave orbital velocities in both canopies. Images were continuously acquired at a frequency of 10 Hz.

339 Plant behaviour characteristics for swaying and whip-like movement under wave motion have been 340 reported elsewhere (Bradley and Houser 2009; Manca 2010) and are illustrated in Fig. 2. However, it 341 should be noted that many transitional states exist between these two main types of plant 342 movement. We analyzed plant movement from plant bending angles in the direction of wave travel (hereafter referred to as 'forward' direction), and counter to direction of wave travel (hereafter 343 344 referred to as 'backward' direction), and the time of maximum stem extension, using 'Kinovea' video analysis software (Kinovea 0.8.15, © 2006 - 2011 - Joan Charmant & Contrib.). The maximum 345 346 bending angle of stems in, forward and backward direction was measured with the 'angle 347 measurement tool' in 'Kinovea'. The time of maximum stem extension was assessed through frame348 by-frame tracking of individual plant stems. In 'Kinovea' tracking of objects (here plant stems) is a 349 semi-automatic process. After manually choosing a well distinguishable point on a plant stem, the 350 point location is computed automatically by recording x (horizontal) and y (vertical) coordinates in 351 pixels. The tracking process can be interrupted and manually adjusted at any time. In each wave test, 352 we recorded stem movement for an interval of 10 - 20 s at the same location in the canopy, thus 353 capturing plant movement under at least four waves. In tests with medium and high hydrodynamic 354 energy, fast canopy movement and high water turbidity, the point location needed to be manually 355 adjusted several times during the tracking process. This may have caused a lower precision of the 356 video analysis in these wave tests. In addition to the analysis of plant movement, the minimum 357 height of the submerged canopy (i.e. canopy height resulting from the maximum bending angle of 358 stems in direction of wave travel) was determined using a measuring tape fixed to the observation 359 window of the flume.

360

361 **2.5 Quantification of wave orbital velocities**

362 Time-series data of orbital velocity under regular non-breaking waves were used to evaluate the 363 effect of canopy movement of Puccinellia and Elymus (observed with the video cameras) on orbital 364 velocities near the sediment bed. The mean peak velocity, both in the direction of wave travel i.e. in 365 'forward' direction (mean peak forward velocity, $U_{peak f}$) and counter to the direction of wave travel 366 i.e. in 'backward' direction (mean peak backward velocity, $U_{peak b}$), were quantified from the 367 horizontal velocity component (component in direction of wave travel) recorded with the EMCMs at 368 a height of 15 cm above the bed. Tt do so, the peak velocities, both in forward and backward 369 direction, were identified for each wave cycle within the complete time series and then averaged 370 over all waves recorded during the respective test ($96 \le N \le 148$).

371 In shallow water environments, wave shape changes with increasing wave height and wave 372 period, from a symmetric sinusoidal pattern to an asymmetric trochoidal shape characterized by 373 steep wave crests and shallower wave troughs. This change leads to asymmetry in forward and 374 backward orbital velocity. The maximum drag force that can be imparted by the waves on the vegetation canopy under a specific level of wave energy is driven by the stronger orbital velocity in 375 376 forward direction under the wave crests. For this reason, we focused on U_{max} recorded within 377 canopies of Puccinellia and Elymus when comparing the responses of the different canopies to wave 378 forcing in terms of movement and their capacities to lessen orbital velocities.

To assess the effect of the presence of *Puccinellia* and *Elymus* on orbital velocities as opposed to unvegetated conditions, we compared U_{peakf} measured within both canopies with U_{peakf} when the canopies were mowed. Differences in orbital velocities between *Puccinellia* and *Elymus*, as well as

between vegetated and mowed conditions, were analyzed for each wave test ($96 \le N \le 148$) with ttests calculated in R 3.1.0 (R Development Core Team, Vienna, AT).

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- 385

2.6 Quantification of physical damage of the vegetation canopy

To assess the physical damage occurring to the vegetated test section as a whole, all floating biomass was collected by net (1 cm mesh) from the water surface at the end of each test, dried and weighed. After the last wave test under vegetated conditions, the whole vegetated test section was mowed to a stem height of 2 - 3 cm (see also section 2.2). To quantify the total dry weight of biomass on the test section, the dry weight of the mowed biomass was added to the dry weight of the floating biomass recovered over ithe course of the experiment.

393 To assess the physical damage to the *Elymus* canopy, the number of *Elymus* stems remaining 394 was counted each time when the flume was drained and the plants emergent. The prerequisite of a 395 stem to be counted was that it was not broken, i.e. stems that were folded but not broken were also 396 counted. Stems were counted at 18 quadrats of 10 x 10 cm located within a distance of 0.7 m into 397 the vegetated test section from the flume side wall. The quadrats were distributed in six sets of three 398 replicates from the front to the rear end of the vegetated test section with two of these sets (i.e. six 399 quadrats) located in the front, middle and rear part of the vegetated test section and accessed from 400 a small walkway along one of the flume side walls. The assessment of physical damage to the *Elymus* 401 canopy as described here was conducted separately from the quantification of stem density for the 402 quantification of biophysical properties of *Elymus* (see section 2.1).

Physical damage to the *Puccinellia* canopy was assessed from photographs of the *Puccinellia* canopy each time the flume was drained at a location close to where the EMCM in the *Puccinellia* canopy was deployed.

406

407 **3 Results**

3.1 Canopy movement and orbital velocity in *Puccinellia* and *Elymus*

409 At low orbital velocity both the *Puccinellia* and *Elymus* canopy showed a swaying movement under 410 wave motion with similar mean peak forward orbital velocitiy $(U_{peak f})$ and mean peak backward 411 orbital velocity $(U_{peak b})$ (Fig. 4, Table 3).

412 At medium orbital velocity, larger differences in U_{peak f} occurred between Puccinellia and Elymus.

These differences were associated with the folding of *Elymus* stems, the transition of swaying to whip-like movement in *Puccinellia* and long wave periods (4 - 5 s).

Folding of *Elymus* stems was first observed at $U_{peakf pred} = 42$ cm s⁻¹, corresponding to a wave 415 416 height of 0.4 m and a wave period of 4.1 s (Fig. 4, wave test 10 in Table 2). Here the bottom stem 417 parts bent to around 30°, while the upper more flexible stem parts folded over at around 8 cm above 418 the bed, resulting in a wide bending angle $(80 - 90^\circ)$ of the *Elymus* canopy as a whole. In comparison, 419 Puccinellia showed a bending angle of 50° (Table 3). The more upright posture of the Puccinellia canopy resulted in a greater flow resistance and an 18 cm s⁻¹ (37%) lower orbital velocity under wave 420 421 forward motion than in *Elymus*. Time trace analysis of plant stem movement indicated a phase 422 difference of around 20 – 40° between canopy movement and wave motion in both the Puccinellia 423 and the *Elymus* canopy (for an illustration of canopy movement and water motion see Appendix Fig. A.1). At $U_{peak f pred}$ = 62 cm s⁻¹ the transition from swaying to whip-like movement occurred in 424 Puccinellia (Fig. 4, wave test 12 in Table 2). The wide bending angles in the direction of wave travel 425 426 (approximately 60°) and the long duration of maximum stem extension (approximately 1.5 s) allowed 427 the flow to pass unimpeded over the deflected canopy the top of which was at a height of around 428 9 cm above the sediment bed for a large part of the wave cycle. In contrast, *Elymus* showed a 429 swaying movement with folding of stems approx. 6 cm above the bed (for an illustration of canopy 430 movement and water motion see Appendix Fig. A.2). Whip-like movement of Puccinellia and hence a decrease in flow resistance led to a 26 cm s⁻¹ (54%) higher orbital velocity under wave forward 431 432 motion in comparison to *Elymus* (Table 2).

At high orbital velocity both *Puccinellia* and *Elymus* exhibited a whip-like movement (Table 3). U_{peakf} in *Puccinellia* exceeded U_{peakf} in *Elymus* by 5 – 18 cm s⁻¹ (6 – 22%; Fig. 4, wave test 14 in Table 2). During wave forward motion, both canopies were in a flattened 'shielding posture' (canopy height above the bed = 7 cm in *Puccinellia*, 5 cm in *Elymus*) and presumably provided low flow resistance. In both *Puccinellia* and *Elymus* a phase difference occurred between canopy movement and wave motion. In *Elymus* the phase difference was much larger (around 90°) than in *Puccinellia* (around 30 – 40°, for an illustration of canopy movement and water motion see Appendix Fig. A.3).

440 # Fig. 4

441 #Table 3

442

The Cauchy number *Ca* ranged in *Puccinellia* from 0.3 - 671 and in *Elymus* from 0.4 - 994 (Fig. 4, Table 4). Small differences (≤ 39) of *Ca* in both canopies at low orbital velocity reflect their similar response to hydrodynamic forcing in terms of canopy movement. From medium orbital velocity onwards differences of *Ca* in *Puccinellia* and *Elymus* increased ($68 \leq X \leq 322$) (Table 4) with higher values of *Ca* in *Elymus* compared to *Puccinellia*. The ratio of canopy height to wave orbital excursion *L* ranged in the low-growing *Puccinellia* from 42.9 - 0.3 and in the tall *Elymus* from 166.9 - 1.2. The onset of whip-like movement was at *L* = 0.6 in *Puccinellia* and at *L* = 1.8 in the *Elymus* canopy.

450 #Table 4

451

452 **3.2** Orbital velocity in *Puccinellia* and *Elymus* under vegetated and mowed 453 conditions

At low orbital velocity, presence of the *Puccinellia* canopy caused a small reduction $(4 - 6 \text{ cm s}^{-1},$ (-18 to -19 %)) and presence of the *Elymus* canopy a small increase in of U_{peakf} . $(2 - 6 \text{ cm s}^{-1} (+13 \text{ to} +21 \%))$. With EMCMs measuring orbital velocity at a precision of ± 10 cm s⁻¹ (see Methods section 2.2) these small differences in U_{peakf} under vegetated and mowed conditions suggest a minor effect of vegetation presence on orbital velocity.

459 At medium orbital velocity, the effect of *Puccinellia* and *Elymus* on *U*_{peakf} varied with water depth 460 and wave period. Under a water depth of 2 m and long wave periods (4.1 s), when both Puccinellia 461 and *Elymus* exhibited a swaying movement, we found *Puccinellia* to reduce U_{peakf} by 16 cm s⁻¹ (35%). 462 The *Elymus* canopy, where the folding of stems occurred, had no significant effect on $U_{peak f}$ (Fig. 5, Table 4). Under a water depths of 1 m and short wave periods (2.9 s), Puccinellia caused an increase 463 of $U_{peak f}$ of 13 cm s⁻¹ (+20%) and *Elymus* a decrease by 7 cm s⁻¹ (-13%). This change in the effect of 464 Puccinellia and Elymus on U_{peak f} occurred simultaneously with the transition from swaying to whip-465 like canopy movement in *Puccinellia* (Fig. 4, 5). 466

Finally at high orbital velocity, when both canopies exhibited a whip-like movement, *Puccinellia* and *Elymus* caused an increase of U_{peakf} by 5 cm s⁻¹ (+13%) and 7 cm s⁻¹ (+13%) respectively (Fig. 5, Table 4).

470 Differences in U_{peakf} when the vegetation was mowed and the predicted peak forward velocity 471 $U_{peakf pred}$ as theoretical value of orbital velocity over a flat, surface without vegetation ranged 472 between 0.5 and 6.6 cm-1 (Table 4). This suggests $U_{peakf pred}$ to be a good proxy for orbital velocities 473 near the sediment bed in absence of vegetation.

474 # Fig. 5

475

476 **3.4 Physical damage to the vegetation canopy**

Cumulatively around 45% of the total 98 kg of above ground biomass was lost under the wave forces applied in the experiment (Fig. 6). Photo documentation of *Puccinellia* and records of stem density in *Elymus* during the course of the experiment revealed that the two canopies differed in their susceptibility to plant stem breakage under increasing orbital velocities. The *Puccinellia* canopy with its high stem flexibility withstood the hydrodynamic forces without substantial damage (Fig. 7) whereas the *Elymus* canopy with its low flexibility experienced severe physical damage in the course of the experiment (Fig. 6). Folding and breakage of *Elymus* stems around 5 – 10 cm above the sediment surface occurred from medium orbital velocities onwards ($U_{peak f pred} \ge 42$ cm s⁻¹ corresponding to wave heights ≥ 0.4 m). In total, a loss of approximately 80% of *Elymus* stems was observed on the 18 10 x 10 cm quadrats distributed over the length of the vegetated test section (Fig. 6). No significant difference was found between stem loss in quadrats in the front, middle and rear part of the vegetated test section (kruskal-wallis-test; chi-squared = 0.34, df = 2, p = 0.84).

Wave tests with $U_{peakfpred}$ of 30 – 76 cm s⁻¹ and wave heights of 0.4 – 0.7 m on day 7 and day 8 of the experiment resulted in folding and breakage of 45% of *Elymus* stems (Fig. 6). This loss of *Elymus* stems occurred simultaneously with the largest share of biomass loss as averaged over the whole test section. Another 35% of *Elymus* stems were lost during wave tests from day 10 to 11, with wave heights up to 0.9 m and $U_{peakfpred}$ up to 90 cm s⁻¹.

494 #Fig. 6

495 #Fig. 7

496

497 **4 Discussion**

498 Understanding the mechanisms of vegetation-induced wave dissipation on the one hand, and 499 vulnerability of the marshes to vegetation damage and erosion on the other hand, is of crucial 500 importance to successfully predict and incorporate the wave dissipation capacity of salt marshes into 501 coastal defence schemes (Howes et al., 2010; Leonardi et al., 2016; Luhar and Nepf 2016; Möller et 502 al., 2014). The near-field scale experimental results presented in this paper provide clear evidence for 503 differences in the interaction between each of two common salt marsh species, Puccinellia and 504 Elymus, and forward orbital velocity near the bed as well as for differences in the susceptibility of 505 both canopies to physical damage under rising orbital velocities and wave energy flux. Our findings 506 provide insights in how the contribution of vegetation to wave dissipation and surface erosion 507 protection varies with plant biophysical characteristics and hydrodynamic conditions and have 508 implications for numerical modelling of the marsh wave dissipation capacity and salt marsh 509 management schemes.

510

511 **4.1 Effect of** *Puccinellia* and *Elymus* canopies on near-bed orbital velocities

512 Low orbital velocity

At low orbital velocities ($U_{peakfpred} \le 32 \text{ cm s}^{-1}$) and *Ca* values ≤ 120 , our results suggest a minor effect of vegetation and its biophysical characteristics on near-bed orbital velocities and bed shear stress. Such findings were also reported by Neumeier and Amos (2006b) who measured a reduction of orbital velocity by 10 – 20% at low orbital velocities and wave energy (h ≤ 0.9 m, H ≤ 0.09 m) in *Spartina anglica* salt marshes of Eastern England, assuming this reduction to be of minor importance for the deposition and erosion of sediments. Wave damping was also observed to be lower for waves of smaller height than for more energetic waves in Maza et al.'s (2015) laboratory experiment, in which *Spartina anglica* and *Puccinellia maritima* species were subjected to waves of between 0.12 and 0.2 m height in < 1.0 m water depth.

522 Medium orbital velocity

At medium orbital velocities ($U_{peak f pred}$ 42 $\leq U_{peak f pred} \leq$ 63 cm s⁻¹) and 141 $\leq Ca \leq$ 473 we found 523 524 larger differences in the effect of *Puccinellia* and *Elymus* on orbital velocity, caused by a different 525 degree of 'canopy flattening' and different susceptibility to stem folding between the two canopies. 526 Differences in the response of Puccinellia and Elymus to medium orbital velocities are also reflected 527 by larger differences in values of Ca between both canopies, compared to low orbital velocities. 528 Lower values of Ca in Puccinellia in comparison to Elymus imply a greater ability of Puccinellia to re-529 orientation after bending and hence a higher flow resistance. This holds true under a water depth of 530 2 m and long wave periods (4.1 s), when stem folding was observed for the first time in *Elymus*. Here 531 we found no significant effect of *Elymus* on orbital velocity. By contrast, *Puccinellia* caused a 532 considerable decline in orbital velocity (-35%), a decrease that may enhance sediment deposition and 533 decrease bed shear stress. In the field, reduction of orbital velocity by Puccinellia could even be 534 higher given the lower stem flexibility of *Puccinellia* in the field compared to the flume (Table 1). In 535 all of the other tests at medium orbital velocity however, higher orbital velocity in Puccinellia 536 suggests a lower flow resistance compared to *Elymus*. This is presumably because the onset of whip-537 like movement occurred in Puccinellia at lower (medium) orbital velocity than in Elymus, an effect 538 that could not be captured by the calculation of *Ca*.

The transition from swaying to whip-like movement occurred in *Puccinellia* at a value of Ca = 319and L = 0.6 and hence at a greater wave orbital excursion and higher orbital velocities as assumed for flexible aquatic vegetation, where properties of whip-like movement are postulated to only start to occur at L values of = 1 (Luhar and Nepf, 2016). In *Elymus* the transition to whip-like movement occurred at Ca = 664 and L = 1.8, suggesting that folding of stems may favour the onset of whip-like movement.

545 High orbital velocity

At high orbital velocities ($U_{peak f pred} \ge 74 \text{ cm s}^{-1}$) and $449 \le Ca \le 994$ both *Puccinellia* and *Elymus* caused an increase of orbital velocity compared to mowed conditions and exhibited a whip-like movement. The reconfiguration of canopies to a flattened 'shielding' posture, close to the soil surface for a large part of the wave cycle, can be expected to protect the bed from erosive processes. However, high orbital velocities above the canopy may reduce the chance of sediment particles settling on the bed, thus leading to a passive protective role of the canopy rather than an active sediment-enhancing role (Neumeier and Ciavola 2004; Peralta et al., 2008).

Apart from high orbital velocities, waves and water levels, long wave periods (4 - 8 s) are 553 554 characteristic for storm surges. The dependence of wave-vegetation interactions on wave period has 555 been observed in many flume, field and modelling studies (Bradley and Houser 2009; Jadhav et al., 556 2013; Lowe et al., 2007; Mullarney and Henderson 2010; Paul and Amos 2011; Maza et al., 2015). It has been suggested that depending on the biophysical properties of the plant species, canopies can 557 act as a band-pass filter preferentially damping short or long-period waves while intermediate 558 559 frequencies pass more easily (Mullarney and Henderson 2010). Moreover, it is to be expected that 560 biophysical plant characteristics impact most on the vegetation-wave interactions at long-period 561 waves as those tend to have larger velocities throughout the water column than short period waves 562 (Anderson et al., 2011).

Our results show that in contrast to medium orbital velocities and long wave periods, where 563 564 Puccinellia and Elymus differed in the degree of canopy flattening and ability to reduce orbital velocity, at high orbital velocities and a wave period of 5.1 s, both Puccinellia and Elymus took a 565 566 flattened posture and caused an increase in orbital velocity compared to mowed conditions. 567 However, both canopies showed differences in their capacity to provide resistance due to relative 568 motion between plants and water (i.e. the phase difference between canopy and water movement). 569 The greater phase difference and lower values of mean peak forward orbital velocity suggest a higher 570 resistance, and hence greater potential for flow and wave dissipation, in the presence of an Elymus 571 canopy.

572 In summary, our results imply a species-specific vegetation control on near-bed orbital velocities, 573 sediment transport and deposition at medium orbital velocities, at least at spatial and temporal 574 scales on which other controls, such as sediment supply and incident hydrodynamic conditions can 575 be assumed to be relatively invariant (French and Spencer 1993). These insights add an additional 576 dimension to existing laboratory studies with real vegetation but relatively low energy conditions 577 (depths \leq 1m; H \leq 0.2 m) in which vegetation density may exert a greater control than species 578 flexibility on wave dissipation (Maza et al., 2015). Our results suggest, however, that the type of 579 vegetation movement which is linked to plant flexibility, remains critical in determining plant-wave 580 interactions and the effects of this interaction on orbital velocity.

581

582 #Table 4

583

584 4.2 Susceptibility of salt marsh vegetation to physical damage under 585 increasing wave forces

586 Throughout the experiment the salt marsh vegetation canopy as a whole experienced moderate 587 physical damage and the sediment surface withstood large wave forces without substantial erosion 588 (Möller et al., 2014; Spencer et al., 2016). This suggests a high resilience of sediment surfaces under a 589 vegetated salt marsh canopy to storm surge conditions. With the root mat remaining intact, damage 590 to the vegetation canopy reported in this paper can be considered to be of a temporary nature 591 meaning that recovery may be expected during the next growing season. This is especially valid for 592 plant species that can reproduce by clonal growth, a characteristic of both the grass species 593 investigated in this study. However, recovery is unlikely to occur between storms clustered over a 594 short interval in the order of weeks, particularly likely in northern winter months when most storm 595 surges occur (Cusack, 2016). The latter may have implications for the coastal protection value of the 596 marsh for reoccurring storms or storms of longer duration (several days). Indeed a recent global 597 analysis on salt marsh erosion and wave measurements by Leonardi et al., (2016) revealed that most 598 of salt marsh deterioration is caused by moderate storms of a monthly frequency while violent 599 storms and hurricanes occurring at a decadal timescale contribute less than 1% to long-term salt 600 marsh erosion rates. Moreover interior marsh surfaces as investigated in our study have been shown 601 to be much less responsive to wave action than fringing marshes (Fagherazzi 2013; Fagherazzi et al., 602 2013; Feagin et al., 2009). Further studies are needed to investigate the links between vegetation 603 and root system characteristics, organic matter dynamics and the erosion stability of marsh edges.

604 The canopies of Puccinellia and Elymus differed in their susceptibility to stem folding and 605 breakage under increasing orbital velocities and wave energy flux. The very low amount of physical 606 damage occurring to Puccinellia can be attributed to its very flexible stems allowing reconfiguration 607 of the canopy to a flat shielding posture close to the bed under high orbital velocities (cf. 608 observations in Bouma et al. 2010; Bouma et al. 2013). A similar strategy to survive under high flow 609 and wave-induced velocities by avoiding high drag forces through reconfiguration is also known for 610 flexible sea grasses (Infantes et al., 2011; Peralta et al., 2008) and freshwater macrophytes (O'Hare et 611 al., 2007; Puijalon et al., 2011; Robionek et al., 2015).

Providing low flow resistance, the direct contribution to hydrodynamic energy dissipation by very flexible plants is small. At the water-sediment interface, however, the flattened plant canopies under high velocities, reduce friction forces and contribute, along with plant roots and sediment organic matter content, to the stabilization of sediment surface and long-term marsh stability (Neumeier and Ciavola 2004; Peralta et al., 2008).

617 In contrast to *Puccinellia*, the less flexible and tall *Elymus* canopy experienced folding and 618 subsequent breakage of stems from medium orbital velocities and above. Turbulence around stumps 619 remaining on the marsh surface after stem breakage can increase bed shear stress and bed erosion 620 through local scour. This is confirmed by a study of Spencer et al., (2016) who investigated soil

surface elevation change in the framework of the present flume experiment. They found surfaces covered by the flattened canopy of *Puccinellia* experienced a lower and less variable elevation loss than those characterized by *Elymus*. The susceptibility of *Elymus* stems to breakage in the field under high orbital velocity may be even higher than that observed in this experiment. On the other hand, the cumulative effects of wave forces on the *Elymus* canopy could also imply that the stem loss experienced at medium orbital velocities enhanced the susceptibility of *Elymus* to folding and breakage at high orbital velocities compared to similar velocities under field conditions.

Physical damage and hence a decline in flow resistance of *Elymus* from medium orbital velocities onwards observed in this study coincided with a leveling-off in the wave-dissipation capacity of the vegetated test section as a whole (Möller et al., 2014). With *Elymus* covering the largest part of the vegetated test section (around 70%) in this flume experiment, this result suggests that changes in vegetation-wave interactions may exert an important control on wave dissipation by salt marshes under increasing orbital velocities and wave energy flux.

634

635 **5 Conclusions**

636 In this paper, we investigated salt marsh vegetation-wave interactions over a wide range of wave 637 conditions, from low to high wave orbital velocities and wave energy flux and in a near-field scale 638 flume experiment. The results of our study show that canopy height and flexibility, as well as incident 639 wave heights, wave periods and water depth, play an important role in the way vegetation interacts 640 with waves. Furthermore, for the conditions and plant species tested here, the ability of vegetation 641 to reduce near-bed wave orbital velocities and vegetation susceptibility to breakage varied with plant 642 biophysical characteristics from an orbital velocity of 42 cm s⁻¹ onwards. To profit from the benefits 643 that plant species differing in biophysical characteristics provide in terms of wave dissipation and 644 surface erosion protection under storm surge conditions, management schemes should aim for the 645 maintenance of plant species diversity. Given the large variability in biophysical properties between 646 salt marsh plant species (Feagin et al., 2011; Rupprecht et al., 2015a) it is recommended that further 647 studies focus on the behavior of a wider range of salt marsh canopies, ideally under the full range of 648 water depth and wave conditions that can be expected to occur on coasts periodically impacted by 649 severe storms. While Elymus athericus and Puccinellia maritima are common species in the NW 650 European region, the occurrence of mono-specific stands of Spartina anglica and Spartina 651 alterniflora along the coastline of the United States and China, as well as NW Europe, calls for a 652 separate investigation of vegetation-wave interactions in these types of marshes. Such studies are 653 needed because these species often feature in coastal wetland creation schemes (Borsje et al., 2011; 654 Kabat et al., 2009; Temmerman et al., 2013). Knowledge on species-specific thresholds of orbital 655 velocities and wave energy flux marking changes in flow resistance, as well as future studies 20

656 providing such thresholds for mixed canopies, might then inform modelling studies generating 657 predictions of marsh stability and resilience over longer time-scales, feeding into the growing body of 658 knowledge that will ultimately allow salt marshes to be fully and effectively incorporated into coastal 659 protection schemes.

660

661 Acknowledgements

We thank all of the staff at the Großer Wellenkanal as well as B. Evans, J. Tempest, K. Milonidis and C. 662 663 Edwards, Cambridge University, and D. Schulze, Hamburg University, for their invaluable logistical assistance, Fitzwilliam College for supporting the research time of I.M., and C. Rolfe, Cambridge 664 665 University, for the soil analysis and Deltares for the support by the Strategic Research Programme on 666 dikes, levees and dams. M.P. acknowledges funding by the German Science Foundation (grant no. PA 2547/1-1). The work described in this publication was supported by the European Community's 7th 667 668 Framework Programme through the grant to the budget of the Integrating Activity HYDRALAB IV, 669 Contract no. 261529 and by a grant from The Isaac Newton Trust, Trinity College, Cambridge.

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 2012
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844 Figures

- 845 Figure 1

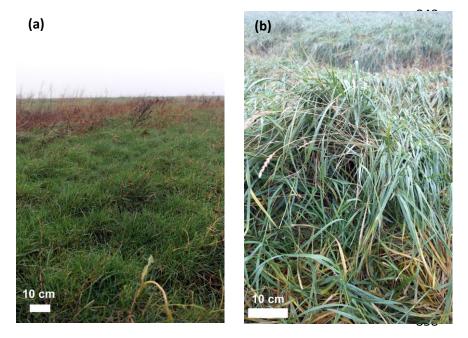


Fig. 1: Canopies of the salt marsh grasses (a) *Puccinellia maritima* and (b) *Elymus athericus* at theNorth Sea Coast in Eastern Frisia, Germany.

873 Figure 2

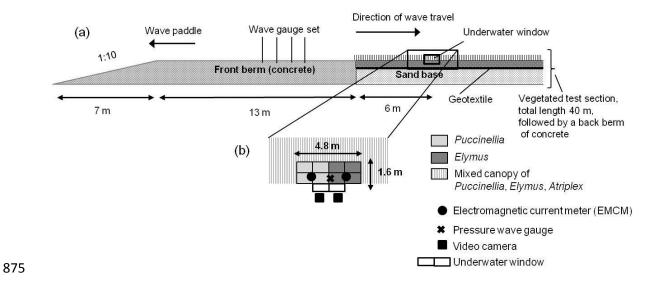


Fig. 2: Large scale flume experiment conducted by Möller et al. (2014). (a) General experimental setup in the GWK (Großer Wellenkanal, Hannover) wave flume, (b) top view of the flume section

878 where vegetation-wave interactions in the canopy of *Puccinellia* and *Elymus* were analyzed.

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881 Figure 3

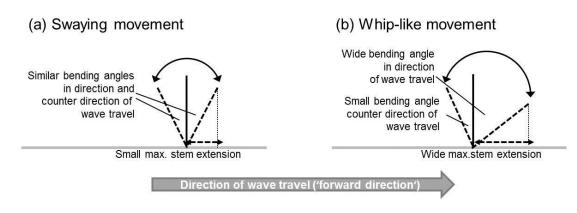
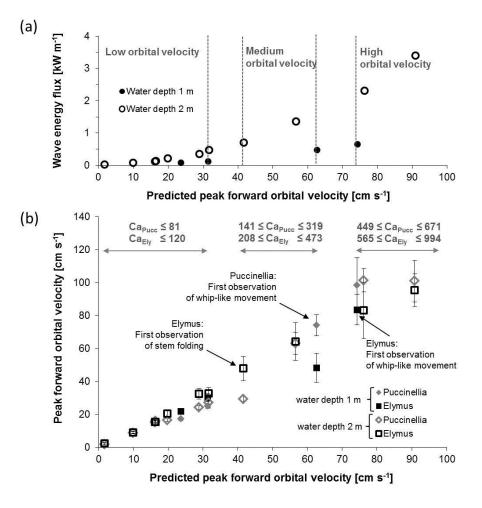


Fig. 2: Schematic of plant movement under wave motion. (a) Bending angles and stem extension
under swaying movement characteristic for low to medium orbital velocities and wave energy flux, (b)
bending angles and stem extension under whip-like movement characteristic for high orbital
velocities and wave energy flux.





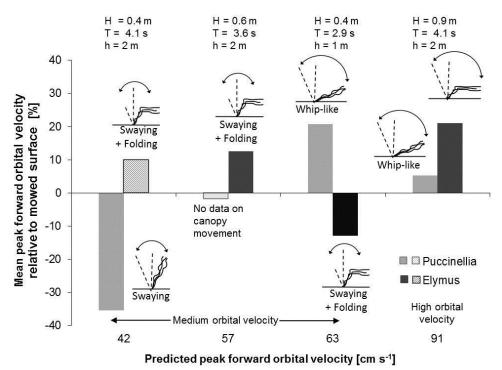
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Fig. 4: (a) Wave energy flux as a function of the predicted peak forward orbital velocity / Relationship between predicted peak forward orbital velocity and wave energy flux and (b) measured peak forward orbital velocity in *Puccinellia* and *Elymus* and range of the Cauchy number (*Ca*, ratio of the hydrodynamic forcing to the restoring force due to plant stiffness) under low, medium and high predicted peak forward orbital velocity. Error bars refer to the mean \pm 1 SD of time series measurements over the complete wave test (96 ≤ N ≤ 148).

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904 Figure 5



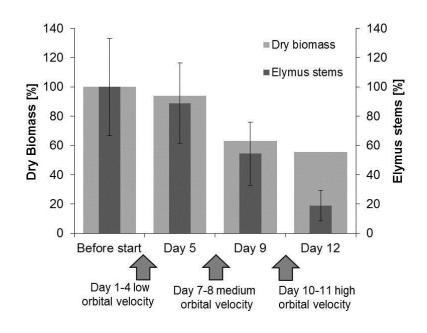
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907 **Fig. 5:** Mean peak forward orbital velocity $(U_{peak f})$ in *Puccinellia* and *Elymus* relative to mowed 908 conditions under low, medium and high predicted peak forward orbital velocity. Negative values 909 indicate a reduction, positive values an increase in $(U_{peak f})$ due to presence of *Puccinellia* and *Elymus*. 910 Hatched columns indicate conditions where no significant differences (t-test; p> 0.01) between $U_{peak f}$ 911 under vegetated and mowed conditions were found.









917 Fig. 6: Total dry plant biomass remaining on the 40 m vegetated test section (see Figure 2) in the 918 flume (light grey bars) and number of *Elymus* stems (dark gray, mean ± 1 SD from 18 10 x 10 cm 919 quadrats distributed over the test section) prior to the first wave test (day 0 of the experiment) and 920 at the three time steps when the flume was drained in the course of the experiment (day 5, day 9 921 and day 12).



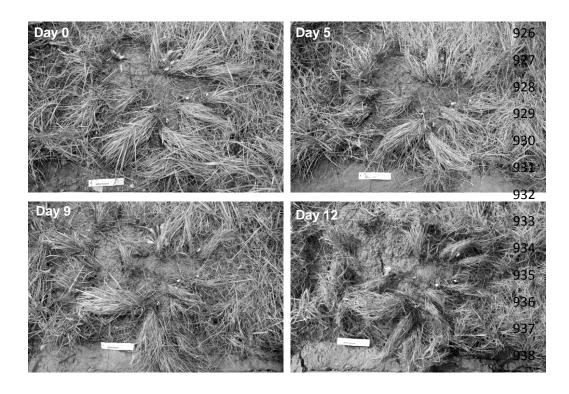


Fig. 7: Photo documentation of the *Puccinellia* canopy prior to the first wave test (Day 0) and at the
three times when the flume was drained (Day 5, 9 and 12) in the course of the experiment. The
photograph of Day 12 shows *Puccinellia* before the marsh platform was mowed i.e. at the end of
wave tests with the vegetated marsh surface.

945 **Tables**

946**Table 1:** Biophysical characteristics (mean values \pm 1 SD) of the *Puccinellia* and *Elymus* canopy at the947test section in the flume and at the field site where the marsh blocks for the flume experiment were948excavated. Young's bending modulus and flexural rigidity and stem diameter were measured with N949= 17 for *Puccinellia* and N = 18 for *Elymus*; stem height with N = 30 and stem density with N = 10 for950both species.

Stem flexibility

Flexural rigidity [Nm² x 10⁻⁵]

Mean

 0.7 ± 0.2

2.1±1.7

 29.9 ± 18.4

 56.9 ± 20.7

Stem

[mm]

Mean

 1.1 ± 0.3

 1.2 ± 0.2

 1.3 ± 0.3

 1.7 ± 0.4

diameter

Stem

height

[mm]

Mean

 220 ± 30

180 ± 30

700 ± 10

 800 ± 10

Stem

m²]

_

_

Mean

density

[number per

1225 ±575

1700 ±200

Stem flexibility

Young's bending

Modulus [MPa]

 111.6 ± 66.3

284.5 ± 369.1

2696.3 ± 1963.8

2514.7 ± 2977.1

Mean

Puccinellia

Puccinellia

(Flume)

(Field) Elymus

(Flume) Elymus

(Field)

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960	Table 2: Hydrodynamic conditions simulated with regular non-breaking waves in the flume
961	experiment. Mean wave height (H), water depth above the marsh platform (h), mean wave period (T),
962	energy flux per meter crest length (P), mean peak forward orbital velocity predicted from wave
963	parameters ($U_{peakfpred}$) and mean peak forward and backward orbital velocity (U_{peakf} , U_{peakb}) recorded
964	within canopies of Puccinellia and Elymus. Wave tests which were repeated after mowing of the
965	marsh platform are shaded in grey. Statistical significance of differences between Puccinellia and
966	<i>Elymus</i> in in U_{peakf} (ΔU_{peakf}) and U_{peakb} (ΔU_{peakb}) verified with t-tests based on (96 \leq N \leq 148) waves.
967	Non significant differences between species (p > 0.05) in U_{peakf} and U_{peakb} are marked with 'ns'.
060	

Test no.	Orbital velocity class	U _{peak f} ^{pred} [cm s ⁻¹]	<i>P</i> [kW m ⁻¹]	<i>h</i> [m]	<i>Н</i> [m]	<i>Т</i> [s]	<i>U_{peak f}</i> [cm s ⁻¹] (mean	± 1 SD)		<i>U_{peak b}</i> [cm s ^{₋1}] (mear	Day		
							Puccinellia	Elymus	∆ U _{peak f}	Puccinellia	Elymus	∆ U _{peak b}	
1	Low	1.8	0.02	2	0.1	1.5	1.9 ± 0.6	2.3 ± 0.6	0.4	-2.8 ± 0.6	-2.2 ± 0.5	0.3	1
2	Low	10.0	0.08	2	0.2	2.1	8.9 ± 0.7	9.1 ± 0.6	0.2	-10.4 ± 0.7	9.6 ± 0.7	0.8	1
3	Low	16.2	0.13	2	0.2	2.9	15.2 ± 0.8	15.5 ± 0.9	0.3	-15.9 ± 1.0	-14.6 ± 0.9	1.3	1
4	Low	16.4	0.13	2	0.2	2.9	16.0 ± 0.9	15.5 ± 0.8	0.5	-15.9 ± 1.1	-13.5 ± 1.4	2.4	3
5	Low	19.8	0.22	2	0.3	2.5	16.5 ± 0.8	20.5 ± 1.6	4.0	-17.7 ± 1.1	-18.2 ± 2.1	0.5	3
6	Low	23.7	0.07	1	0.2	2.1	17.2 ± 1.0	21.9 ± 1.2	4.7	-19.8 ± 1.1	-18.9 ± 1.2	1.0	4
7	Low	28.8	0.36	2	0.3	3.6	24.2 ±1.2	32.6 ± 3.2	8.4	-20.5 ± 1.5	-24.1 ± 3.5	3.6	3
8	Low	31.4	0.12	1	0.2	2.9	25.1 ± 1.4	30.1 ± 2.4	5.0	-21.5 ± 1.5	-24.4 ± 2.6	2,9	4
9	Low	31.6	0.48	2	0.4	2.9	27.2 ± 3.1	32.9 ± 3.3	5.7	-30.5 ± 2.1	-25.5 ± 2.5	5.0	7
10	Medium	41.6	0.71	2	0.4	4.1	29.4 ± 1.7	47.9 ± 7.3	18.5	-34.1 ± 1.8	-38.9 ± 5.4	4.8	7
11	Medium	56.6	1.36	2	0.6	3.6	63.2 ± 6.7	64.3 ± 11.5	ns	-48.6 ± 2.4	-46.7 ± 9.4	ns	7
12	Medium	62.7	0.47	1	0.4	2.9	74.2 ± 6.5	48.2 ± 8.7	26.0	-41.5 ± 2.9	-50.5 ± 8.7	9.0	8
13	High	74.3	0.65	1	0.5	3.3	98.5 ± 16.8	83.5 ± 9.2	5.0	-50.5 ± 9.2	-48.2 ± 9.2	2.3	11
14	High	76.2	2.31	2	0.7	5.1	101.4 ± 7.0	83.2 ± 17.1	18.2	-41.0 ± 3.1	-37.2 ± 10.1	3.8	8
15	High	90.9	3.39	2	0.9	4.1	100.9 ± 12.6	95.4 ± 9.8	5.5	-73.7 ± 4.4	62.8 ± 9.5	10.9	10

Table 3: Observed characteristics of vegetation-wave interactions, Cauchy number (*Ca*; ratio of the hydrodynamic forcing to the restoring force due to plant stiffness), ratio of canopy height to wave orbital excursion (*L*) and effect of vegetation on peak forward orbital velocity (U_{peakf}) in *Puccinellia* (*Pucc*) and *Elymus* (*Ely*). Wave tests that were repeated after mowing of the marsh platform are shaded in grey. Due to high water turbidity bending angles could not be measured for either *Puccinellia* or *Elymus* in the wave test 13 nor for *Puccinellia* in the wave test 11.

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Test no.	Orbital velocity class	U _{peak f} pred [cm s ⁻¹]	<i>h</i> [m]	Н [m]	Т [s]	Movem	ent	Bending a in/counte travel		Ca	Ca		L		Effect or compare condition	d to mowed
						Pucc	Ely	Pucc	Ely	Pucc	Ely	∆ Ca	Pucc	Ely	Pucc	Ely
1	Low	1.8	2	0.1	1.5	No	No	upright canopy	upright canopy	0.3	0.4	0.1	42.9	166.9	-	-
2	Low	10.0	2	0.2	2.1	SW	SW	10°/10°	5°/5°	8.0	11.4	3.9	5.4	21.0	-	-
3	Low	16.2	2	0.2	2.9	SW	SW	20°/20°	10°/10°	21.5	31.8	10.3	2.4	9.3	-	-
4	Low	16.2	2	0.2	2.9	SW	SW	20°/20°	10°/10°	21.8	32.3	10.5	2.4	9.2	-	-
5	Low	19.8	2	0.3	2.5	SW	SW	20°/20°	10°/10°	31.9	47.2	15.3	2.3	8.9	-	-
6	Low	23.7	1	0.2	2.1	SW	SW	20°/20°	10°/10°	45.6	67.5	21.9	2.3	8.8	RED	INC
7	Low	28.8	2	0.3	3.6	SW	SW	35°/35°	25°/25°	67.80	100.4	32.6	1.1	4.2	-	-
8	Low	31.4	1	0.2	2.9	SW	SW	35°/35°	15°/15°	80.00	118.5	38.5	1.2	4.8	-	-
9	Low	31.6	2	0.4	2.9	SW	SW	40°/40°	20°/20°	81.4	120.5	39.1	1.2	4.8	RED	INC
10	Medium	41.6	2	0.4	4.1	SW	SW	50°/50°	Stem folding	140.6	208.2	67.5	0.7	2.6	RED	NS
11	Medium	56.6	2	0.6	3.6	-	SW	-	Stem folding	260.9	386.1	125. 3	0.6	2.2	NS	INC
12	Medium	62.7	1	0.4	2.9	WP	SW	60°/35°	Stem folding	319.3	472.6	153. 3	0.6	2.4	INC	RED
13	High	74.3	1	0.5	3.3	WP	WP	-	-	448.9	664.5	215. 6	0.5	1.8	-	-
14	High	76.2	2	0.7	5.1	WP	WP	60°/25°	Stem folding	472.5	699.4	226. 9	0.3	1.1	-	-
15	High	90.9	2	0.9	4.1	WP	WP	60°/25°	Stem folding	671.4	993.7	322. 4	0.3	1.2	INC	INC

Abbreviations used in Table: SW = Swaying movement; WP = Whip-like movement; RED = reduction; INC = increase;
 NS = no significant effect

Table 4: Mean peak forward orbital velocity (U_{peakf}) within canopies of *Puccinellia* and *Elymus* and when both canopies were mowed. Statistical significance of differences between U_{peakf} under vegetated and U_{peakf} under mowed conditions in *Puccinellia* and *Elymus* respectively ($\Delta U_{Pucc}, \Delta U_{Ely}$) was verified with t-tests based on (96 $\leq N \leq 148$) waves. Negative values of ΔU_{Pucc} and ΔU_{Ely} indicate a reduction, positive values an increase of U_{peakf} due to vegetation presence. Non significant values (p > 0.01) are marked with 'ns'.

Test no.	Orbital velocity class	U _{peak f pred} [cm s ⁻¹]	<i>h</i> [m]	<i>Н</i> [m]	Т [s]	Puccinellia U _{peak f} [cm s ⁻¹] (mea	n ± 1 SD)		Elymus U _{peak f} [cm s ⁻¹] (mean ± 1 SD)			
						vegetated	mowed	Δ U _{Pucc}	Vegetated	mowed	ΔU_{Ely}	
6	Low	24.7	1	0.2	2.1	17.2 ± 1.0	21.0 ± 1.8	-3.8	21.9 ± 1.2	19.5 ± .3	2.4	
9	Low	31.6	2	0.4	2.9	27.2 ± 3.1	33.6 ± 3.1	-6.4	32.9 ± 3.3	27.2 ± .5	5.7	
10	Medium	42.3	2	0.4	4.1	29.4 ± 1.7	45.6 ± 2.0	- 16.2	47.9 ± 7.3	43.5 ± .7	ns	
11	Medium	58.3	2	0.6	3.6	63.2 ± 6.7	64.4 ± 3.6	ns	64.3 ± 1.5	57.2 ± .5	7.1	
12	Medium	61.9	1	0.4	2.9	74.2 ± 6.5	61.4 ± 3.5	12.8	48.2 ± 8.7	55.3 ± .0	-7.1	
15	High	90.1	2	0.9	4.1	100.9 ± 2.6	96.0 ± 5.6	4.9	95.4 ± 9.8	78.9 ± .9	16.5	

1023 Appendix

A.1

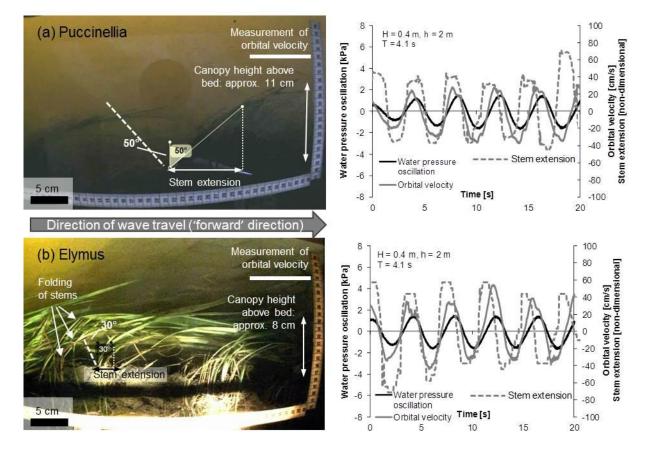


Fig. A.1: Vegetation-wave interactions under medium orbital velocity (predicted peak forward orbital velocity 42 cm s⁻¹), water depth (h) = 2 m, wave height (H) = 0.4 m and wave period (T) = 4.1 s (wave test 10, Table 2). Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in the direction of wave motion). (a) Swaying movement of the Puccinellia canopy and (b) Swaying movement of the Elymus canopy, both recognizable from similar bending angles and orbital velocities in forward and backward direction of wave-induced oscillatory flow. Note that due to stem folding lower stem parts of *Elymus* bent to smaller angles (30°) than upper more flexible stem parts resulting in bending angles of 90° of the Elymus canopy as a whole Mean peak forward orbital velocity in *Puccinellia* with its intact stems was 40% lower than in *Elymus* where folding of stems occurred (see Fig. 4).

A.2

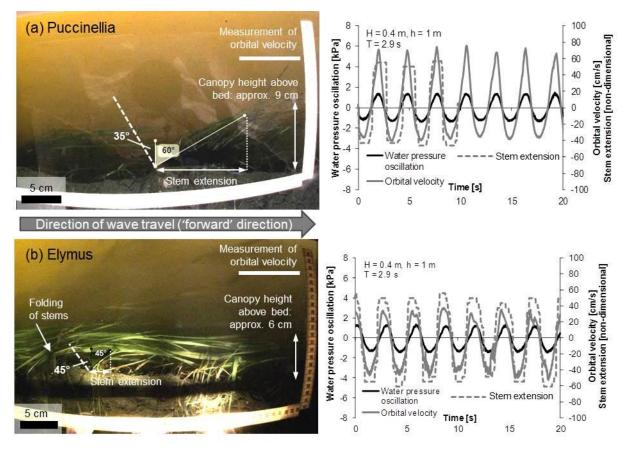


Fig. A.2: Vegetation-wave interactions under medium orbital velocity (predicted peak forward orbital velocity 63 cm s⁻¹) water depth (h) = 1 m, wave height (H) = 0.4 m and wave period (T) = 2.9 s (wave test 12, Table 2). Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in direction of wave motion). (a) Whip-like movement of the Puccinellia canopy recognizable from wide bending angles and high orbital velocity in forward direction of wave-induced oscillatory flow. (b) Swaying movement of the *Elymus* canopy recognizable from similar bending angles and orbital velocities in forward and backward direction of wave-induced oscillatory flow. Note that due to stem folding lower stem parts of *Elymus* bent to smaller angles (45°) than upper more flexible stem parts resulting in bending angles of 90° of the Elymus canopy as a whole. Following its whip-like movement mean peak forward orbital velocity in Puccinellia was approx. 50% higher than in *Elymus* (see Fig. 4).

A.3

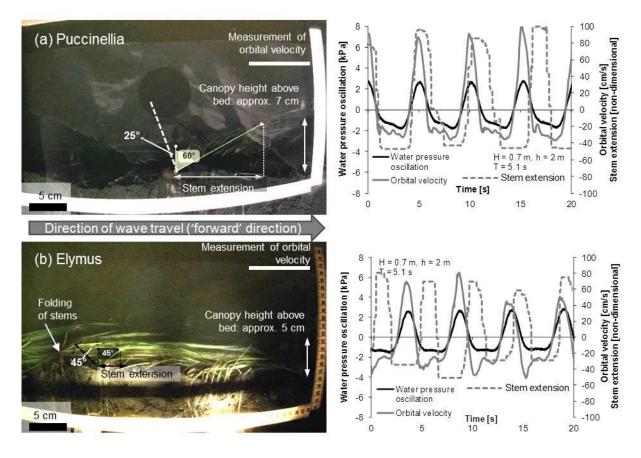


Fig. A.3: Vegetation-wave interactions under high orbital velocity (predicted peak forward orbital velocity 76 cm s⁻¹) water depth (h) = 2 m, wave height (H) = 0.7 m and wave period (T) = 5.1 s (wave test 14, Table 2). Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in the direction of wave motion). (a) Whip-like movement of the Puccinellia canopy and (b) whip-like movement of the Elymus canopy, both recognizable from wide bending angles and high orbital velocity in forward direction of wave-induced oscillatory flow. Note that due to stem folding lower stem parts of *Elymus* bent to smaller angles (45°) than upper more flexible stem parts resulting in bending angles of 90° of the *Elymus* canopy as a whole. Mean peak forward orbital velocity in Puccinellia was 20% higher than in Elymus (see Fig. 4). One reason for this may be the lower phase difference between canopy movement and water motion in Puccinellia.

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