Climate change in salt marshes

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Effects of hydrodynamic forcing, sea level rise and higher temperatures on coastal vegetation

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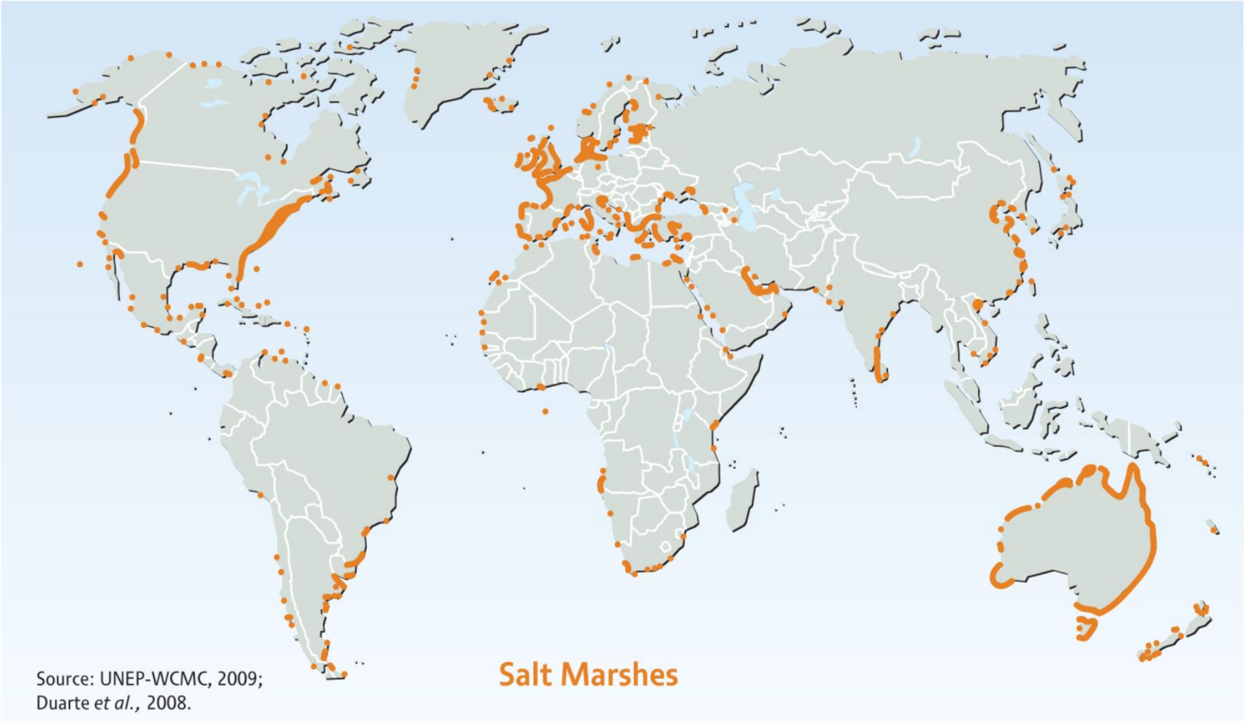
Contents

1 General introduction

Salt marshes

Salt marshes are intertidal wetland ecosystems that can be found between the marine and terrestrial environment. They form in wave-sheltered areas with high sedimentation rates such as estuaries, coastal plains, lagoons und landward sides of barrier islands (Mitsch et al. 2009; Scott et al. 2014). Salt marshes occupy approx. 45,000 km^2 of the total global land area (Greenberg et al. 2006), of which 2,300 km^2 are situated in Europe (Dijkema 1997, Fig. 1).



Source: UNEP-WCMC, 2009;
Duarte *et al.*, 2008.

Figure 1 Global distribution of salt marshes from Nellemann (2009).

Vegetation and zonation

The vegetation of salt marshes is largely dominated by grasses, herbs and shrubs that are adapted to regular flooding and high salinities. The vertical distribution of individual salt-marsh species is usually restricted to certain hydrological conditions, i.e. inundation frequency and duration with seawater, which is often coupled with marsh elevation relative to mean high tide (Bockelmann et al. 2002). Three vegetation zones are most commonly used to refer to local abiotic conditions and species composition in NW European salt marshes: the pioneer zone, low marsh and high marsh. The pioneer zone is situated next to the unvegetated mudflat starting at an elevation of approx. 40 cm below mean high tide (Essink et al. 2005). The pioneer zone is flooded daily and its typical vegetation consists of *Salicoria europea* and *Spartina anglica*. The higher elevated low marsh is flooded during springtides, which is estimated to happen 100 – 400 times per year (Essink et al. 2005). In comparison with the pioneer zone and high marsh, the species composition of the low marsh is more diverse, including species such as *Puccinellia maritima*, *Halimione portulacoides Limonium vulgare*, *Artemisia maritima* or *Aster tripolium* (Esselink et al. 2000; Suchrow and Jensen 2010). The high marsh is flooded only during storm surges in autumn and winter and its vegetation is often dominated by *Elymus athericus*, or *Festuca rubra* (Andresen et al. 1990; Wanner et al. 2014; Suchrow and Jensen 2010). For most marshes, the vegetation zonation reflects natural temporal dynamics in vegetation cover, also known as vegetation succession (Leeuw et al. 1993). At the beginning of marsh development, pioneer species colonise muddy sediments where they increase sediment settlement eventually leading to an increase in marsh surface elevation. The elevated marsh surface provide conditions under which low marsh species can establish. With further sedimentation, low marsh species are replaced by high marsh species forming the late-successional stage of the marsh. In addition to a vertical elevation gradient, tidal marshes that develop in estuaries are characterised by a horizontal salinity gradient with decreasing salinity from the mouth to the source of a river leading to a division into salt, brackish and freshwater marshes (Engels et al. 2011).

Salt marshes are not alone shaped by natural processes but also by human intervention. In northern Europe, for example in the Wadden Sea region, humans have modified large salt-marsh areas for centuries (Adam 2002). They created artificial drainage systems and sedimentation fields to promote vertical accretion and thereby the formation of marshes which were then used for grazing or for agricultural purposes (Esselink et al. 2000). In addition, due to the construction of dikes, large areas of former salt marshes have been disconnected from tidal flooding reducing the overall area of salt marshes by e.g. more than 80 % along the Dutch Wadden Sea coast during the last 800 years. However, since the 1980ies nature conservation interest increased and led to a transformation of many areas into nature reserves or national parks where management and human impacts were reduced (Bakker et al. 2003).

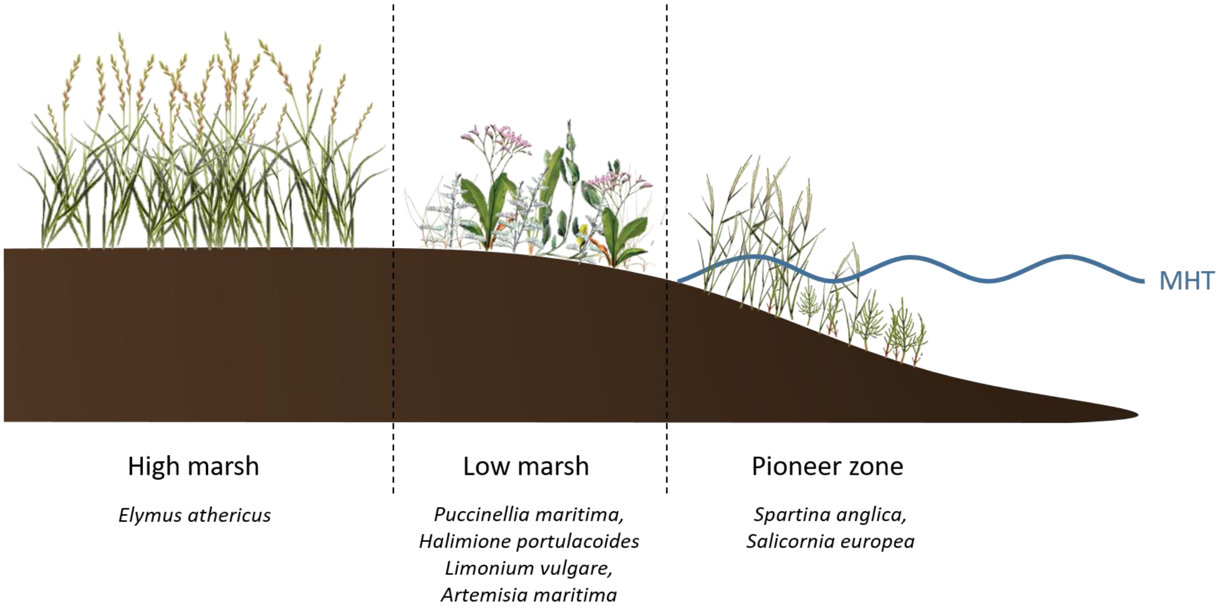


Figure 2 Typical vegetation zonation of NW European salt marshes including commom salt-marsh species; modified after Nationalparkverwaltung Schleswig-Holsteinisches Wattenmeer (2017).

Ecosystem services

Salt marshes are increasingly recognised as valuable ecosystems because they provide many benefits relevant for the human society, the so-called ecosystem services. Salt marshes supply nursery grounds for commercially relevant fish species (Bolle et al. 2009) as well as areas for breeding, feeding or staging for many bird species (Zedler and Kercher 2005). More recently, it has been shown that salt marshes contribute to climate change mitigation through their ability to sequester carbon over long time scales (Mcleod et al. 2011). This is mainly due to the capture of allochthonous carbon from adjacent marine ecosystems as well as a high net primary productivity while microbial decomposition of soil organic matter is reduced (Reddy and DeLaune 2008). Another important ecosystem service of salt marshes is the coastal protection function hampering coastal flooding and shoreline retreat. Storms and waves can have highly destructive impacts on coastal areas. At the same time, these areas are more densely populated by humans than at the global average (Small and Nicholls 2003). To guarantee the protection of coastal communities also in the future, it is necessary to better understand underlying processes of coastal protection (e.g. wave attenuation and marsh resilience). Generally, above- and belowground parts of the vegetation contribute differently to coastal protection. Aboveground parts act as obstruction and thereby reduce current velocity, wave action and flow turbulence (Yang 1998), while belowground parts prevent erosion by stabilising the substrate (Spencer et al. 2016a; Battisti et al. 2019).

Wave attenuation in salt marshes is a substantial part of coastal protection and is usually assessed by studying the reduction of incident wave height while waves are traveling across the marsh surface. In these studies, wave heights are often expressed as significant wave heights, which are defined as mean of the highest third of recorded wave heights. Wave measurements in salt marshes of Essex, England, showed that over a 310 m long transect 92 % of the incident significant wave height was reduced (Möller and Spencer 2002). In the same study, they observed that more than 40 % of the wave energy was dissipated in the first 10 m of the salt marsh. To isolate the vegetation effect on wave attenuation from locally varying environmental effects (e.g. slope) and to test whether salt-marsh vegetation provides effective wave attenuation even under extreme wave events, Möller et al. (2014) conducted a true-to-scale flume experiment. They created hydrodynamic conditions typical for storm surges in NW European salt marshes and showed that the vegetation was able to reduce significant wave height by between 15 and 60 % over a 40 m distance. However, it needs to be considered that the wave attenuation capacity of individual ecosystems vary in a non-linear way. Beside the effects of local geomorphology and hydrodynamic conditions of the system, the variation in wave attenuation often originates from species-specific differences in plant properties (Koch et al. 2009). Aboveground biomass (Bouma et al. 2010), stem density (Bouma et al. 2005) and stem flexibility (Paul et al. 2016) are among these properties since they add friction and thereby reduce wave energy. Whether tidal marshes will contribute to coastal protection also in the future does not only rely on plant properties or hydrodynamic conditions directly affecting wave attenuation but also on the persistence of these ecosystems.

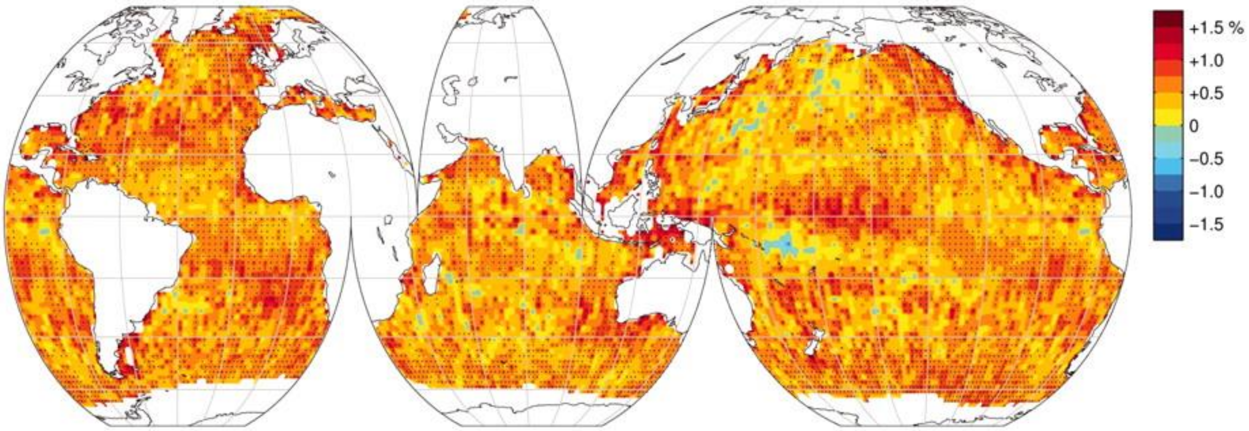
Threats

The persistence of salt marshes is today threatened by anthropogenic pressures like land-use, eutrophication and climate change. These stressors lead to a salt-marsh loss of 1-2% of the global area per year (Duarte et al. 2013). For salt marshes, major climate change related threats are an intensification of storms (hence hydrodynamic conditions), accelerated sea level rise and increasing temperatures. Recent developments and projections concerning these climate change factors as well as expected impacts on the vegetation of salt marshes will be discussed in the following paragraphs.

Increased storminess

When evaluating how future wind climates will affect the vegetation of salt marshes and thereby their coastal protection function, it is important to incorporate trends that have been observed over the past years. A global analysis of satellite altimeter data ranging from 1985-2008 did not detect any changes in mean wind speed or significant wave height but showed an increase in extreme events (99th percentile) of both parameters (Young et al. 2011, Fig. 3). Moreover, extreme significant wave heights progressively increased with higher latitudes (> ±35°). Similarly, upward trends in frequency of storm days and magnitude of extreme wind speeds have been demonstrated for Europe, where highest values were observed for North-Western Europe and the North Sea region (Donat et al. 2011). Since the causes of the trends have not been investigated in these studies, caution needs to be exercised when relating these trends to changes in climate (e.g. global warming). Projections of future wind and wave climate are dominated by large variations and uncertainties. This is mainly due to ‘the small number of studies, the lack of consistency of the wind projections between models, and limitations in the models' ability to simulate extreme winds' (Seneviratne et al. 2012). However, there is more scientific consensus regarding projections of other climate change factors such as accelerated sea level rise or global warming, which also include potential impacts on the wind and wave conditions. For example, researchers of the Intergovernmental Panel on Climate Change (IPCC) reported that an increase in ocean temperatures already caused an intensification of storms and that sea level rise will amplify the impact of storms and wave action (Masson-Delmotte et al. 2018).

99th percentile wind speed (1991-2008)



99th percentile significant wave height (1985-2008)

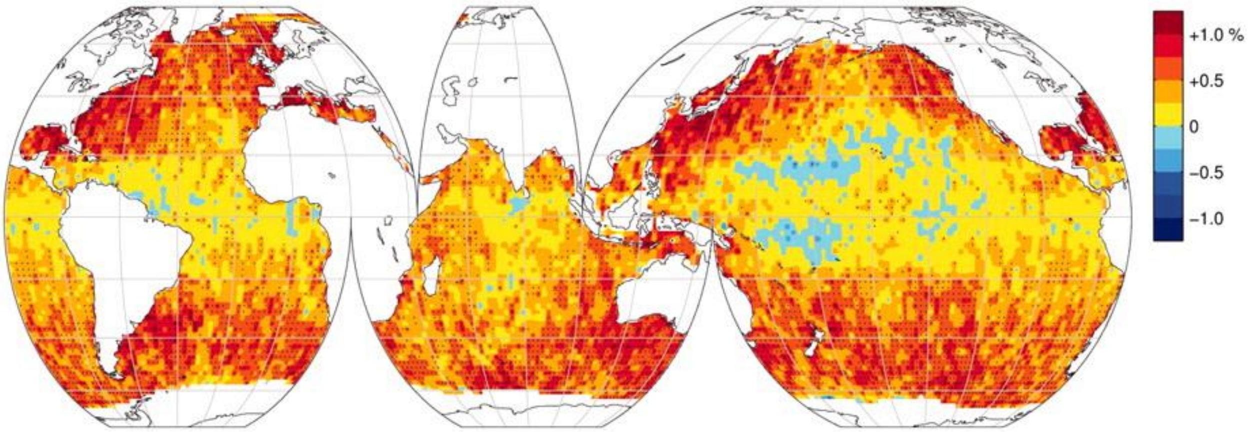


Figure 3 Trends in extreme wind speeds and significant wave height (99th-percentile) for the period from 1985 to 2008 and in percent per year. Dots indicate significant point values, from Young et al. (2011).

In the past, positive as well as negative effects of extreme storm and wave conditions on marsh stability have been reported. On the one hand, overwash events during storm surges increase sediment deposition onto the marsh platform and thereby facilitate vertical accretion and marsh resilience (Walters and Kirwan 2016). On the other hand, wind waves can cause severe damage to the marsh often through erosion directly at the marsh edge (Leonardi and Fagherazzi 2015; Schwimmer 2001). It has been found that for many locations, including the Venice lagoon and several sites in the USA, that wave impact was responsible for the marsh edge retreat and thus the reduction in local marsh area (Marani et al. 2011; Bendoni et al. 2016; Leonardi et al. 2015). By developing a model that analyses sedimentation processes and spatial marsh development focusing on the marsh edge, van de Koppel et al. (2005) discovered one potential explanation for marsh edge retreat under wave forcing. They found that with increasing sedimentation, the marsh edge development approaches a critical threshold above which storm-induced waves are likely to cause vegetation collapse, cliff erosion and salt-marsh loss. So far, studies investigating wave impacts on marsh stability mainly focused on erosion while other processes and plant-wave interactions such as wave-induced plant damage are poorly understood. Yet, studies suggest that wave-induced plant damage might be affected by plant properties such as stem flexibility and plant height (Vuik et al. 2018; Coops and van der Velde 1996). However, according to Vuik et al. (2018), a species-specific validation remains indispensable. Apart from species-specific differences, seasonality in vegetation properties potentially needs to be considered as well, as in temperate and boreal regions, aboveground parts of many salt-marsh species die-off in autumn and their biomechanical plant properties (e.g. stem flexibility) may therefore undergo considerable modifications in the course of a year. As biomechanical properties have the potential to affect the vulnerability to wave-induced plant damage, it becomes clear that further investigations on the effect of seasonality on plant resistance are needed. Consequently, this lack of knowledge together with projections of the future wind climate and the evidence of wave-induced marsh retreat, point towards the need to better understand marsh resilience against an increased storminess. In particular, plant damage through wave impact as well as determinants of plant resistance required further investigation as they might limit future coastal protection function in salt marshes.

Accelerated sea level rise

Accelerated sea level rise is a consequence of thermal water expansion with higher temperatures as well as an increase of total ocean water mass, which is caused by the melting of water storages like glaciers and ice sheets. Moreover, local changes in the sea level might also be affected by isostatic adjustment or anthropogenic processes (e.g. land subsidence through ground water abstraction, Huthnance et al. 2016). Global average sea level rise increased since the early 20th century from 1.3 mm/year (1901-1971) over 1.9mm/year (1971-2006) to 3.7 mm/year (2006-2018) (IPCC 2021). For NW European coasts, such as the North Sea region, a sea level rise of 1.5 mm/year have been reported for the 1900 to 2011 period by Wahl et al. (2013). It is expected, that mean sea level will continue to rise over the 21st century (IPCC 2021). Depending on the greenhouse gas (GHG) emission scenarios, global sea level rise is expected to range from 0.28-0.55 m (very low GHG emissions) to 0.63-1.01 m (very high GHG emissions) by 2100. Models that have been developed to evaluate future marsh resilience under projected accelerated sea level rise indicate that marsh persistence might be threatened. Crosby et al. (2016) predict that in 60-91 % of the studied salt marshes in Europe and USA, sea level rise will exceed accretion rates by the end of the century. Furthermore, according to Nicholls (2004), 5-20% of the global coastal wetlands could be lost due to sea level rise by 2080. However, following Kirwan et al. (2016), many predictions overestimate marsh vulnerability because they do not consider biophysical feedbacks (e.g. vertical accretion) counteracting sea level rise.

Nevertheless, the majority of salt marshes kept pace with recent rates of sea level rise, through their ability to accrete vertically and the feedback that more flooding leads to more sedimentation (Kirwan and Megonigal 2013). Globally, average accretion rates of coastal wetlands (mangroves, sea grasses, salt marshes) were about 2-3mm/year (Scott et al. 2014), whereas rates of mainland salt marshes in the North Sea region ranged between 2 and 29 mm/year (Bakker et al. 2016). How marshes accrete vertically is dependent on marsh type and often tidal amplitude (Allen 2000; Nolte et al. 2013a). Minerogenic marshes that form in areas with high sediment input through coastal waters and often a relatively high tidal amplitude, accrete as described above: the aboveground biomass of the vegetation reduces water flow velocity, which results in a decrease in the sediment-loading capacity of the water and an increase in sediment settlement (Morris et al. 2002; Yang 1998). In organogenic marshes that have little sediment input and often a low tidal amplitude, vertical accretion is mainly derived from belowground accumulation of organic matter, eventually leading to an expansion of soil volume and peat formation (Nolte et al. 2013a). In both cases, when accretion rates are too low and threshold values of sea level rise are exceeded, plant growth is negatively affected, leading to a negative feedback loop, which ensues marsh submergence and finally marsh loss (Chmura 2013; Kirwan and Guntenspergen 2012). In the past, marsh loss through submergence have been demonstrated for several areas including the Mississippi Delta (Baumann et al. 1984), Venice Lagoon (Carniello et al. 2009) and Chesapeake Bay (Kearney et al. 1988). Since the vegetation of salt marshes contributes significantly to vertical accretion, it is vital to investigate how it is responding to accelerated sea level rise. Previous studies have shown that responses of marsh vegetation to sea level changes are highly species-specific (Kirwan and Guntenspergen 2015; Langley et al. 2013; Morris et al. 2013). Even within species, there can be a considerable variability in plant responses due to a high degree of phenotypic plasticity and genetic diversity (Beierkuhnlein et al. 2011; Valladares et al. 2014). Thus far, however, assessments of plant responses to sea level rise have been restricted to the species or community level and therefore did not consider intraspecific variability. Investigations on the intraspecific variability in plant response to increased flooding frequencies might therefore hold major implications for a better understanding of marsh resilience to sea level rise.

Global warming

Global mean temperatures have increased and during the last four decades, this upward trend of warming further increased successively. In fact, the increase of global mean land and ocean surface temperatures reached +0.85°C from 1880 to 2012 (IPCC 2014), and further increased to +1.09°C between 2011-2020 (relative to the period 1850–1900, IPCC 2021, Fig. 4). The rate at which global mean temperatures will further rise depends on future GHG emissions. Under very low GHG emissions, it is very likely that at the end of this century global surface temperature will be approx. +1.4°C, while under very high GHG emissions it could be +4.5°C (relative to the period 1850–1900) (IPCC 2021).

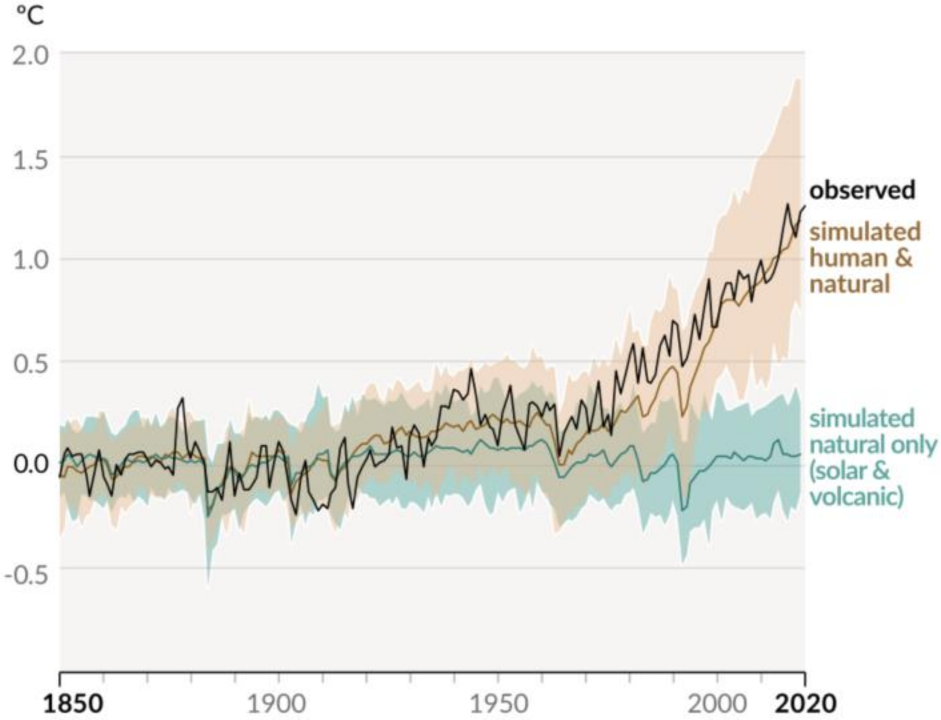


Figure 4 Annually averaged changes in global surface temperature over the past 170 years (black line), relative to the period between 1850 and 1900, and in comparison to the temperature response to both human and natural drivers (brown), and to only natural drivers (green). Colored lines show the average, while the shades indicate the very *likely range* simulations, from IPCC 2021.

Effects of global warming on salt marshes has been mainly studied by investigating its indirect effects via sea level and potentially storminess in the past. In contrast, potential direct effects of increased temperatures on the persistence of salt marshes have been subject to a few studies only. Generally, it has been shown that in other ecosystems, higher temperatures can increase the vegetation's productivity which in most cases results in a higher biomass (Rustad et al. 2001). An increase in biomass under warming has also been found for salt-marsh species

(Charles and Dukes 2009; Gray and Mogg 2001). Plant productivity and thus biomass might be increased under warming as metabolic processes are temperature-dependent and take place at a faster rate when temperature increases. Moreover, it has been shown that increased temperatures can extend the growing season for trees and shrubs in Europe (Menzel and Fabian 1999), which could affect biomass productivity as well. Whether the growing season of the salt-marsh vegetation is similarly extended under warming needs to be investigated still. As vegetation responses to environmental changes have often been shown to be species-specific, differences in the response to warming between different marsh species are likely but should be experimentally verified nonetheless. Facing current global warming projections, further investigations need to be carried out on warming-induced changes in biomass and especially phenology of salt-marsh vegetation. An extension of the growing season might not only affect biomass production but also the condition the vegetation is in. In NW European salt marshes, aboveground parts of the vegetation usually die-off in autumn limiting their contribution to wave attenuation during the storm surge season, which is from autumn until early spring. An early green-up in spring and/or delayed senescence in autumn due to higher temperatures might therefore have major impacts on the wave attenuation capacity as well as vegetation's resistance and thus coastal protection.

Objectives of this thesis

The overarching aim of this study was to investigate how climate change factors such as an increased storminess, accelerated sea level rise and higher temperatures affect the vegetation of salt marshes and thereby the coastal protection function. For this purpose, it was necessary to firstly determine plant properties that influence tidal marsh resistance against extreme hydrodynamic forcing. Subsequently, plant response to increased flooding frequencies as well as experimental warming were assessed, focusing on properties that are important for wave attenuation and marsh stability. Consequently, objectives of this thesis can be structured as follows:

Impact of extreme wave conditions on tidal marsh vegetation

In a true-to-scale flume experiment, single seedlings and fully-developed canopies of tidal marsh species are exposed to storm surge conditions to assess determinants for plants' vulnerability. In the first study, survival rates of seedlings of four pioneer species with distinct morphologies are compared (chapter 2). In the second study, fully-developed canopies of two salt-marsh species from different vegetation zones are used to compare wave-induced plant damage between the species (chapter 3). Additionally, prior to wave exposure, senescence is induced in half of the plants to examine potential seasonal effects on plants' resistance (autumn vs. summer condition). In these studies, biomechanical, biochemical and morphological plant properties are quantified to detect causes of potential species-specific or seasonal differences.

Plant response to increased flooding frequencies

A factorial marsh organ experiment is conducted to compare the plant responses of two genotypes of the dominant salt-marsh grass *Elymus athericus* to increased flooding frequencies (chapter 4). Above- and belowground growth parameters that are known to affect marsh accretion, are quantified to reflect potential intra-specific differences in plant performance and adaptability to sea level rise.

Plant response to experimental warming

Lastly, plant responses to increased temperatures are investigated in a whole ecosystem warming experiment in a salt marsh at the German North Sea coast (Box 1). Spectral reflectance (NDVI) of the canopy is monitored to quantify expected shifts in the length of growing season under warming, which might hold significant implications for biomass production and thus wave attenuation capacity.

2

Survival of the thickest? Impacts of extreme wave-forcing on marsh seedlings are mediated by species morphology

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Abstract

Although tidal marshes are known for their coastal defense function during storm surges, the impact of extreme wave forcing on tidal marsh development is poorly understood. Seedling survival in the first season after germination, which may involve exposure to extreme wave events, is crucial for the natural establishment and human restoration of marshes. We hypothesise that species-specific plant traits plays a significant role in seedlings survival and response to wave induced stress, i.e. through stem bending and uprooting. To test this hypothesis, seedlings of pioneer species (*Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani*, *Spartina anglica* and *Puccinellia maritima*) with contrasting biophysical traits were placed in the Large Wave Flume in Hannover (Germany) and exposed to storm wave conditions.

Seedlings of *P. maritima* and *S. anglica* experienced a lower loss rate and bending angle after wave exposure compared to *S. tabernaemontani* and especially *B. maritimus*. The higher loss rates of *B. maritimus* and *S. tabernaemontani* result from deeper scouring around the stem base. Scouring depth was larger around stems of greater diameter and higher resistance to

bending. Here, *B. maritimus* and *S. tabernaemontani* have both thicker and stiffer stems than *S. anglica* and *P. maritima*. Our results show that especially seedlings with thicker stems suffer from erosion and scouring, and have the highest risk of being lost during extreme wave events. This implies that for successful seedling establishment and eventually the establishment of a mature tidal marsh vegetation, the species composition and their capacity to cope with storm wave disturbances is crucial.

Introduction

Understanding the mechanisms that facilitate or hinder plant establishment on tidal flats is fundamental for successful tidal marsh restoration and creation, which is increasingly implemented for delivery of a multitude of ecosystem services, including the nature-based mitigation of coastal hazards related to global change (Narayan et al. 2016; van der Nat et al. 2016; Oppenheimer et al. 2019). Despite being the focus of this increased attention, tidal marsh ecosystems are still under threat due to environmental change and anthropogenic pressures, such as sea level rise, and local factors, such as marsh conversion to human land use (Lotze et al. 2006; Nicholls and Cazenave 2010; van Asselen et al. 2013).

To counteract loss or create new tidal marshes as nature based solutions, a variety of methods are used to (re-)establish ecological functioning. In practice, tidal marsh (re-)establishment requires the presence of a suitable habitat for marsh development, such as suitable bed elevation (i.e. tidal inundation frequency) and hydrodynamic conditions that allow seedling establishment and growth (Wolters et al. 2008; Zhao et al. 2020). There are several options to initiate the growth of marsh vegetation, i.e. (i) by adult propagule settlement, (ii) lateral clonal expansion of existing marsh plants or (iii) seedling establishment (Balke et al. 2014; Hu et al. 2015). Aside from a detailed understanding of the conditions under which seeds of tidal marsh plants can germinate and establish (Hu et al. 2015), it might be even more important to know how seedlings can survive energetic environments to facilitate and ensure successful marsh restoration and creation.

Studies on seedling survival often focus on the initial establishment phase, i.e. the phase where the seedlings become independent of the resources in the seed (Balke et al. 2014; Zhu et al.

2014). After initial seedling establishment in calm growing conditions, potential storm events in the course of the growing season might exert strong mechanical stress on the developing seedlings (Paul et al. 2016; Rupprecht et al. 2017) and may limit their survival. Yet many studies on seedling survival are conducted under relatively low levels of hydrodynamic exposure (Silinski et al. 2015; Cao et al. 2018; Xie et al. 2019). In contrast, little is known about survival in the period between initial seedling establishment and fully grown, patch forming pioneer vegetation, when the plants could still be vulnerable to more extreme hydrodynamic disturbances. On the one hand storm surges are difficult to investigate in the field due to their sporadic nature and relative unpredictability in terms of timing of occurrence, magnitude and precise meteorological characteristics (Hansen et al. 2019). On the other hand storm surges and storm waves are difficult to simulate in lab conditions without encountering significant scaling issues (Spencer et al. 2015; Masselink et al. 2016).

Fundamental knowledge on the processes that determine seedling survival under storm conditions is required to support the implementation of successful restoration of tidal marshes and their valuable ecosystem services. Structural failure of plants due to hydrodynamic stress is initiated by (1) drag forces acting on the plant shoots (Henry et al. 2015; Paul et al. 2016) and can be facilitated by (2) sediment scour around the stem base (Friess et al. 2012). Drag forces result from friction between the water flow and the plant shoot (e.g. Dean and Dalrymple 1991, Denny 1994), which is known to be a function of hydrodynamic forces (i.e. flow velocities), plant morphology (i.e. shoot surface area) and stem biomechanical properties (i.e. stem stiffness) (Paul et al. 2016; Vuik et al. 2018). Recent studies highlight that such species-specific plant traits also affect the plant’s capacity to cope with mechanical stress from hydrodynamic forces (Silinski et al. 2018; Schoutens et al. 2020). For example, if the drag forces exceed the shoots’ resistance against breakage, the stem will buckle or will break which can be fatal for the survival of the plant (Vuik et al. 2018). Moreover, when drag forces exceed the root anchoring strength, the seedling will be dislodged and will be flushed away by waves and currents. For the anchoring strength of the seedling, the root growth and structure are crucial (Peralta et al. 2006; Szmeja and Gałka 2011). Additionally, anchoring strength decreases through the development of scour holes around the stem base resulting from turbulence, leading to reduced contact area between roots and soil. Scour hole volume around single shoots has been shown to be a function of hydrodynamic forces, morphological and biomechanical plant properties (Bouma et al. 2009a), and sediment properties (Lo et al. 2017). Additionally, scouring around patches of multiple shoots growing close to each other, has been reported to depend also on the shoot density within the patch (e.g. Bouma et al. 2009b, Duggan-Edwards et al. 2020). When scour decreases the anchoring strength up to a point where drag forces can dislodge the complete plant, it will be flushed away and lost (Clark et al. 2015). The role of plant traits on drag forces and scouring processes during storm wave conditions remains unclear.

In the present study we experimentally assess the survival rates of four different species of pioneer tidal marsh seedlings with distinct morphologies, under storm wave conditions. More specifically, we examine the cause of structural failure, i.e. stem bending and uprooting by storm waves and how this relates to species-specific plant traits. Drag force proxies and scouring were quantified. Plant morphological and biomechanical properties were measured to support discussion of potential explanations of species differences in survival, damage, scouring and drag forces. With this discussion we aim to increase insights into the link between species-specific plant traits and the capacity of the seedlings to survive storm wave conditions.

Methods

Studied species

To test the hypothesis that plant traits exert a significant influence on the survival of pioneer marsh seedlings under storm wave conditions, four NW European pioneer marsh species with distinct morphologies were selected: *Bolboschoenus maritimus* (L.) Palla, *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla, *Spartina anglica* C.E. Hubb. and *Puccinellia maritima* (Huds.) Parl. *B. maritimus* and *S. tabernaemontani* are pioneer species in brackish marshes, while *P. maritima* and *S. anglica* are found in pioneer salt marshes. All four species can spread by clonal outgrowth (via rhizomes or stolons) of existing adult plants but can also colonise bare mudflats by seed dispersal. After flowering in summer, seeds can spread by the wind or tide in autumn followed by germination in spring. *B. maritimus* is often found as pioneer species in brackish marshes forming monospecific patches/zones parallel to the marsh shoreline. They form tall, thick shoots (up to 2.5 m high) with leaves. *S. tabernaemontani* can be found in the same brackish environment of pioneer marshes (Heuner et al. 2019; Elsen et al. 2019). It grows in monospecific stands and produces tall and thick stems (up to 2.0 m high) without leaves. *P. maritimus* is typically found in pioneer (to mid-successional) salt marshes characterised by sheltered conditions. It forms dense tufts (up to 0.7 m high) of thin flexible stems with leaves spread over the soil surface. The salt-marsh coloniser *S. anglica* is a pioneer that grows in dense tussocks of thin stems with leaves (up to 1.5 m high) under highly dynamic conditions often covering the lowest parts of the marsh.

Experimental setup

Preparation of experimental plant units

Upon stratification (4 °C during the night and room temperature during the day), germination of seeds was initiated on moist substrate. Three weeks after the start of the stratification (mid-June 2018), the seedlings were first planted in fertilised (slow release Osmocote, Substral) sand from the Scheldt estuary (SW Netherlands) and grown in greenhouse conditions. Five weeks later, the seedlings were transplanted in large sediment boxes (120cm by 80cm, 40 cm soil depth) that were later placed in the flume. The sediment in the boxes was composed of 32% silt and clay (< 63 µm), and 31%, 11%, 24%, and 2% very fine (63 – 125 µm), fine (125 – 200 µm), medium (200 – 630 µm), and coarse sand (> 630 µm), respectively, with a mean grainsize of 152.02 µm. As the sediment comes from the intertidal zone of the Scheldt estuary, this particle size distribution is representative for tidal marshes and mudflats in this estuary. Seedlings were planted 15 cm apart in a grid of 4 by 6 with a distance of 20 cm from the front and the back and 15 cm from the sides of the sediment box to minimise interference between the individuals and still enabling plantation of a reasonable amount of individuals (24 per sediment box) in the available space of the sediment boxes to allow statistical analyses (Fig. 1). Throughout the entire preparation period, the boxes were stored outside and the substrate was kept moist by irrigation with freshwater. The seedlings were 10 to 14 weeks old during the experiment.

Spatial and temporal setup

The experiment was carried out over a three week period (13-31 August 2018) in the Large Wave Flume (Grosser Wellenkanal, GWK) of the Forschungszentrum Küste (FZK), Hannover, Germany. In the middle of the wave flume (310 m long, 5 m wide and 7 m deep), an elevated platform (40 m long) was split over its length into separate zones (Fig. 1). The zones (horizontally separated by 10 m of platform) consisted of lowered gaps in the platform in which sediment boxes with plants were placed so that the surface of the sediment boxes was level with the platform surface. In addition to the experiment with seedlings described in this paper, which was performed in one such zone, other sediment boxes in other zones contained parallel experiments of which the results will be reported elsewhere. In the seedling zone, four sediment boxes were placed, each box contained 24 individual seedlings of one of the four different plant species. This set-up with sediment boxes excludes flume wall-edge erosion effects (Möller et al. 2014). One set of four boxes was placed in the flume for a whole week and then replaced by a new set of four boxes in the next week. Hence, for the three week period of the experiment, three sets of four sediment boxes filled with seedlings were prepared.

We highlight that the three consecutive weeks do not represent three replicate runs with the same wave conditions. Instead, over the three-week course of the experiment, a sequence of different wave conditions was applied (further called wave runs). Every week, four different wave runs were applied on day 2, 3, 4 and 5, with a daily increase in the intensity of simulated wave conditions (Table 1). This set-up gave us a total of 12 different wave runs covering a wide range of (extreme) hydrodynamic wave conditions. We chose this design to limit the risk of having a too narrow range of wave conditions for which either (i) all wave conditions would be too harsh and all seedlings would flush away after the first wave run or (ii) all wave conditions would be not harsh enough and none of the species would show any response. Instead, applying a wide range of wave conditions allowed us to identify species-dependent differences in seedling response. However, this choice and practical limitations (oa. in terms of time and resources) implied that we could not do replicate wave runs under exactly the same wave and plant conditions. Every daily wave run consisted of a JONSWAP wave spectrum of 1000 random waves (i.e. waves of different height and period as experienced typically on the shores of the North Sea) with an inundation depth of 1.5 m approximating storm surge conditions in temperate regions (Table 2). Wave and water depth conditions were selected to mimic conditions that (a) are typical of those experienced at marsh margins around the North Sea basin (e.g. Spencer et al. 2015), (b) generate high bed shear stresses, but also (c) maintain relative uniformity of hydrodynamic forcing along the individual successive experimental zones on the raised platform. Only during the last wave run (on day 4 of week 3) were monochromatic waves used to allow higher time-averaged wave induced bed stresses to be simulated (see Table 1), which could not be achieved through an irregular wave spectrum. In between the daily wave runs the flume was drained slowly over several hours in order to prevent erosion on the sediment surface and drag on the seedlings. Once the flume was drained, in between every daily wave run, the effects of the preceding inundation and wave conditions on the plant seedlings and sediment surface were measured, but the same boxes with sediments and plants were kept in the flume for 5 days. Hence, for four days (days 2-5), the seedlings and sediment surfaces were exposed to an accumulating load of wave energy resulting from the four consecutive wave runs.

Table 1 Incoming wave conditions measured at the start of the experimental platform. Significant wave height (H_s, m) and significant wave period (T_s, s) are shown per week and per wave run. Every wave run consisted of 1000 waves. Note that apart from the monochromatic waves during wave run 4 of week 3 (italics), all wave runs had randomly generated waves representative for North Sea conditions (JONSWAP spectrum).

		H_s (m)			**T_s (s)**		
		Week 1	**Week 2**	**Week 3**	**Week 1**	**Week 2**	**Week 3**
Wave run	**1**	0.30	0.68	0.68	2.58	3.80	4.02
	2	0.40	0.68	0.77	4.22	3.80	5.63
	3	0.58	0.78	0.78	3.56	5.66	5.63
	4	0.69	0.78	*0.71*	5.23	5.63	*6.00*

Table 2 Field studies with recordings of a maximum significant wave height (H_s, m) and inundation depths (h, m) at the marsh edge as compared to the conditions in this flume experiment.

Publication	**H_s (m)**	**h (m)**	**Study site**
This flume study	**0.78**	**1.5**	
Möller et al. 1999	0.58	1.39	North Norfolk Coast, UK
Ysebaert et al. 2011	0.64	1.86	Yangtze, CN
Yang et al. 2012	0.73	1.71	Yangtze, CN
Vuik et al. 2016	0.69	1.90	Western Scheldt, NL
Schoutens et al. 2019	1.00	3.85	Elbe, GE
Zhu et al. 2020	0.87	2.20	Wadden Sea Coast, NL

Hydrodynamic measurements

Wave-induced current velocities were recorded directly in front (0.30 m) of the seedling zone (Fig. 1). High-frequency (25 Hz) flow velocity measurements were conducted with Acoustic Doppler Velocimeters (ADVs) positioned in the middle of the flume width at 0.05 m above the bottom of the experimental platform. Wave gauge arrays mounted against the flume side wall were installed at the start of the experimental platform (Fig. 1). From these measurements, the significant wave height and period (mean of the highest third of recorded wave heights, H_s or wave periods T_s respectively) were derived (Table 1). Over the course of the four days for which individual seedling boxes were retained in the flume, the wave exposure of the seedlings and sediment surfaces progressively increased. The plant and sediment surface responses recorded on each day thus represent change induced through the previous day's wave run, but, for days 3, 4, and 5, the reported change is that which has resulted from all preceding wave runs during that week, i.e. is relative to day 1 of the experiment. The accumulated wave load (action, S) for each wave run was calculated from the orbital flow velocities as the kinetic energy times the exposure time (i.e. number of wave oscillations times the representative wave period) and has the unit Joules-second (Js) (see supplementary info for the full method).

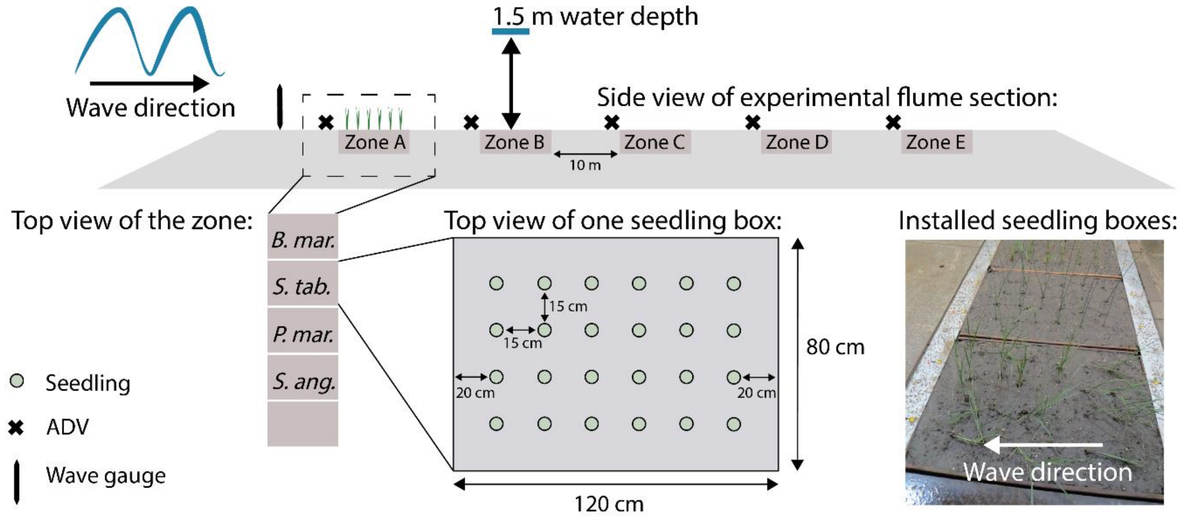

Figure 1 Schematic overview of the experimental setup in the Large Wave Flume (GWK, Hannover, Germany). On the elevated platform, installed in the flume, one zone was used to install four boxes with seedlings. Each box contained 24 seedlings of one species. The picture on the right illustrates the seedling boxes installed in the flume platform.

Plant trait dependent response to storm waves

Plant damage and vitality

Seedling response to storm wave exposure was quantified daily after each wave run and was compared to the initial seedling condition before the first wave run of the week. Remaining seedlings were counted and the angle, perpendicular to the sediment bed, of the standing stem was measured in categories ranging from '<18°', '18°-36°', '36°-54°', '54°-72°' and '72°-90°' (the latter representing the seedlings that were almost completely bent over on the sediment bed). Seedlings that were missing were categorised as 'lost shoot'. When a shoot was lost, the cause (uprooting, i.e. including loss of below-ground roots; or stem breakage, i.e. below-ground roots still present) was recorded.

Damage resulting from drag forces and erosion

Scouring and erosion features

Structure from motion (SFM) photogrammetry of the sediment surfaces was used to quantify the degree of erosion, including local scouring around the individual shoots, and in certain cases larger-scale erosion features in the sediment boxes. Pictures (ca. 300) were taken daily from various angles in between wave runs, after which they were processed in Agisoft Photoscan Professional software to produce three-dimensional point clouds. For the processing of the SFM photographs to accurate ground geometry and the spatial co-registration of successive point clouds, self-adhesive fiducial markers were placed at fixed positions on metal fixings around the experimental zone. Point clouds were scaled and co-registered to a reference cloud (Day 1 of the week, before any wave run) that had previously been scaled and registered to a lower resolution (5 mm) point cloud derived from an overhead laser scanner. Comparisons between clouds were conducted using the M3C2 plugin for Cloud Compare (Lague et al. 2013). The M3C2 distances, projected onto the reference cloud, were then rasterised on a 1 mm grid prior to further analysis in R (R Core Team 2019). From this raster, the sediment elevation was extracted as rings of 2 mm thickness designated here by their outer radius. Differentiation between scour features and pallet erosion was achieved through visual inspection of images.

Drag forces on plants

Hydrodynamic drag forces can initiate severe mechanical stresses when applied to plant structures. It is known that such hydrodynamic drag forces depend on flow velocities, shoot biomass and shoot stiffness (Vogel 1996). In this paper, shoot biomass, shoot length and flexural stiffness were used as proxies for drag forces experienced by the four species.

Plant morphology and biomechanics

Plant morphological properties (shoot biomass, shoot length, basal stem diameter) were quantified for all four species as follows. Aboveground biomass was harvested for every surviving seedling after the last wave run of each week. Belowground biomass, as proxy for anchoring capacity, was sampled on 5 replicate seedlings per species by digging up all the roots and rinsing the sediment off. After biomass collection, the samples were dried for 72h at 70 °C and weighed. Root:shoot ratios were calculated as the mean belowground biomass divided by the mean aboveground biomass and the error bars were obtained through a propagation formula. Shoot lengths and basal stem diameters were measured on all 24 seedlings of every species each week.

Biomechanical properties (second moment of area, Young's modulus and flexural stiffness) were quantified for all four species by three-point bending tests (Niklas 1992; Rupprecht et al. 2015). Per week, 5 seedlings per species were harvested after the last wave run to test for flexural strength of the shoots. The tests were performed using a universal testing machine (Instron 5942, precision ± 0.5%) with a 10 kN load cell (Instron Corporation, Canton, MA, USA). Prior to testing, the diameters of the stems were measured with a caliper. The supports of the machine, on which the plant shoots were horizontally placed, were fixed at a distance of 15 times the stem diameter to diminish shear stress on the supports during the tests (Usherwood et al. 1997). The most basal part of the stem was placed on the two supports after which a force was applied on the center of the stems at a displacement rate of 10 mm min^{-1}. The Instron Bluehill 3.0 software accompanied by the device creates a stress-strain curve, i.e. a graph describing the relation between vertical deflection of the stem (D; on the X-axis) and the bending force of the stem (F; on the Y-axis) which enables the calculation of the slope from the elastic deformation zone on the curve (F/D). From this slope, the flexural stiffness (EI in Nm^2) was calculated as:

$$\text{(eq 1.)} \qquad EI = (s^3 F)/(48D),$$

where s is the distance between the supports. Next, the second moment of area (I in m4), a measure for the structural geometry (i.e. shape) of the stem, was calculated. The formula used for round stems (*S. tabernaemontani, P. maritima and S. anglica*) is:

$$\text{(eq 2.)} \qquad I = \pi r^4/64,$$

where r is the diameter of the stem's cross section, and the formula for the triangular stems of *B. maritimus* is:

$$\text{(eq 3.)} \qquad I = bh^3/36,$$

where b is the base and h is the height of the triangular cross section. Using the flexural stiffness and the second moment of area, we calculated Young's modulus (E in Nm^{-2}), which is a measure for the strength of the stem material, as $E = EI/I$.

4.3.6 Data analysis

Probabilities of damage were compared between species with two-proportion z-tests. Species-specific differences in scouring depth in response to storm wave conditions as well as species differences in plant traits (morphological and biomechanical properties) were tested with one-way ANOVAs or the non-parametric alternative Kruskal-Wallis test. These were followed by a multiple pairwise comparison with a post-hoc Tukey honest significant difference test or with a non-parametric pairwise comparison using Wilcoxon rank sum test with Bonferroni correction. Linear regression was applied to check for a relationship between scour depth and stem diameter and Pearson correlation coefficient was calculated. To test if shoot length is important for the risk of getting damaged we used a logistic mixed effect model with 'damage' after the 4th wave run of the week as the response variable ('damaged' and 'not damaged'), the 'week' of the experiment was added as random variable and 'species' was added as random variable nested in 'week'. The significance of the shoot length was tested with a Likelihood Ratio test (Zuur et al. 2009). All statistical analyses were performed in R 3.5.3 (R Core Team 2019) applying a significance level of $p < 0.05$ for all tests. Normality of the residuals was tested based on visual inspection with histograms and Q-Q plots and homogeneity of variance was tested with scale-location plots. To meet normality assumptions, a log transformation was applied to the aboveground biomass data.

Results

Storm wave induced damage

Simulated storm waves had an increasing significant wave height H_s every consecutive wave run in a week (Table 1). The waves had an H_s ranging from 0.30 m up to 0.78 m and a significant wave period T_s ranging between 2.6 s and 6.0 s. As seedlings were exposed to 4 consecutive wave runs in one week, the experienced stress on any specific day was the result of the effect of any preceding wave runs that week, including the run on the day of, and preceding, the measurement of plant characteristics. Thus, the accumulated wave load was calculated (Fig. 2). With an accumulated wave load of 819 Js, the first week represented the calmest storm conditions of the experiment. The accumulated wave load in week 2 (1667 Js) and week 3

(1454 Js) were similar to each other, although the specific wave characteristics differed (Table 1).

After exposure to storm-wave conditions, the damage (i.e. stem bending angle and seedling loss) observed was highest for the *B. maritimus* and *S. tabernaemontani* seedlings (Fig. 2). Seedlings of *S. anglica* and *P. maritima* hardly showed noticeable damage, while up to 100 % of the *B. maritimus* seedlings showed damage from wave exposure. The main damage in *B. maritimus* were bent shoots and over the three weeks less than 15 % of the shoots were lost. *S. tabernaemontani* seedlings had better survival rates and after four wave runs, the *S. tabernaemontani* seedlings had more than 57 % chance to remain upright in contrast to 26 % for *B. maritimus* seedlings (z-test Chi-squared = 13.18, df = 1, $p < 0.05$). Most damage in *S. tabernaemontani* seedlings only started from wave run 3 onwards, but was still limited, i.e. after the fourth wave run, *S. tabernaemontani* seedlings had less than 15 % chance of being bent by > 72° while this was more than 40 % for *B. maritimus* seedlings (z-test Chi-squared = 10.04, df = 1, $p < 0.05$). Interestingly, all seedlings that were lost suffered from stem breakage, mainly at the base of the stem. No cases were observed of seedlings that were uprooted, i.e. completely eroded and washed away including their roots. Apart from some exceptions, the stems bent or broke at the stem-root connection.

Scouring processes

To gain insights in why damage differs between the species, we investigated two groups of processes that can generate wave-induced damage to the plants: (1) proxies for drag forces and (2) erosion processes such as scouring. Measurements of sediment scouring around individual plant stems, induced by turbulence, indicate a difference between species (Kruskal-Wallis Chi-squared = 128.5, df = 1, $p < 0.05$) that is in line with the observed species differences in seedling damage (Fig. 3). Especially close to the seedling stems, *B. maritimus* and *S. tabernaemontani* produced deeper scour holes (median values of 1.0 cm) compared to *P. maritima* and *S. anglica* (only a few millimeter). The scour holes around *P. maritima* were shallower and narrower compared to the scour holes around *B. maritimus* and *S. tabernaemontani*. Least scour was observed around *S. anglica*.

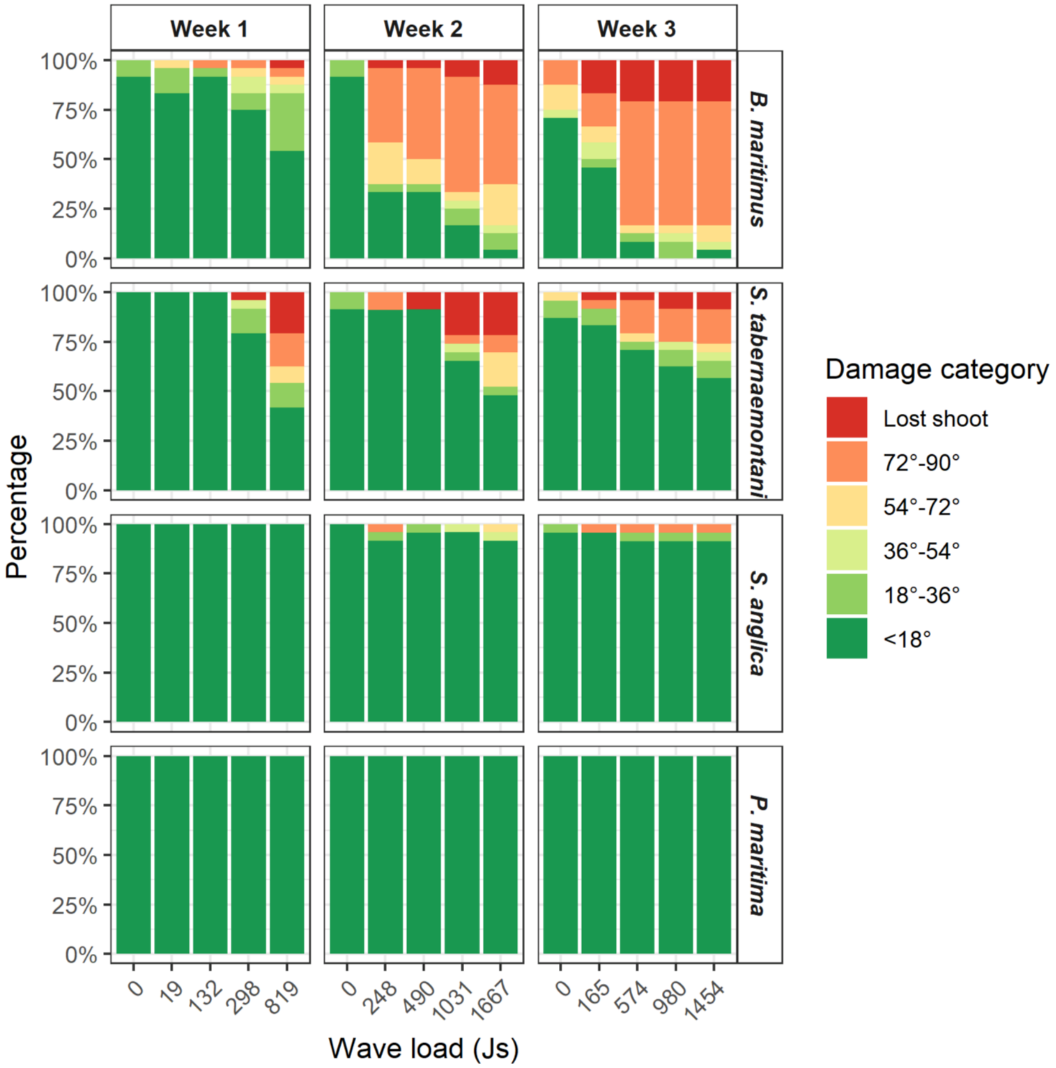

Figure 2 Percentage of seedlings (n = 24) that experienced damage caused by storm-wave exposure for the four species. Damage is quantified in six categories ranging from < 18° (i.e. no or negligible damage), to higher bending angles (increasing damage), to completely lost shoots (due to breakage at the stem base). The first day represents the initial starting situation before any wave exposure (wave load is zero). The accumulated wave load (Js) after each daily wave run is indicated on the x-axis.

Around some of the seedlings, the sediment was slightly elevated (in the order of magnitude of a few millimeters), which may be within registration errors, due to small deposition of elsewhere eroded sediments or due to slight swelling of the clay and silt rich sediment surface during the experiment.

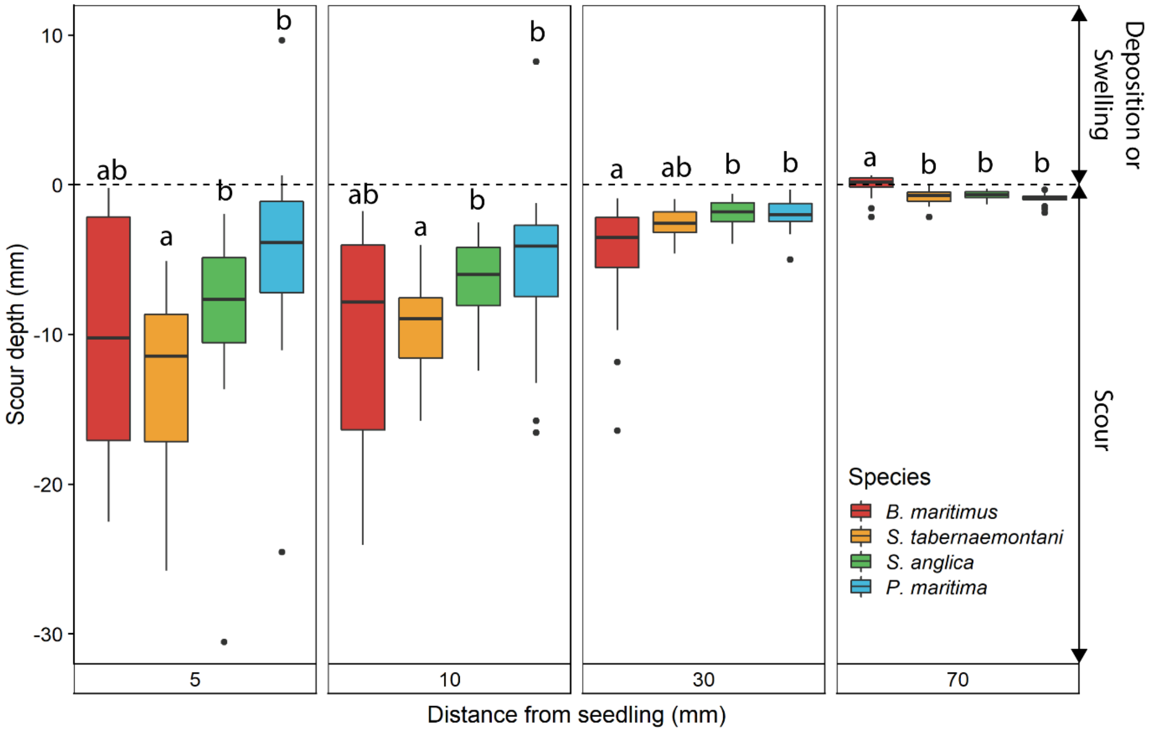

Figure 3 Median scour depth at four circular distances from the seedlings plotted as boxplots per species at the end of the 4th wave run of week 3 (i.e. the week with most extreme wave conditions) (n = 72). Erosion features, not linked to scour around the seedlings, are not shown in this figure, i.e. edge erosion induced from the edge of the sediment box or erosion induced by a pebble in the sediment. Different letters indicate significant differences as obtained by a non-parametric pairwise comparison using Wilcoxon rank sum test with Bonferroni correction.

Link between damage and erosion processes

In general, the seedlings that were not damaged did not suffer from strong erosion features, even after several wave runs (Fig. 4). *B. maritimus* seedlings that were lost due to shoot breakage at the stem base showed relatively shallow (< 10 mm) erosion features in contrast to the seedlings of *S. tabernaemontani* (> 10 mm) that were lost also due to shoot breakage. The deeper erosion features around *B. maritimus* seedlings were observed around seedlings that suffered from damage by stem bending but where the shoot was still attached. Each successive wave run resulted in higher bending angles which were also corresponding with deeper erosion features. This pattern was less pronounced in *S. tabernaemontani*, however it should be noted that the number of seedlings suffering from damage by bending were low for this species. The *S. tabernaemontani* seedlings that did suffer damage, showed an increase in erosion depth in the last wave run of the week. In general, when a shoot started to show damage, this coincided with a step-wise change to much higher bending angles (bending angle > 18°) bypassing intermediate bending angle categories. Partial uprooting was observed for multiple seedlings, however all roots remained anchored in the sediment and hence no complete root dislodgement was recorded.

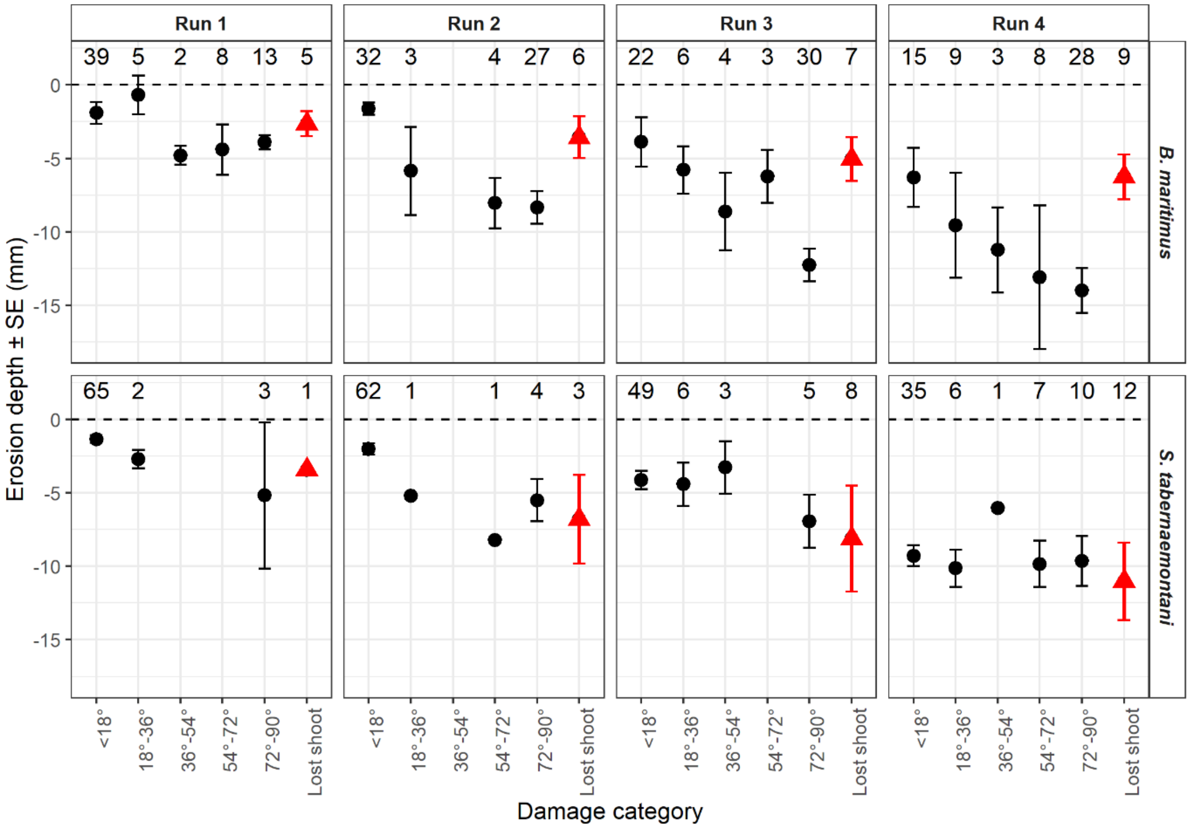

Figure 4 Mean erosion depth (mm ± SE) at 10 mm from the seedling per damage category for *B. maritimus* and *S. tabernaemontani* plotted per wave run, pooled over the three weeks to increase the number of observations in every damage category. The numbers indicate the count of seedlings per calculated mean. Shoots that were lost by breakage at the stem base are indicated with red triangles.

In order to explore species differences in scouring depth, we further investigated species differences in plant traits that were expected to affect the scour intensity around plants, i.e. basal stem diameter and stem flexibility. Basal stem diameters of *B. maritimus* and *S. tabernaemontani* were similar to each other and significantly larger than for the other two species (Fig. 5a). *P. maritima* had the lowest stem diameter (mean of 0.9 mm), however it should be noted that seedlings of *P. maritima* sprout multiple stems and leaves from the crown. Three-point-bending tests showed that in agreement with these thicker diameters for *B. maritimus* and *S. tabernaemontani*, their second moment of area was significantly bigger than for *S. anglica* and *P. maritima* (Fig. 6c). Since no species differences in Young's modulus were found except for the higher values of *P. maritimus* during the three-point bending test, the flexural stiffness of *B. maritimus* and *S. tabernaemontani* was higher, causing higher resistance against bending with the flow (Fig. 6a-b).

Proxies for drag force and anchoring capacity

Plant traits were used as proxy for drag force to explain species differences in damage. Shoot length was highest for *S. tabernaemontani* seedlings followed by *B. maritimus* (Fig. 5b). Both species had a significantly longer shoot length (almost double the length) compared to *S. anglica* and *P. maritima*. Seedlings that suffered from damage had significantly longer shoots compared to the seedlings that remained upstanding (damage category < 18°) (Likelihood ratio test: Chi-squared = 5.07, df = 1 $p < 0.05$). Aboveground dry biomass of *B. maritimus* seedlings collected after the 4th wave run of the week was more than twice as high (average of 0.52 ± 0.04 g per seedling) as compared to the other species (Fig. 5c). There was a non-significant difference in aboveground biomass between *S. tabernaemontani* and *S. anglica* (Tukey HSD $p = 0.1$). The aboveground biomass of *P. maritima* was lowest compared to the other species. Both shoot length and aboveground biomass indicate a higher drag force for *B. maritimus* and *S. tabernaemontani* and lowest drag force for *P. maritima*. In addition to the morphological proxies for drag force, the biomechanical proxy, i.e. flexural stiffness (described above), are in line with this result (Fig. 6a). Higher resistance against breaking (i.e. higher flexural stiffness) of *B. maritimus* and *S. tabernaemontani* indicate higher drag forces compared to *S. anglica* and *P. maritima* that both have low resistance against bending (low flexural stiffness).

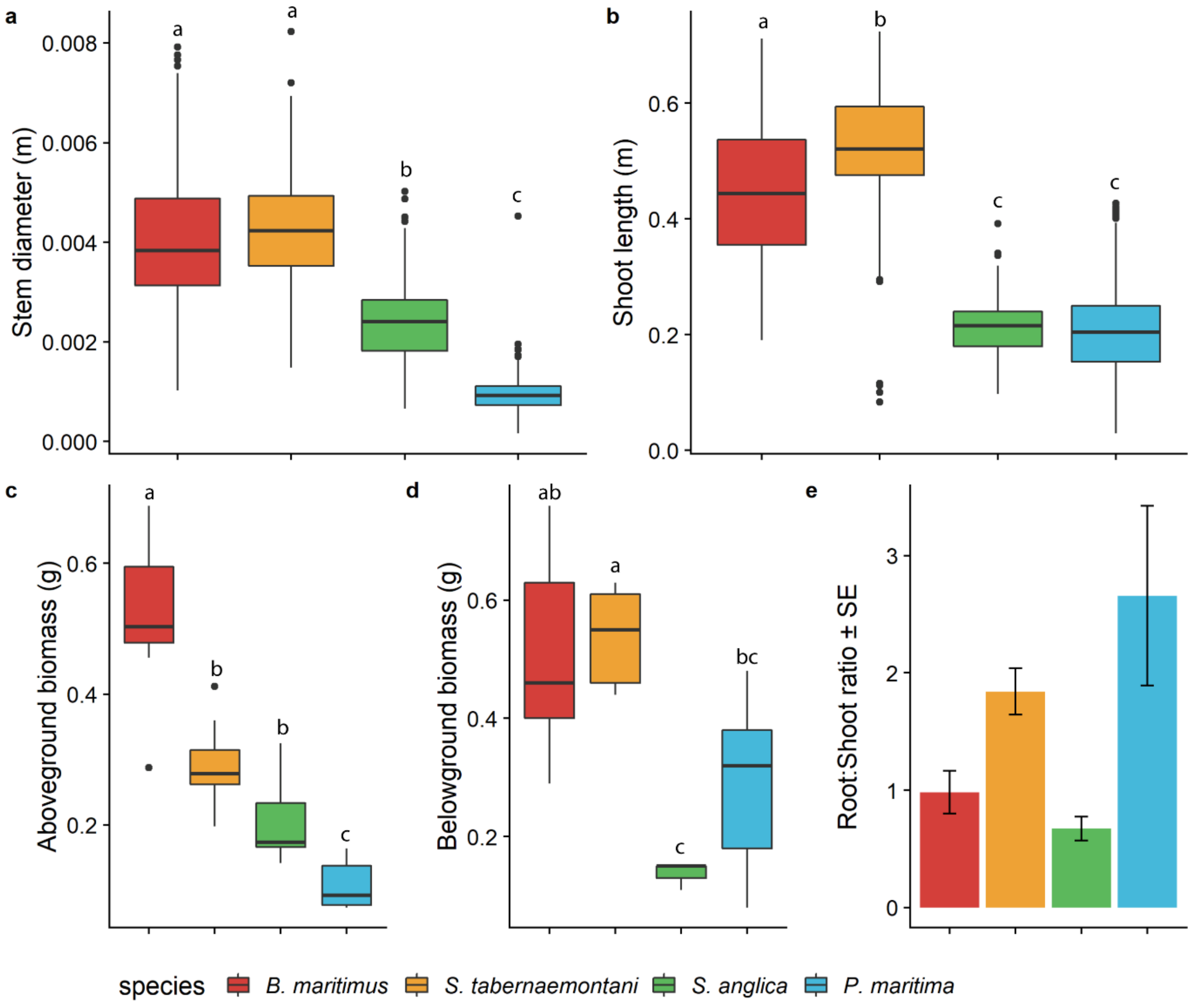

Figure 5 Plant morphogical properties as proxy for drag forces and driving force for scour. (a) Basal stem diameter and (b) shoot length per species (n = 72) are plotted as boxplots. (c) Aboveground dry biomass per seedling (n=8) and (d) belowground dry biomass per seedling (n=5) are plotted as boxplots and (e) root:shoot ratios per species ± SE (n = 1). Letters indicate the significant differences obtained by one-way ANOVAs followed by a post-hoc Tukey HSD test.

Belowground biomass was biggest for *B. maritimus* and *S. tabernaemontani* (Fig. 5d). Root:Shoot ratios indicate highest investment in root biomass for *S. tabernaemontani* and *P. maritima* seedlings which invested twice as much biomass in belowground parts compared to investments in shoots (Fig. 5e). In contrast to the absolute values for dry belowground biomass, *B. maritimus* invested a similar amount of biomass in its aboveground and belowground parts. *S. anglica* seedlings invested less in belowground biomass as the root:shoot ratio was below one.

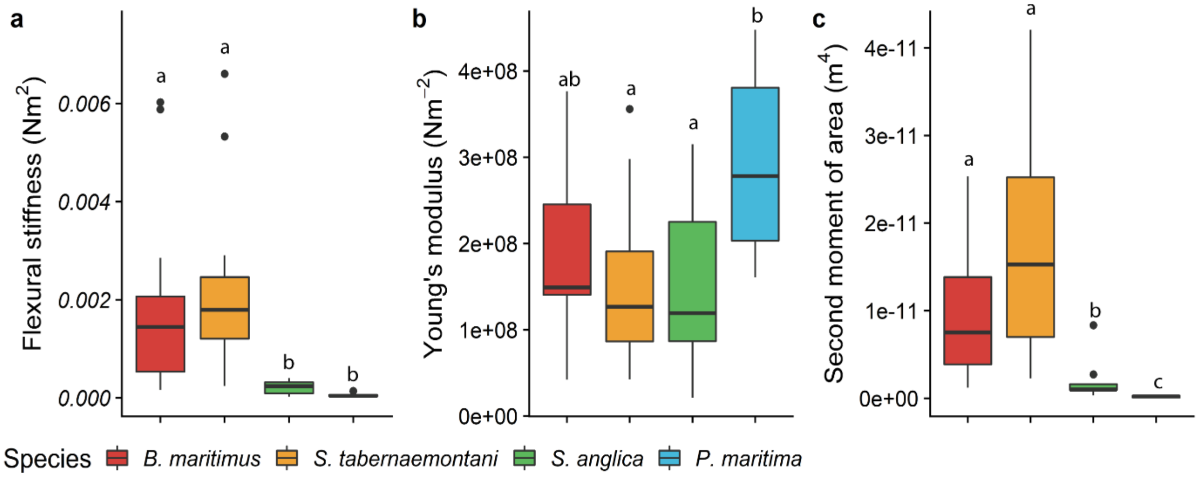

Figure 6 Biomechanical properties per species sampled over the three weeks represented as boxplots (n is, respectively, 15 for *B. maritimus* and *S. tabernaemontani* and 13 for *S. anglica* and *P. maritima*). Letters indicate the significant differences between species tested with a one-way ANOVA followed by a Tukey HSD test.

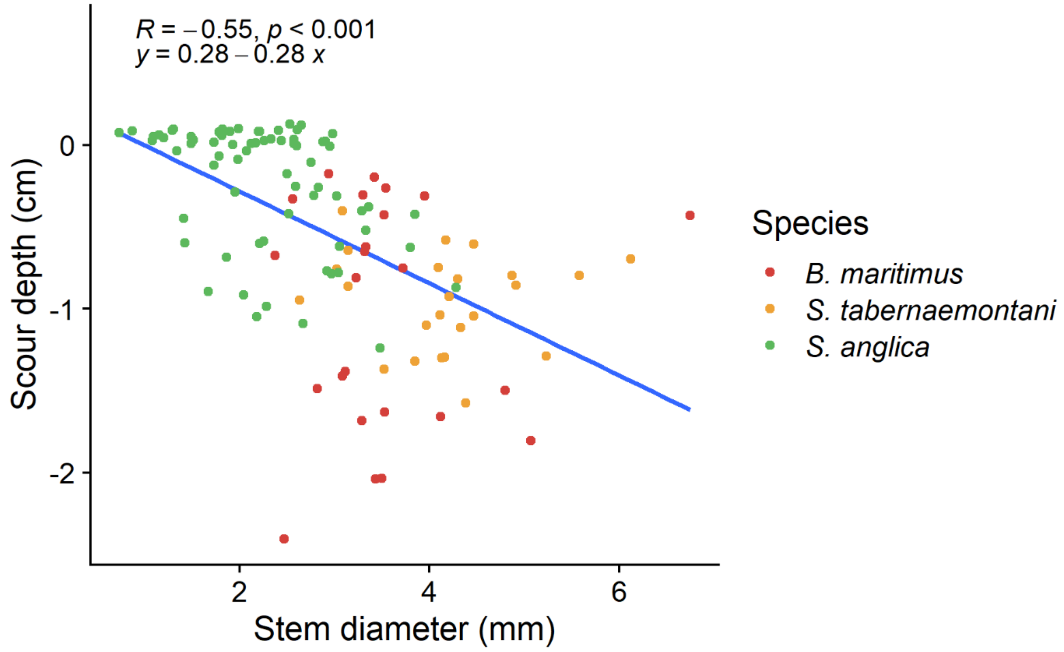

Figure 7 Scour depth (m) plotted against basal stem diameter (mm) across the three single-stem species (*B. maritimus*, *S. tabernaemontani* and *S. anglica*) showed a negative correlation indicated by the Pearson correlation coefficient (*R*).

Despite the spread, a significant trend of deeper scour holes with increasing stem diameter was observed over all three species characterised by a single stem (Regression analysis: $F_{3,114} = 31.08$, $p < 0.05$, $R^2 = 0.45$, non-scour-related erosion features were excluded from the analysis) (Fig. 7). Due to the multiple stems of *P. maritima*, which act more as a tussock, this species was excluded from the analysis. *S. anglica* had the smallest stem diameters. Therefore, scour depth was generally lower compared to *B. maritimus* and *S. tabernaemontani*.

Discussion

The results of this large wave-flume experiment show that the survival rate of seedlings in response to storm waves is plant trait dependent. More specifically, seedling survival decreases when the seedling has plant traits that increase the potential drag force and scouring around the stem. This knowledge has multiple implications for marsh (re-)establishment and should be taken into consideration when modeling and planning tidal marsh restoration and creation projects.

Plant-trait dependent loss of seedling shoots

Both *B. maritimus* and *S. tabernaemontani* showed a similarly high loss of shoots, while this was negligible for *S. anglica* and *P. maritima* (Fig. 2). Dislodgement is considered the main cause of death for young seedlings during germination and the initial establishment phase, even under calm wave conditions (Balke et al. 2013; Zhu et al. 2014; Cao et al. 2018). However, in this study we did not observe complete dislodgment of seedlings, including their roots, under storm wave conditions. All observed losses of *B. maritimus* and *S. tabernaemontani* shoots happened through basal stem breakage, predominantly at the connection between the stem and the roots. It is known from previous studies that long shoots increase the drag forces pulling on the stems which makes them more vulnarable to breaking (Albayrak et al. 2014). Hence our results confirm that the higher loss rate by stem breakage for *B. maritimus* and *S. tabernaemontani* seedlings (Fig. 2), is related to their significantly higher shoot lengths as compared to the two other species in our experiments (Fig. 5). Stem breakage of adult shoots of these two species mainly occurs several centimeters above the sediment surface at the end of the growing season when the shoots are deteriorating as part of the seasonal growth cycle (Vuik et al. 2018; Schoutens et al. 2019; Zhu et al. 2020). Our experiments show that seedling stems typically first bend and then break at the shoot-root interface. It should be noted that the question of whether shoot breakage leads to permanent loss of the seedlings, cannot be confirmed from our experiments. The ability of a shoot to break close to the root connection may be seen as a strategy to avoid drag forces and scouring, while the remaining root network might prevent the sediment surface from eroding (Spencer et al. 2016a; Wang et al. 2017). Hence, damage by stem breakage in the short term could reduce the risk for complete root dislodgement, thus allowing regrowth of shoots from the roots and facilitating seedling survival over the longer term. Such a survival strategy by stem breaking under storm waves and regrowth from surviving roots was also suggested by Rupprecht et al. (2017) for an adult canopy of the high marsh species *Elymus athericus*. Fast regrowth of shoots is also what we observed from the cut-off outgrown shoots of *B. maritimus* and *S. tabernaemontani*.

Plant trait dependent bending of shoots

Applying a wide range of different wave runs with different wave conditions allowed us to demonstrate that species-specific responses also depend on the wave conditions (Fig. 2). The calmest wave conditions in this experiment show very small (or no) differences in species response while heavier wave conditions show increaslingly larger species-specific responses. This proves that it are the more extreme wave conditions that are most selective in terms of species response. *B. maritimus* suffered the most among all studied species with bent shoots or shoots lying flat on the sediment surface after an accumulative wave loading of ≥ 132 Js (Fig. 2). Here, we argue that this species-dependent difference in shoot bending may be the result of two mechanisms: scouring around stems and drag forces exerted by the waves on the stems. First, the seedlings of *B. maritimus,* with greatest bending angles (Fig. 2), also had the deepest scour holes (Fig. 3), which resulted in partial uprooting. This suggests that the loss of the anchoring strength of the roots may have contributed to reduced ability of the shoots to keep an upstanding position. Although scour holes around *S. tabernaemontani* were of similar dimensions (Fig. 3), no uprooting was observed indicating that the root system of this species develops at several centimeters below the sediment surface. As *S. tabernaemontani* did not experience uprooting, this may partly explain why it also experienced less bending as compared to *B. maritimus* seedlings. *S. anglica* and *P. maritima* showed least percentages of shoot bending (Fig. 2) and lowest scouring depths (Fig. 3). Overall, this suggests that shoot bending is positively related to the depth of scouring holes across the studied species.

Moreover, our results showed that across the studied species, the scouring depth is deeper around stems with a larger diameter (Fig. 7). Here, it should be noted that although *S. anglica* had thicker stem diameters, the seedlings of *P. maritima* form grass clumps with multiple stems sprouting from the crown which will likely act as one entity causing more turbulence and thus more scour compared to *S. anglica*. Scour is the result of the interaction between hydrodynamics (wave induced currents in this experiment) and a physical obstacle (seedlings in this experiment) that creates turbulent flow. Since hydrodynamic forces were the same for all seedlings, the stem shape was the key variable to explain the observed differences in scouring depth. It has been shown that the dimensions of scour holes are related to the diameter of the obstacle (Bouma et al. 2009a). Additionally and in accordance with literature, thicker stems were found to have a higher flexural stiffness, which limits their tendency to bend over with the flow. Interestingly, studies on scouring around engineered structures, like bridge pillars, showed that when the angle of the obstacle to the incoming flow is wider, i.e. the obstacle is bent over in the direction of the flow, the turbulence generated around the object changes and creates less deep scouring compared to objects of the same dimensions that stand perpendicular against the flow (Kitsikoudis et al. 2017). Applying this to plant shoots, stiffer stems, that have more tendency to stand perpendicular against the flow, will generate deeper scour holes compared to more flexible stems that bend over to reduce the angle with respect to the flow direction (Bouma et al. 2009a; Yagci et al. 2016).

Secondly, to explain why *B. maritimus* suffers much more from structural bending of the stem compared to *S. tabernaemontani*, we also consider the expected drag forces acting on the seedlings. Both stem diameters and stem lengths are similar for both species, however, an important difference is the aboveground biomass, which is almost double for *B. maritimus* as compared to the biomass of *S. tabernaemontani* (Fig. 5). The absence of leaves in *S. tabernaemontani* lowers their aboveground biomass which reduces the frontal area and hence, is expected to reduce the experienced drag (Paul et al. 2016; Silinski et al. 2016). *S. anglica* and *P. maritima* do have leaves, but these were small (Figs. 4.5 and 4.6) and thus contribute little to the expected drag forces (Paul et al. 2016; Vuik et al. 2018). Apart from aboveground biomass, a higher shoot stiffness is also expected to result in increased drag force and to induce more wave-induced damage on the stem (Rupprecht 2017). Our results also indicate that flexural stem stiffness was highest for the *B. maritimus* and *S. tabernaemontani* (Fig. 6a), which were the species that showed the highest percentages of stem bending (Fig. 2). Overall, our result confirm that plant traits responsible for an increase of drag forces, also increase the damage experienced by the seedling.

The role of a root network

All four species in this experiment are able to grow clonally by producing an extended root network of rhizomes or, in the case of *P. maritima*, aboveground stolons (Charpentier and Stuefer 1999; Sosnová et al. 2010; Silinski et al. 2016). During the experiment, the seedlings were between 10 and 14 weeks old which for *B. maritimus* and *S. tabernaeomontani* had resulted in clonal outgrowth and well developed roots (Figs. 4.5d and 4.5e). Although outgrown shoots were cut off prior to the wave runs, the belowground network of rhizomes was able to maintain an anchoring capacity that was strong enough to avoid complete uprooting during the experiment. Hence, despite their age which results in a more developed shoot that increases the drag forces, a more developed belowground biomass (Fig. 5e) seems to compensate this increased stress (Balke et al. 2013; Cao et al. 2020). It is known from other ecosystems that anchoring capacity is positively correlated with root properties such as rooting depth, structural complexity and root biomass (Peralta et al. 2006; Schwarz et al. 2010; Edmaier et al. 2014), but research on root networks in tidal marsh vegetation remains sparse (Friess et al. 2012). Apart from the root properties of the seedlings, the cohesiveness of the sediment bed plays a role in the anchoring capacity and resistance against dislodgement of the seedlings (Edmaier et al. 2014; Schwarz et al. 2015; Lo et al. 2017). Highly cohesive sediments have a higher shear strength which prevents erosion (e.g. scouring) and potential uprooting, even under storm wave conditions (Möller et al. 2014; Spencer et al. 2016a).The sediment used in this experiment was fairly cohesive (32% < 63 µm), implying that erosion and uprooting might have been more prominent in less cohesive, more sandy sediment. Fast developing belowground root networks are likely to be an important survival strategy of developing seedlings, which may facilitate marsh establishment. Moreover, root development is regulated by multiple environmental variables such as oxygen limitation (Bouma et al. 2001), bioturbation and salt stress, which are conditions that were not varied in this study. Therefore, detailed studies of the root development in the first growing season with a focus on rooting depth and outgrowth by rhizomes can provide crucial insights into spatial and temporal patterns of colonisation and survival of marsh plant seedlings (Balke et al. 2014; Cao et al. 2018, 2020).

Simulated storm-wave and local environmental conditions

The hydrodynamics created in this experiment were simulating storm waves that matched or exceeded most severe wave conditions measured in the field in marsh pioneer zones (Table 1). Important to note is that storm wave exposure under field conditions has a duration of multiple hours which is longer than the short term exposure in this experiment. Moreover, water depths in this study (1.5 m) were rather deep. Although such water depths may indeed typically occur during storm surges at the moment of peak water level (Table 2), tidal water level variations in marsh pioneer zones may also lead to storm wave conditions coinciding with much shallower water depths. Therefore, it should be noted that even higher shear stress can be expected under storm conditions coinciding with more shallow water and breaking wave conditions (Fagherazzi and Wiberg 2009; Leonardi et al. 2015; Pascolo et al. 2018).

Interestingly, the two species that were most damaged (i.e. *S. tabernaemontani* and *B. maritimus)*, grow in the brackish water zone of estuaries. Along estuarine salt gradients, the brackish water zone is more upstream, where open water surfaces are typically smaller, and thus wind fetch length and wave loading during storms are expected to be smaller. The two species that were least affected in our experiments (i.e. *P. maritima* and *S. anglica*), grow in the salt water zone, in what are often more exposed areas closer to the mouth of estuaries where storms energies are higher (van der Wal et al. 2008; Callaghan et al. 2010; Yang et al. 2012). This suggests that the natural hydrodynamic growth conditions of the species may have played a role in the selection of species traits that allow salt-marsh plants to cope better with storm waves as compared to brackish marsh species, althoug many other factors such as tolerance to salt stress will play a role, and more research is needed to further investigate this hypothesis. For example, studies on adult plants have already shown different responses to hydrodynamic forces in relation to their species-specific plant traits (e.g. Bouma et al. 2010; Silinski et al. 2016; Rupprecht et al. 2017; Vuik et al. 2018; Zhu et al. 2020; Schoutens et al. 2020).

Implications for planning of marsh restoration and creation

Our results indicate that, depending on the pioneer marsh species, storm wave events can be a bottleneck for the success of marsh establishment in the first growing season. This has implications for the selection and design of suitable marsh restoration or creation sites, a practice that is frequently adopted to enhance or increase the delivery of valuable ecosystem services such as biodiversity conservation, coastal defense, and carbon sequestration (Barbier et al. 2011). Apart from well-documented site characteristics, such as suitable intertidal elevation and soil conditions (Wolters et al. 2008; Zhao et al. 2020), and proximity to existing marshes for seed dispersal (Morzaria-Luna and Zedler 2007; Zhu et al. 2014), our findings stress that site exposure to risks of storm waves is one of the factors that should be taken into account in marsh restoration or creation projects. The latter is expected to become increasingly relevant, as in many coastal areas, storm activity is expected to increase over the coming decades due to climate change (Bender et al. 2010; Vitousek et al. 2017; Habel et al. 2020).

From our findings it becomes evident that, when planning and designing sites for marsh restoration and creation projects, it is important to evaluate the risk of damage and disturbance cauased by storm waves beyond an initial window of opportunity for seed dispersal and germination (Bouma et al. 2014). For example, tidal marsh creation in a brackish water environment, where the pioneer species are *B. maritimus* and *S. tabernaemontani*, will be more vulnarable to storm waves in the first growing season. In contrast, the seedlings of pioneer salt water species such as *S. anglica* and *P. maritima* are better able to withstand the storm waves. Moreover we argue that, depending on the location, a low disturbance period for seed germination (i.e. previously identified to be 3 days up to 4 weeks, Hu et al. 2015) might not be sufficient for successful marsh establishment, as marsh seedlings (here grown for 10 – 14 weeks) can still be disrupted by storm waves. Furthermore, the increased storminess due to global climate change might affect the frequency and duration of windows of opportunity for seedling survival and therefore the chance of marsh establishment (Balke et al. 2014). To mitigate the risk for potential disturbance such as through storm wave events, artificial wave damping structures (such as wood branch fences; Dao et al. 2018) can be used to create temporary sheltered conditions, which can facilitate the growth of seedlings into mature plants and improve the success of the restoration. Indeed, over time, the clonal outgrowth and the formation of a root network seems to secure the survival chance of marsh plants. This type of density-dependent feedback through clonal outgrowth and tussock formation is known to contribute importantly to the stability of more mature marshes (Bouma et al. 2009b; Bricker et al. 2018). Hence, temporary fences constructed to create wave sheltered environments so as to facilitate seedling establishment, may be removed after several years once dense vegetation patches have formed.

Finally, knowledge on the impact of extreme wave events on the probability of seedling establishment is often a big uncertainty in predicting marsh establishment, and is consequently not considered in existing marsh evolution models (Mariotti and Fagherazzi 2010; Hu et al. 2015; Poppema et al. 2019). Large scale flume experiments such as reported in this study, can help to better define processes and parameters that need to be included in marsh development models to improve their predictive capability. As pointed out by Hanley et al. 2020, knowledge on the scale of individual plants is crucial to optimise the succes rate of large scale marsh restoration and creation projects that are key to adapt our coastal areas to the predictions of increased storminess.

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3

Species-specific and seasonal differences in the resistance of salt-marsh vegetation to wave impact

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Abstract

The coastal protection function provided by the vegetation of tidal wetlands (e.g. salt marshes) will play an important role in defending coastlines against storm surges in the future and depend on how these systems respond to such forcing. Extreme wave events may induce vegetation failure and thereby risking loss of functionality in coastal protection. However, crucial knowledge on how hydrodynamic forces affect salt-marsh vegetation and whether plant properties might influence plant resistance is missing. In a true-to-scale flume experiment, we exposed two salt-marsh species to extreme hydrodynamic conditions and quantified wave-induced changes in plant frontal area, which was used to estimate plant damage. Additionally, some plants were artificially weakened (via drought) as we expected seasonal changes in plant resistance, as the leaves and stems of examined species die off during the winter and their biophysical properties may undergo considerable modifications. Morphological, biomechanical as well as biochemical plant properties were assessed to better explain potential differences in wave-induced plant damage. Our results indicate that the plants were more robust than expected, with pioneer species *Spartina anglica* showing a higher resistance than the high-marsh species *Elymus athericus*. Furthermore, wave-induced plant damage mostly occurred in the upper part of the vegetation canopy and thus higher canopies (i.e. *Elymus athericus*) were more vulnerable to damage. Besides a taller canopy, *Elymus athericus* had weaker stems than *Spartina anglica*, suggesting that biomechanical properties (flexural stiffness) also played a role in defining plant resistance. Under the highest wave conditions, we also found seasonal differences in the vulnerability to plant damage but only for *Elymus athericus*. Although we found higher concentrations of a strengthening compound (biogenic silica) in the plant material of the weakened plants, the flexibility of the plant material was not affected indicating that the drought might not has been applied long enough. Nevertheless, this study yields important implications since we demonstrate a high robustness of the salt-marsh vegetation as well as species-specific and seasonal differences in the vulnerability to plant damage.

Introduction

Salt marshes are intertidal wetlands that are widely distributed along the coastlines from middle to high latitudes. They are increasingly recognised as contributing to the provision of valuable ecosystem services such as climate change mitigation through long-term carbon sequestration (Mcleod et al. 2011) or coastal protection through wave attenuation (Möller et al. 2014). To a great extent, the provision of these ecosystem services is determined by the vegetation of salt marshes which mainly consists of highly specialised grasses, herbs and shrubs that are adapted to high salinities and regular flooding (Adam 2002). Despite their value, the persistence of salt marshes is threatened by anthropogenic pressures like their embankment, land-use change, eutrophication and climate change, leading to a salt-marsh loss of 1-2 % of the global area per year (Duarte et al. 2013). From all climate change factors, so far the impact of accelerated sea level rise on marshes has been most widely studied (Spencer et al. 2016b; Schuerch et al. 2018), while other climate change effects such as the projected changes in storm intensities and thus hydrodynamic forcing has still received relatively less attention (Leonardi et al. 2018; Armitage et al. 2020).

Previous research examining the interaction of hydrodynamic forces and salt-marsh vegetation mainly focused on the wave attenuation capacity of salt marshes, i.e. the effect of vegetation on waves. These studies compared the wave attenuation capacity of different plant species as well as whole ecosystems, or aimed to find determinants of effective reduction in wave energy (Anderson and Smith 2014; Möller et al. 2003; Pinsky et al. 2013). In a true-to-scale flume experiment, Möller et al. (2014) showed that the vegetation of NW European salt marshes is able to reduce significant wave height by between 15 % and 60 % over a 40 m distance under storm surge conditions. Additionally, the authors observed that the behavior of the tall grass *Elymus athericus* under the action of waves differed from that of the much shorter *Puccinellia maritima*, suggesting that plant-wave interactions and thereby wave attenuation capacity is dependent on species-specific traits such as plant height, plant density, and rigidity (Rupprecht et al. 2017). These species traits eventually affect vegetation properties as aboveground biomass (Bouma et al. 2010; Ysebaert et al. 2011), stem density (Bouma et al. 2005; Anderson and Smith 2014) and biomechanical properties (e.g. stem flexibility, Riffe et al. 2011, Paul et al. 2016), all mediating wave attenuation. However, the vegetation's ability to reduce wave energy is also depending on hydrodynamic conditions like inundation depth and wave orbital velocity (Garzon et al. 2019; Koch et al. 2009; Gedan et al. 2011b). For example, above certain values of orbital velocity, stem breakage and biomass loss may lead to a decrease in wave attenuation (Vuik et al. 2018; Rupprecht et al. 2017). Yet, studies investigating these limits, i.e. defining hydrodynamic conditions above which salt-marsh vegetation experiences severe physical damage, as well as factors that influence plants resistance, are rare.

The few studies that focused on physical damage induced by waves all suggest that the plant damage is species-specific (Coops and van der Velde 1996; Heuner et al. 2015; Vuik et al. 2018; Schoutens et al. 2021). Furthermore, the observed differences between species have been attributed to differences in stem flexibility (Coops and van der Velde 1996; Heuner et al. 2015; Vuik et al. 2018) and plant height (Vuik et al. 2018) and, in the case of seedling survival, stem diameter (Schoutens et al. 2021). A stem breakage model developed by Vuik et al. (2018) combined plant morphology (stem height and diameter), flexural strength of the stems and wave-induced bending stress to determine hydrodynamic forces above which stems break or fold. It was found that shorter species were more flexible than taller ones and have a lower probability of stem breakage. However, according to Vuik et al. (2018), a species-specific validation remains indispensable.

Apart from species-specific differences, seasonality in vegetation properties needs to be considered when evaluating the resistance of salt-marsh vegetation and their role for wave attenuation capacity (Zhang et al. 2022; Schoutens et al. 2019). In temperate and boreal regions, aboveground parts of many salt-marsh species die-off in autumn, but remain as dead standing biomass in winter until storms induce breakage of stems or leaves and eventually carry the litter away. While transforming from a vital to senescent or even dead state, the plant material undergoes major physiological changes that affect biomechanical properties like stem flexibility (Zhu et al. 2020; Coops and van der Velde 1996; Schulze et al. 2019). The seasonal vegetation response was also confirmed by the stem breakage model of Vuik et al. (2018), which suggested that the salt-marsh grass *Spartina anglica* is more vulnerable to stem breakage in November compared to December or April. During the storm surge season in temperate regions (from autumn until early spring), the coastal protection provided by salt marshes is most needed. However, the protection capacity in winter might be hampered due to changes in plant resistance and wave-induced damage. To our knowledge, it has never been experimentally tested whether seasonal changes in biomechanical or even morphological vegetation properties directly affect plant resistance to extreme wave conditions.

To improve our understanding on how plant's vulnerability to wave-induced damage differs between species and seasonal conditions, we thus conducted a controlled flume experiment. We exposed two NW European salt-marsh grass species (*Spartina anglica*, *Elymus athericus*) to progressively increased wave energies and measured plant response as well as biomechanical, biochemical and morphological plant properties. Since *Spartina anglica* usually grows in the pioneer zone of the marsh (low elevations, at the marsh edge), we expected a higher resistance to hydrodynamic forcing and thus lower vulnerability to wave-induced plant damage than for *Elymus athericus,* which typically grows at higher elevations that are less frequently flooded. Furthermore, prior to wave exposure, we induced senescence in half of the plants to create a weakened ‘autumn treatment’. We hypothesised that the plant’s resistance to hydrodynamic forcing is negatively affected by the autumn treatment due to changes in their biomechanical properties.

Material & Methods

This flume experiment was conducted in the Large Wave Flume (Großer Wellenkanal (GWK) of the Forschungszentrum Küste (FZK) Hanover, Germany) in which salt-marsh plants, that have been previously collected in the field, were exposed to extreme hydrodynamic conditions. In addition to recordings of plant response to wave exposure (i.e. wave-induced plant damage), plant properties were assessed.

Plant material

For this study we used *Spartina anglica* (C. E. Hubb) and *Elymus athericus* (Link) Kerguélen, two clonal grass species that are widely distributed in NW European salt marshes. In March 2018, plants were collected in salt marshes of Paulinaschor (*Spartina anglica,* 51°20'56.2"N 3°43'37.4"E) and Zuidgors (*Elymus athericus,* 51°23'13.6"N 3°49'18.5"E) along the Western Scheldt estuary in the Netherlands. They were excavated in sods (20 cm x 20 cm) and transported to the Royal Netherlands Institute for Sea Research (NIOZ) in Yerseke, the Netherlands, where they were kept in the greenhouse until they were planted. Before planting the sods, boxes (120 cm x 80 cm x 40 cm, hereafter referred to as pallets) were lined with an impermeable foil and filled with sediment taken from a marsh of the Scheldt estuary (see Schoutens et al. (2021) for soil properties). Ten holes (2 mm diameter) on each side of the pallet were drilled to allow for drainage after inundation. In April, six sods per pallet were arranged together to create a dense canopy. The sods were planted at one end of the pallet to allow the waves to run up over an unvegetated strip before reaching the vegetation (Fig. 1A, B).

To assess seasonal differences in plant response to hydrodynamic forces, half of the plants were subjected to an ‘autumn treatment’ while the others remained as ‘summer treatment’. The ‘autumn’ treatment was achieved by creating a drought, since the plant stress response (e.g. to drought) shares many similarities with the process of natural plant senescence at the end of the growing season (Gepstein and Glick 2013; Sade et al. 2018). To create a drought, pallets of the ‘autumn treatment’ were covered for six weeks prior to the flume experiment to exclude rainfall while the ‘summer treatment’ pallets were kept irrigated with freshwater (Schoutens et al. 2021). Hereafter, the term treatment is used to refer to the condition of the vegetation (summer/autumn).

Flume set up

The experiment in the Large Wave Flume (300 m x 5 m x 7 m) was carried out over three weeks in August 2018. For addressing different research questions within the RESIST project, five zones in total (10 m apart) were used to investigate the effect of increased hydrodynamic forces on different types of marsh vegetation as well as their soil surface. For instance, in Schoutens et al. (2021), we reported the results for one specific zone where we tested the resistance of seedlings to strong waves. Within each zone five pallets were placed next to each other over the flume width and between concrete blocks which had the same height as the pallets (Fig. 1C). The present study only focusses on one other zone, where we specifically tested the resistance of mature shoots of *Spartina anglica* and *Elymus athericus,* both in summer and autumn treatment, resulting in four pallets within this zone, while one pallet was left empty. Each Monday for the three weeks of the experiment, we placed a new (replicate) set of pallets into the flume and carried out baseline measurements.

Hydrodynamic conditions

Hydrodynamic conditions were the same as reported in Schoutens et al. (2021). Each day from Tuesday to Friday, we created a sequence of waves that are hereafter referred to as ‘wave runs’. Wave runs consisted of 1000 randomly generated waves (JONSWAP spectrum, Hasselmann et al. 1973) that were monitored with wave gauges and from which we calculated significant wave height (H_s) and significant wave period (T_s). The still water level was 1.5 m

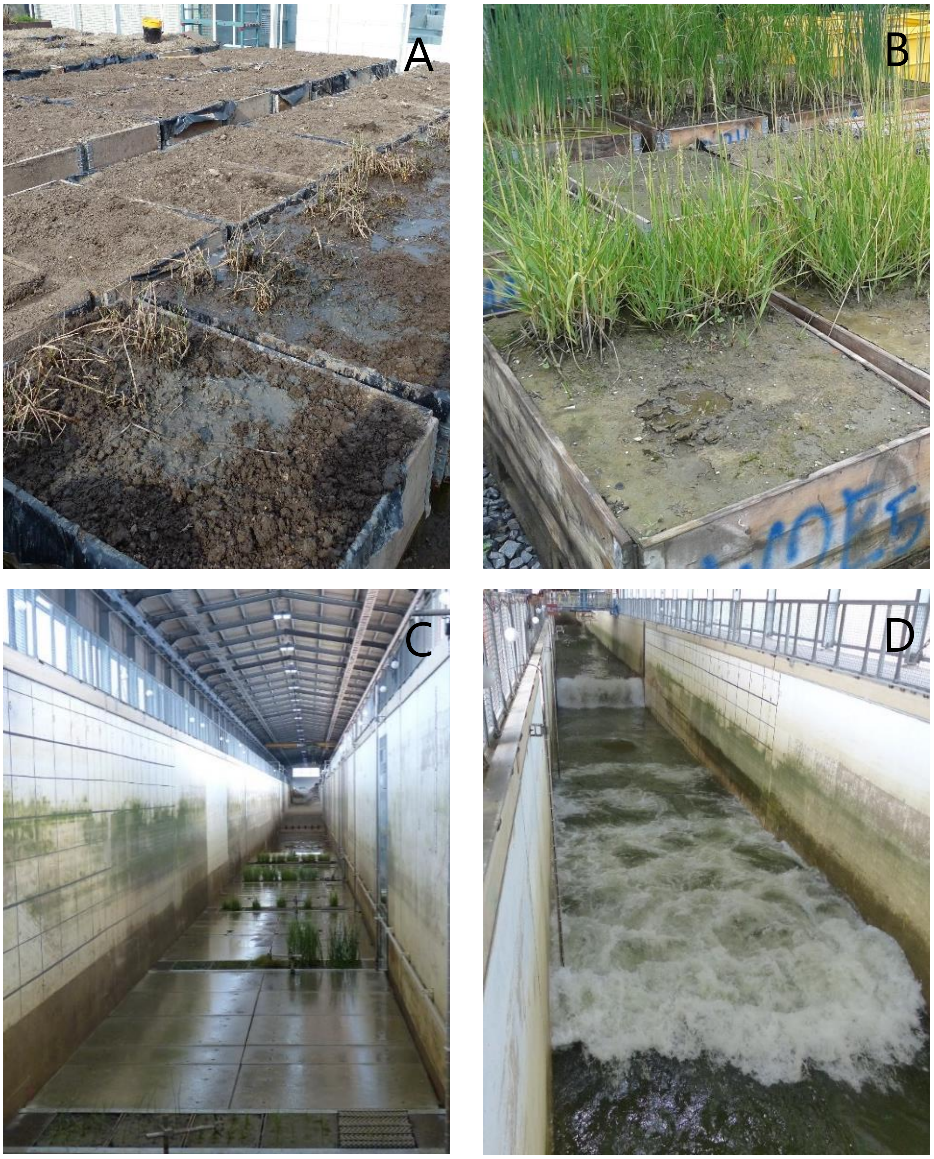

Figure 1 Sediment boxes after planting (A) and prior to placement into the flume (B). Experimental setup within the Large Wave Flume (Großer Wellenkanal (GWK) of the Forschungszentrum Küste (FZK) Hanover, Germany) after draining (C) and during a wave run (D).

above the sediment surface for all wave runs. We increased bed orbital velocity by increasing wave height and/or wave period in subsequent wave runs over the course of days and weeks (Table 1), which also implies a cumulative wave exposure experienced by the vegetation and sediment per week. In the third week, pallets were moved forwards along the test section in the direction of the wave paddle to further increase hydrodynamic forces. The wave conditions generated in this flume experiment were comparable to natural storm surge conditions in temperate regions (Schoutens et al. 2021). After each wave run, we slowly drained the flume to record potential impacts of hydrodynamic forcing on the vegetation (details in next section).

Table 1 Wave conditions measured in front of the first zone generated in this flume experiment and shown per week and wave run. All wave runs consisted of randomly generated waves except for the last wave run (wave run 4 in week 3, italic), where monochromatic waves were used to increase bed shear stress beyond that which can be generated by random wave sequences (see also Schoutens et al. (2021)).

		Significant wave height (H_s, in m)			Significant wave period (T_s, in seconds)		
		Week 1	Week 2	Week 3	Week 1	Week 2	Week 3
Wave run	1	0.30	0.68	0.68	2.58	3.80	4.02
	2	0.40	0.68	0.77	4.22	3.80	5.63
	3	0.58	0.78	0.78	3.56	5.66	5.63
	4	0.69	0.78	*0.71*	5.23	5.63	*6.00*

Vegetation response: Δ frontal area and mean vegetation height

To measure plant damage non-destructively, we used the photo-method described by Möller (2006). Every day, a red screen with a scale attached was placed behind the vegetation to increase contrast between vegetation and background (Fig. 2A). Side-on photographs (Fig. 2B) were taken of the vegetation from the back of the pallet (i.e. facing the back of the flume) always at the same position, height and distance to the screen. This was achieved by putting a calibrated camera to permanent fixings mounted on the experimental platform. Photographs were cropped and corrected for distortion in MATLAB (The MathWorks Inc. 2019) before pixels were classified into either vegetation or background pixel using an unsupervised classification tool and followed by manual class allocation in ArcGIS (ESRI 2020). Similarly to Rupprecht et al. (2015), these obtained binary images (Fig. 2C) were used to perform further program routines in MATLAB to generate information on vegetation structure, adapting the protocol developed by Möller (2006, MATLAB program available on request). Vegetation structure parameters included projected plant frontal area (the proportion of vegetation to background pixel) per pixel column and per horizontal subsections, as well as the vegetation profile (highest vegetation pixel per pixel column). While projected plant frontal area per pixel column was further processed as described below, plant frontal area per horizontal subsections was used to illustrate potential changes in the spatial distribution of the vegetation in each photograph.

Projected plant frontal area per pixel column was spatially referenced and converted into 1 cm wide columns (starting from the bottom left of the image). The data was averaged over 5 cm wide vertical subsections. Every second subsection, as well as the left and right outer edges (6 cm each), were removed to reduce potential impacts from adjacent subsections and pallets, respectively. To detect potential changes in plant frontal area due to wave exposure (indicating plant damage), we calculated the difference between projected plant frontal area prior to (Monday) and after wave exposure (Friday) per week (designated as Δ plant frontal area). It should be noted that changes in plant surface area might result from plant damage but also from reconfiguration of shoots and leaves. Estimations for vegetation height were obtained from vegetation profile data of the photographs taken prior to wave exposure. That data was averaged over the same 5 cm wide vertical subsections as for Δ plant frontal area and designated as mean vegetation height.

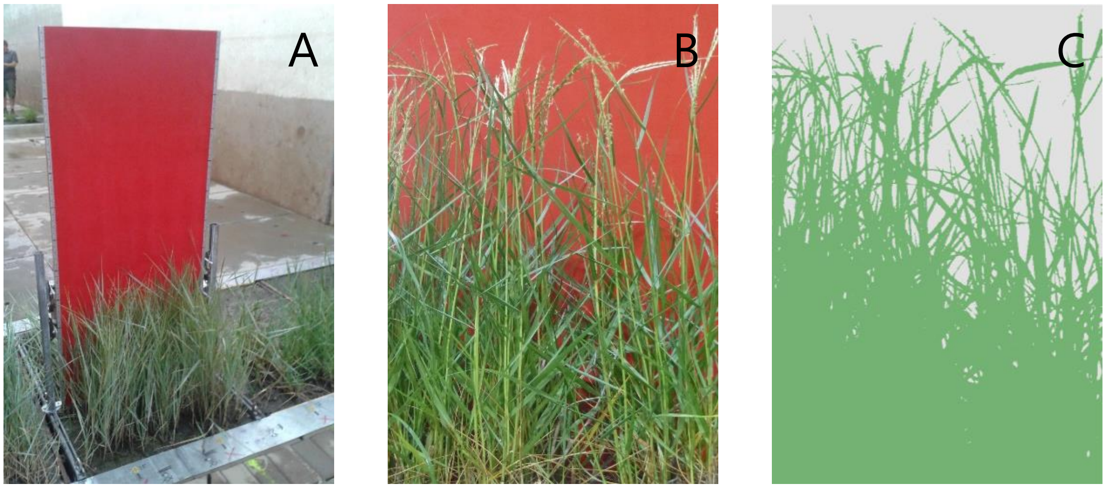

Figure 2 The red screen with scales attached on the sides (A) that was used to take side-on photographs of the vegetation. After they have been cropped and corrected for distortion (B) photographs were converted into binary images (C).

Biomechanical plant properties

Three-point bending tests were performed to measure stem flexibility as potential explanatory factor of plant damage under hydrodynamic forcing. Each week prior to and after wave exosure, five stems per species-treatment combination were cut at random at the soil surface. The bottom part of the stem was shortened to a length that was not exceeding a stem diameter-to-length ratio of 1:15 to avoid shear stress while testing (Niklas 1992). Bending tests were performed with a universal test machine, including flexure fixture and a 5 kN load cell (Instron Corporation, Canton, MA, USA). Following Rupprecht et al. (2015) and Schulze et al. (2019), a force-displacement curve was created to determine the linear slope indicating elastic behavior that was then used to calculate flexural stiffness. Flexural stiffness or flexural rigidity describes the ability of the stem to resist bending, i.e. high values indicate high stem stiffness and thus low flexibility. It combines the information on the stem's material property expressed by the Young's bending modulus and the stem's morphology expressed by the second moment of area which both contribute to overall flexural stiffness. The second moment of area is a term to include stem morphology (i.e. shape and diameter). Since the second moment of area can be derived from the stem's dimensions, we were able to calculate Young's bending modulus, which is only describing the flexibility of the material but without taking stem morphology into account. Equations for calculating flexural stiffness, second moment of area and Young's bending modulus can be found in the appendix.

Biochemical plant properties

Biogenic silica, lignin and cellulose are known to affect the rigidity of plant tissue (Schoelynck et al. 2010; Schoelynck et al. 2012; Turner et al. 2001) and thus Young's bending modulus. Potential differences in concentrations of these strengthening compounds could provide additional explanations for differences in stem flexibility and therefore plant resistance to hydrodynamic forcing. Plant material that was harvested for flexibility measurements was dried for 72 hours at 70°C and afterwards ground with a mixer mill (MM400, Retsch, Germany). For analyzing lignin and cellulose content, we used the Van Soest method (Van

Soest 1963) whereas the biogenic silica content was determined by applying the DeMaster alkaline extraction method (DeMaster 1981).

Statistical analyses

To test whether Δ plant frontal area (difference between projected plant frontal area prior to and after wave exposure), flexibility parameters (Young's bending modulus, flexural stiffness) and concentration of strengthening compounds (cellulose, lignin, biogenic silica) differed between species, treatments and weeks, factorial ANOVAs were applied. Accordingly, species, treatment, and week, as well as their interactions, were set as explanatory variables. After visually checking ANOVA assumptions following Zuur et al. (2010), flexibility parameters (Young's bending modulus, flexural stiffness) were log transformed to meet normality assumptions. Plant material that was harvested for flexibility measurements and biochemical analyses was tested for differences between the two harvesting days (Monday and Friday). Since we did not find any differences, we merged the data per week. To detect significant differences between species, treatments, and weeks, post hoc tests (Tukey's HSD, honest significant difference) were applied. A linear regression was performed to examine the relationship between Δ plant frontal area and mean vegetation height for the entire data set and separately for each species-treatment combination. To test whether biogenic silica concentration affect the flexibility of the plant material (Young's bending modulus) another linear regression with these two variables was conducted. For this regression, Young's bending modulus needed to be averaged per measurement day to be in the same format as the biogenic silica data. All statistical analyses were performed using R version 4.1.1. (R Core Team 2021).

Results

Plant damage under wave exposure

Δ plant frontal area, as indicator for plant damage, differed significantly between species, treatments, and weeks (Table 2). Additionally, the three-way-interaction of these factors had a significant effect on Δ plant frontal area as well. In general, *Elymus athericus* showed a stronger reduction in frontal area compared to *Spartina anglica* (*Elymus*: -985.31 ± 950.66

mm^2/mm, *Spartina*: -6.44 ± 499.91 mm^2/mm, Fig. 3, mean ± SD), implying that *Elymus athericus* lost more biomass due to wave exposure than *Spartina anglica*. Summer and autumn treatments of *Spartina anglica* showed similar response in Δ plant frontal area and decreased from week to week. This decrease was also found for *Elymus athericus* in autumn condition, but in comparison with *Spartina anglica* it was much more pronounced in *Elymus athericus*. In the third week, the difference in Δ plant frontal area between the summer and autumn treatment of *Elymus athericus* was highly significant (Fig. 3) while differences between summer and autumn treatment were not significant for all other weeks for *Elymus athericus* and were never significant for *Spartina anglica*.

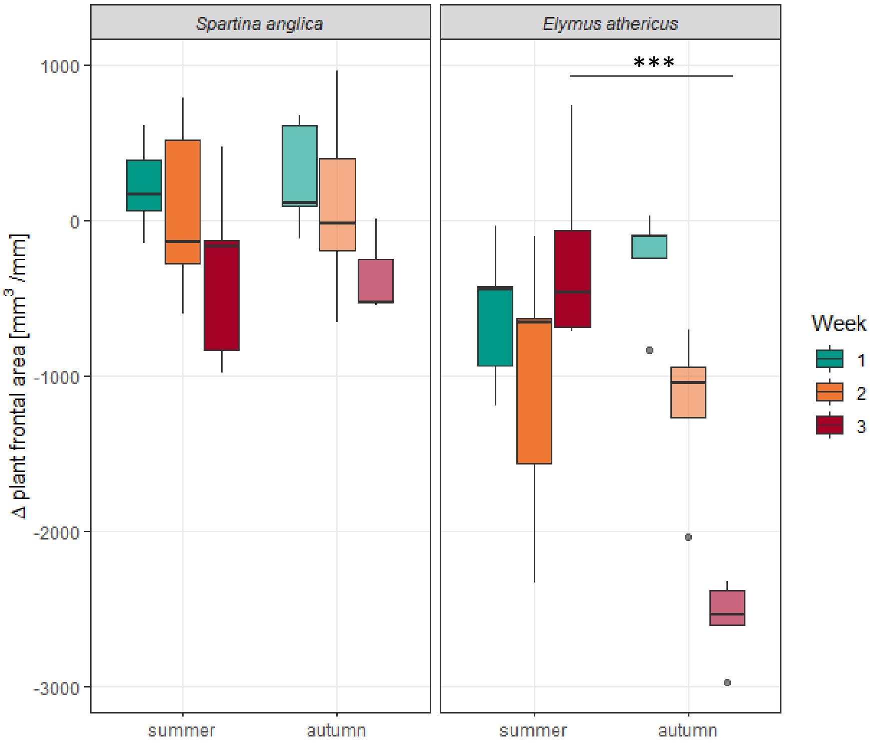

Figure 3 Δ plant frontal area (difference between prior to and after wave exposure) per week of *Spartina anglica* and *Elymus athericus* in summer and autumn condition. Asterisks show significant differences between the summer and autumn treatment within the same species and week based on Tukey's HSD post hoc test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 2 Summary statistics of factorial ANOVAs for testing the effect of species, treatment and week (and their interaction) on Δ plant frontal area, Young's bending modulus (MPa), flexural stiffness (Nm^2) and biogenic silica concentration (mg/g dry weight). Cellulose and lignin are not included since no significant effects were detected (n.s. = not significant).

	Δ plant frontal area		Young's bending modulus		Flexural stiffness		Biogenic silica	
	F value	p value	F value	p value	F value	p value	F value	p value
Species	54.83	<0.001	64.98	<0.001	111.41	<0.001	50.99	<0.001
Treatment	6.72	<0.05	1.98	n.s.	2.63	n.s.	16.00	<0.01
Week	11.77	<0.001	20.05	<0.001	7.05	<0.01	10.25	<0.01
Species x treatment	7.44	<0.01	3.43	n.s.	0.09	n.s.	3.52	n.s.
Treatment x week	10.48	<0.001	0.27	n.s.	0.38	n.s.	2.45	n.s.
Species x week	1.45	n.s.	2.21	n.s.	9.32	<0.001	1.99	n.s.
Species x treatment x week	9.04	<0.001	2.05	n.s.	0.32	n.s.	0.16	n.s.

Considering the spatial distribution of the vegetation in each photograph (Fig. 4), the area from the bottom of the photograph to 20 cm height was completely saturated with vegetation for both species. For *Elymus athericus,* the area from 20 to 40 cm was likewise saturated, while wave-induced changes in frontal area became visible in this section on photographs of *Spartina anglica*. However, most changes in frontal area were detected in the upper section (>40 cm) for all species-treatment combinations. Here, frontal area tended to decrease over the course of days and weeks, which was most pronounced in the autumn treatment of *Elymus athericus*, indicating that plant damage was restricted to biomass removal from the top of the vegetation.

Morphological properties and plant damage

The linear regression between mean vegetation height (in mm) and Δ plant frontal area showed a negative relationship ($R^2 = 0.36$, $p < 0.001$, Table 3) indicating an increase in plant damage (as Δ plant frontal area decreased) with increasing vegetation height (Fig. 5). Additionally, mean vegetation height clearly differed between both species, i.e. *Elymus athericus* being taller than *Spartina anglica* (Fig. 5). For both species, autumn treatments were slightly taller than summer treatments (*Spartina anglica*: 624.1 ± 98.5 mm (summer) and 658.9 ± 145.6 mm (autumn), *Elymus athericus*: 832.7 ± 121.3 mm (summer) and 929.9 ± 92.4 mm (autumn)). However, no significant linear relationships between mean vegetation height and

Δ plant frontal area were found for single species-treatment combinations except for the summer treatment of *Elymus athericus* (Table 3). This implies that canopy height alone did not explain observed differences in plant damage between the other species-treatment combinations.

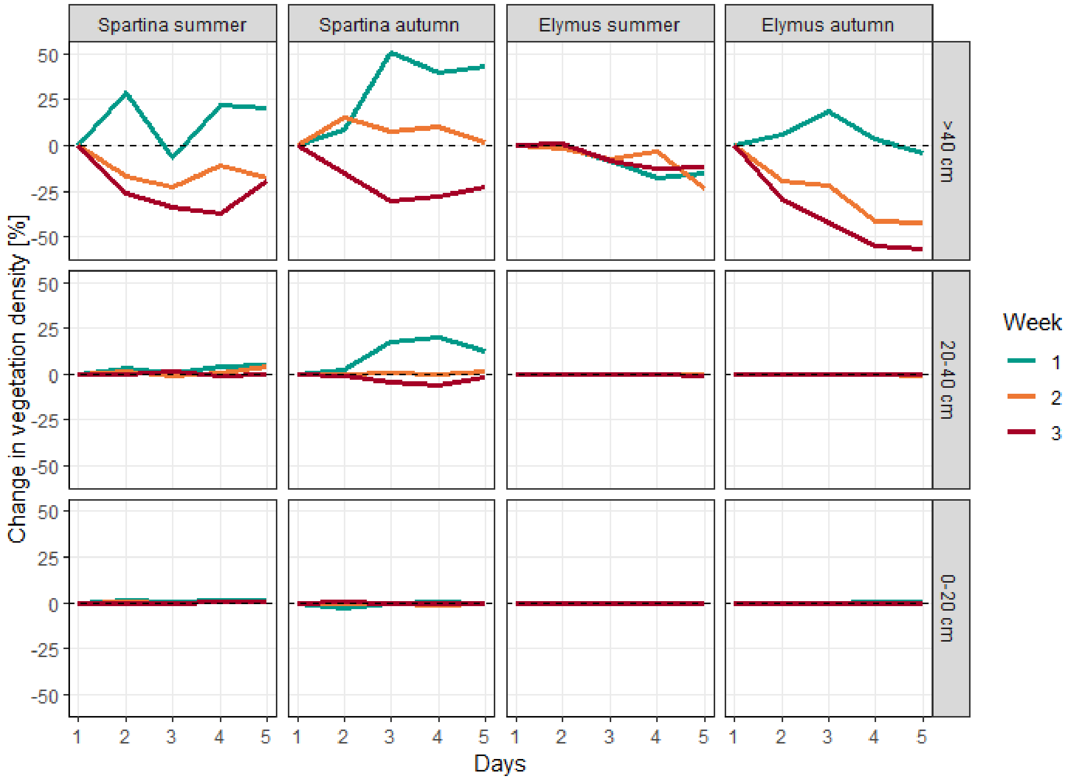

Figure 4 Change in projected plant frontal area in percent (relative to the condition prior to wave exposure on day 1) of three different horizontal subsections shown per day, week and species-treatment combination. Dashed lines indicate a plant frontal area equivalent to the initial state on day 1 of the experimental week (i.e. 100 %).

Table 3 Results of linear regression analyses testing the relationship between mean vegetation height and Δ plant frontal area for the different species-treatment combinations as well as the entire data set (n.s. = not significant).

Species	Treatment	Estimate	Std. Error	t value	Pr(>|t|)
Spartina anglica	summer	-0.769	1.467	-0.524	n.s.
	autumn	-1.594	0.823	-1.938	n.s.
Elymus athericus	summer	-3.306	1.355	-2.440	**<0.05**
	autumn	-1.066	3.128	-0.341	n.s.
All data		-3.184	0.557	-5.718	**<0.001**

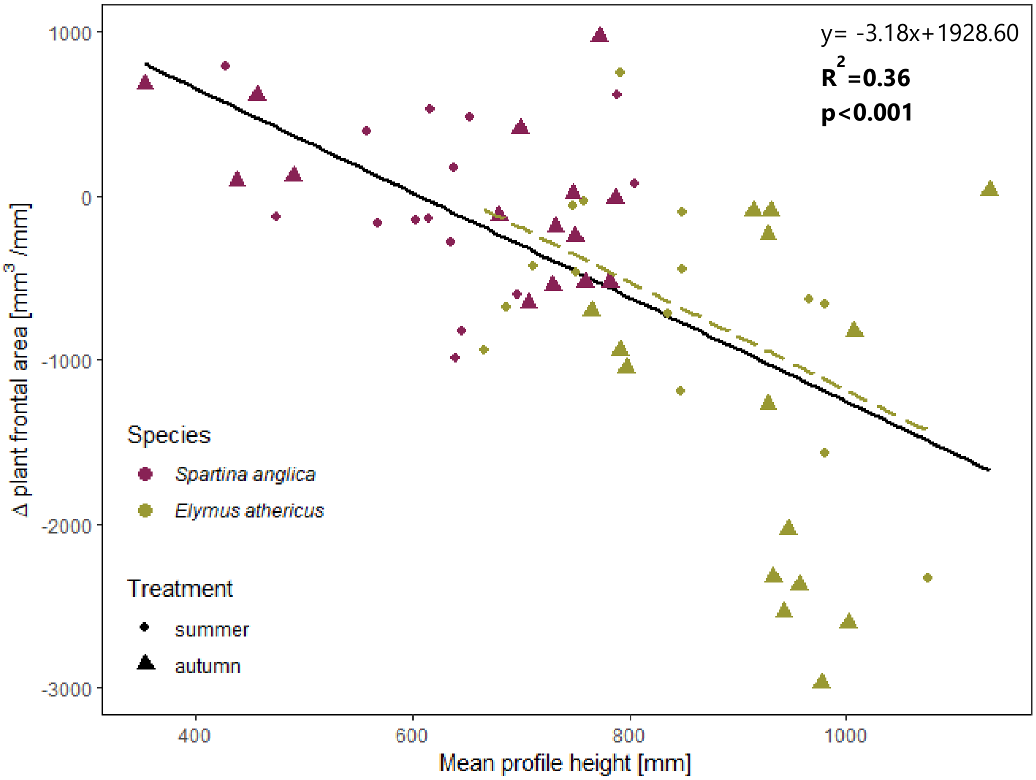

Figure 5 Linear regression showing the significant negative relationship between mean vegetation height (in mm, measured prior to wave exposure) and Δ plant frontal area of the entire data set (black line, *Spartina anglica* and *Elymus athericus* including both summer and autumn treatment). The dashed line indicates the significant linear relationship between mean vegetation height and Δ plant frontal area of the summer treatment of *Elymus athericus* only, while the ones of the other species-treatment combinations were not significant (Table 3) and therefore not shown here.

Biomechanical plant properties and plant resistance

Young's bending modulus differed significantly between species and weeks, but no significant effects of treatment and the interactions between factors were found (Table 2). In general, Young's bending modulus of *Elymus athericus* was twice as high as that of *Spartina anglica* (*Elymus*: 1169.82 ± 646.86 MPa, *Spartina*: 553.74 ± 315.04 MPa, Fig. 6), indicating a higher stiffness of the plant material of *Elymus athericus*. From week to week, Young's bending modulus increased, a trend that was more pronounced for *Elymus athericus*.

Similarly, flexural stiffness, which describes the absolute strength of plant stems (material stiffness + stem morphology), differed significantly between species and weeks (Table 2). Furthermore, the interaction of species and week had a significant effect on flexural stiffness of the vegetation. Flexural stiffness of *Spartina anglica* was four times higher than of *Elymus athericus* (*Spartina*: 6.56 ± 4.39 Nm^2*10^{-3}, *Elymus*: 1.61 ± 1.59 Nm^2*10^{-3}), indicating that *Spartina anglica* stems had a higher resistance to -bending than the ones of *Elymus athericus*. Yet no clear trend was recognizable for *Spartina anglica,* we found a slight increase in flexural stiffness for *Elymus athericus* from week to week (Fig. 7).

Biochemical properties and plant resistance

We found no significant effects of species, treatment or week on the lignin and cellulose concentration of the plant material harvested in our flume experiment. Biogenic silica concentration, however, was significantly affected by species, treatment, and week but no significant interaction was found (Table 2). Biogenic silica concentration in the plant material of *Elymus athericus* was almost twice as high as of *Spartina anglica* (*Elymus*: 7.14 ± 1.66 mg/g dry weight, *Spartina*: 4.84 ± 0.85 mg/g dry weight). Plants that had been exposed to the autumn treatment had higher biogenic silica concentrations than those of the summer treatment, but this was only significant in *Elymus athericus* (Table 4). Regardless of the species-treatment combinations, biogenic silica concentrations of the third week were significantly higher than those measured in the first and second week (*1*: 5.50 ± 1.99 mg/g dry weight, *2*: 5.45 ± 1.07 mg/g dry weight, *3*: 7.02 ± 1.75 mg/g dry weight). Highest concentrations for biogenic silica were detected in the autumn treatment of *Elymus athericus* (Table 4). The biogenic silica concentration and Young's bending modulus showed a significant positive relationship, indicating an increase in the stiffness of the plant material with increasing biogenic silica concentration (Fig. 8).

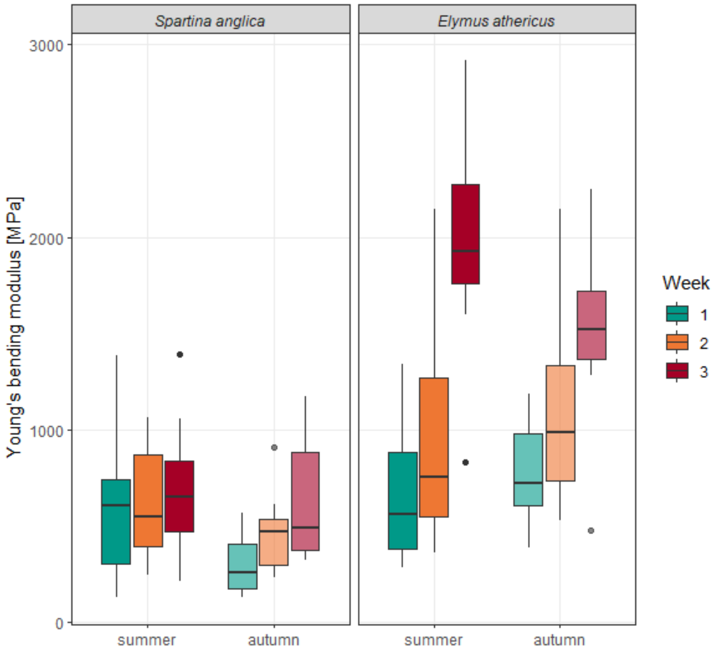

Figure 6 Young's bending modulus (MPa) per week of *Spartina anglica* and *Elymus athericus* in summer and autumn condition.

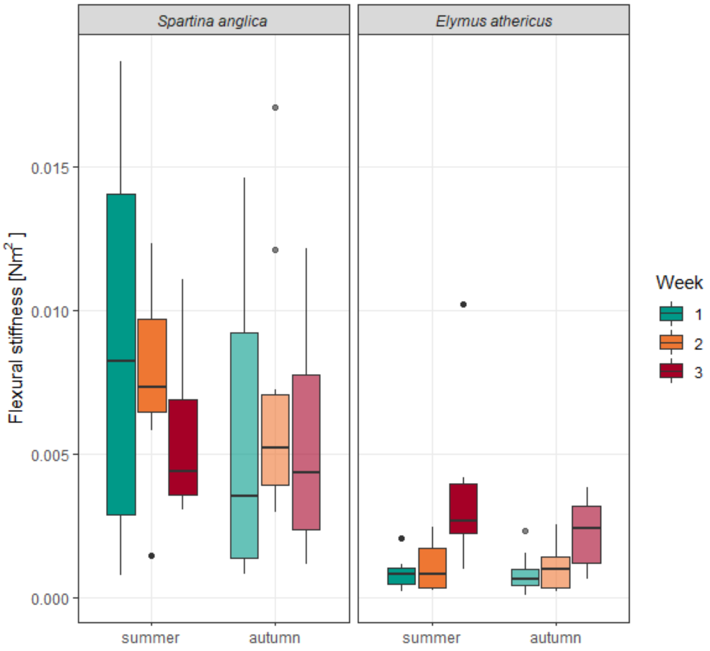

Figure 7 Flexural stiffness per week of *Spartina anglica* and *Elymus athericus* in summer and autumn condition.

Table 4 Strengthening compound concentration of plant material of two salt-marsh species in summer and autumn condition averaged over weeks (mean ± SD in mg/g dry weight). Different letters indicate significant differences between species-treatment combinations according to a Tukey test at $p < 0.05$.

	Spartina anglica		*Elymus athericus*	
Compound	summer	autumn	summer	autumn
Cellulose	276.75 ± 16.16^{a}	240.08 ± 90.34^{a}	214.72 ± 28.88^{a}	246.46 ± 25.55^{a}
Lignin	42.44 ± 26.29^{a}	29.84 ± 20.67^{a}	31.28 ± 12.20^{a}	29.47 ± 9.67^{a}
BSi	4.50 ± 0.80^{a}	5.18 ± 0.82^{ab}	6.20 ± 1.06^{b}	8.09 ± 1.66^{c}

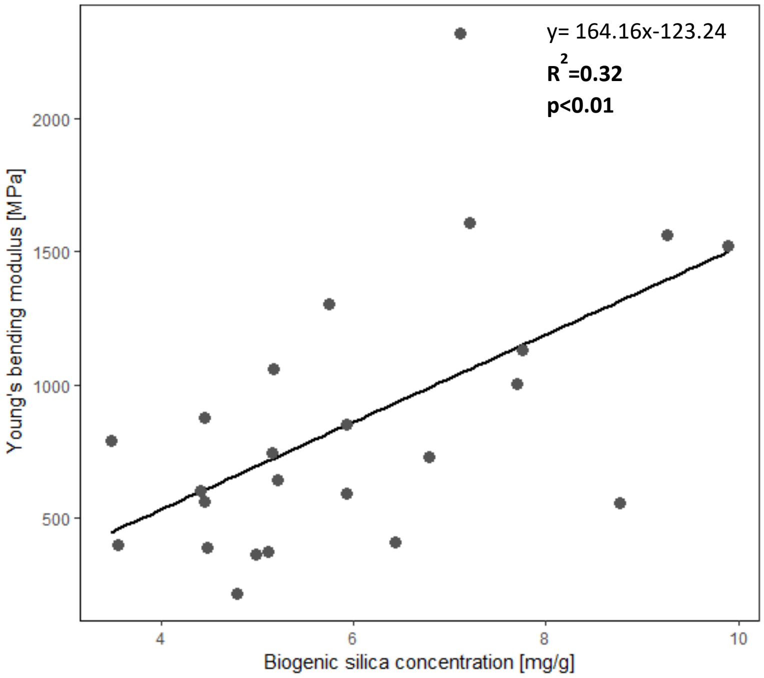

Figure 8 Linear regression showing the significant positive relationship between Young's bending modulus and biogenic silica concentration. The data includes both species, treatments and all three weeks.

Discussion

Our study investigated the resistance of salt-marsh vegetation to wave-induced plant damage, which is a relevant question as climate change may induce changes in wave forcing on marshes, and as damage to marsh vegetation may imply loss of valuable ecosystem services. So far, studies investigating how hydrodynamic forces affect marsh vegetation focused exclusively on vital vegetation (Rupprecht et al. 2017; Heuner et al. 2015). Seasonal differences in vegetation condition were only accounted for in modelling studies (Vuik et al. 2018) and in field studies (Schulze et al. 2019; Zhu et al. 2020; Schoutens et al. 2019) not directly quantifying plant damage. This flume experiment was designed to compare wave-induced plant damage of two salt-marsh species under both summer (vital) and autumn (weakened) conditions. Furthermore, we aimed to assess whether species-specific or seasonal differences in plant damage are caused by potential differences in biomechanical, biochemical and/or morphological plant properties. In accordance with our first hypothesis, the wave forcing caused significantly more damage (measured as Δ plant frontal area) to *Elymus athericus*, than to *Spartina anglica*. Moreover, we found indications of higher plant damage in the autumn treatment compared to the summer treatment in *Elymus athericus*, but not in *Spartina anglica*, only partly supporting our second hypothesis. In the following paragraphs, we will discuss factors that may have affected our results, focusing on measured variables (canopy height, biomechanical and biochemical plant properties) and whether they are suitable determinants of plant resistance to wave-induce plant damage.

In comparison with *Elymus athericus*, the plant damage of *Spartina anglica* was relatively low. *Spartina anglica* is typically growing in pioneer marsh zones and is therefore regularly exposed to higher wave intensities, which may lead to a higher resistance, as compared to *Elymus athericus*, which grows typically in high, wave-sheltered marsh zones (Suchrow and Jensen 2010). This adaptation mechanism has also been suggested as a possible explanation for thicker reed (*Phragmites spp*) stems at an exposed site on the southern shore of the Baltic Sea (Möller et al. 2011) and has been shown to exist for other marsh pioneer species (Silinski et al. 2018). Even seedlings already display different levels of plant resistance to hydrodynamic forcing depending on their site of origin, with salt-marsh species being less damaged by hydrodynamic forcing than brackish-marsh species (Schoutens et al. 2021).

Vegetation height

Our results indicate that wave-induced plant damage mostly occurs in the upper part of the vegetation canopy (Fig. 4) and that higher vegetation canopies (e.g. *Elymus athericus*) are more vulnerable to damage (Fig. 5). An increase in plant damage with increasing plant height was also described by Vuik et al. (2018). Taller plants might be more affected by wave impact because wave orbital motion and thereby wave energy is greatest at the water surface and decreases with water depth (Anderson and Smith 2014; Möller and Christie 2019). Although plants under the autumn treatment were slightly taller than under the summer treatment, these differences might not have been big enough to affect the plants vulnerability to plant damage since we have not found significant relationships through our linear regression analyses (except for *Elymus athericus* in summer condition, Table 3). This suggest that vegetation height alone did not entirely explain observed pattern e.g. the higher plant damage in the autumn treatment compared to the summer treatment of *Elymus athericus*. However, it should be noted that one value of *Elymus athericus* under the autumn treatment stands out (mean vegetation height = 1131.68 mm, Δ plant frontal area = 31.89 mm^2/mm, Fig. 5) which might have affected the insignificance of the relationship.

Biomechanical plant properties and plant damage

Canopy height may correlate with biomechanical plant properties because taller species tend to have stiffer stems than shorter ones (Zhu et al. 2020). In our study, this difference between taller and shorter species was only true for Young's bending modulus, which describes the stiffness of plant material itself without taking stem morphology into account. Here the plant material of the taller species (*Elymus athericus*) was indeed stiffer. However, when considering the absolute strength of the stems by integrating stem morphology (i.e. flexural stiffness), the taller species *Elymus athericus* had weaker stems than the shorter *Spartina anglica* (Fig. 7), which might have contributed to the higher vulnerability to wave-induced plant damage found for *Elymus athericus*. Flexural stiffness of *Elymus athericus* (1.61 ± 1.59 Nm^2*10^{-3}) was similar to values Rupprecht et al. (2015) reported for salt marshes in the Dengie Peninsula, England, (1.23 ± 0.64 Nm^2*10^{-3}). Nevertheless, flexural stiffness of *Spartina anglica* (6.56 ± 4.39 Nm^2*10^{-3}) was much higher in our study compared to Rupprecht et al. (2015) (3.51 ± 0.58 Nm^2*10^{-3}). Neither Young's bending modulus nor flexural stiffness were affected by the summer and autumn treatments (Table 2). Since the increase in Young's bending modulus over the weeks was also present in the autumn treatments, it might suggest that the peak in plant stiffness with further maturation was not reached and the drought treatment was not long enough.

Biochemical plant properties and plant resistance

We have not found any significant differences between species nor treatments in strengthening compounds except for biogenic silica. Biogenic silica increases rigidity and, in contrast to cellulose and lignin, its incorporation is at lower energetic costs (Schoelynck et al. 2010). In comparison with *Spartina anglica*, biogenic silica concentrations were much higher for *Elymus athericus,* which might have resulted in the higher stiffness of the plant material (Young's bending modulus) since a positive relationship between these two variables has been shown to exist for the entire data set (Fig. 8). We also found significant higher biogenic silica concentrations in the plant material of the autumn treatment in comparison with the summer treatment (Table 2 and 4). However, these differences between the treatments can not be translated into a higher stiffness of the plant material since we have not found an effect of the treatment on Young's bending modulus. The seasonal differences in biogenic silica concentration might have contributed to a higher stiffness of the plant material, if the drought treatment were to have been applied for longer.

Methodological considerations

Autumn treatment – Applying a drought to create an autumn treatment seems to have worked well for *Elymus athericus* since biomechanical properties of the autumn treatment correspond well with data gathered in the field in early spring i.e. before the onset of plant growth (flexural stiffness, our study: 1.40 ± 1.09 Nm^2*10^{-3}, field: 1.54 ± 0.58 Nm^2*10^{-3}, Schulze et al. 2019). In contrast, *Spartina anglica* seemed to be barely affected by the drought treatment. This could be explained by *Spartina anglica* being a C4 plant, which generally results in higher water use efficiency and tolerance against drought (Taylor et al. 2014). An alternative to a drought treatment would have been to reduce light availability and temperature to induce an autumn condition but this was not logistically possible.

Photo method – For our study, using the photo method for detecting plant damage fast and non-destructively generated relatively good results. This is especially true for higher wave intensities resulting in major changes in plant frontal area. In the first week, however, wave intensities were not high enough to cause distinguishable damage but rather caused a rearrangement and straightening of the vegetation under inundation, which eventually led to positive values in Δ plant frontal area. For future research on wave-induced plant damage, we recommend to use less dense vegetation if it is not possible/desirable to create extreme wave conditions.

Effect of weeks – Lastly, plant damage of both species increased (i.e. Δ plant frontal area decreased) from week to week (Fig. 3). This can be explained by the hydrodynamic forces, which were set to increase successively. Moving of the pallets in the direction of the wave paddle in the third week further increased hydrodynamic forces potentially resulting in an amplification of plant damage, which was observed for *Elymus athericus* (in autumn condition) and perhaps even implies a threshold effect for this particular species-treatment combination. However, we noticed upward trends from week to week also in other variables that were independent of wave conditions such as Young's bending modulus, flexural stiffness and biogenic silica concentration. These trends might be due to natural development as plants matured outside the wave flume prior to the placement on the flume test section, which was inevitable but should be born in mind when interpreting our results.

Although we created storm surge conditions that are typical for the NW European salt marshes, the vegetation was more robust than expected. This finding is of great importance as it provides additional support for the high resilience of salt marshes to storm impact. A species-specific characterization with respect to the vegetation's vulnerability to wave-induced damage is important to faster assess the status and predict future responses of a salt marsh, and of course adapt management if necessary. Furthermore, we need to investigate how climate change (e.g. increased warming) affects biomechanical and morphological plant properties, which have been shown to clearly affect plant's vulnerability to wave-induced damage. It is interesting to note here that recent studies report that *Elymus athericus* has formed a new genotype that is growing at lower elevations and appears to be better adapted to higher flooding frequencies (Veeneklaas et al. 2013; Reents et al. 2021). *Elymus athericus* is highly competitive and has, due to the new genotype, the potential to outcompete other species and further establish in lower parts of the marsh. Investigations on whether this genotype exhibits a higher resistance against increased hydrodynamic forces, is required to improve predictions on potential shifts in species composition and thereby marsh resilience in the future.

However, it is worth noting that, over longer (decadal) time scales, the susceptibility of aboveground biomass to breakage or loss may in fact reduce the risk for uprooting and hence allow the belowground biomass to remain intact during severe storm impact, as noted by Schoutens et al. (2021). Without removal of the aboveground parts of the plant, wave-forces can translate into stresses at the water/sediment interface around the plant stem that may produce scour, associated loss of sediment, and ultimately the potential uprooting of the plant itself. Following this, another focus for future studies should be to investigate whether wave-induced plant damage and thus aboveground biomass loss ultimately have a positive or negative effect on the longer-term survival chances of the vegetation and thereby provision of wave attenuation under altered future environmental conditions.

Acknowledgements

This study was conducted as part of the RESIST project (‘Response of Ecologically-mediated Shallow Intertidal Shore Transitions to extreme hydrodynamic forcing’) in which we aimed to investigate how tidal marsh vegetation (different species, life stages and densities) is affected by extreme hydrodynamic forces and how this vegetation contributes to sediment stabilization. The work described in this publication was supported by the European Community’s Horizon 2020 Research and Innovation Programme through the grant to HYDRALAB-PLUS (contract no. 654110). Svenja Reents was funded by the German Research Foundation (DFG, Deutsche Forschungsgemeinschaft, project no. 401564364) and Ken Schoutens by the Research Foundation Flanders, Belgium (FWO, PhD fellowship for fundamental research, 1116319 N). Additional support was provided by the RESIST-UK project (UKRI Natural Environment Research Council grant no. NE/R01082X/1). We would like to thank the team from the Forschungszentrum Küste (FZK) as well as Meline Brendel, Helen Brooks,

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Supplementary material

Calculations of Young's bending modulus and flexural stiffness were based on Usherwood et al. (1997). Accordingly, flexural stiffness *EI* was calculated as follows

$$EI = \frac{s^3 F}{48D}$$

where *s* is the distance between the two support bars of the testing machine, *F* the applied force and *D* the corresponding vertical deflection of the stem. The second moment of area *I* can be derived from the stem's dimensions and using the equation for circular stem shapes

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

where *d* is the stem diameter. Young's bending modulus *E* was eventually calculated by dividing flexural stiffness *EI* by the second moment of area *I* as follows

$$E = \frac{EI}{I}$$

4

Plant genotype determines biomass response to flooding frequency in tidal wetlands

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Abstract

The persistence of tidal wetland ecosystems like salt marshes is threatened by human interventions and climate change. Particularly the threat of accelerated sea level rise (SLR) has recently gained increasing attention by the scientific community. However, studies investigating the effect of SLR on plants and vertical marsh accretion are usually restricted to the species or community level and do not consider phenotypic plasticity or genetic diversity. To investigate the response of genotypes within the same salt-marsh species to SLR, we used two known genotypes of *Elymus athericus* (Link) Kerguélen (low-marsh and high-marsh genotypes). In a factorial marsh organ experiment we exposed both genotypes to different flooding frequencies and quantified plant growth parameters. With increasing flooding frequency, the low-marsh genotype showed higher aboveground biomass production compared to the high-marsh genotype. Additionally, the low-marsh genotype generally formed longer rhizomes, shoots and leaves, regardless of flooding frequency. Belowground biomass of both genotypes decreased with increasing flooding frequency. We conclude that the low-marsh genotype is better adapted to higher flooding frequencies through its ability to allocate resources from below- to aboveground biomass. Given the strong control of plant biomass production on salt-marsh accretion, we argue that these findings yield important

implications for our understanding of ecosystem resilience to SLR as well as plant-species distribution in salt marshes.

Introduction

Salt marshes are wetland ecosystems predominantly found along coastlines where they form a transition zone between the marine and the terrestrial environment. Salt marshes provide important ecosystem services like protection of coastlines against storm surges by wave attenuation (Möller et al. 2014), supply of nursery grounds for commercially important fish (Bolle et al., 2009) and mitigation of climate change by long-term carbon sequestration (McLeod et al., 2011). However, human interventions such as land reclamation, eutrophication and climate change threaten the persistence of salt marshes, causing loss rates of 1-2 % of the global area per year (Duarte et al., 2008). Particularly the threat of accelerated sea level rise (SLR) has recently gained increasing attention by the scientific community (FitzGerald et al. 2008; Kirwan and Megonigal 2013; Schuerch et al. 2018).

Generally, up to a certain locally varying threshold of SLR, salt marshes are able to keep up with rates of SLR through their ability to accrete vertically (Kirwan and Megonigal, 2013). During this process, salt-marsh plants act as 'ecosystem engineers' because their aboveground biomass reduces water flow velocity and hydrodynamic forces, which results in a decrease in the sediment-loading capacity of the water and an increase in sediment settlement (Morris et al. 2002; Yang 1998). Furthermore, a high belowground biomass production and decreased decomposition rates in oxygen-deficient soils lead to an accumulation of organic matter and thereby expansion of soil volume. Whether above- or belowground processes predominantly contribute to vertical accretion, depends on the marsh type (i.e. minerogenic vs. organogenic) and often depends on local tidal amplitude (Allen 2000; Kirwan and Megonigal 2013; Nolte et al. 2013a). Yet, in both cases, biomass production of the marsh vegetation is an important driver of accretion. When accretion rates are too low and threshold values of SLR are exceeded, plant growth is negatively affected, leading to a negative feedback loop, which ensues marsh submergence and finally marsh loss (Chmura 2013; Kirwan and Guntenspergen 2012).

Recently, more studies have therefore been focusing on salt-marsh resilience to projected rates of SLR by studying the vegetation response. To examine how vegetation responds to changes in flooding regimes, so called 'marsh organ' experiments have been proven as convenient and insightful approaches. A marsh organ consists of several mesocosms arranged next to each other and along an elevational gradient. Kirwan and Guntenspergen (2012), for example, placed a marsh organ in a brackish marsh to examine the effect of varying sea levels on plant growth of two marsh species and what possible implications this may have on accretion processes. They observed that marsh elevation within the tidal frame determines whether root biomass increases or decreases with SLR. In contrast to belowground productivity, aboveground biomass response was species dependent. Numerous other studies confirmed that responses of marsh plants to sea level changes are highly species-specific (Eleuterius and Eleuterius 1979; Kirwan and Guntenspergen 2015; Langley et al. 2013; Morris et al. 2013). Therefore, the effect of SLR on plant biomass production, and thus the ability of the ecosystem to accrete vertically, can only be understood if SLR-induced shifts in plant species composition also are taken into account.

However, such studies on the effect of SLR on plants are usually restricted to the species or community level (Kirwan and Guntenspergen, 2015; Langley et al., 2013; Morris et al., 2013). They usually do not consider the high degree of phenotypic plasticity and genetic diversity within many species, as for instance evident between different locally adapted populations (Valladares et al. 2014). Yet, understanding a species' adaptive genetic plasticity can be crucial to evaluate its response to environmental change (Razgour et al. 2019). Indeed, in some cases environmental change can in fact induce larger variability in plant biomass production within than between species (Beierkuhnlein et al., 2011). We therefore argue, that intraspecific differences in the biomass response to SLR of salt-marsh plants are likely relevant and require more attention by the scientific community to understand ecosystem resilience.

To investigate the response of genotypes within the same salt-marsh species to SLR, we used two known genotypes of the grass *Elymus athericus* (Link) Kerguélen. This species is widely distributed in NW European salt marshes and usually grows in high-elevated and therefore less-frequently flooded zones of the salt marsh (= high marsh) (Nolte et al. 2019). In the high marsh, the tall grass forms dense, monospecific stands with a low local plant species diversity (Bakker et al., 2003). Recently, however, populations of *E. athericus* have been observed spreading into lower and thus more frequently flooded zones of the marsh (= low marsh) (Olff et al. 1997; Veeneklaas et al. 2013). Low- and high-marsh genotypes are visually distinguishable, as the low-marsh genotype develops a specific phenotype different from the high-marsh genotype (Bockelmann et al. 2003). If genotypes respond differently to increased flooding frequencies, for instance in biomass productivity, it might affect salt-marsh responses to SLR.

The aim of this study was to investigate potential adaptations of the low-marsh genotype to increased flooding frequencies, to improve current evaluations of salt-marsh resilience to SLR. To test the hypothesis that the low-marsh genotype performs better at increased flooding frequencies than the high-marsh genotype, which would be reflected in above- and belowground growth parameters like biomass production and shoot, leaf and rhizome lengths, we conducted a factorial marsh organ experiment. We exposed both genotypes of *E. athericus* to three different flooding frequencies and quantified plant growth parameters to compare their performance and assess morphological adaptations of the low-marsh genotype.

Material and methods

Plant collection and culture

Plants were collected in April 2015 from a salt marsh on the Dutch Island Schiermonnikoog (53°30′N, 6°16′E) from stands that have previously been identified to be dominated by genetically distinct populations of *E. athericus*, i.e. high-marsh (HM) and low-marsh (LM) genotypes (Bockelmann et al., 2003). On Schiermonnikoog, *Elymus athericus* can be found in higher and lower elevated sites, which are inundated 20 – 125 and 90 – 270 times per year, respectively (Bockelmann et al., 2003). Soil salinities range from 22 to 29 ppt (Bolhuis et al. 2013). Plants and soil were extracted in the form of intact sods to keep them alive during transport. In Hamburg, soil was removed and roots were rinsed before both genotypes were planted separately in trays with standardised potting soil. Until the start of the experiment (i.e.

for 24 months), plants were kept under identical environmental conditions in a common garden at the Institute of Plant Science and Microbiology. Ramets of these plants were used for this study. In July 2017, single plants of similar biomass were selected based on visual assessment (no obvious outliers), transplanted to separate pots and randomly assigned to the flooding treatments (described in 2.2). Initial shoot length and shoot number was tested for differences between genotypes and flooding frequencies to ensure that results were not biased by unequal plant size at the beginning of the experiment. There were no significant differences regarding shoot length (genotype: F = 0.787, p = 0.380; flooding frequency: F = 0.127, p = 0.881; genotype*flooding frequency: F = 0.231, p = 0.795) and number of shoots (genotype: Wald = 2.203, p = 0.137; flooding frequency: Wald = 0.357, p = 0.837; genotype*flooding frequency: Wald = 0.005, p = 0.997). The pots were 15 cm in diameter, 17 cm in height and had holes in the bottom to facilitate drainage. They were filled with salt-marsh soil taken from the salt marsh at Sönke-Nissen-Koog, Germany (54°36’N, 8°49’E) which was sieved (with a 1 cm mesh) and homogenised beforehand (see Nolte et al. (2013b) for soil properties). Eight replicates (i.e. single plants in separate pots) per genotype were assigned to one of three flooding treatments, so that a total number of 48 plants were used in this study.

Experimental set-up

Plants were placed onto three steps (step height: 20 cm) within a tidal-tank facility (Hanke et al., 2015), to create three different flooding frequencies. The tidal tank is located outdoors at the Institute of Plant Science and Microbiology and has a total volume of 6.75 m^3 (dimensions: 3 x 1.5 x 1.5 m). A pump was used to fill and empty the tidal tank at regular intervals to mimic tides by alternating between three different maximum water levels. Pots were fully drained between flooding events. Flooding with the respective maximum water level reached 3 cm above soil surface, lasted two hours and took place twice a day. The lowest step was flooded every day, which represented the highest frequency. The flooding of the middle step (moderate flooding frequency) happened weekly, while plants on the highest step were flooded only every two weeks (lowest flooding frequency). Highest and lowest flooding frequency reflect the natural flooding gradient between pioneer zone and high marsh in many NW European salt marshes, including the site where our plants were collected (Bockelmann et al., 2002). A CTD diver combined with a baro diver (Van Essen Instruments, Delft, The Netherlands) was used to monitor flooding cycles. Artificial sea salt (AB Aqua Medic GmbH, Germany) was suspended in tap water to create a salinity of about 20-22 ppt. To minimise the impact of other effects than flooding frequency and genotype, the pots were circulated on each step, other seedlings and algae were removed once a week. Concurrently, water level and salinity were checked as well. The experiment ran for approx. 12 weeks from mid-July to early October 2017.

Measurements

Biomass

At the end of the experiment (2nd of October 2017), the plants were harvested, separated into above- and belowground biomass, dried for two days at 70°C and weighed. Belowground biomass was divided into rhizomes and roots and weighed. The length of rhizomes was also recorded. Additionally, above- and belowground biomass were used to calculate the belowground:aboveground ratio.

Plant growth

At the beginning and the end of the experiment, plant shoot and leaf length as well as number of shoots and leaves were measured. The difference between both measurements was calculated and designated as Δ. Only living plant material was taken into account and length measurements (leaf and shoot length) were carried out on the longest leaves or shoots.

Statistical analysis

Data were tested for normality by applying the Shapiro-Wilk-Test. Except count data (e.g. number of leaves), all parameters were normally distributed and therefore further analysed applying factorial ANOVAs. Due to the well-balanced study design, potential moderate deviations from homogeneity of variance between groups were considered unimportant for ANOVA testing (Box 1954; McGuinness 2002). Each analysis included genotype and flooding frequency as well as their interaction as explanatory variables. To detect significant differences between treatments (flooding frequency and genotype), post-hoc tests (Tukey's HSD) were conducted. To analyse count data, i.e. number of shoots and number of leaves, generalised linear models (GLM) were applied assuming a Poisson distribution and including the explanatory variables genotype and flooding frequency, as well as two-way interaction effects. Each GLM was checked for overdispersion (Pearson Chi2 dispersion parameter) and was refitted afterwards if necessary, using the standard procedure of the applied program. All statistical analyses were performed using STATISTICA 13 (StatSoft Inc., Tulsa, OK, USA).

3 Results

Biomass

Total biomass, defined as the sum of dry above- and belowground plant biomass, differed significantly between genotypes and flooding frequencies (Table 1). In addition, the interaction of both factors showed a significant effect on total biomass. Total biomass production of the high-marsh genotype decreased steadily with increasing flooding frequency, whereas the total biomass of the low-marsh genotype decreased less distinctly (Fig. 1a). The difference between low-marsh and high-marsh genotypes was most pronounced at the highest flooding frequency. In fact, the low-marsh genotype produced almost twice as much total biomass at highest flooding frequency as the high-marsh genotype (LM: 4.61 ± 0.70 g and HM: 2.66 ± 0.52 g, mean ± standard deviation).

Genotype and flooding frequency as well as their interaction had a significant effect on the aboveground biomass production. Aboveground biomass of the high-marsh genotype decreased with increasing flooding frequency from 3.31 ± 0.57 g to 2.03 ± 0.38 g (Fig. 1b). However, aboveground biomass production of the low-marsh genotype remained constant at about 3.46 ± 0.45 g on all flooding frequencies.

In contrast to the genotype-specific aboveground biomass response to flooding, belowground biomass of both genotypes decreased with increasing flooding frequency (Fig. 1c). Results indicate a more pronounced effect of flooding frequency on belowground biomass production compared to the factor genotype (Table 1). Under all flooding frequencies, the low-marsh genotype produced slightly more belowground biomass than the high-marsh genotype (LM: 1.63 ± 0.78 g, HM: 1.30 ± 0.76 g).

Root biomass production (belowground biomass without rhizomes) was significantly affected by flooding frequency ($F = 10.69$, $p < 0.001$), but did not differ between genotypes. Root biomass decreased with increasing flooding frequency for both genotypes (Fig. 1d). In contrast, biomass of rhizomes was significantly affected by both genotype and flooding frequency (Table 1). Mean rhizome biomass of the low-marsh genotype was higher than of the high-marsh genotype (LM: 0.55 ± 0.50 g, HM: 0.26 ± 0.28 g) with the most pronounced differences on lowest and highest flooding frequency (Fig. 1e). In some cases, the low-marsh genotype formed very long rhizomes (up to 166 cm length, coiled around the soil). On average, rhizomes of the low-marsh genotype were nearly twice as long as those of the high-marsh genotype (LM: 51.43 ± 41.11 cm, HM: 26.63 ± 27.23 cm, Table 2). Genotypes significantly differed in the length of rhizomes ($F = 6.102$, $p < 0.05$, Table 1). Belowground:aboveground-ratio was significantly affected by flooding frequency (Table 1) and decreased with increasing flooding frequency (Fig. 1f).

Table 5 Summary statistics of main response variables in the experiment testing for effects of flooding and genotype of *Elymus athericus* on its biomass and growth. Count variables (number of shoots, number of leaves) are analysed through GLM, all other variables by a two-way factorial ANOVA. Significant p-values are shown in bold letters. Means and standard errors are shown in Figures 1 and 2.

		genotype (df =1)		flooding frequency (df = 2)		genotype * flooding frequency (df = 2)	
Response variable	statistical test	test statistic	p-value	test statistic	p-value	test statistic	p-value
Total biomass [g]	factorial ANOVA	F = 13.18	**≤ 0.001**	F = 18.24	**≤ 0.001**	F = 3.36	**≤ 0.05**
Aboveground biomass [g]	factorial ANOVA	F = 13.84	**≤ 0.001**	F = 6.38	**≤ 0.01**	F = 4.77	**≤ 0.05**
Belowground biomass [g]	factorial ANOVA	F = 4.31	**≤ 0.05**	F = 21.93	**≤ 0.001**	F = 0.53	0.59
Δ Shoot length [cm]	factorial ANOVA	F = 7.77	**≤ 0.01**	F = 0.32	0.73	F = 1.03	0.37
Δ Leaf length [cm]	factorial ANOVA	F = 5.09	**≤ 0.05**	F = 1.08	0.35	F = 1.42	0.25
Δ Number of shoots	GLM	Wald = 0.00	0.95	Wald = 5.87	0.05	Wald = 0.78	0.68
Δ Number of leaves	GLM	Wald = 0.44	0.51	Wald = 19.69	**≤ 0.001**	Wald = 1.60	0.45
Root biomass [g]	factorial ANOVA	F = 0.03	0.86	F = 10.69	**≤ 0.001**	F = 0.07	0.93
Rhizome biomass [g]	factorial ANOVA	F = 6.49	**≤ 0.05**	F = 3.84	**≤ 0.05**	F = 0.51	0.60
Rhizome length [cm]	factorial ANOVA	F = 6.10	**≤ 0.05**	F = 1.67	0.20	F = 0.45	0.64
Belowground:Aboveground	factorial ANOVA	F = 0.34	0.56	F = 14.56	**≤ 0.001**	F = 0.13	0.88

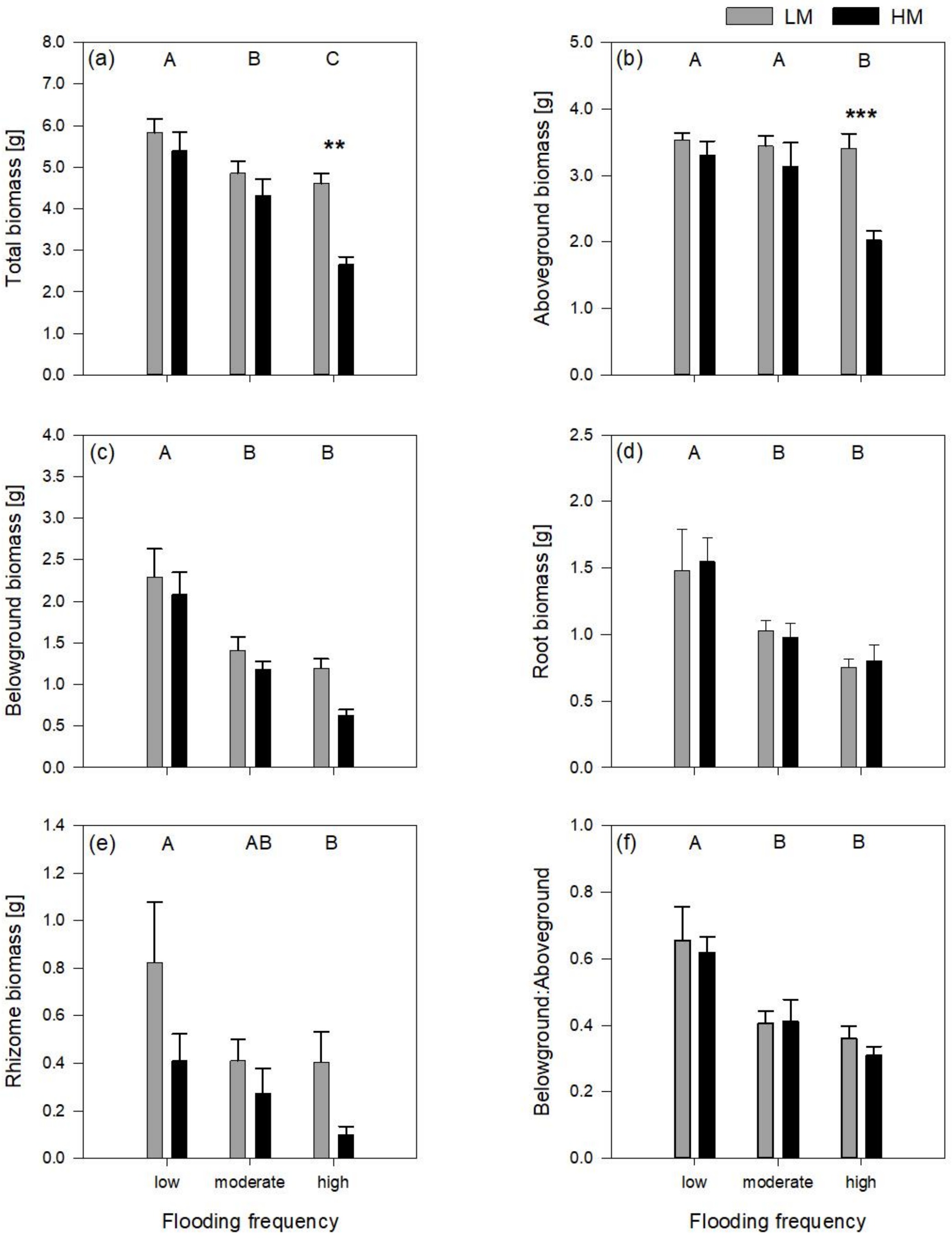

Figure 1 Total biomass (a), aboveground biomass (b), belowground biomass (c), root biomass (d), rhizome biomass (e) and belowground-aboveground ratio (f) of both genotypes on three different flooding frequencies (mean + standard errors). Stars show significant differences between low-marsh (LM) and high-marsh (HM) genotypes within the same flooding treatment based on Tukey's HSD post-hoc test (* $p < 0.05$; **$p < 0.01$; *** $p < 0.001$). Capital letters indicate significant differences between flooding frequencies. For statistics see Table 1.

Leaf and shoot length

The increase in shoot and leaf length significantly differed between genotypes (Table 1). Regarding leaf length, the high-marsh genotype showed approximately the same increase on all flooding frequencies (1.9 ± 4.45 cm). The low-marsh genotype had similar increases of leaf lengths at the lowest flooding frequency but showed pronounced increases of leaf length with increasing flooding frequency (7.03 ± 2.17 cm) (Fig. 2a). Increase in shoot length of the low-marsh genotype was twice as high as that of the high-marsh genotype (LM: 10.78 ± 6.18 cm, HM: 5.57 ± 6.58 cm, Fig. 2b).

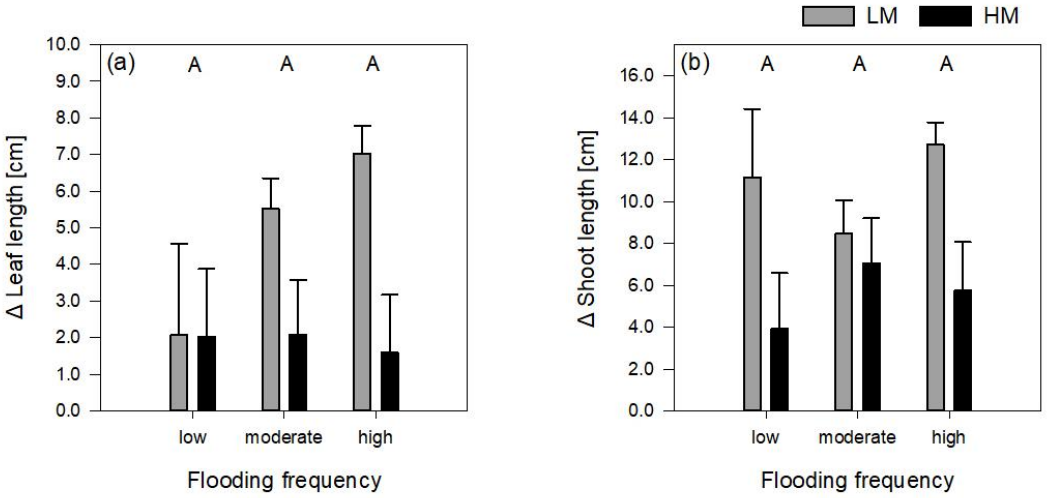

Figure 2 Delta leaf length (a) and delta shoot length (b) of both genotypes on three different flooding frequencies (mean + standard errors). Capital letters indicate significant differences between flooding frequencies. For statistics see Table 1.

Δ Number of leaves and shoots

Neither genotype nor flooding frequency had a significant effect on the increase in number of shoots (Table 1). However, for the increase in number of leaves, a significant effect of flooding frequency was detected (Wald = 19.69, p < 0.001). With highest flooding frequency, both genotypes produced the lowest number of new leaves (LM: 10.4 ± 4.0, HM: 8.9 ± 2.1; Table 2).

Table 2 Mean and standard error (SE) of rhizome length [cm], delta number of leaves and delta number of shoots for different combinations of factors genotype and flooding frequency. LM = low-marsh genotype, HM = high-marsh genotype.

			Rhizome length		Δ Number of leaves		Δ Number of shoots	
genotype	flooding frequency	N	mean	SE	mean	SE	mean	SE
LM	low	8	63.38	15.13	15.88	2.43	7.00	0.82
HM	low	8	37.13	9.85	18.00	3.19	8.13	1.52
LM	moderate	8	45.28	10.35	21.75	2.45	9.50	0.78
HM	moderate	8	32.81	11.76	16.88	3.42	8.50	1.65
LM	high	8	45.63	18.10	10.43	1.53	6.25	1.18
HM	high	8	9.94	2.91	8.86	0.80	5.88	1.08

Discussion

Assessments of plant responses to changed hydrological conditions (e.g. SLR) have thus far focused mainly on comparisons on species level. However, variability in plant responses within species can be considerably higher than between species (Beierkuhnlein et al., 2011). In this study, we therefore investigated differences in plant response between genotypes of the same species (*Elymus athericus*) to better understand the importance of intraspecific variability for evaluations of future ecosystem functionality and resilience. We found, in line with our hypothesis on biomass production, that the low-marsh genotype performs better than the high-marsh genotype under increased flooding frequency. Additionally, the low-marsh genotype generally formed longer rhizomes, shoots and leaves, regardless of flooding frequency (Fig. 1 & 2). We argue that these findings yield important implications for our understanding of ecosystem resilience to SLR as well as plant-species distribution in salt marshes.

We found a higher total biomass of the low-marsh genotype, which was particularly pronounced under high flooding frequency (Fig. 1a). This result indicates a better adaptation of the low-marsh genotype to lower elevated, more frequently flooded conditions. When separating above- and belowground biomass, the high-marsh genotype showed a decrease of both biomass parameters with increasing flooding frequency. Aboveground biomass is important for maintaining photosynthesis (Johnson 2016), so that its reduction can be interpreted as reduction in performance as well. In contrast to the high-marsh genotype showing a marked reduction in aboveground biomass, the low-marsh genotype maintained aboveground biomass across all flooding treatments.

We also found a decrease of belowground biomass with increasing flooding frequency in both genotypes. This can be interpreted as an adaptive trait, because a reduction of belowground biomass reduces the number of respiring roots and thereby improves the diffusion of oxygen to the roots (Naidoo and Naidoo 1992; Voesenek et al. 1989). In line with these results, an increased aboveground biomass production while belowground biomass decreased was found for other flooding adapted plant species such as *Taxodium distichum, Danthonia montevidensis* and *Paspalum dilatatum* (Megonigal and Day 1992; Rubio et al. 1995).

The difference in aboveground biomass response between the two genotypes seems to be mainly explained by genotype-specific increases in leaf and shoot length, whereas the number of both remained similar (Fig. 2, Table 1). Likewise, Voesenek et al. (1989) found a marked increase in leaf length in the flooding adapted *Rumex palustris* under waterlogging, but no increase in number of leaves. The distinct increase in leaf and shoot length in addition to the simultaneous reduction of belowground biomass of the low-marsh genotype of *Elymus athericus* found in our study, indicate resource allocation as response to flooding. For other species it was found that reallocated resources fuel elongation of shoots and leaves to maintain gas exchange and avoid light dissipation through water (Blanch et al. 1999; Grace 1989). Our results suggest that this response may be also present in *E. athericus*, which could improve its chances of survival under higher flooding frequencies e.g. due to accelerated SLR.

Vertical accretion in the minerogenic salt marshes of the Wadden Sea is primarily driven by sedimentation (Allen, 2000; Nolte et al., 2013b), which is strongly controlled by the sediment-trapping capacity of the aboveground biomass (Morris et al., 2002; Yang, 1998). The strong aboveground biomass response to increased flooding frequencies of the low-marsh genotype found in our study may therefore have a positive effect on vertical accretion rates and thereby marsh resilience to rising sea levels.

E. athericus is not the only salt-marsh species characterised by a high degree of genetic diversity. In previous studies, genotypes of several salt-marsh grasses have been described and tested for intraspecific differences in plant response to changing environmental conditions, including *Puccinellia maritima*, *Phragmites australis* and *Spartina alterniflora* (Gray 1985; Seliskar et al. 2002; Mozdzer and Megonigal 2012; Proffitt et al. 2003). They showed high genotypic variations affecting colonisation success, species composition and even ecosystem function.

Compared to the root biomass of both genotypes, which responded similarly and decreased with increasing flooding frequency, rhizome length differed significantly between the genotypes (Table 1). The formation of longer rhizomes by the low-marsh genotype, especially under high flooding frequency, could serve as an escape strategy to expand into more favourable habitats (Hartnett and Bazzaz 1983; Lovett-Doust 1981). In previous studies, it was reported that *E. athericus* usually expands via a 'phalanx' growth strategy, which means that parental plants invest in many but rather short rhizomes to utilise resources in a favourable habitat (Bockelmann and Neuhaus 1999). Field observations of the same authors and results of our study, however, indicate that *E. athericus* is able to alter its strategy to the 'guerrilla' form, by producing longer rhizomes. The 'guerrilla' strategy is usually found in plants characteristic for early successional stages as it enables plants to spread quickly and exploit new favourable areas (Lovett-Doust, 1981). However, overall rhizome length of our study should be interpreted with caution because of potential edge effects caused by the experimental mesocosms.

The change of expansion strategy together with a better adaptation to higher flooding frequencies may lead to a displacement of the high-marsh genotype under accelerated SLR. However, until now, the Wadden Sea salt marshes are able to cope with current rates of sea level rise due to high accretion rates (Nolte et al. 2013b; Esselink et al. 2017). If rates of SLR remain stable, the low-marsh genotype of the tall grass *E. athericus* has the potential to expand further into the low marsh and outcompete other species via light competition, potentially reducing local species diversity.

Methodological considerations

We suggest that the experimental setup including a tidal tank and steps proved suitable to investigate the effects of different flooding frequencies on salt-marsh vegetation. Nevertheless, we recommend repeating this experiment in situ, for example as a transplant experiment, to estimate actual effect size under more natural conditions, as drainage and plant-soil interactions might have been different in the tidal tank and could have affected biomass production.

Conclusion

The present work revealed marked differences in the plant biomass response to changes in flooding frequency between two genotypes of the dominant European salt-marsh grass *Elymus athericus*. Furthermore, we observed large differences in rhizome production between genotypes, which is interpreted as a change in growth strategy. The alteration of its growth strategy and the higher aboveground biomass productivity of the low-marsh genotype implies a larger potential of the low-marsh genotype to invade and establish at lower elevations of the tidal frame. Considering the generally low plant species diversity of salt marshes (e.g. Wanner et al. 2014; Silliman 2014) and the strong feedbacks between plant growth and accelerated SLR (Kirwan and Megonigal, 2013), it is possible that intraspecific variation and adaptive capacity in salt-marsh plants acts as an important but overlooked mediator of ecosystem resilience.

Acknowledgements

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5

BOX: The effect of experimental warming on the phenology of salt-marsh vegetation: implications for future wave attenuation

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Introduction

Facing the consequences of climate change like sea level rise and changes in storm intensities, salt marshes will play an increasingly important role in future coastal protection. The vegetation of salt marshes contributes significantly to the protection function as the plants reduce erosion and act as obstruction to hydrodynamic forces resulting in wave attenuation (Möller et al. 2014). Yet, how other global change factors such as higher temperatures will affect salt marshes and their potential to protect our coasts against high wave intensities, e.g. during storm surges, is largely unknown.

Apart from hydrodynamic conditions, the wave attenuation capacity of a marsh is determined by vegetation properties such as canopy height (Zhu et al. 2020), stem flexibility (Paul et al. 2016) and aboveground biomass (Bouma et al. 2010). Biomass is assumed to increase under warming as higher temperatures increase plant's productivity (Rustad et al. 2001). Since a higher biomass enhances the wave attenuation capacity of a marsh, an increase in temperatures (e.g. due to global warming) might have a positive effect on the coastal protection function in the future. A warming-induced increase in biomass may not only be caused by the stimulation of the photosynthetic rate (Sage and Kubien 2007), but also indirectly by an extended growing season. By analysing phenological data from 1959 to 1993, Menzel and Fabian (1999) reported that an increase in air temperature caused an earlier onset of spring and a delayed autumn for trees and shrubs in Europe. Whether the vegetation of salt marshes respond in the same way to increased temperatures has not been investigated yet. Besides effects on biomass, an earlier green-up and/or delayed senescence could affect the plant’s vitality status and biophysical properties at the start and/or end of the storm surge season which might be of significance for the coastal protection function of salt marshes.

Other studies have quantified phenological shifts using remotely sensed data and calculating the Normalised Difference Vegetation Index (NDVI) (Zhou et al. 2001; Mo et al. 2019). Vegetation indices such as the NDVI describe the spectral reflectance or ‘greenness' of the vegetation, so they can be used to measure the length of the growing season quantitatively. Whether these shifts in the growing season do also exist in salt marshes is largely unknown. Yet, it was found that the peak day in NDVI correlated with air temperature and that this peak day moved from July to August during the past 30 years in salt marshes in Louisiana, USA (Mo et al. 2019). However, such observational studies correlating shifts in phenology to air temperature changes should be validated by experimental approaches.

In a world-unique whole ecosystem warming experiment we increased air and soil temperature in a salt marsh at the German North Sea coast. We used spectral reflectance sensors to continuously assess the NDVI of the canopy to quantify the expected shifts in the growing season due to warming (i.e. earlier green-up in spring and/or delayed senescence in autumn).

Methods

The MERIT (Marsh Ecosystem Response to Increased Temperatures) experiment is located at Hamburger Hallig, Germany (54° 35′ 58″ N, 8° 49′ 8″ E), and consists of 27 plots. In addition to ambient temperature (‘control’) plots, two warming treatments (+1.5°C, +3°C) have been established by using a combination of active belowground (heating cables) and passive aboveground (open-top chambers) warming. Furthermore, three replicates per temperature treatment were placed in each of the three vegetation zones (Pioneer Zone, Low Marsh, High

Marsh) typically found in NW European salt marshes (Esselink et al. 2017). In every plot, spectral reflectance sensors (SRS, METER Group, Inc. USA) were installed approx. 1.5 m above the vegetation. Sensors measured the reflected radiation in two wavelengths (650 and 810 nm) that allowed for the calculation of the NDVI. Additionally, one hemispherical sensor was used to measure incident radiation to account for changes in atmospheric conditions. NDVI was calculated as follows:

$$NDVI = \frac{Rn/In - Rr/Ir}{Rn/In + Rr/Ir}$$

where *Rn* and *Rr* stand for the reflected near-infrared and red radiation from the canopy while *In* and *Ir* is the incident radiation in the near-infrared and red region, respectively. Measurements were controlled and logged on data loggers (CR1000, Campbell Scientific, USA) at hourly intervals from mid-March to mid-October 2019 and 2020.

Results

Generally, overall timing and length of the growing season differed between both years independently of temperature treatments and zones (Fig. 1). NDVI values in spring 2019 (days 85-145) were higher than those measured around the same time in 2020, indicating an earlier green-up in 2019 than in 2020. This difference could have been caused by the steep increase in air temperature from January until March in 2019 (Fig. 2). NDVI values in autumn (days 235-300) were quite similar for both years. However, in 2019, there was a distinct decrease in NDVI, while values just started to decrease for the same time in 2020 suggesting that the end of the growing season was not captured in 2020. For this box, data sets of both years were analysed separately.

Pioneer zone

In the pioneer zone, for both years, an earlier green-up in spring was observed for plants under the +3°C warming treatment, since their NDVI signal increased steeper and were higher than those of control plots and under the +1.5°C treatment (Fig. 1, Fig. 3). In autumn of both years, however, the NDVI of the +3°C warmed plants decreased to the level of the controlled plots whereas the plants under the +1.5°C treatment showed increased NDVI values (Fig. 1, Fig. 3).

The pioneer zone generally showed a lower NDVI signal probably due to higher proportion of bare soil and deposited sediment on leaves and stems of vegetation after inundation. Very low NDVI values that are not following the overall trend indicate flooding events since the NDVI of the vegetation becomes negative when inundated.

Low marsh

Vegetation response in the low marsh showed a different pattern between both years. In 2019, only the +3°C warming treatment showed an earlier green-up in spring. In late summer and autumn of the same year, highest NDVI values were observed for the +1.5°C treatment while the NDVI signal of the +3°C treatment decreased and followed trends of the control plots. In 2020, however, no clear effect of warming was observed. In spring and in the course of the year, NDVI values of the +1.5°C were much lower than those from the +3°C treatment and control plots (Fig. 1, 3). In comparison with the almost monospecific stands in pioneer zone and high marsh, the low marsh has a more diverse species composition that partly differs between plots and included species that form large, colourful flower stands (*Limonium vulgare*) or have greyish-blue leaves due to glandular trichomes (*Artemisia maritima*). This complexity in vegetation composition might have affected the reflectance signal. Interestingly, after NDVI decreased in early July 2020, NDVI started to increase again in mid-July (around day 200, Fig. 1). At the same time, precipitation and air temperature increased (Fig. 2), and thus probably enhanced growing conditions and therefore might had an impact on the plant response.

High marsh

In the high marsh, the vegetation of both warming treatments showed an earlier green-up (i.e. higher NDVI values) at the beginning of the growing season than the control plots, which was consistent for both years (Fig. 1, Fig. 3). Higher NDVI values under warming were also visible in autumn but only in 2019 (Fig. 1, Fig. 3).

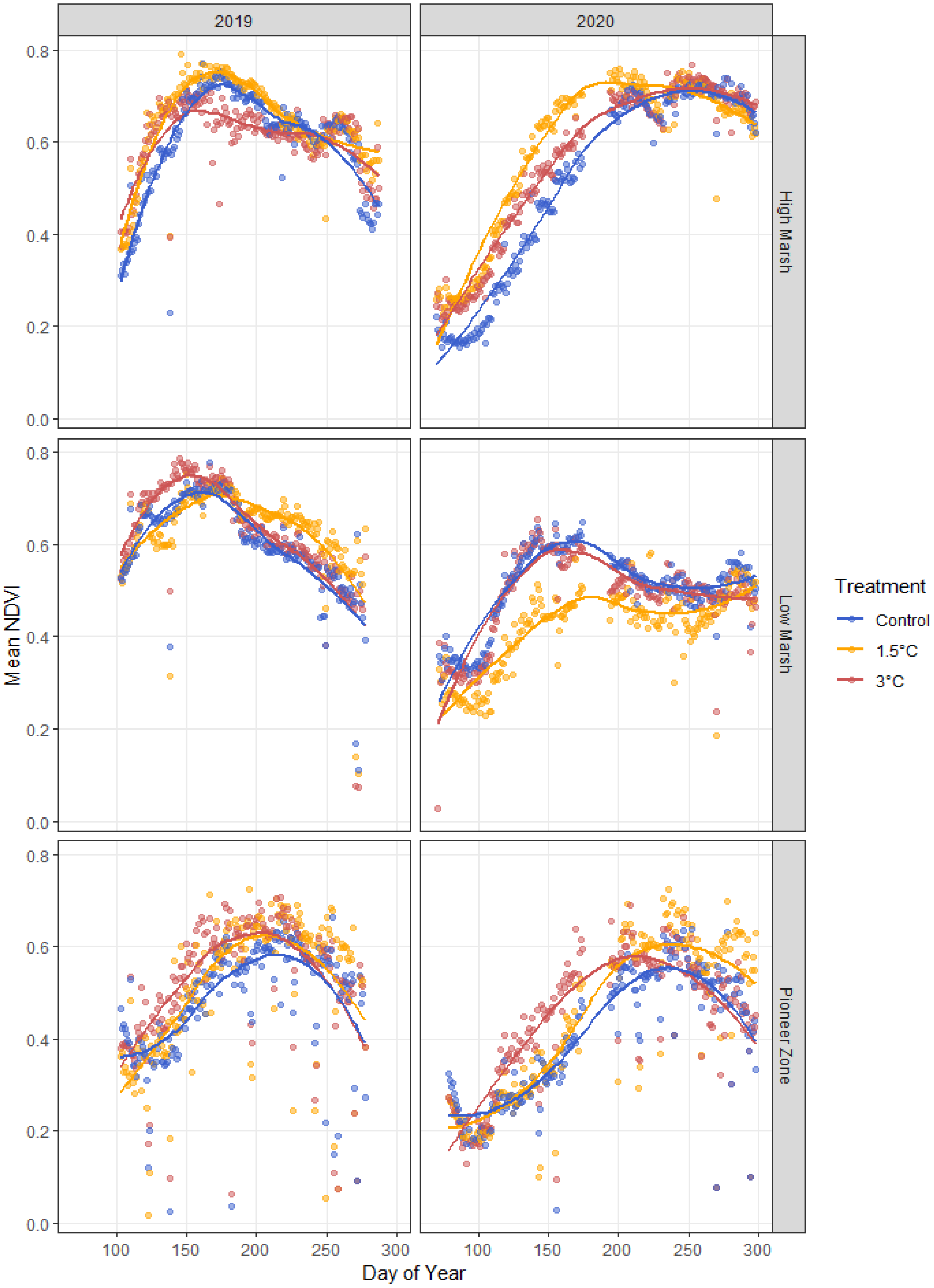

Figure 1 Normalised Difference Vegetation Index (NDVI) averaged over all three replicates per day of year, zone and temperature treatment for 2019 (left) and 2020 (right).

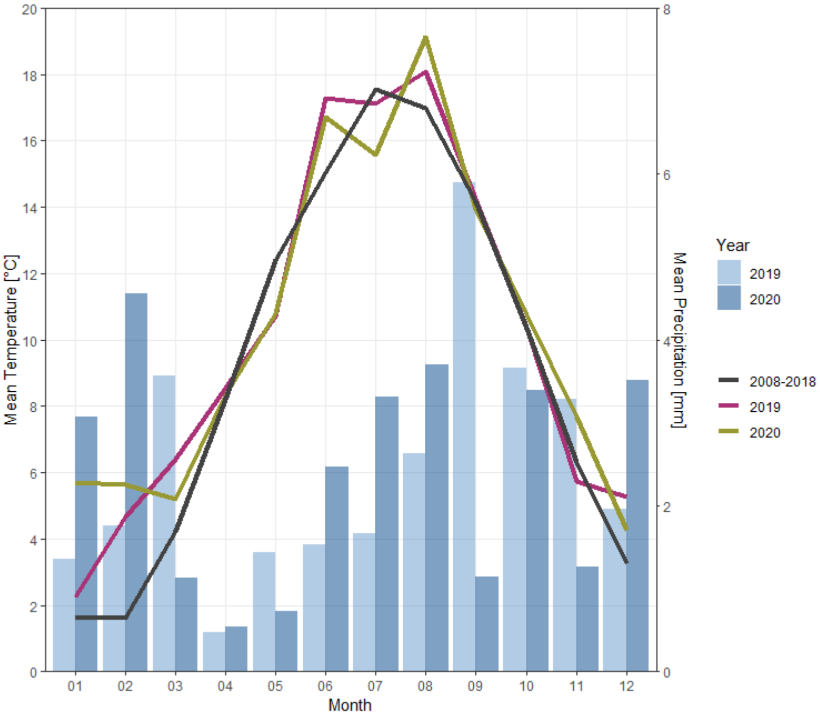

Figure 2 Mean temperature (lines) and precipitation (bars) per month for 2019 and 2020. The black line shows mean temperatures of the 10 previous years. Data was provided by the German weather service (Deutscher Wetterdienst, DWD).

To summarise, the distinct earlier green-up and the delayed senescence (in 2019) found in the high marsh suggest that the warming treatment induced a longer growing season here. NDVI signals measured in the low marsh are more difficult to interpret which is, most probably, due to the diverse canopy. The vegetation in the pioneer zone showed an increase in NDVI under warming but this was mainly restricted to spring and early summer. In general, the vegetation in spring seemed to be more sensitive to changes in temperature, which was also demonstrated in other studies (Menzel and Fabian 1999). We also found warming-induced increases in NDVI in autumn 2019. We recommend continuing NDVI measurements in the MERIT experiment both in spring and in autumn to capture green-up and the end of the growing season for several years. The longer growing season we observed e.g. in the high marsh, suggests that more biomass was produced that in turn has the potential to enhance wave attenuation capacity. Harvested biomass of the MERIT experiment will be used to verify our conclusions. Additionally, effects of warming on other plant properties (i.e. stem flexibility, biochemical properties) that are critical for withstanding hydrodynamic forces and therefore important for wave attenuation will be investigated as well.

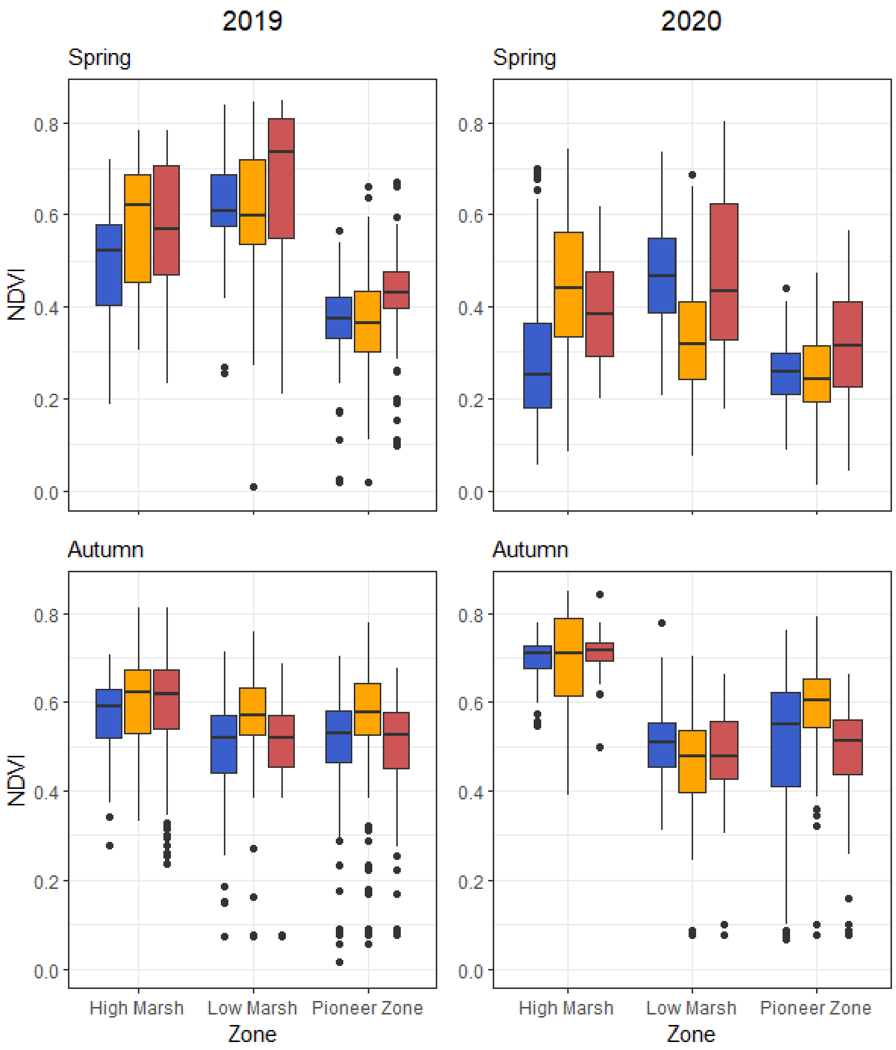

Figure 3 NDVI in spring (top) and autumn (bottom) of 2019 (left) and 2020 (right) per zone and temperature treatment (blue = control, yellow = +1.5°C, red = +3°C). Spring was defined as the time from 27.3. – 27.05. and autumn from 20.09. until the end of measurements (approx. mid of October)

6

Synthesis

The aim of this thesis was to examine how climate change factors, such as extreme wave forcing, sea level rise and increased temperatures, affect the vegetation of tidal marshes. Particular focus was laid on the determination of plant properties that might be important for withstanding extreme wave impact and therefore potentially hold major implications for the evaluation of marsh stability and coastal protection in the future. More particularly, in a true-to-scale flume study, single seedlings (chapter 2) and fully-developed canopies (chapter 3) of different tidal marsh species were exposed to extreme hydrodynamic conditions to quantify wave-induced plant damage and to discover potential determinants of plant resistance. In the third study, the effect of increased flooding frequencies on two genotypes of the salt-marsh grass *Elymus athericus* was compared to assess the intraspecific variability in plant biomass response and detect responsible adaptation mechanisms (chapter 4). Lastly, the effect of experimental warming on plant growth was investigated by increasing soil and air temperature in a Wadden Sea salt marsh (chapter 5). The synthesis is divided into three main sections. In the first part of the synthesis, I will summarise key findings of the four studies, while in the second part, a connection between these findings will be established, thereby bringing it to a broader perspective. Eventually, I will close the synthesis with future research opportunities and the overall conclusion of this thesis.

Key findings

Seedling survival under storm surge conditions (chapter 2)

While tidal marshes are increasingly recognised for their role in coastal protection, the global marsh area is decreasing. Therefore, the interest in the restoration and creation of tidal marshes is growing. Seedling establishment is an important part of the initiation of marsh vegetation growth but the survival of seedlings might be limited by high wave intensities during storm surge events. This survival limitation might become even more relevant with expected future changes in the wind and wave climate. In this flume experiment, we therefore exposed seedlings of four pioneer marsh species differing in morphology, to storm surge conditions to gain insights into the link between species-specific plant properties and seedling survival. We found that seedlings of the two species that usually grow in brackish marshes (*Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani*) showed more wave-induced plant damage than seedlings of the salt-marsh species (*Spartina anglica*, *Puccinellia maritima*). Stem bending and breaking was mostly restricted to the stem base while no seedling was lost due to uprooting. Young's bending modulus, which describes the flexibility of the plant material, did not differ between the seedlings of the four species. However, absolute stiffness of the seedlings stem (flexural stiffness) of the brackish-marsh species was higher compared to the salt-marsh species due to the larger stem diameter. Moreover, the greater stem length and aboveground biomass of seedlings of both brackish-marsh species most likely led to a higher drag force, which could explain the higher vulnerability to stem breakage. Besides plant properties that affect drag forces on the stems, another mechanism that probably has affected the seedlings' vulnerability was scouring around the stems. The larger stem diameter and higher flexural stiffness of the seedlings of the brackish-marsh species most probably caused deeper scour holes that in turn co-occurred with the greatest bending angles of the plant stems (i.e. more plant damage).

Wave-induced plant damage in mature canopies (chapter 3)

In the same flume experiment, we also used fully developed canopies to further examine plants' resistance to wave impact, but this time focusing on two salt-marsh species. The two species originate from different zones of the marsh (*Spartina anglica* = pioneer zone, *Elymus athericus* = high marsh) and are therefore expected to differ in their resistance to hydrodynamic forcing and thus vulnerability to wave-induced plant damage. In addition, we aimed to assess how the plant material changes in the course of a year, which also includes biomechanical properties. To investigate whether these seasonal effects in turn influence the plants' resistance to hydrodynamic forcing, we induced senescence in half of the plants to create a weakened 'autumn treatment'. Generally, both salt-marsh species showed a high resistance against the wave conditions we created in the flume. Nevertheless, we found species-specific differences in the vulnerability to wave impact with *Elymus athericus* being more affected than *Spartina anglica*, especially under higher wave intensities. Furthermore, plant damage was mostly restricted to the upper part of the vegetation. Since *Elymus athericus* was taller and had weaker stems than *Spartina anglica*, canopy height and flexural stiffness seem to be determining factors of plant damage in this study. Furthermore, we found seasonal differences in plants' vulnerability but only in *Elymus athericus* and under highest wave conditions with plants under the autumn treatment showing more damage than the control treatment. Differences in plant properties between the autumn and control treatment could not be clearly detected, except in the concentration of a strengthening compound (biogenic silica), which is known to increase plants' stiffness. As neither Young's bending modulus nor flexural stiffness were affected by the autumn treatment, we suggest that the autumn treatment was not applied long enough.

Plant response to increased flooding frequencies (chapter 4)

Accelerated sea level rise is already occurring along many coastlines and is threatening the persistence of salt marshes in some regions. Changes in the flooding regime have been shown to affect growth responses (e.g. biomass productivity) of the vegetation, which often were accompanied by changes in marsh resilience. Yet, how plants response to environmental changes, such as accelerated sea level rise, is highly species-specific. Even within the same species, there can be a high degree of phenotypic plasticity and genetic diversity resulting in a high variability in plant responses as for instance evident between different locally adapted populations (e.g. genotypes). In a tidal tank experiment, we therefore compared plant responses to increased flooding frequencies of two genotypes of the salt-marsh grass *Elymus athericus*. Since one genotype has been observed spreading into lower and thus more frequently flooded zones of the marsh (i.e. low marsh), we expected a better adaptation of this genotype to higher flooding frequencies, which would be reflected in plant growth parameters. Generally, with increasing flooding frequencies, we found a higher total and aboveground biomass of the low-marsh genotype compared to the genotype that is exclusively growing in the high marsh (high-marsh genotype), indicating a better performance of the low-marsh genotype to increased flooding frequencies. The higher aboveground biomass was caused by an elongation of stems and leaves, which thereby probably enabled the plants to grow out of the water column and to maintain photosynthesis. Furthermore, we observed that the low-marsh genotype formed longer rhizomes, especially under highest flooding frequencies, which usually allows the plants to spread quickly and exploit new favourable areas. This change in growth strategy, together with the higher aboveground biomass productivity of the low-marsh genotype implies a better adaptation to higher flooding frequencies and thus a larger potential of the low-marsh genotype of *Elymus athericus* to invade and establish at lower elevations of the tidal frame.

Plant response to increased temperatures (chapter 5)

Increased temperatures have been shown to enhance the productivity of plants in the temperate zone, as metabolic processes are temperature-dependent and take place at a faster rate when temperature rises. Besides an increased biomass, an extended growing season (earlier green-up in spring and/or delayed senescence in autumn) as consequence of higher temperatures might hold important implications for biomass production and thus marsh resilience and coastal protection. In a warming experiment in which the ambient air and soil temperature of a Wadden Sea salt marsh was increased by approx. +1.5°C and +3°C, NDVI was recorded for two years (2019 and 2020) to track potential phenological changes due to experimental warming. Warming treatments and NDVI recordings covered the three vegetation zones usually found in NW European salt marshes (pioneer zone, low marsh, high marsh), which all differed in their NDVI signal. In general, we observed an earlier green-up of the vegetation in response to warming in the pioneer zone and high marsh for both years as well as in the low marsh in 2019. Additionally, there seems to be a delay in senescence for autumn 2019 in the high marsh under the 3°C treatment as well as in the low marsh and pioneer zone under the 1.5°C treatment, while we were unable to capture the end of the growing season in 2020. Although the signal in autumn was less distinct in comparison to data acquired in spring, our results suggest that experimental warming indeed caused an extension of the growing season.

The impact of climate change factors on tidal marsh vegetation

Based on the results we obtained in the flume studies, the next section will evaluate and synthesise the insights we gained into the impact of waves on marsh vegetation as well as plant properties that proved to affect plant resistance. Subsequently, I will elaborate on how some of these plant properties might be influenced by climate change factors (accelerated sea level rise and higher temperatures) by referring to the studies described in chapter 4 and 5.

Marsh vegetation response to hydrodynamic forcing in relation to vegetation properties

When comparing the plant response of seedlings and mature vegetation to increased hydrodynamic forcing, we found some similarities but also dissimilarities. In seedlings as well as mature vegetation, we found that the differences in their resistance to wave impact correspond well to the differences in wave exposure at their site of origin. With respect to seedling survival, this became apparent in the higher robustness of the species originating from salt marshes compared to the brackish-marsh species. For the mature vegetation, the plants' origin within the same marsh system could be found with higher plant resistance of species growing in the pioneer zone compared to high-marsh species. The relationship between wave exposure at the site of origin and plant resistance might be explained by varying degrees of adaptation in the studied species. This means that over time, plant properties might have been gradually selected that are beneficial for plants' survival including resistance to wave impact. However, environmental conditions at these sites may change e.g. due climate change, maybe even at a faster rate than plant adaptation takes place. Therefore, we need to understand how climate change factors can affect the plant properties that influence resistance and whether they differ between species. This characterisation is important to faster assess the status, predict future responses of a marsh and allows adapting management if necessary.

One plant property that has affected plant resistance of seedlings as well as mature canopies was **vegetation height**. In both flume studies, we observed that taller species were more negatively affected by wave impact. Our results thereby confirm the increase in plant damage with increasing vegetation height, which was also proposed by a stem breakage model of Vuik et al. (2018). One explanation for this could be that taller plants might be more negatively affected by wave impact because wave orbital motion and thereby wave energy is greatest at the water surface and decreases with water depth (Anderson and Smith 2014; Möller and Christie 2019, Fig. 1). Additional support for this argument is provided by our observation that plant damage of the mature vegetation was mostly restricted to the upper part of the canopy. Interestingly, this was not the case for the seedlings as here plant damage occurred at the shoot-root interface although the seedlings (brackish-marsh species) had approximately the same height as the mature canopies of *Elymus athericus* and *Spartina anglica*. Further discussions on why plant damage occurred at different parts of the vegetation can be found later in this section. Another reason for the effect of vegetation height on plant damage might be that an increase in vegetation height also increases drag forces acting on the plant stem (Albayrak et al. 2014). Drag forces describe the forces of resistance while an object moves through a fluid or in case of vegetation, fluid moves past the plants. Besides vegetation height, another important factor influencing drag is plant frontal area, which often relates to aboveground biomass and stem flexibility (Bouma et al. 2005; Bouma et al. 2010; Paul et al. 2016).

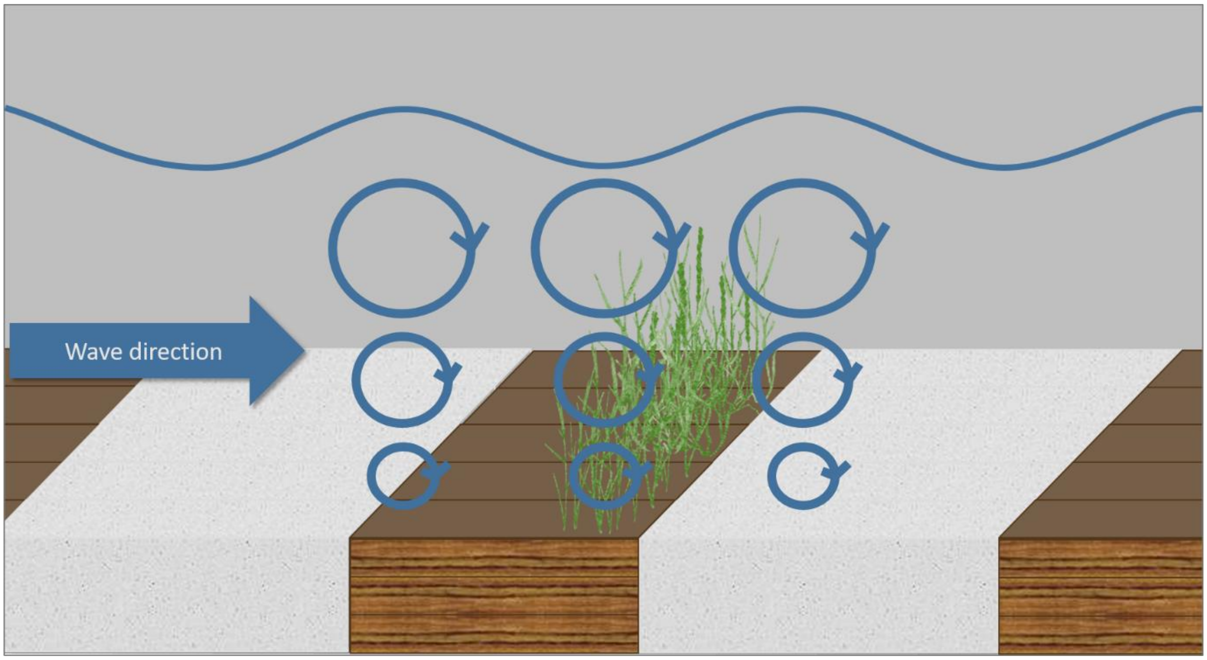

Figure 1 Diagrammatic view of the orbital motion within the water column, illustrating decreasing wave energy with water depth (referring to the flume experiment).

Similar to vegetation height, an increase in **aboveground biomass** also increases drag and is therefore expected to have an impact on wave-induced plant damage. In line with this, in our first flume study, seedlings of species that displayed a high aboveground biomass (brackish-marsh species) were found to be more vulnerable to wave impact than seedlings of species with a lower aboveground biomass (salt-marsh species). Although not described in the study, aboveground biomass was also assessed in the second flume study focusing on mature vegetation. Despite the fact that the number of observations were too low to conduct a statistical analysis, figure 2 still provides some insight into potential differences in aboveground biomass production between *Spartina anglica* and *Elymus athericus*. *Elymus athericus*, which showed more wave-induced plant damage than *Spartina anglica*, also had a higher aboveground biomass, further supporting our conclusion that aboveground biomass indeed influences the plants' vulnerability to damage. Nevertheless, this relationship does not hold for the seasonal treatment comparison, as the higher biomass for example of *Elymus athericus* under the summer treatment does not coincide with a higher vulnerability to plant damage.

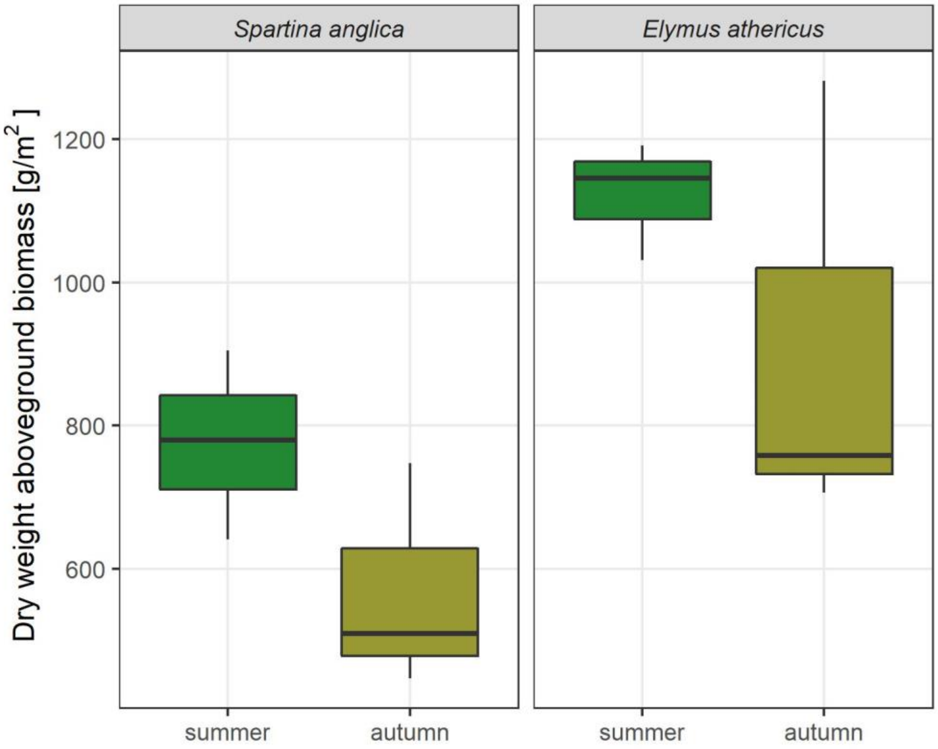

Figure 2 Aboveground biomass of mature canopies of *Spartina anglica* and *Elymus athericus* in summer and autumn condition, assessed in the second flume study (chapter 3).

Stem flexibility (or flexural stiffness) is another key plant parameter, which has been shown in a study by Paul et al. (2016), to be more important than biomass. Stem flexibility controls the degree of bending with the flow, which in turn reduces effective plant frontal area and thus drag (Fig. 3). The effect of stem flexibility on plant resistance leads to two contrasting plant adaptation strategies. On the one hand, a high stem flexibility allows the plant to move and bend under the flow, which reduces drag and thereby the risk of plant damage (avoidance strategy). On the other hand, a low stem flexibility (i.e. high stiffness) results in a high mechanical resistance to breaking but only to certain level of hydrodynamic forces above which the risk of stem breakage increases (tolerance strategy) (Silinski et al. 2015; Heuner et al. 2015). In the seedling survival study, we observed that stiffer species were more vulnerable to plant damage than flexible species. However, the opposite was found for the mature vegetation, as *Spartina anglica* had stiffer stems than *Elymus athericus*, but was barely affected by wave impact. This contrasting response might indicate that the different life stages pursue different strategies to cope with hydrodynamic stress, which has been previously hypothesised for *Scirpus maritimus* (= *Bolboschoenus maritimus*, Silinski et al. 2015). Survival chances of seedlings may increase when being flexible hence avoiding stress, which allows them to invest resources to further establish e.g. by developing a dense root system. If the root system is developed, the plants' resources can be used to enhance the growth and strength of stems as well as leaves, thereby promoting their capability to tolerate hydrodynamic stress.

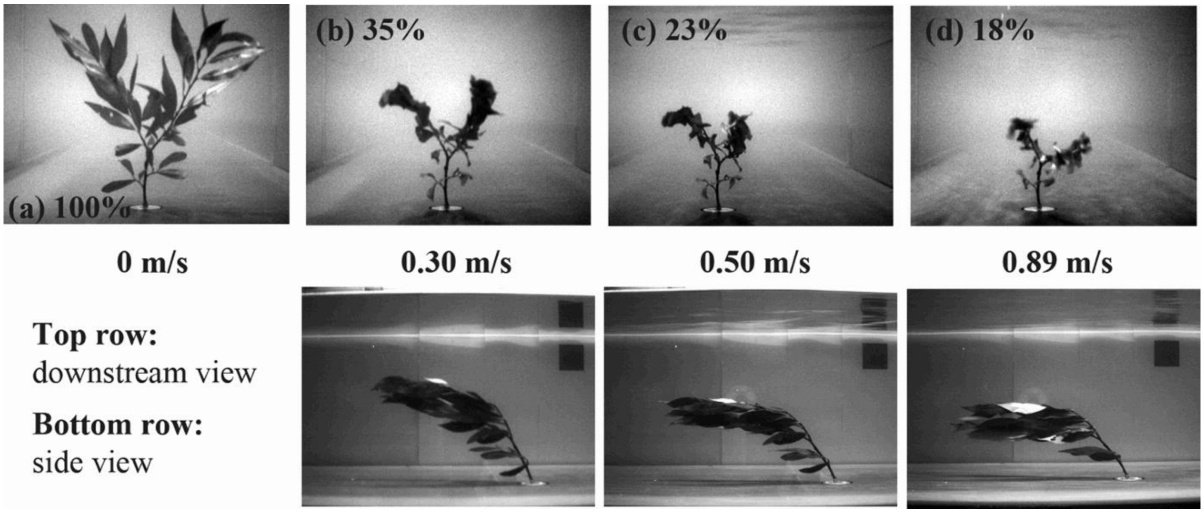

Figure 3 Frontal area and side view of a submerged willow twig under different flow velocities in m/s. The reduction of frontal area compared to the no-flow case is indicated is shown in percent, from Aberle and Järvelä (2013).

The strengthening of the plant material is usually achieved by the incorporation of structural components such as cellulose, lignin or biogenic silica into the plant cell wall. By analysing these **biochemical plant properties** of the mature salt-marsh vegetation in the second flume study, we aimed to better understand the relationship between structural compounds, stem flexibility and plant resistance. However, the only differences between species and season treatments were found for biogenic silica. The higher biogenic silica concentration of *Elymus athericus* probably have led to an increase in Young's bending modulus, a parameter that was used to describe the stiffness purely of the plant material by excluding effects of stem morphology. Although we found a higher biogenic silica concentration in the plant material of the autumn treatment, we did not find seasonal differences in Young's bending modulus. While Young's bending modulus was useful to provide insights into the plant material properties of the different species and effects of seasonal treatment, the absolute stem flexibility or flexural stiffness proved to be more important for determining plant resistance in our flume studies.

When comparing wave impact on the seedlings and mature vegetation, one important variable has not been directly measured but needs to be acknowledged as potential influencing factor: the **vegetation density** differed between both life stages as we used single seedlings that were planted 15 cm apart from each other and a dense canopy of the mature vegetation. The high density of the mature vegetation has possibly reduced the impact of the waves by supporting the upright posture of the vegetation as well as reducing range of motion of the individual stems whereas the seedlings were able to move back and forth unimpeded. This range of motion could also have affected at which height the stems broke since we observed that most seedlings first bend and then break at the shoot-root interface. Consequently, a reduced range of motion due to a higher density of the mature vegetation canopy might explain why we observed plant damage in the upper part of the mature vegetation rather than at the shoot-root interface. Moreover, in another flume study by Rupprecht et al. (2017), less dense canopies of *Elymus athericus* showed very high bending degrees under wave forcing (up to 90°), which resulted in stem breakage at 5-10 cm above the soil surface. Although it seems that vegetation density has an effect on plant resistance to wave impact, it has not been subject to any investigations yet.

To synthesise, the findings of the two flume studies suggest that best estimations for plant resistance to wave impact can be derived from factors influencing drag. These are vegetation height and aboveground biomass, both defining plant frontal area, and stem flexibility. These factors often correlate, for example, taller plants usually have stiffer stems since a certain mechanical strength is required to support aboveground features (Jagels et al. 2018). In line with this, positive correlations between vegetation height and stem stiffness were shown for several marsh species (Zhu et al. 2020; Vuik et al. 2018). However, it should be noted that there are exceptions to this principle as we found in our second flume study that in comparison with *Spartina anglica*, *Elymus athericus* was taller but had weaker stems. We therefore recommend a species-specific characterisation with respect to the plant properties we have shown being most important for defining plant resistance. This could even include different life stages, as the plant response to hydrodynamic forcing clearly differed between the seedlings and the mature vegetation. Furthermore, we suggest to further examine the effect of vegetation density on the plants' vulnerability to wave impact.

Effects of accelerated sea level rise and warming on plant resistance

How climate change factors such as accelerated sea level rise and global warming might affect plant resistance to wave impact can be derived from experiments using tidal tanks and experimental warming, respectively. Results of the tidal tank experiment described in chapter 4 indicate that the low-marsh genotype of *Elymus athericus* is indeed better adapted to increased flooding frequencies, which probably explains its expansion into the low marsh. Besides higher flooding frequencies, the low marsh and its respective vegetation might also be exposed to higher hydrodynamic forcing than the high marsh, which could limit the further establishment of *Elymus athericus* in the low marsh. We saw that, in response to increased flooding frequencies, the low-marsh genotype produced longer stems and thus a higher aboveground biomass than the high-marsh genotype. A higher aboveground biomass and longer stems increases the plant frontal area, which leads to higher drag forces that act on the stem and thereby induce a higher plant vulnerability to wave impact. Consequently, the plant response of the low-marsh genotype might have negative effects on its resistance. However, stem flexibility, which has been shown to be equally important for determining plant resistance, has not been assessed in the tidal tank experiment. If the stems of the low-marsh genotype are also stiffer than of the high-marsh genotype, the negative effect of the higher aboveground biomass and longer stems on plant resistance might be compensated. The determination of stem flexibility of the low-marsh genotype is therefore necessary to better evaluate its chances of a successful establishment in the low marsh and thus under higher hydrodynamic forcing. Furthermore, we need to consider that the tidal tank did not simulate any hydrodynamic forcing, which might have affected the growth response of the vegetation.

Experimental warming was found to extend the growing season, as indicated by NDVI recordings showing an earlier green-up in spring and a delayed senescence in autumn in the MERIT experiment. A warming-induced extension of the growing season has previously been shown to increase biomass productivity in several ecosystems, which might suggest that the extended growing season we observed in the MERIT experiment could similarly result in a higher biomass productivity. Since biomass can be increased either by stem and leaf elongation or a higher stem density, impacts of warming on plant resistance might vary significantly. While a higher biomass through stem or leaf elongation might have negative effects (if stems do not become stronger too), a higher stem density might be beneficial as a dense canopy provides structural support between adjacent stems and reduces the range of motion of the stems. Passive warming via open-topped chambers in a salt marsh in Massachusetts caused an increase in aboveground biomass of *Spartina alterniflora*, which has been attributed to the elongation of stems while stem density was not affected by higher temperatures (Charles and Dukes 2009). Although, in the same study, an increase in stem length has also been demonstrated for *Spartina patens* and *Distichlis spicata*, their aboveground biomass was not affected by warming. This indicates that their stems grew longer but thinner, thereby decreasing stem strength and that the response of salt-marsh vegetation to warming is species-specific. Therefore, a deeper discussion on how warming-induced increases in biomass might affect plant resistance to wave impact requires further investigations. Nevertheless, the extension of the growing season might not only affect plant resistance due to differences in biomass productivity but also due to differences in the plants' vitality in the case of an extreme event such as a storm surge. In the flume experiment, we saw that the weakened *Elymus athericus* (autumn treatment) was more vulnerable to wave impact than the healthy control canopies (summer treatment). The delayed senescence in autumn we observed for salt-marsh plants under warming might therefore decrease plants' vulnerability as the vegetation might be still in a pre-senescence condition when first storms of the storm surge season start to occur.

Future research perspectives

Plant responses to wave impact as well as other environmental stressors have previously been shown to be highly species-specific, as species display different sets of plant properties, all affecting their resistance (Heuner et al. 2015; Schoutens et al. 2019). Therefore, additional marsh plant species, including those from different geographic regions (e.g. *Spartina alterniflora*) should be included in future research. It is similarly important to investigate how the species composition of tidal marshes might change in response to climate change. Previous studies revealed that an increase in temperature or salinity has the potential to affect the species composition in salt marshes (Baldwin and Mendelssohn 1998; Gedan et al. 2011a) and hence probably the properties of the community. It is therefore essential to gain further knowledge of the plant resistance of individual species as well as potential shifts in the species composition to assess marsh resilience and thus the potential of marshes for future coastal protection.

Investigating impacts of single climate change factors on tidal marsh vegetation, as presented in this thesis, provides a baseline for future studies, but many knowledge gaps currently remain. Therefore, these studies should aim to examine the interaction of multiple climate change factors and their impacts on coastal vegetation as it allows for a more realistic approach and thereby a more precise assessment of marsh resilience and stability in the future. Accordingly, more studies have recently been published that experimentally tested for example the effect of warming combined with either elevated CO_2 or reduced precipitation on tidal marsh vegetation, generating interesting insight into the interactions of these factors (Charles and Dukes 2009; Gray and Mogg 2001; León-Sánchez et al. 2020). However, experiments simulating higher hydrodynamic forces in combination with other climate change factors that would allow gaining knowledge of processes relevant for future coastal protection, are technically difficult and have not been conducted yet. This knowledge gap could be addressed by focussing on potential effects of a combination of climate change factors on canopy height and aboveground biomass, but also include stem flexibility as it plays a central role in defining plant resistance.

Although this thesis focused primarily on implications for coastal protection, obtained results might also affect plant resistance to other stresses and thus the provision of other ecosystem services in tidal marshes. For example, the increased vegetation height we observed in the low-marsh genotype of *Elymus athericus* enabled the plants to resist higher flooding frequencies, but also increased aboveground biomass, which is known to positively affect vertical accretion in tidal marshes (Fig. 4). Accordingly, Battisti (2021) suggest in a recent review, that further research should investigate how potential changes in the sets of plant properties that determine plant resistance to one stress also relate to the resistance to other stresses, which would facilitate evaluations of overall marsh resilience. However, before relating the plant properties discussed in this thesis to other stresses (e.g. higher temperature, salinity), I recommend to further investigate mechanisms relevant for plant resistance to wave impact by addressing the knowledge gaps mentioned above.

The processes I focused on in this thesis relate to natural marsh dynamics and anthropogenic climate change, while the effect of more direct human intervention was mostly excluded. Direct human interventions such as agricultural use or the erection of artificial sea defense structures (e.g. sea walls) might hamper these natural dynamics. For example, livestock grazing for agricultural or nature management or nature management purposes has an impact on vegetation canopy height and species composition (e.g. Bakker et al. 2020), with likely implications for the coastal protection function of tidal marshes. Furthermore, it is expected that salt marshes will migrate further inland in response to accelerated sea level rise. However, sea walls will probably restrict this spatial expansion in many regions in NW Europe, which might lower marsh resilience and increase the risk of salt-marsh loss (Schuerch et al. 2018). Consequently, the impact of human intervention on marsh resilience in the face of climate change will be another important aspect future research should focus on.

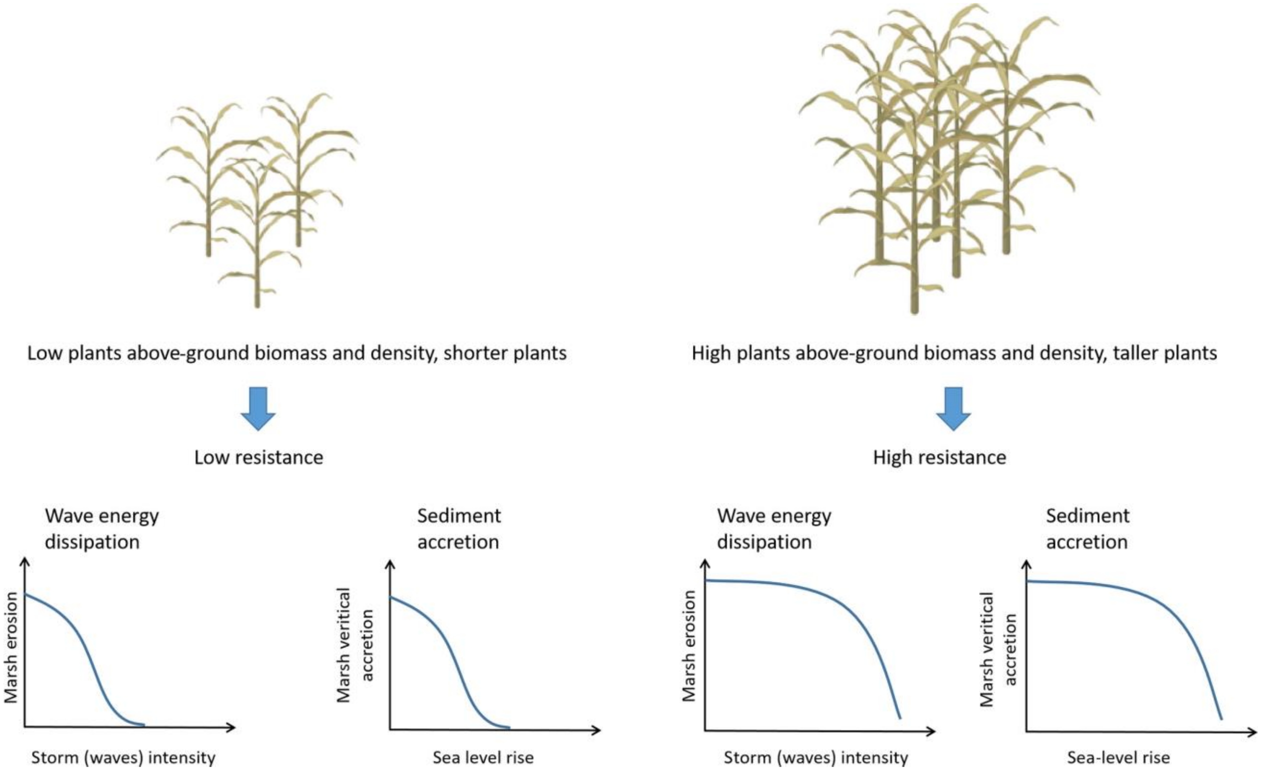

Figure 4 Conceptual diagram illustrating how the same set of plant properties (e.g. plant density, stiffness and aboveground biomass) influences the ecosystem resistance to multiple stress types (e.g. wave energy and sea-level rise), from Battisti (2021).

Conclusions and outlook

Overall, the plant properties assessed for this thesis proved useful to differentiate levels of plant vulnerability to wave impact between tidal marsh species. However, there are plant properties that might be worth examining as well (e.g. stem density). Furthermore, the high robustness against hydrodynamic forcing we found for the studied species holds additional support for the high resilience of tidal marshes to storm impact. However, it should be noted that the conditions generated in the flume experiment reflect present storm surge conditions found in front of many NW European salt marshes. Nevertheless, the wave-induced plant damage we detected provides valuable insights into the hydrodynamic conditions the vegetation is able to withstand. In both flume studies, we found that especially the more intense wave conditions generated the most distinct differences in plant resistance between species and treatments. Although uncertainties exists regarding future wave climate projections, findings of this thesis suggest that an increase in wave intensities might increase the susceptibility of the vegetation to severe physical damage as well. Moreover, factors influencing or relating to the aboveground biomass of the vegetation (vegetation height, frontal area or density) as well as stem flexibility seem to be key elements for determining plant resistance. It might be therefore advisable to focus on these properties when evaluating marsh resilience to future environmental changes. Furthermore, accelerated sea level rise (in the case of the low-marsh genotype) as well as increased temperatures has been shown to have positive effects on aboveground biomass features. A higher aboveground biomass under these climate change factors has the potential to enhance marsh stability as biomass increments has been shown to be positively correlated with vertical accretion rates. However, it remains unknown how accelerated sea level rise and warming might affect stem flexibility, which greatly increases the uncertainty of the conclusions drawn in this thesis.

To summarise, this thesis provides new insights into the impact of hydrodynamic forcing on tidal marsh vegetation. While we found species-specific differences, both seedlings and mature canopies have generally been shown to be very resistant against wave impact. Furthermore, important plant properties that determine plant resistance have been identified. We found that these are affected by climate change factors, namely higher flooding frequencies and temperatures. Even though knowledge gaps remain regarding further climate change parameters and the interaction of these factors, the results presented in this thesis hold major implications for the coastal protection function of tidal marshes in the future.

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Summary

Salt marshes are coastal ecosystems that are able to provide many valuable ecosystem services such as carbon sequestration or coastal protection. Despite their value, the global area of salt marshes is declining, mainly due to anthropogenic effects including global climate change. Climate change factors that might threatening the persistence of salt marshes in the future are sea level rise and higher temperatures as well as changes in the wind climate affecting local hydrodynamic conditions. Although salt marshes are formed in highly dynamic environments, their stability may be disturbed by more extreme events like a series of several storm surges that might lead to vegetation failure and a reduced marsh stability. So far, studies investigating wave impacts on marsh stability mainly focused on erosion while other plant-wave interactions such as wave-induced plant damage are poorly understood. This thesis aimed to address this knowledge gap by investigating the effect of different climate change factors on marsh vegetation. In a true-to-scale flume study, single seedlings (chapter 2) and fully-developed canopies (chapter 3) of different tidal marsh species were exposed to storm surge conditions to quantify wave-induced plant damage and potentially discover determinants of plant resistance. Furthermore, two genotypes of a salt-marsh grass were used to assess intraspecific variability in plant responses to increased flooding frequencies (chapter 4). Lastly, plant response to increased temperatures were investigated in a whole ecosystem warming experiment in a salt marsh at the German North Sea coast (chapter 5).

In both flume studies (chapter 2 and 3), we were able to detected wave-induced plant damage, which provides valuable insights into plant resistance to extreme hydrodynamic conditions. Regardless of life stage, wave-induced plant damage differed significantly between studied species, which can be attributed to species-specific differences in plant properties. These plant properties were vegetation height and aboveground biomass, both defining plant frontal area, and stem flexibility. We found that species with a high frontal area (high aboveground biomass and/or longer stems) were more vulnerable to wave-induced plant damage because the these aboveground features most probably increased drag. Flexible species, however, were less

affected by wave impact probably because they were able to bend under the flow, which reduced the effective frontal area and thereby drag.

The tidal tank experiment with the two genotypes of the salt-marsh grass *Elymus athericus* (chapter 4) revealed that the intraspecific variability in plant response to increased flooding frequencies can be substantial. We found that the genotype that has recently been observed spreading into lower parts of the marsh (low-marsh genotype), produced more aboveground biomass in response to higher flooding frequencies than the genotype that is exclusively growing in the high marsh (high-marsh genotype). The higher aboveground biomass was caused by an elongation of stems and leaves.

By increasing air and soil temperature in a salt marsh at the German North Sea coast, we were able to investigate plant responses to increased temperatures (chapter 5). Recordings of the spectral reflectance of the vegetation (NDVI) showed an earlier green-up of the vegetation in spring and a delayed senescence in autumn, suggesting an extension of the growing season under warming. As it has been shown for other ecosystems that extensions in the growing season resulted in a higher biomass, we might assume that the warming in the studied salt marsh similarly increased biomass productivity.

Although the studied species seemed very robust to wave impact, we still observed noticeable plant damage under conditions that reflected typical storm surge conditions in many NW European salt marshes. Our findings therefore suggest that an increase in wave intensities might increase the susceptibility of the vegetation to severe physical damage as well. Furthermore, plant properties assessed in this thesis proved useful to explain different levels of plant resistance to wave impact. Accelerated sea level rise (in the case of the low-marsh genotype) as well as increased temperatures seemed to have positive effects on aboveground biomass features, which might enhance marsh stability as biomass productivity plays an important role in vertical accretion. Even though knowledge gaps remain regarding further climate change parameters and the interaction of these factors, the results presented in this thesis hold major implications for the evaluation of marsh resilience and coastal protection in the future.

Zusammenfassung

Salzmarschen sind für ihre Fähigkeit bekannt wertvolle Ökosystemdienstleistungen wie die Kohlenstofffixierung oder die Küstenschutzfunktion bereitzustellen. Trotz ihrer Bedeutung nimmt die globale Fläche der Salzmarschen vor allem aufgrund anthropogener Einflüsse jährlich ab. Zu diesen anthropogenen Einflüssen die den Fortbestand der Salzmarschen in der Zukunft gefährden könnten, zählen auch die Folgen des Klimawandels wie z.B. der Anstieg des Meeresspiegels, die globalen Erwärmung oder Veränderungen des Windklimas (und die damit verbundene Wellenbelastung). Obwohl Salzmarschen in hochdynamischen Systemen entstehen, kann ihre Stabilität durch extremere Ereignisse, wie zum Beispiel einer Reihe von aufeinanderfolgenden Sturmfluten, gestört werden. Schwerwiegende Schäden an der Vegetation und eine Verringerung der Salzmarsch-Stabilität können die Folgen sein. Studien, die die Auswirkungen von hydrodynamischen Kräften auf die Stabilität von Salzmarschen untersuchten, konzentrierten sich bisher hauptsächlich auf die Erosion, während andere Faktoren wie welleninduzierte Pflanzenschäden kaum erforscht sind. Ziel dieser Dissertation war es demnach die Auswirkungen verschiedener Klimawandelfaktoren auf die Vegetation der Salzmarschen zu untersuchen. In einer maßstabsgetreuen Wellenkanal-Experiment wurden einzelne Jungpflanzen (Kapitel 2) und voll entwickelte Pflanzenbestände (Kapitel 3) verschiedener Salzmarscharten verschiedenen Wellenintensitäten ausgesetzt. Hierbei wurden welleninduzierte Pflanzenschäden quantifiziert und mögliche Bestimmungsfaktoren der Widerstandfähigkeit der Vegetation untersucht. In einem weiteren Experiment wurden zwei Genotypen der Salzmarschart *Elymus athericus* verwendet, um die intraspezifische Variabilität der Pflanzenreaktion auf erhöhte Überflutungshäufigkeiten zu ermitteln (Kapitel 4). Des Weiteren, wurde die Reaktion von Pflanzen auf erhöhte Temperaturen in einem Erwärmungsexperiment in einer Salzmarsch an der deutschen Nordseeküste untersucht (Kapitel 5).

In beiden Wellenkanalstudien (Kapitel 2 und 3) beobachteten wir eine hohe Robustheit der Vegetation gegenüber den generierten Wellenbedingungen. Dennoch konnten wir welleninduzierte Pflanzenschäden nachweisen, die wertvolle Erkenntnisse über die

Widerstandsfähigkeit der Pflanzen gegenüber extremen hydrodynamischen Bedingungen liefern. Unabhängig vom Lebensstadium der Vegetation unterschied sich das Ausmaß der Pflanzenschäden signifikant zwischen den untersuchten Arten, was auf artspezifische Unterschiede in den Pflanzeneigenschaften zurückzuführen ist. Diese Pflanzeneigenschaften waren die Vegetationshöhe, die oberirdische Biomasse und die Flexibilität der Pflanzenstängel. Pflanzenarten mit einer hohen oberirdischen Biomasse oder Vegetationshöhe wiesen eine höhere Anfälligkeit für welleninduzierten Pflanzenschaden auf. Eine mögliche Erklärung hierfür ist, dass mit zunehmender oberirdische Biomasse vermutlich auch die Zugkräfte die auf den Stängel wirken zunehmen. Flexible Arten waren hingegen weniger von der Wellenbelastung betroffen, was darauf zurückgeführt werden könnte, dass sie sich unter der Strömung biegen konnten und somit Zugkräfte verringerten.

Das Überflutungs-Experiment mit den beiden Genotypen von *Elymus athericus* (Kapitel 4) zeigte, dass die innerartliche Variabilität in der Pflanzenreaktion auf erhöhte Überflutungshäufigkeiten erheblich sein kann. Wir fanden heraus, dass einer der beiden Genotypen (*low-marsh genotype*), als Reaktion auf höhere Überflutungshäufigkeiten mehr oberirdische Biomasse produzierte als der zweite Genotyp (*high-marsh genotype*). Zusätzlich konnte die Biomassezunahme durch eine Verlängerung der Stängel und Blätter erklärt werden.

Im Erwärmungsexperiment (Kapitel 5) konnte gezeigt werden, dass höhere Temperaturen ein früheres Aufgrünen der Vegetation im Frühjahr und eine verspätete Seneszenz im Herbst bewirkte, was die Vegetationsperiode verlängerte. Da sich für andere Ökosysteme gezeigt hat, dass eine Verlängerung der Vegetationsperiode zu einer höheren Biomasseproduktion führt, kann davon ausgegangen werden, dass die Erwärmung die Biomasseproduktivität der Salzmarschvegetation in ähnlicher Weise erhöht.

Obwohl die untersuchten Arten eine hohe Widerstandsfähigkeit gegenüber den generierten Wellenbedingungen besaßen, konnte dennoch Pflanzenschaden festgestellt werden. Es bleibt anzumerken, dass die erzeugten Wellenbedingungen aktuellen Sturmflutbedingungen nordwesteuropäischer Salzmarschen entsprechen. Eine Zunahme der Wellenintensität könnte somit auch die Anfälligkeit der Vegetation für schwere Schäden erhöhen.

Darüber hinaus erwiesen sich die in dieser Arbeit untersuchten Pflanzeneigenschaften als geeignet, um Unterschiede der Pflanzenresistenz gegenüber Welleneinwirkung zu erklären. Zudem beeinflusste die Erwärmung und die gesteigerte Überflutungshäufigkeit die oberirdische Biomasseproduktion positiv. Da die Biomasseproduktion eine essentielle Rolle im vertikalen Marschaufwuchs spielt, hätte der Meeresspiegelanstieg und die Erwärmung das Potential die Stabilität der Salzmarschen zu verbessern. Obwohl andere Klimawandelfaktoren und deren Interaktion noch nicht vollständig untersucht sind, tragen die in dieser Arbeit präsentierten Ergebnisse zu einer verbesserten Beurteilung der zukünftigen Widerstandsfähigkeit der Salzmarschen und somit der Küstenschutzfunktion bei.

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Author’s contribution

Chapter 2

Survival of the thickest? Impacts of extreme wave-forcing on marsh seedlings are mediated by species morphology

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Svenja Reents contributed to the design and implementation of the flume experiment. Svenja Reents planned and carried out vegetation response measurements (survival, bending angle, height and diameter measurements, three-point bending test, biomass) as well as commented the manuscript.

Prof. Dr. Kai Jensen

Author's contribution

Chapter 3

Species-specific and seasonal differences in the resistance of salt-marsh vegetation to wave impact – *in review*

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Chapter 4

Plant genotype determines biomass response to flooding frequency in tidal wetlands

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Svenja Reents contributed to the design and conducted the tidal tank experiment. Svenja Reents analysed the data and wrote the first draft of the manuscript.

Prof. Dr. Kai Jensen

Eidesstattliche Versicherung

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