Traits of tidal marsh plants determine survival and growth response to hydrodynamic forcing: implications for nature-based shoreline protection

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ABSTRACT: Tidal marshes are increasingly valued for their nature-based shoreline protection function, as they reduce waves, currents and erosion. The effectiveness of this function depends on the ability of tidal marsh plants to grow and survive under pressure from waves and currents. However, how this varies with species-dependent plant traits is poorly understood. We performed a field transplantation experiment to quantify species-specific growth responses to different levels of hydrodynamic exposure and tidal inundation for 3 NW European marsh species: *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis*. In this order, these species showed increasing shoot stiffness, length and biomass, which are traits that increase hydrodynamic drag forces experienced by plants. Increased exposure to tidal inundation and hydrodynamics reduced the growth of all 3 species, but species with lower biomass and shorter, thinner and more flexible shoots could better cope with higher hydrodynamic exposure and tidal inundation. Furthermore, transplants of *S. tabernaemontani* (i.e. the species with the lowest shoot stiffness, length and biomass that survived under all tested conditions) developed smaller, thinner and more flexible shoots in response to higher hydrodynamic exposure and inundation. Hence our study indicates that similar inter- and intra-specific plant traits drive plant growth in response to hydrodynamics and inundation. This suggests that the spatial distribution of species typically observed in tidal marshes results not only from species-specific tolerance to tidal inundation gradients but also from hydrodynamic gradients. Allowing enough space for development of species zonation may be important to increase the efficiency of nature-based shoreline protection by tidal marshes.

KEY WORDS: Plant traits · Growth response · Hydrodynamic exposure · Tidal inundation · *Schoenoplectus tabernaemontani* · *Bolboschoenus maritimus* · *Phragmites australis*

1. INTRODUCTION

Climate change-induced sea level rise and increasing storminess emphasize the need for sustainable shoreline protection strategies for often densely populated, low-lying coastal zones, river deltas and estuaries (Hallegatte et al. 2013, Temmerman et al. 2013, Auerbach et al. 2015, Tessler et al. 2015). Conservation and restoration of coastal vegetated wetlands, such as tidal marshes and mangroves, is increasingly

proposed and implemented as a nature-based climate adaptation strategy to complement man-made shoreline protection infrastructure such as dikes, which are common across the NW European coast (Schoonees et al. 2019, Smith et al. 2020). Tidal marshes in front of dikes attenuate waves (Vuik et al. 2016, Schoutens et al. 2019), tidal currents (Carus et al. 2016, Schoutens et al. 2019), storm surges (Smolders et al. 2015, Stark et al. 2016) and erosion (Lo et al. 2017), thereby reducing wave loads on dikes, lowering the risk of dike failure during storms and even limiting damage to the hinterland when dikes breach (Zhu et al. 2020a). Not only do tidal marshes provide this protective function, they also deliver a multitude of other valuable ecosystem services that benefit nature and society (Barbier et al. 2011).

The capacity of marsh plant species for nature-based shoreline protection depends on (1) their effectiveness to temper waves, currents and erosion, but also (2) their ability to grow and persist under the effects of waves and currents. Hydrodynamic attenuation has been the subject of multiple studies, showing that the effectiveness of wave and current attenuation depends on plant morphological traits such as high biomass (Paul & Amos 2011, Shepard et al. 2011, Schoutens et al. 2020), high density of shoots (Shepard et al. 2011, Vuik et al. 2016), high shoot lengths (Garzon et al. 2019) and stiff shoots (Rupprecht et al. 2017, Schulze et al. 2019, Schoutens et al. 2020). These plant traits increase friction (i.e. hydraulic resistance) on waves and tidal currents, thereby contributing to decrease the hydrodynamic forces and reduce the risk of erosion in marshes and on the dikes behind marshes (Möller et al. 2014, Schoutens et al. 2019). Concerning plant growth, fewer studies have identified the mechanisms determining the ability of marsh plants to withstand waves and tidal currents. Recent studies suggest that a trade-off exists between the capacity of plants to attenuate hydrodynamic forces and their capacity to cope with and grow under hydrodynamic forces (Heuner et al. 2015, Schoutens et al. 2020). These studies suggest that plant traits that enhance the reduction of hydrodynamic forces, such as having a high biomass and stiff shoots, also lead to higher drag forces exerted by the flow on the plants and thus higher mechanical stress experienced by the plants (Bouma et al. 2005).

The growth responses to mechanical stress from hydrodynamic forces have been studied in multiple aquatic ecosystems (e.g. Gaylord et al. 2003 and Demes et al. 2013 on kelp vegetation; Puijalon et al. 2008 and Schoelynck et al. 2015 on freshwater macrophytes; Peralta et al. 2006 and La Nafie et al. 2012 on seagrasses). In tidal marshes, key knowledge gaps on species-specific plant growth response to wave exposure remain. A limited number of short-term (minutes to hours) flume studies showed that drag forces on plants and dislodgment of plants in response to hydrodynamic forces increased with species-specific plant traits such as shoot stiffness (Bouma et al. 2005, Silinski et al. 2016b, Schoutens et al. 2021). Only few experimental studies have shown the longer-term (months) implications of hydrodynamic forces on intra-specific variations in plant growth during at most one summer growing season (Coops et al. 1996, Silinski et al. 2016a, 2018, Cao et al. 2020). These studies revealed that stronger hydrodynamic forces resulted in seedling mortality, reduced growth and increased shoot flexibility. To our knowledge, however, no experimental studies have shown growth responses to hydrodynamic forces over multiple growing seasons. In particular, there are no field experiments in temperate-climate marshes that identified how hydrodynamic forces from waves and currents affect plant survival during winter seasons, when plants are largely dormant, and then affect regrowth of shoots from the roots and rhizomes during the subsequent growing seasons. Yet, such knowledge is key if we want to understand under which wave and current conditions tidal marshes can be conserved, restored or created by plantings, e.g. for nature-based shoreline protection. Further, such knowledge is essential for developing models enabling the prediction of the biogeomorphic evolution of marshes (Schwarz et al. 2018, Gourgue et al. 2020) and their nature-based contribution to shoreline protection (Marijnissen et al. 2020, Willemsen et al. 2020).

Marshes that are most vulnerable to shoreline erosion are often the small fringes (i.e. 10–100 m) along embanked shorelines of estuaries and coasts, where hydrodynamic forces are dominant. These smaller fringing marshes in front of embankments are of particular interest to policymakers and shoreline managers, because of their function as nature-based shoreline protection in addition to man-made structures like dikes landward of the fringing marshes (van der Nat et al. 2016, van Loon-Steensma & Schelfhout 2017, Schoonees et al. 2019). In contrast, in wide marshes (i.e. 100s to 1000s m wide) the presence of a less-effective wave-attenuating species may be compensated for by the large width of the marsh providing significant wind wave attenuation (Shepard et al. 2011, Li et al. 2014, Xue et al. 2021). The species composition and their spatial distribution might play an important role in determining the

capacity to attenuate hydrodynamic forces such as waves and currents (van Loon-Steensma et al. 2016, Schoutens et al. 2020). Moreover, increasing storminess and sea level rise might increase landward marsh edge erosion, reducing the width of the marsh in front of the dike (Torio & Chmura 2013, Borchert et al. 2018).

Apart from waves and currents, other environmental stress factors are known to affect plant growth in tidal marshes, including tidal inundation, salinity, pollutants, sediment grain size, competition and grazing. In particular, the spatial distribution of species has been related to spatial variation in environmental stressors, as the capacity of species to cope with these stress factors determines where they survive (Pennings et al. 2005, Silvestri et al. 2005, Rasser et al. 2013, Bang et al. 2018, Veldhuis et al. 2019). Most research on tidal marsh plant zonation has focused on the role of abiotic drivers such as species tolerance to salt gradients (Engels et al. 2011) and inundation frequency and time (Castillo et al. 2000, Fariña et al. 2009), and how this affects biotic interactions via competition or facilitation between species (Bertness 1991). How species-dependent tolerance of marsh plants to waves and currents contributes to spatial plant zonation, in addition to other factors like tolerance to tidal inundation time, is much less studied (Heuner et al. 2019). That is, the ability of tidal marsh vegetation to cope with waves and tidal currents might play a role in the species zonation along a hydrodynamic exposure gradient from high exposure close to the shore towards lower exposure further inland (Bruno 2000, Schoutens et al. 2020). This means that some species might have plant properties that allow them to grow in more wave-exposed conditions compared to other species that lack these properties. Phenotypic plasticity to waves and currents may further affect growth and alter plant traits (Carus et al. 2016, Silinski et al. 2018) and thus modify their ability to withstand hydrodynamic forces. Although knowledge on phenotypic plasticity, long-term growth and survival is crucial for marsh management and restoration projects, little is known on how co-occurring species differing in traits respond to gradients in contrasting hydrodynamic exposures.

Here we experimentally quantified the relative effects of hydrodynamic forces from waves and currents, in addition to tidal inundation, on the growth and morphology of 3 different co-occurring pioneer species of temperate-climate brackish tidal marshes. Over 2 subsequent growing seasons, including the winter dormant season, we investigated how species responses differ in relation to species-specific plant traits through a field transplantation experiment, in which we applied *in situ* manipulation of the hydrodynamic forces along an inundation gradient. Based on the findings from this experiment, we aim to enhance insight in the role of hydrodynamic forces, in addition to tidal inundation, on species-specific plant growth.

2. MATERIALS AND METHODS

2.1. Study area and species description

This study took place in the brackish zone of the Elbe estuary, Germany (Fig. 1), where groundwater salinity ranges between 0.3 and 1.2 PSU (Schulte Ostermann et al. 2021) and the semi-diurnal tide has an average tidal range of 2.8 m (data for 2018–2019 for the tide gauge station of Brokdorf; Küstendaten, Federal Waterways and Shipping Administration [Wasserstraßen- und Schifffahrtsverwaltung des Bundes], https://www.kuestendaten.de/). Transplantation locations were selected on an intertidal flat using the following selection criteria: (1) absence of vegetation, so that transplanted plants were not affected by existing vegetation; (2) tidal flat location with similar surface elevations (i.e. similar tidal inundation frequency and time) to where pioneer vegetation was present in adjacent areas; and (3) tidal flat should be exposed to incoming waves at high tides. Along the marshes of Hollerwettern, we found a location with these conditions (53° 50′ 0.7″ N, 9° 22′ 6.0″ E). The tidal flat at this location has a gentle slope of ≤1° perpendicular to the estuary tidal channel with a median grain size <125 µm. There was a trend of larger grain sizes with increasing inundation depth, where hydrodynamic exposure is larger (Table S1 in the Supplement at www.int-res.com/articles/suppl/m693p107_supp.pdf). The tidal flat is exposed to the dominant wind and wave direction coming from west to south as illustrated by the windrose diagram in Fig. 1b, with a wind fetch length at high tide of ca. 3 km.

The species selected for this study were *Schoenoplectus tabernaemontani* (C. C. Gmel.) Palla (formerly *Scirpus tabernaemontani*), *Bolboschoenus maritimus* (L.) Palla (formerly *Scirpus maritimus*) and *Phragmites australis* (Cav.) Trin. ex Steud. (Fig. S1). These 3 species are typically found along the brackish zone of the Elbe estuary and other NW European estuaries, growing in distinct zones parallel to the marsh edge in which they are the dominant species in their respective zones: *S. tabernaemontani* typically grows in a
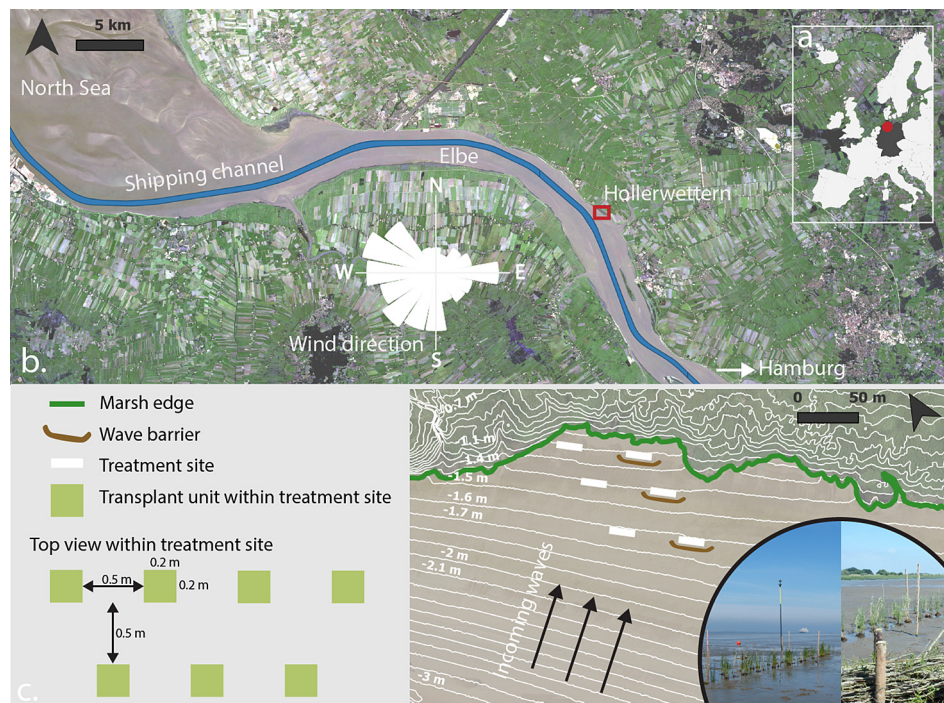
Fig. 1. (a) Study area in the Hollerwettern marshes, situated in the brackish part of the Elbe estuary in NW Germany. (b) The shape of the estuary in combination with the dominant wind directions illustrate that the Hollerwettern marsh is a wave-exposed site. Wind conditions during the experimental period in 2018–2019 are shown in the windrose diagram. (c) The experimental setup was a factorial design of 2 hydrodynamic exposure treatments spread over 3 elevations (i.e. inundation treatments) representing 6 treatment sites. Sheltered wave and flow conditions were created with wooden wave barriers which were placed outside the wake zones of other barriers. Inset pictures show transplant units without (left) and with (right) wave barrier. In each treatment site, 20 transplant units of each species were installed in 2 staggered rows and in random order. Elevations relative to Mean High Water are visualized with contour lines

zone at the waterfront of marshes, followed in landward direction by a zone of *B. maritimus* and then *P. australis* (Schoutens et al. 2020). Apart from seed dispersal, the 3 species reproduce by clonal outgrowth through rhizomes or by dispersal of root fragments, e.g. released from marsh erosion. During the winter period, the aboveground biomass of the 3 species dies back and can get washed away by the waves and tides. In the next growing season, new shoots sprout from the surviving belowground biomass. *S. tabernaemontani* produces round, leafless stems up to 2.0 m and grows from thick rhizomes that form a sparse root network. *B. maritimus* grows as a triangular shoot up to 2.5 m tall and forms a dense root network of rhizomes and tubers. The hollow stems of *P. australis* can reach up to 4.0 m in brackish marshes and are supported by a densely branched network of rhizomes.

2.2. Set-up of transplantation experiment

Sites for transplantation of the 3 species were selected at 3 different intertidal elevations (corresponding to different tidal inundation times and depths), and in each elevation zone, 2 sites were established, of which one was exposed to and the other sheltered from incoming waves. The 3 elevations represent inundation depths under which at least 1 of the 3 species can be found in natural marshes. During 2 growing seasons, from March 2018 until August 2019, 3 wave barriers (24 m wide and 0.7 m high) were installed, 1 at each of the 3 selected elevations (Fig. 1), to create wave-sheltered conditions at the naturally wave-exposed site. The barriers were made from horizontally piled wooden branches that were fixed in between 2 rows of poles which were hammered vertically into the soil (Fig. 1). The orientation of the barriers was perpendicular to the dominant incoming wave direction from the SW. Edge effects were limited by extending the barrier 2 m further than the transplanted vegetation. The outer ends of the barrier were placed at a slight angle to provide an even better protection from incoming waves, in a direction that slightly deviated from the SW. Large deviation in wave direction is not expected due to wave refraction over the tidal flat,

which is expected to result in dominant southwestern wave directions more or less perpendicular to the tidal flat slope (Fig. 1). In addition to the 3 wave sheltered sites, 3 wave-exposed sites (i.e. without wave barriers) were installed at the same elevations. Although the sites were positioned near each other to ensure similar conditions, they were positioned far enough (at least 30 m) from each other to ensure that the wave barriers did not affect the plant growth at the wave-exposed treatment sites (without barriers) (Fig. 1).

Transplantation took place in April 2018 at the start of the growing season. In order to excavate a consistent amount of marsh soil for every transplant, a metal clump-extractor was used to create marsh soil transplant units with a surface area of 0.20 × 0.20 m and a depth of 0.30 m. At each of the 6 treatment sites, 20 transplants from each of the 3 species were planted equally spaced at 0.50 m from the adjacent transplant unit. The total of 60 transplant units per treatment site were transplanted in 2 spatially staggered rows parallel to the wave barrier (Fig. 1). All 360 transplant units were taken from the adjacent marsh and directly planted at the experimental sites. In December 2018, when aboveground vegetation was low, the wave barriers were washed away. The barriers were rebuilt in March 2019, before the start of the next growing season.

2.3. Growth response and species-specific plant traits

The following plant traits were quantified, which are known to affect the capacity of the plants for nature-based attenuation of waves and currents. For each transplant, shoots were counted monthly from March 2018 until August 2019. At all 6 sites, canopy height (average of the 3 highest shoots per transplant) was measured monthly for 10 randomly selected surviving transplant units per species and was used as a measure for average shoot length of the transplant. Basal shoot diameters were measured monthly at every site for 10 shoots from different transplant units per species. Spatial outgrowth was quantified as the largest horizontal distance between shoots grown from the transplanted unit and was measured at every site for 10 transplant units per species. In August 2019, at the end of the experiment, aboveground biomass was harvested from all treatments in case they survived. Upon drying at 70°C for 72 h, biomechanical properties were quantified on 20 individuals for each species per treatment. For more details

on the methods to quantify biomechanical properties, see Schoutens et al. (2021).

2.4. Hydrodynamics and sediment dynamics

Hydrodynamic conditions were measured at the different sites to make sure that the barriers created an environment sheltered from waves and currents as compared to the sites without barriers. Tides, waves and current velocities were measured with automated pressure sensors (P-Log3021-MMC, Driesen & Kern) and acoustic Doppler velocity sensors (Vector ADV, Nortek).

The pressure sensors were placed in front of the transplanted vegetation at an elevation of 0.07 m above the sediment surface and recording at 8 Hz. The pressure data were converted into water surface elevation using a Matlab routine, accounting for corrections for atmospheric pressure and depth-dependent pressure, followed by calculations of the following wave characteristics: significant wave height (H_s, mean of the highest third of recorded waves) and $H_{1/100}$ (mean of the highest 1% of recorded waves) over 10 min time intervals. For more details on this method, see Belliard et al. (2019). The water surface elevation data were also used to calculate tidal inundation characteristics such as inundation time per tide (I_{time}), mean inundation depth at high water (I_{depth}) and inundation frequency (i.e. proportion of high tides inundating the sites).

The ADV sensors measured flow velocities at 1 Hz at 0.10 m above the sediment surface. After filtering out low-quality data based on the signal to noise ratio and the beam correlations, the planar flow velocity (U, m s^{-1}) was calculated as $U = \sqrt{u^2 + v^2}$ with u and v being the mean flow velocities (m s^{-1}) in the 2 horizontal dimensions perpendicular to each other, calculated over 10 min time intervals.

Hydrodynamic exposure or the presence of a barrier can alter the sediment dynamics. Therefore, sediment bed level changes were quantified with a combination of a real-time kinematics GPS and laser leveler over the first growing period in 2018, revealing a vertical accuracy on the order of ±2 cm. At the start of the second growing season in March 2019, a triangular sedimentation erosion bar (SEB) setup was installed at every site (i.e. 6 in total) to increase the vertical accuracy of the bed level change measurements up to an order of ±2 mm (van Wijnen & Bakker 2001, Nolte et al. 2013). Monthly SEB measurements were made from March 2019 until the end of the experiment in August 2019.

2.5. Data analysis

Survival and growth response quantified through shoot counts were compared using a generalized linear model with negative binomial distribution to account for the many 'zero' counts ('glm.nb' function in the R package 'MASS', https://rdocumentation.org/packages/MASS/versions/7.3-57). Both treatments, i.e. the hydrodynamic treatments and the tidal inundation treatments, were added as independent variables. The date of sampling was added to include the effect of seasonal variation. Separate models were made for each species since comparing shoot counts between the different species would not be meaningful without normalizing against typical shoot densities observed in the natural marsh populations. The factorial design of this transplantation experiment allowed us to test the effect of inundation and wave exposure on shoot morphological properties such as shoot length, stem diameter and above-ground shoot biomass and whether the size of the effect differs among the 3 species. To make interspecific comparisons, shoot length, stem diameter and above-ground biomass were normalized for the mean value of the respective property in the adjacent natural marsh population (Table 1, data used from Schulte Ostermann et al. 2021), i.e. values >1 indicate a higher performance and values <1 indicate a lower performance of the respective variable compared to the natural population. The responses at the end of the growing season in 2019 were compared in a 3-way ANOVA including species, wave exposure and inundation stress as independent variables. Within every species, the ANOVA was followed by a post hoc comparison between the combined treatments using a Tukey HSD test. All statistical analyses were performed in R 4.0.3 (R Core Team 2020), and results were considered significant at p < 0.05 for all tests. All p-values <0.001 are reported as '<0.001', p-values <0.05 are reported as '<0.05', and p-values >0.05 are reported as 'ns' or the exact number. Assumptions were checked based on visual inspection with histograms and Q-Q plots.

3. RESULTS

3.1. Hydro- and morphodynamic conditions within the experimental treatments

Hydrodynamic forces from waves and currents were stronger at the exposed sites (Table 2; Figs. S2 & S3). Significant wave heights and mean flow velocities were higher at the exposed sites compared to the sheltered sites, and this difference increased with decreasing tidal inundation depths (i.e. up to a maximum of 16% higher significant wave heights and 21% higher flow velocity). The deepest inundated sites had an inundation time which was approximately 1.5 h longer and a Mean High Water depth that was around 0.40 m deeper than the shallowest inundated sites (Table 2). Inundation frequency was >98% for all sites, meaning that they were inundated during nearly every high tide. Over the entire period of the experiment, all sites experienced both periods of erosion and accretion (Table 2; Fig. S4). Erosion mainly occurred during the winter period when waves were largest, and accretion in spring and summer when waves were smaller. During the winter period from December 2018 to March 2019, the wave barriers were damaged during storms, and this was associated with erosion up to 15 cm observed on several of the sheltered and exposed sites (Fig. S4).

3.2. Effects of hydrodynamic exposure and inundation on shoot numbers

Transplantation to deeper and longer-inundated sites, i.e. with higher inundation time (>405 min) and depth (>1.29 m) (Table 1), reduced the number of shoots per transplant in all 3 species (Fig. 2, p < 0.001). Interestingly, there was a big difference in shoot numbers between the 2 growing seasons (Fig. 2). During the second growing season, at the shallow inundation sites, the *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* plants produced

Table 1. General description of the growth conditions where the 3 transplanted species grow naturally in the adjacent tidal marshes of Hollerwettern, Germany. Elevations relative to the tidal range and distance to the marsh edge (±SD) indicate that the sampling of all 3 natural populations occurred on locations which were sheltered from incoming waves and currents. Data on shoot length, stem diameter and above-ground biomass measured on these populations were published by Schulte Ostermann et al. (2021) and were used here to normalize the data measured from the transplants

	Elevation	Distance to marsh (m)
Schoenoplectus tabernaemontani	0.70 ± 0.13	5.7 ± 3.0
Bolboschoenus maritimus	0.88 ± 0.11	38.1 ± 15.1
Phragmites australis	1.08 ± 0.05	86.6 ± 35.2

Table 2. Summary of the main hydrodynamic properties per treatment combination over the entire monitoring campaign; mean of the significant wave heights ($H_s \pm$ SD), mean maximum wave height ($H_{1/100} \pm$ SD), single maximum wave height (H_{max}), mean planar flow velocity ($U \pm$ SD), mean inundation depth at high water (I_{depth}), mean inundation time per tide (I_{time}), elevation relative to Mean High Water (E_{MHW}) and elevation variation (E_{var}), calculated as the maximum elevation − minimum elevation over the time period

Inundation	Wave	H_s (m)	$H_{1/100}$ (m)	H_{max} (m)	U (m s^{-1})	I_{depth} (m)	I_{time} (min)	E_{MHW} (m)	E_{var} (cm)
Shallow	Exposed	0.088 ± 0.06	0.11 ± 0.08	0.71	0.06 ± 0.05	1.15	379	−1.17	13.6
	Sheltered	0.085 ± 0.05	0.10 ± 0.07	0.7	0.06 ± 0.04	1.13	373	−1.18	14.0
Inter-	Exposed	0.084 ± 0.06	0.11 ± 0.08	0.68	–	1.38	425	−1.35	7.6
mediate	Sheltered	0.071 ± 0.05	0.09 ± 0.07	0.5	–	1.29	405	−1.39	17.4
Deep	Exposed	0.085 ± 0.06	0.11 ± 0.08	0.89	0.19 ± 0.09	1.58	462	−1.62	5.9
	Sheltered	0.078 ± 0.06	0.10 ± 0.08	0.78	0.15 ± 0.08	1.52	451	−1.63	14.8

more shoots, while *Phragmites australis* formed a similar amount of shoots compared to the first season. In the deep inundation treatments, the seasonal difference diminished as shoot numbers of all species were strongly reduced. The number of shoots was highest in *S. tabernaemontani*, followed by *B. maritimus*. In the second growing season, *S. tabernaemontani* grew less than 50 shoots per transplant

when inundated more than 1.29 m and more than 405 min per tide, i.e. deep inundation treatment, while the other species hardly grew any shoots starting from an intermediate inundation stress. Already in the first growing season, *P. australis* transplants died off at the intermediately and deeply inundated sites. Hydrodynamic exposure decreased the number of shoots in *B. maritimus* and *S. tabernaemontani*
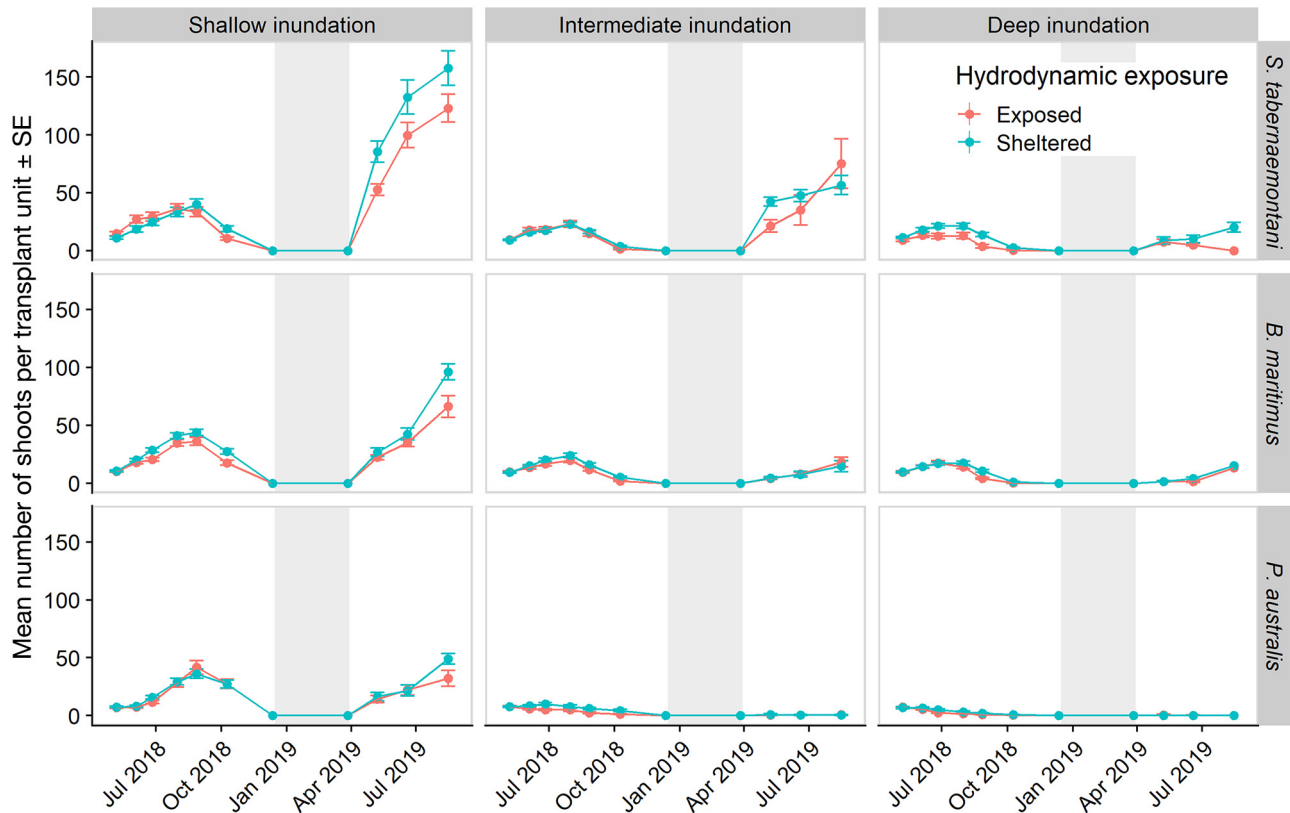

Fig. 2. Number of shoots of *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis* per transplant unit for both hydrodynamic exposure treatments and 3 inundation treatments. The shoots were counted over 2 growing seasons (2018–2019). Grey boxes indicate the winter season when aboveground biomass died off and was flushed away by the tides

(p < 0.05). The low number of shoots for *P. australis* did not allow the detection of significant differences between the exposed and sheltered sites. The different responses of shoot numbers to hydrodynamic exposure was only visible when the stress from tidal inundation was low enough.

3.3. Effects of hydrodynamic exposure and inundation on shoot diameter, shoot length and biomechanical properties

In the natural marsh of Hollerwettern, where plant material was collected for the transplantation experiment, plant morphological measurements of the natural population showed a clear species-specific difference in plant traits (Fig. 3).

Both the inundation stress and the hydrodynamic exposure had a negative effect on basal shoot diameter and shoot length (Figs. 4 & 5), but the response to these stressors was species-specific (Table 3). *S. tabernaemontani* was able to cope better with the combined stressors from tidal inundation and hydrodynamic exposure, followed by *B. maritimus* and *P. australis*, which had a strongly reduced growth compared to the natural population. In *S. tabernaemontani* transplants, increased inundation stress and increased hydrodynamic exposure resulted in thinner basal stem diameters and shorter shoots. Except for the exposed, deep inundation treatment, *S. tabernaemontani* transplants grew shoots that were consistently thicker and longer compared to the natural population. *B. maritimus* grew thinner and shorter shoots with increasing inundation stress; however, no significant differences between the hydrodynamic exposure treatments were found. Under shal-

low inundation, shoots of *B. maritimus* were up to twice as thick and 1.3 times longer compared to the natural population. In the 2 deeper inundation treatments, the basal shoot diameters of *B. maritimus* were more comparable to the natural population, whereas the shoot lengths were shorter compared to the natural population. In *P. australis*, no differences in treatment response were observed, and compared to the natural population, the basal stem diameter of the remaining shoots was halved and the shoot lengths were less than half of the normal length.

Biomechanical properties such as Young's modulus and flexural stiffness were not affected by the inundation treatment nor the hydrodynamic exposure treatment, except for *S. tabernaemontani* shoots in the shallow inundation sites, which were stiffer on the sheltered sites as compared to the exposed shoots (ANOVA, $F_{1,77} = 15.3$; p < 0.001). More details are given in Table S2.

3.4. Effects of hydrodynamic exposure and inundation on lateral expansion and overall biomass

The 3 species in this transplantation experiment reproduce primarily by clonal outgrowth, which is important for the long-term survival of the species. Outgrowth of the transplants in the second growing season was reduced with increasing stress from inundation, while no significant response to hydrodynamic exposure was observed. Outgrowth of the transplants in the second growing season did show a species-specific response and was highest in *S. tabernaemontani*, which expanded in multiple directions forming a star-like pattern of shoots (Fig. 6). The transplants of *B. maritimus* also expanded, albeit
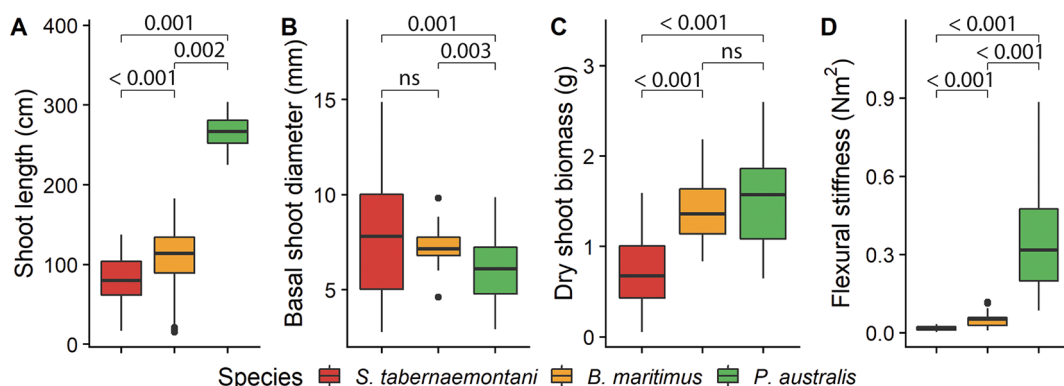

Fig. 3. Plant morphological traits in the adjacent natural marsh (Hollerwettern) for *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis*. Shoot length (m), basal shoot diameter (mm), dry shoot biomass (g) and shoot flexural stiffness (Nm²) were quantified at peak biomass (data from Schulte Ostermann et al. 2021). Differences between the species are indicated with significance levels obtained with ANOVA. Boxplots show the median, interquartile range, minimum and maximum whiskers, and outliers
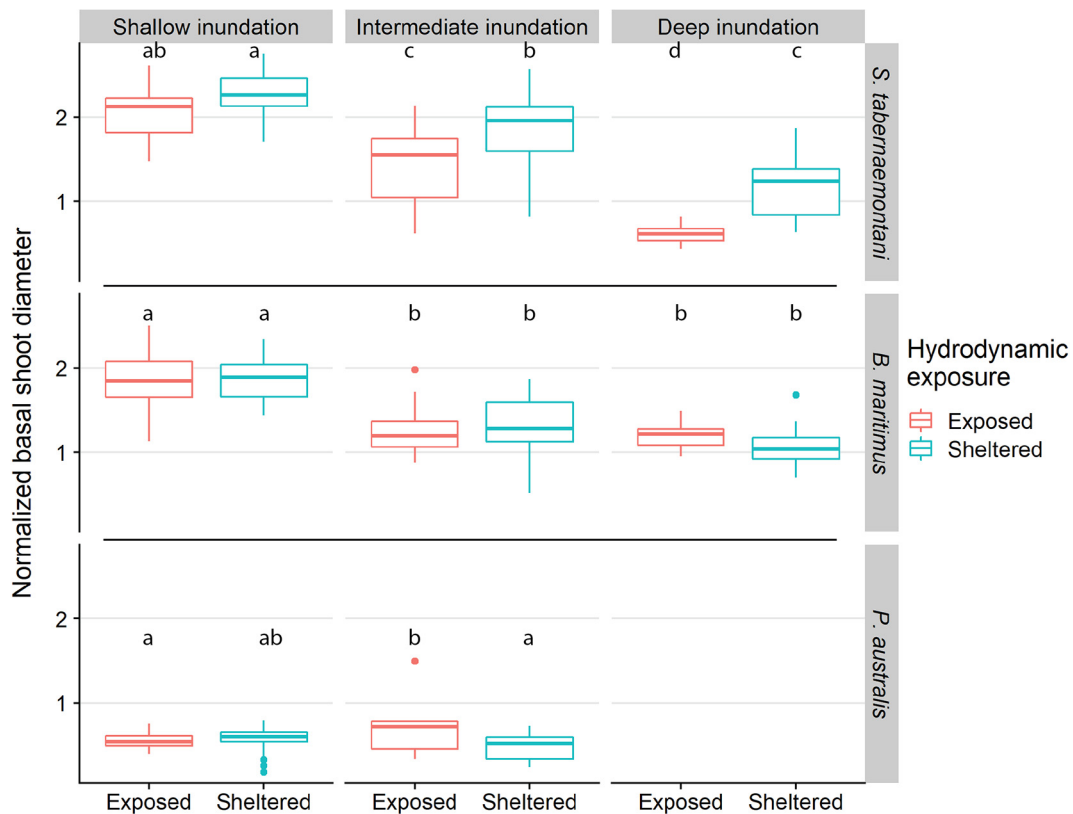
Fig. 4. Shoot basal diameter of *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis* normalized by shoot diameters in the natural marsh (see Fig. 3) at peak biomass for the 2 hydrodynamic exposure treatments and the 3 inundation treatments. Differences between the combined treatments were tested with ANOVA for every species and followed by a post hoc Tukey's HSD test; significant differences are indicated by different letters. Box plot parameters as in Fig. 3

to a lesser extent compared to *S. tabernaemontani*. *P. australis* hardly expanded, and the few surviving transplants had the same diameter as when the experiment started (Fig. 6).

Although there seems to be a trend of decreasing shoot biomass with increasing inundation stress (Table 3), this trend was not consistent for all species with remaining shoots (Fig. 7). Nevertheless, biomass die-off in the deep inundation treatment for *B. maritimus* and in both the intermediate and deep inundation treatment for *P. australis* did show a negative effect on the survival and hence shoot biomass production as a result of increased inundation stress. Hydrodynamic exposure had a similar negative effect on the shoot biomass, but this was not significant for *S. tabernaemontani* and only significant in the intermediate inundation treatment for *B. maritimus* shoots. The remaining *P. australis* biomass in the shallow inundation treatments did not differ either. Shoot biomass of the transplants was lower in all treatments compared to the natural population, except for the shallow inundation and sheltered,

intermediate inundation treatments of *S. tabernaemontani* and *B. maritimus*, which had a similar biomass compared to the natural population. Only the sheltered, shallow inundated transplants of *S. tabernaemontani* grew a higher (by 1.5×) shoot biomass.

4. DISCUSSION

Our findings highlight that plants with a higher capacity to grow under hydrodynamic forces have inter- and intraspecific traits that are known to reduce mechanical stress from waves and currents. Species-specific growth responses to wave and current exposure is likely to contribute to spatial species zonation. Previous studies on nature-based shoreline protection by tidal marsh plants have identified species traits that increase their effectiveness to attenuate waves and currents (Bouma et al. 2005, 2010, Vuik et al. 2016, Schulze et al. 2019, Schoutens et al. 2020). In contrast, relatively little is known about how species traits affect the capacity of species to
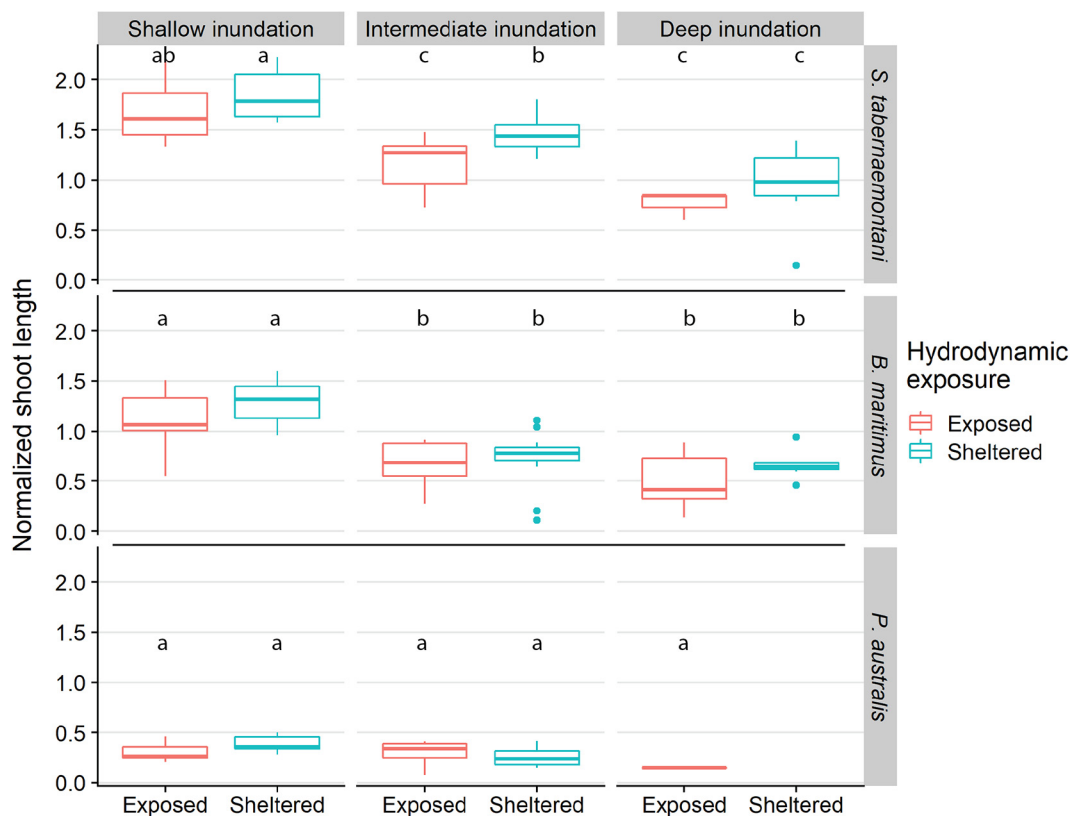
Fig. 5. Shoot lengths of *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis* normalized by shoot lengths in the natural marsh (see Fig. 3); details as in Fig. 4

survive and grow under the influence of different levels of exposure to waves and currents. Yet, such knowledge on species-dependent growth responses to wave and current exposure is crucial to manage and restore marshes for nature-based shoreline protection. Here, we showed in a 2 yr field transplantation experiment, that in addition to tidal inundation, exposure to waves and currents also decreases the growth of 3 tidal marsh species, with the magnitude of growth reduction being species specific.

Table 3. ANOVA table for the linear model made for normalized shoot diameters, normalized shoot lengths and normalized stem biomass at peak biomass in August 2019. Both the hydrodynamic exposure treatment (exposed or sheltered) and the inundation treatment (shallow, intermediate or deep) were tested across the 3 species (*Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis*). Significant variables (p < 0.05) are indicated in **bold**

Variable	df	Diameter		Length		Shoot biomass	
		F	p	*F*	p	*F*	p
Wave	1	26.6	**<0.001**	19.6	**<0.001**	22.0	**<0.001**
Inundation	2	134.8	**<0.001**	129.5	**<0.001**	13.9	**<0.001**
Species	2	553.5	**<0.001**	537.2	**<0.001**	71.1	**<0.001**
Wave × inundation	2	1.8	0.2	0.4	0.7	4.5	**<0.05**
Wave × species	2	8.8	**<0.001**	1.8	0.2	4.6	**<0.05**
Inundation × species	3	8.8	**<0.001**	9.0	**<0.001**	4.3	**<0.05**
Wave × inundation × species	1	0.4	0.5	0.004	0.9	1.7	0.2

4.1. Species-specific response to tidal inundation and hydrodynamic forces

Tidal inundation had a negative effect on the shoot numbers, but with a species-specific magnitude (Fig. 2). Apart from limited light availability during inundation, water submergence creates anaerobic conditions which can suppress the growth of vegetation, e.g. by anaerobic formation of phytotoxic compounds surrounding the roots (Hellings et al. 1992, Coops et al. 1996, Engloner 2009). Many tidal marsh species developed morphological adaptations
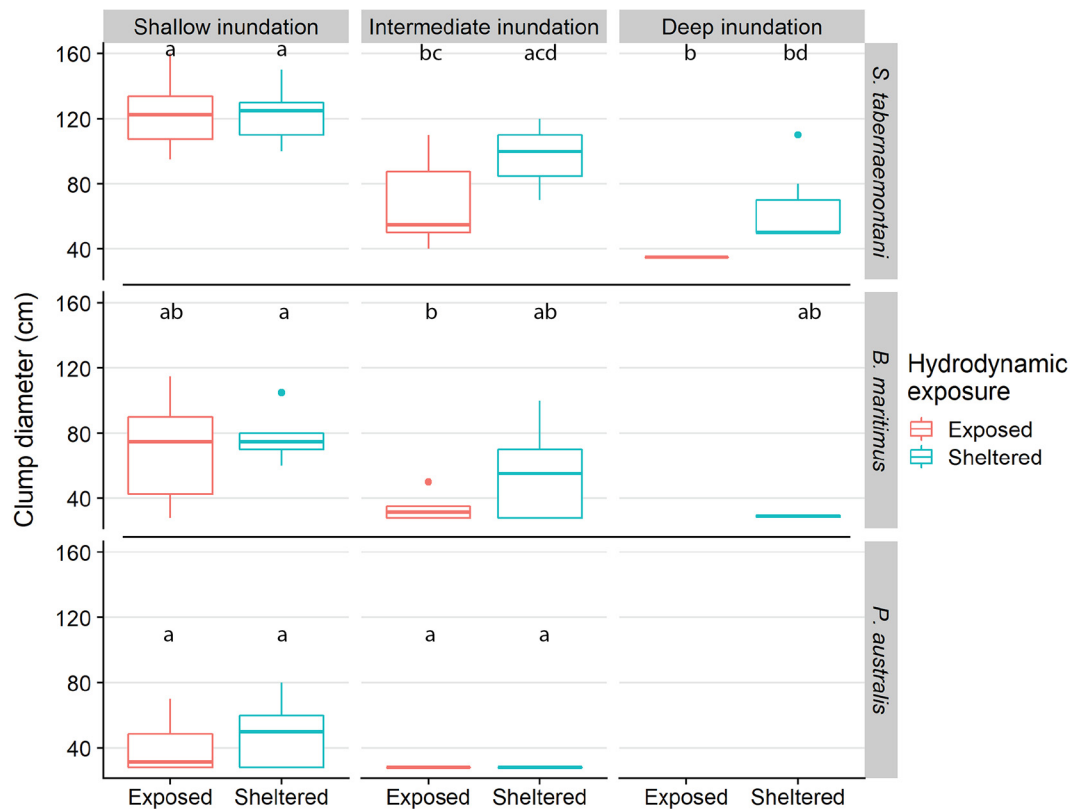
Fig. 6. Outgrowth of the transplants of *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis* in the second growing season, expressed as clump diameter (i.e. biggest diameter of the transplant); details as in Fig. 4

to these anaerobic conditions of which oxygen supply to their root system is most common, i.e. species grow aerenchyma tissue that allows oxygen transport from aerated organs such as leaves towards the root system (Armstrong et al. 2006, Lemoine et al. 2012). The thicker stems of *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* provided structural rigidity in this study, which might result from more aerenchyma tissue in response to oxygen deprivation (Albert et al. 2013). In contrast, more aerenchyma and thicker stems are also linked to a softer and thinner epidermic layer, i.e. less amount of strength molecules (e.g. cellulose, lignin) and less structural rigidity, which increases the stem flexibility (Shah et al. 2017, Silinski et al. 2018). Growing shoots that stay emerged during flooding facilitates and ensures the oxygen supply to the roots (Maricle & Lee 2002) and hence allows the plants to cope with increased tidal inundation (Colmer & Flowers 2008). However, this strategy can only work when shoots do not break due to hydrodynamic forces.

In addition to the tidal inundation treatments, plant growth and development were hampered in the wave- and current-exposed sites for *B. maritimus*

and especially for *S. tabernaemontani*, compared to the sheltered sites, but the plants were still able to survive (Figs. 4, 5, 7). This result suggests that both species were, to some extent, able to grow under the increased mechanical stress from waves and currents, which is most likely a result of species-specific plant morphological traits (Fig. 3). Plant traits such as small, flexible shoots found in the natural population of *S. tabernaemontani* and to a lesser extent *B. maritimus* reduce drag, hence increasing the capacity to cope with waves and currents (Bouma et al. 2005, Puijalon et al. 2011, Paul et al. 2016, Schoutens et al. 2020, Schulte Ostermann et al. 2021). These are plant morphological traits that are often found in species growing under mechanical stress (Anten et al. 2005, Anten & Sterck 2012). For some wetland species, shoot elongation in response to inundation stress was described as part of a so-called escape strategy, i.e. the shoots grow to stay emerged from the water (Garssen et al. 2015). This suggests that inundation stress and mechanical stress from hydrodynamic forces might have contrasting effects on plant growth.

For *Phragmites australis*, the observed response to tidal inundation stress might be enhanced by an indi-
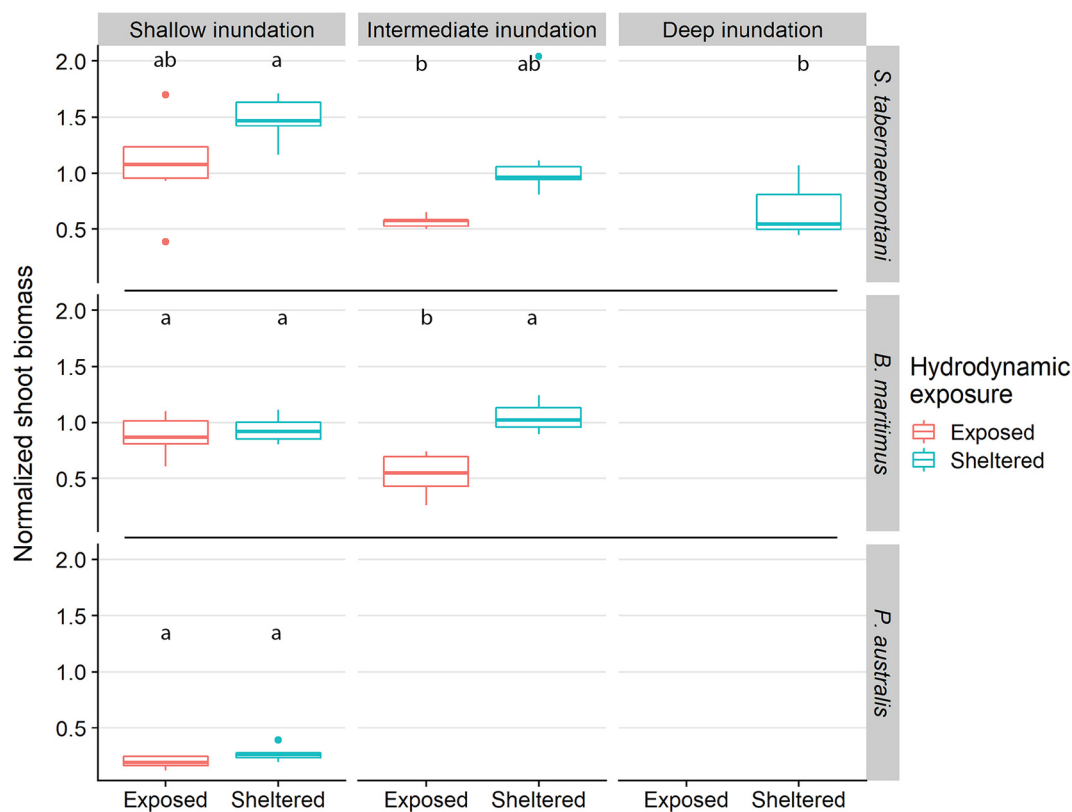
Fig. 7. Dry shoot biomass of *Schoenoplectus tabernaemontani*, *Bolboschoenus maritimus* and *Phragmites australis* harvested in August 2019, normalized by shoot biomass in the natural marsh at peak biomass (see Fig. 3); details as in Fig. 4

rect response to damage from hydrodynamic exposure. *P. australis* grows relatively stiff stems in natural populations (see Fig. 3 and Coops & Van der Velde, Schoutens et al. 2020, Zhu et al. 2020b, Zhang & Nepf 2021), but shoots with a higher stiffness are more susceptible to stem breakage (Shah et al. 2017, Zhu et al. 2020b). Immediately from the first growing season after transplantation, *P. australis* produced few shoots, which could suggest a mechanical growth restriction by breakage of young stiff shoots. *P. australis* is prone to drowning when shoots are cut during the growing season as a result of an impaired oxygen supply to the roots and the loss of photosynthetic activity (Hellings et al. 1992, Rolletschek et al. 2000, Asaeda et al. 2003). For the shoots that did survive, growth was hampered, e.g. by mechanical stress. Hence, the amount of photosynthetically active leaf surface is reduced, which might increase the susceptibility to other stressors, such as oxygen deprivation by tidal inundation stress.

Apart from direct stress responses induced by the experimental treatments in this study, the observed stress responses of the species could be the result of a species-specific capacity to cope with the stress

from the transplantation itself, e.g. change in local sediment properties or damage to the roots. Transplantation success of marsh plants is typically optimized by providing enough belowground biomass of nearby populations from species that have a high capacity to expand clonally (Thomsen et al. 2005, Ott et al. 2019, Popoff et al. 2021). Although no control transplantation was performed, we know from literature on previous transplantation treatments that the 3 species in this study are well able to handle the disturbance of a transplantation (Coops & Van der Velde 1996, Amsberry et al. 2000, Silinski et al. 2016a, Taylor et al. 2019).

Indirect effects of the applied treatments might also play an important role in the growth response. For example, the hydrodynamically driven grain-size distribution (Table S1) results in coarser sediments in places with increased hydrodynamic exposure, more inundation alters the redox potential of the soil, and sheltered conditions might increase sediment accretion and potential burial of young shoots. Although sediment dynamics in this experiment were mostly limited outside the period of the growing season, we acknowledge that sediment dynamics and sediment

characteristics can alter the growth of the root network, which is important for the long-term survival of the marsh plants (Bradley & Morris 1990, Chen et al. 2012, Jafari et al. 2019). Moreover, both direct and indirect effects of synergetic stressors should be considered (Veldhuis et al. 2019). For example, the presence of grazers will reduce aboveground biomass and wave attenuation capacity, but it promotes belowground biomass production which could increase the stability of the sediment bed (Pagès et al. 2019). Although changes in belowground biomass were not measured in our experiment, the inclusion of belowground biomass dynamics should be considered in future research.

4.2. Phenotypic plasticity in response to tidal inundation and hydrodynamic forces

Apart from plant trait differences between species, a similar trend of intraspecific varying plant traits was also found in response to the different inundation and hydrodynamic exposure treatments. Within the species that was able to survive and grow under all tested conditions (i.e. *S. tabernaemontani*), the transplants developed smaller, thinner and more flexible shoots in response to higher exposure to waves and currents and increasing tidal inundation, which was similar to the response in interspecific variation in plant traits. Interestingly, when comparing morphological traits in the transplantation experiment with the natural population, *S. tabernaemontani* grew thicker and taller shoots on the sites with shallow and intermediate inundation (Figs. 4 & 5), which resulted in a stronger stem geometry (i.e. high moment of area, see Table S2) and stiffer shoots. This suggests that in these treatments, stress from hydrodynamic exposure and tidal inundation were relatively low for *S. tabernaemontani*. Since all transplant units were spaced evenly apart from each other to limit potential competition between them, this enhanced growth capacity compared to the natural population might result from better resource availability and less competition between shoots in the transplants (Shen et al. 2020). Phenotypic plasticity as a growth response to waves or currents has been previously reported for *B. maritimus*, as it grows shorter and more flexible shoots with thicker stem diameters in response to increasing exposure to waves and currents (Carus et al. 2016, Silinski et al. 2018). Interestingly, this response can vary depending on the species and habitat-specific conditions, e.g. for *Juncus roemerianus* and *Spartina alterni-*

flora, thinner stem diameters in response to wave exposure were reported (Temple et al. 2021).

Variation of plant traits in response to environmental stress creates variation in the functional role of the plants and their bio-physical interactions within the environment (Heuner et al. 2015, Renzi et al. 2019, De Battisti 2021). The intra- and interspecific variations of plant traits generate different ecosystem engineering capacities, e.g. plant traits that generate more friction with the water have a stronger wave-attenuation effect which will promote sedimentation and limit erosion risk (Silinski et al. 2018, Schoutens et al. 2020). In this context, plant traits are linked to species habitat, i.e. seagrasses benefit from being flexible, limiting their capacity to accrete sediments, but maintaining the submerged conditions (Bouma et al. 2005). Variability in plant traits will therefore generate spatial variability in bio-physical interactions, which is important for the geomorphology of the marsh, e.g. sedimentation–erosion processes (Bouma et al. 2009, Corenblit et al. 2015). The balance between the strength of the bio-physical interactions, generated through the plant traits, and the environmental stressors will therefore create large-scale geomorphological patterns such as cliffs and channels (van de Koppel et al. 2005, Brückner et al. 2019).

Interestingly, the adaptive nature of tidal marsh plants and their plant trait-based variation in functionality can improve the resilience of the ecosystem to a range of environmental settings (De Battisti 2021).

4.3. Consequences for species spatial distribution in pioneer tidal marshes

The spatial distribution of species within tidal marshes is traditionally thought as being predominantly the result of the balance between competition and tolerance to environmental stress factors, typically tidal inundation and salinity (Pennings & Callaway 1992, Wang et al. 2010, Janousek & Mayo 2013, Rasser et al. 2013). Our study indicates that species-specific tolerance to waves and currents can play an additional role in the spatial distribution of pioneer tidal marsh plants. The high capacity of *S. tabernaemontani* to grow under hydrodynamic forces allows this species to colonize areas where other species might not be able to grow. The establishment of *S. tabernaemontani* leads to attenuation of waves and currents within and behind patches of *S. tabernaemontani* (Schoutens et al. 2020) and as such is expected to create more sheltered conditions that may facilitate the establishment of other species, less

tolerant to waves and currents, such as *B. maritimus.* Subsequently, the presence of those 2 species zones can create even more wave and current attenuation and hence create the environmental conditions that allow the establishment of species such as *P. australis.* Wave-induced species distribution in pioneer tidal marshes has been suggested in other studies (Heuner et al. 2019, Schoutens et al. 2020, Zhu et al. 2020b). Although the growth response to waves and currents was less clear for *B. maritimus* and *P. australis,* tidal inundation is likely to be the dominant stressor which diminishes the potential effects of wave exposure on survival or growth. To make the growth response to hydrodynamic exposure more apparent, future research should consider increasing the elevation range towards higher sites, reducing the tidal inundation stress and/or increasing the differences between the hydrodynamic exposure treatments.

4.4. Species-specific survival chances determine the shoreline protection capacity of tidal marshes

Nature-based shoreline protection capacity of tidal marshes depends on (1) the wave and current attenuation capacity of marsh plants and (2) their ability to cope with the exposure to waves and currents. Our results emphasize an apparent trade-off between these 2 aspects, i.e. that species growing at the wave-exposed marsh edge have plant traits (smaller, more flexible shoots) that reduce the drag forces on their shoots, but the same plant traits reduce their wave-attenuation capacity, which has been hypothesized before (Schoutens et al. 2020). Studies on wave and current attenuation use plant traits of natural populations or plants that were grown under ideal conditions (Suzuki et al. 2012, Möller et al. 2014, Vuik et al. 2016, Garzon et al. 2019, Willemsen et al. 2020). The effectiveness of attenuating hydrodynamics is then described based on the plant traits of idealized species. However, when considering tidal marsh restoration and (re-)establishment, the new environmental conditions (e.g. in case of strong hydrodynamic exposure and high tidal inundation stress) might alter the growth and plant traits of some species, which also changes the expected wave- and current attenuation capacity of the newly formed marsh. Nevertheless, we argue here that the traits that allow plants to grow in more exposed sites create more sheltered conditions in the landward direction and there facilitate the growth of species that otherwise would not have been able to cope with the stronger hydrodynamic forces. Such facilitation implies that tidal

marshes might be able to survive more exposed conditions than previously thought. Nevertheless, growth facilitation between different marsh species zones will only work when there is enough space for the marsh to develop different vegetation zones. At many shorelines all over the world, land use change has reduced the spatial extent of tidal marshes drastically (Duarte 2009, Davidson 2014, Crosby et al. 2016, Spencer et al. 2016). Moreover, sea level rise and increased hydrodynamics (e.g. shipping) will enhance the so-called 'coastal squeeze', increasing hydrodynamic exposure of tidal marshes (Torio & Chmura 2013, Borchert et al. 2018, Valiela et al. 2018). This trend will make the existing space for interspecific growth facilitation and tidal marsh development even smaller. However, we argue that providing enough space for tidal marsh development and species facilitation is important to ensure shoreline protection throughout changes in the hydrodynamic conditions which as a result may improve marsh resilience to environmental change (Renzi et al. 2019).

Our findings have practical implications for restoration and conservation of natural shorelines, a measure that is often applied to improve the ecosystem service functions of tidal marshes, such as biodiversity conservation, water quality improvement, carbon sequestration and coastal defense (Barbier et al. 2011). Firstly we argue that, when space allows, interspecific facilitation of plant growth and survival results in a species distribution which increases the effectiveness of the hydrodynamic attenuation function of the marsh. Secondly, the presented results can help to identify sites that are suitable for tidal marsh restoration in terms of suitable site exposure to waves and currents and tidal inundation. This type of data is also highly useful for improving models that predict species occurrence and that can be used in restoration projects (Gourgue et al. 2020). More specifically, species-specific growth rates under a range of hydrodynamic conditions could be used to calibrate and validate such models (van de Koppel et al. 2005, Mariotti & Fagherazzi 2010, Hu et al. 2015, Carus et al. 2017). Rather than e.g. planting seedlings, creating enough space for a suitable environment where species with the right plant traits can grow might be even more important for long-term survival of tidal marshes and therefore their shoreline protection capacity.

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