

**Vegetation Properties and Sedimentation in
Salt Marshes:
Implications for Wave Attenuation and
Marsh Survival**

Dissertation

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1 General introduction

1.1 Salt marshes and ecosystem services

Coastal salt marshes develop in sheltered saltwater environments close to the sea level and form a transition between the sea and the land (e.g. Bakker 2014). They predominantly develop in temperate to subpolar zones and are mostly being outcompeted by mangroves in subtropical and tropical regions, although a coexistence as a mangrove-salt-marsh ecotone is well described (Feller et al. 2017; Kelleway et al. 2017; Fig. 1.1). Globally, salt marshes cover up to 55000 km² whereas mangroves cover around 138000 km², although mangroves may increase their competitive advantage on salt marshes in tropical and subtropical areas even further due to climate change (Guo et al. 2013; Friess et al. 2020). The biggest threat for salt marshes, however, is the direct loss to human influences: on the one hand through wetland conversion and modifications, on the other hand through effects of the anthropogenically accelerated climate change and SLR (sea-level rise; Crosby et al. 2016; Fitzgerald and Hughes 2019; IPCC 2019). For example, in dense populated and urbanised coastlines of Europe and the USA, embankment often prevents a landward migration of salt marshes resulting in a coastal squeeze (Borchert et al. 2018). An ongoing loss of these highly vulnerable and valuable ecosystems would be associated with losses of biodiversity and the so-called ecosystem services they provide to humans. These ecosystem services can be divided into several categories such as supporting (e.g. fish nursery, habitat provisioning, primary production), provisioning (e.g. food supply to humans), regulating (e.g. climate regulation through carbon sequestration, coastal protection through wave attenuation) and cultural (e.g. tourism, education; Barbier et al. 2011). However, ecosystems can also have negative effects on humans (e.g. being sources for diseases or danger to human wellbeing), which led to the concept of Nature's Contributions to People (NCP) including both positive and negative effects (Kadykalo et al. 2019; Friess et al. 2020).

An increasing recognition of salt marsh ecosystem services and the role of salt marshes for biodiversity protection has consequently led to a rising concern regarding salt marsh loss.

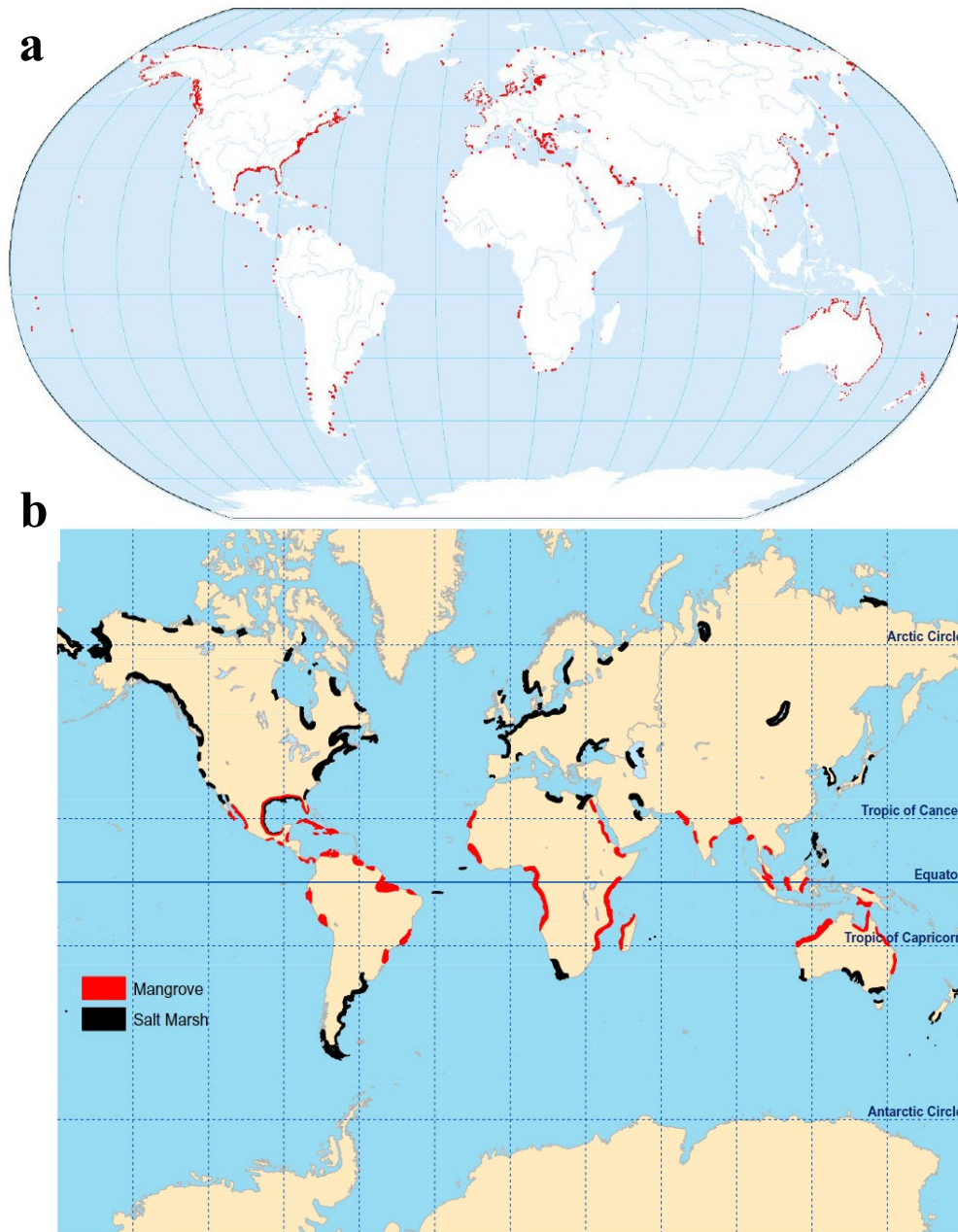


Figure 1.1 a) Global occurrences of coastal salt marshes shown as red contours. Source: UNEP-WCMC; McOwen et al. 2017; map updated in 2020 **b)** Global distribution of mangroves (red) and salt marshes (black). Shown are coastal marshes and inland marshes. Source: D’Odiroco et al. 2013.

1.2 Salt marsh development and succession

In Northwestern Europe, coastal salt marshes show a spatial vegetation zonation pattern consisting of monospecific stands of single species or mixtures of species which are

characteristic for the respective marsh zone (Oloff et al. 1997). Usually, the zones are arranged along an elevational gradient from the tidal flats towards the high marsh gradually facing changing environmental conditions, such as differences in flooding frequency and duration, wave forcing, flow velocity, salinity, waterlogging and nutrient availability (Pennings 1992; Fig. 1.2).

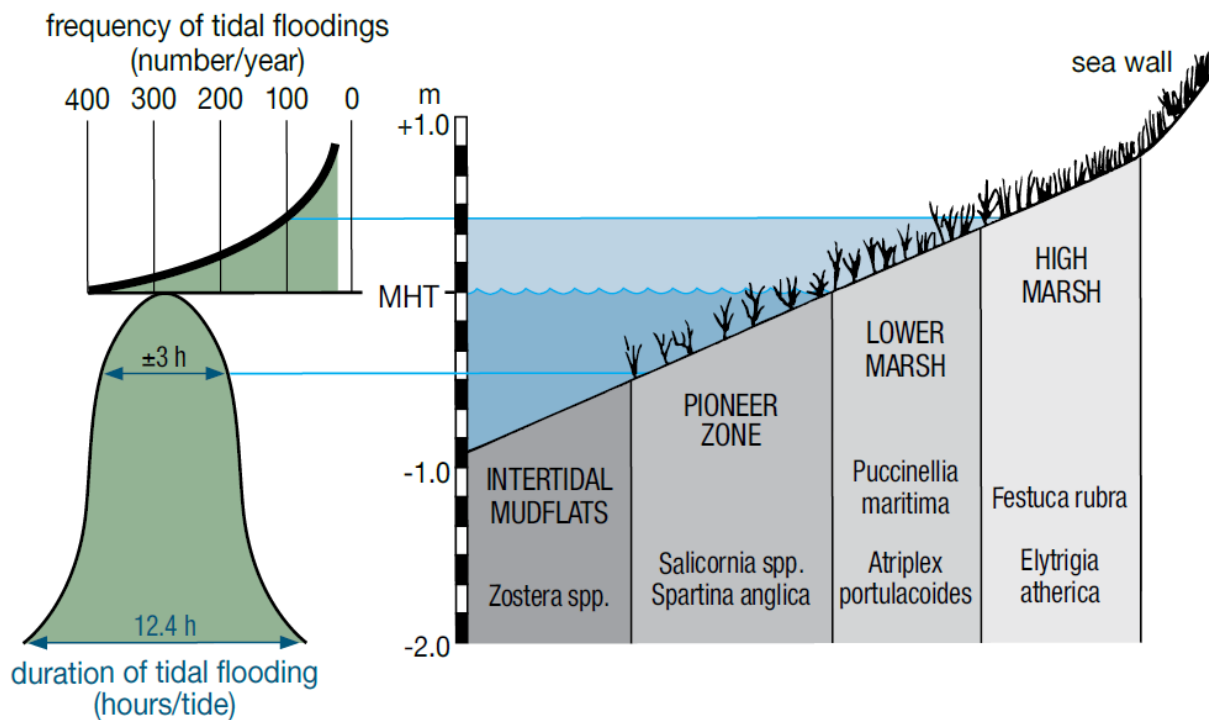


Figure 1.2 Typical zonation of salt marshes in Northwestern Europe in relation to flooding frequency and duration (MHT=mean high tide). Source: Bakker 2014.

Differences between salt marsh plant species in terms of competitive ability and adaptation to stressful conditions (e.g. salinity, soil moisture, flooding duration and frequency, nutrient availability) lead to discrete boundaries of marsh vegetation zones. According to the so called stress-to-competition-hypothesis, it is generally accepted that plant species with a strong competitive ability and a poor adaptation to stressful abiotic conditions colonize the lesser stressful higher marsh zones, whereas plant species with a lower competitive ability and a better adaptation to stressful conditions colonize lower marsh zones (Pennings et al. 2005). Besides the chemical abiotic stressors such as salinity or redox potential, physical stressors need to be

taken into account as a colonization of low marsh zones requires an adaptation to wave forcing either by minimizing (avoidance strategy; i.e. flexible stems) or withstanding physical stress from wave forcing (tolerance strategy; i.e. stiff stems; Schulze et al. 2019). In Northwestern European salt marshes, typical species of the pioneer zone are *Spartina anglica* and *Salicornia europea*. Key species of plant communities of low marshes are *Aster tripolium*, *Halimione portulacoides* and *Puccinellia maritima*. High marshes often show monospecific stands of *Elymus athericus* or *Festuca rubra* (Suchrow and Jensen 2010). This spatial zonation can also be seen as representing the temporal succession of salt marsh vegetation. Marsh colonization usually is initiated by pioneer plant species, which are able to establish on the bare intertidal flats below mean high tide level. These pioneer plants, which are adapted to daily flooding and long inundation times, contribute to the stabilisation of sediments by their root system (Hemminga et al. 1998). Hydrodynamic forces that coincide with every flooding event can be reduced by pioneer species due to their specific biophysical plant properties such as high biomass or high stem densities (Peralta et al. 2008; Schulze et al. 2019) leading to increased deposition rates of allochthonous sediment (Van Hulzen et al. 2007). This process of sediment deposition (specified as $\text{g m}^{-2} \text{yr}^{-1}$) is usually measured in short timescales such as single inundation events or after every spring-neap cycle (Nolte et al. 2013a, b). Sediment deposition then causes a rise in elevation (mm yr^{-1}), which leads to a progressive succession and replacement of pioneer species by low marsh species and species of later successional stages (Rupprecht et al. 2015b). With increasing elevation of the marsh, vegetation development is further favoured. This process is described as accretion, which is the vertical growth of the marsh platform by allochthonous sediment input and autochthonous organic production, also considering auto-compaction, compaction by trampling and erosion (Nolte et al. 2013b).

On larger temporal scales (decades to centuries), salt marshes may establish and erode periodically. The vegetated marsh platform is regularly flooded by the tide from the seaward marsh edge and by a network of tidal creeks leading to a positive surface-elevation change of

the marsh in the long term (Fig. 1.3a). This net elevation change and a further expansion towards the intertidal flats and deeper waters can be a critical stage for the marsh, as a steepening (Fig. 1.3b) of the edge can result in a formation of cliffs therefore increasing the vulnerability of the marsh edge (van de Koppel et al. 2005). Severe storm surges and wave forcing may then initiate vegetation collapse and erosion at the marsh edge leading to partial losses of the vegetated marsh platform (Fig. 1.3c).

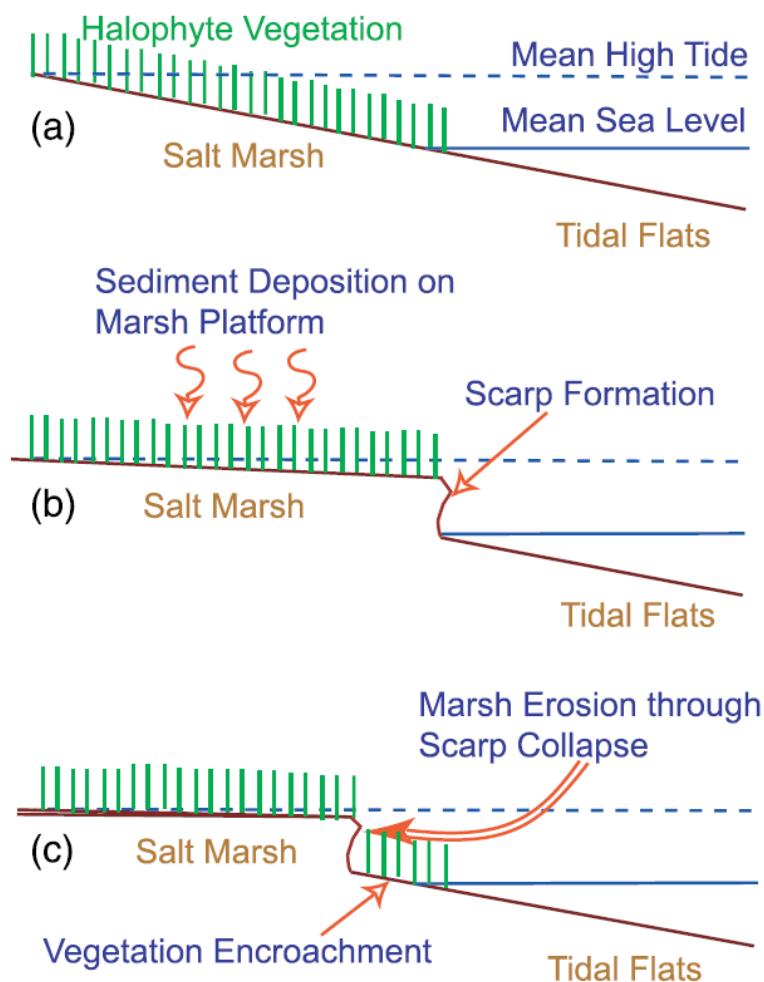


Figure 1.3 Cyclical establishment and erosion of salt marshes. **a)** Vegetation encroachment on a tidal flat. **b)** Regular sediment deposition and sufficient accretion rates lead to a positive surface-elevation change and therefore promoting scarp formation at the marsh edge. **c)** The scarp collapses and erodes due to storm surges and high wave forcing. Eventually, pioneer vegetation recolonizes the eroded area. Source: van de Koppel et al. 2005; Fagherazzi et al. 2020.

1.3 Historical development and man-made threats to salt marshes

For long times, civilizations have considered coastal wetlands as worthless areas with no value for coastal inhabitants and human societies. Therefore, coastal salt marshes and other wetlands were traditionally converted and exploited for agricultural and industrial purposes (Kirwan and Megonigal 2013). Estimations of global loss rates add up to 1-2% per year for salt marshes and to 1-3% per year for mangroves (Duarte et al. 2008). Consequently, approximately 87% of the world's wetlands have been lost in the past 300 years while 35% of all coastal wetlands have been lost in the last decades only (Friess et al. 2020). On a local scale, human modifications include alterations with hydrological purposes such as dredging, ditching and leveeing as well as embanking. On a regional scale, land subsidence caused by groundwater withdrawal threatens marshlands and, for example, led to drowning and extinction of large parts of coherent marshland at the Gulf of Mexico or in the San Francisco Bay area (Kennish 2001; Sarika and Zikos 2020). In the Wadden Sea, 15000 km² of coastal wetlands including salt marshes and tidal flats have been converted to date due to the aforementioned impacts (Airoldi and Beck 2007). On a global scale, the persistence of the currently existing salt marshes around the world is furthermore threatened by global warming and associated sea-level rise (Crosby et al. 2016). As landward migration of salt marshes is often prevented by seawalls, the combination of embankment and anthropogenically driven sea-level rise can strongly contribute to marsh loss (Wolters et al. 2005). Global-scale assessments of sea-level rise within recent years show average rates of approx. 3 mm yr⁻¹ (Chen et al. 2017; IPCC 2019) implying that salt marshes need to gain elevation by sediment input at minimum equally to rates of SLR. Nevertheless, varying regional conditions can lead to noticeable deviations from the global mean (Vermeersen et al. 2018). For northern parts of the Wadden Sea, even higher sea-level rise rates of up to 4 mm yr⁻¹ were described (Wahl et al. 2013).

The Wadden Sea is considered Europe's largest area of marshes and intertidal flats and consists of approx. 4500 km² of tidal flats as well as 400 km² of salt marshes stretching from Esbjerg

(Denmark) to Den Helder (Netherlands). Overall, 20% of European salt marshes are represented by Wadden Sea marshes (Esselink et al. 2017). Throughout the last century, high losses of salt marshes occurred due to land reclamation and the construction of coastal defence measures. However, Wadden Sea salt marshes, which can be separated into foreland marshes (mainland marshes with an anthropogenic origin), back-barrier marshes (mostly natural marshes) and Hallig marshes (remnants of former mainland marshes, now marsh islands), showed an expansion within the last 20 years (Esselink et al. 2017; Fig.1.4). Back-barrier marshes (islands) showed an expansion of 40%, whereas Hallig island marshes neither expanded nor shrank. Mainland marshes showed a slight expansion, mainly in the state of Schleswig- Holstein in Germany (Esselink et al. 2017; Fig. 1.4).

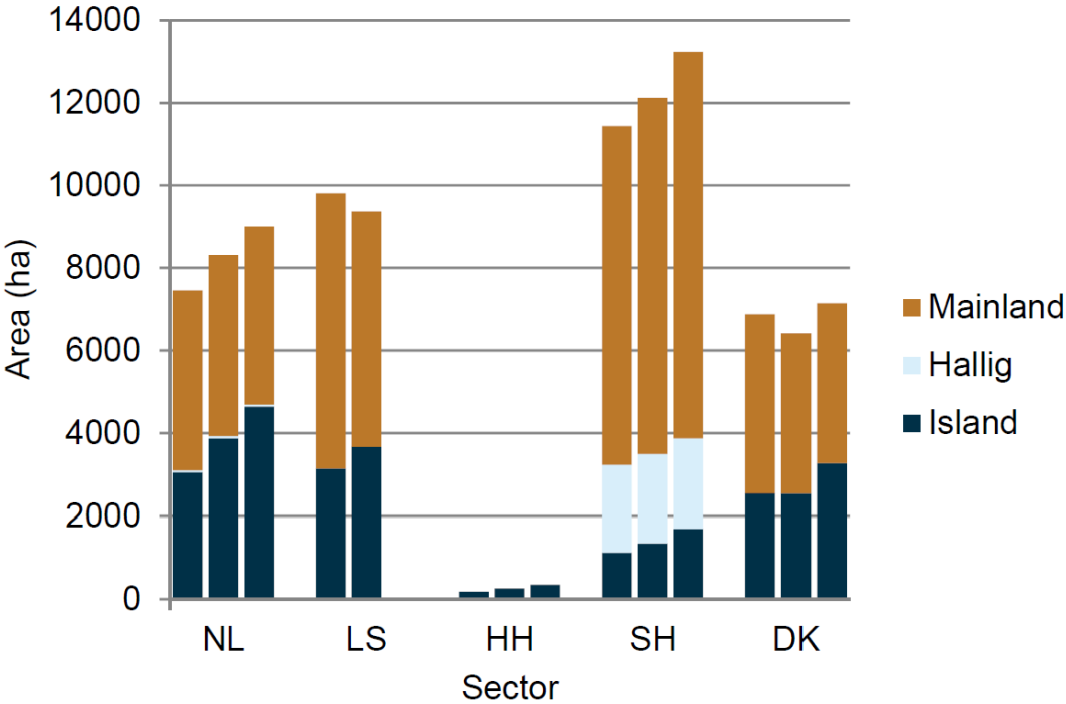


Figure 1.4 Areal extent of salt marshes in the Netherlands (NL), Germany (LS=Lower Saxony, HH=Hamburg, SH=Schleswig-Holstein) and in Denmark (DK). The data are based on three surveys (1995/2001, 2002/2007 and 2008/2014; left to right). Source: Esselink et al. 2017.

While on the one hand the tidal flats were almost unaffected by humans in the past, the artificially created mainland marsh type accounts for 60% of the 400 km² of Wadden sea salt

marshes which underwent a high degree of human modifications (Reise et al. 2010; Fig. 1.5). Approx. 1000 years ago, land reclamation started with the installation of dikes and foreland sedimentation fields made of e.g. brushwood groynes in order to facilitate sediment deposition and accretion. Once a salt marsh has established due to increased accretion rates and establishment of pioneer vegetation, the outer dike was shifted seaward (Reise 2005). As a result, the reclaimed area was used as farmland once the soil has been drained and soil salinity has been washed out. Without human intervention, salt marshes would likely have a greater extent than today stretching kilometres from the tidal flats to the hinterland. A regular flooded treeless plain with a salinity gradient from salty (tidal flats) to brackish and fresh (hinterland marsh) would allow freshwater marsh species such as common reed to establish along an elevational gradient above the salt marshes. In the transition zone towards the pleistocene sandy geest, extensive bog landscapes would develop. Today, the majority of Wadden Sea salt marshes are fragmented and structured by artificial drainage systems resulting in rectangular shaped sedimentation fields (Fig. 1.5). In the 1990's, the maintenance of these drainage systems was reduced in the Wadden Sea due to newly developed management strategies of the National Park Administration in 1992 (Stock et al. 2005).

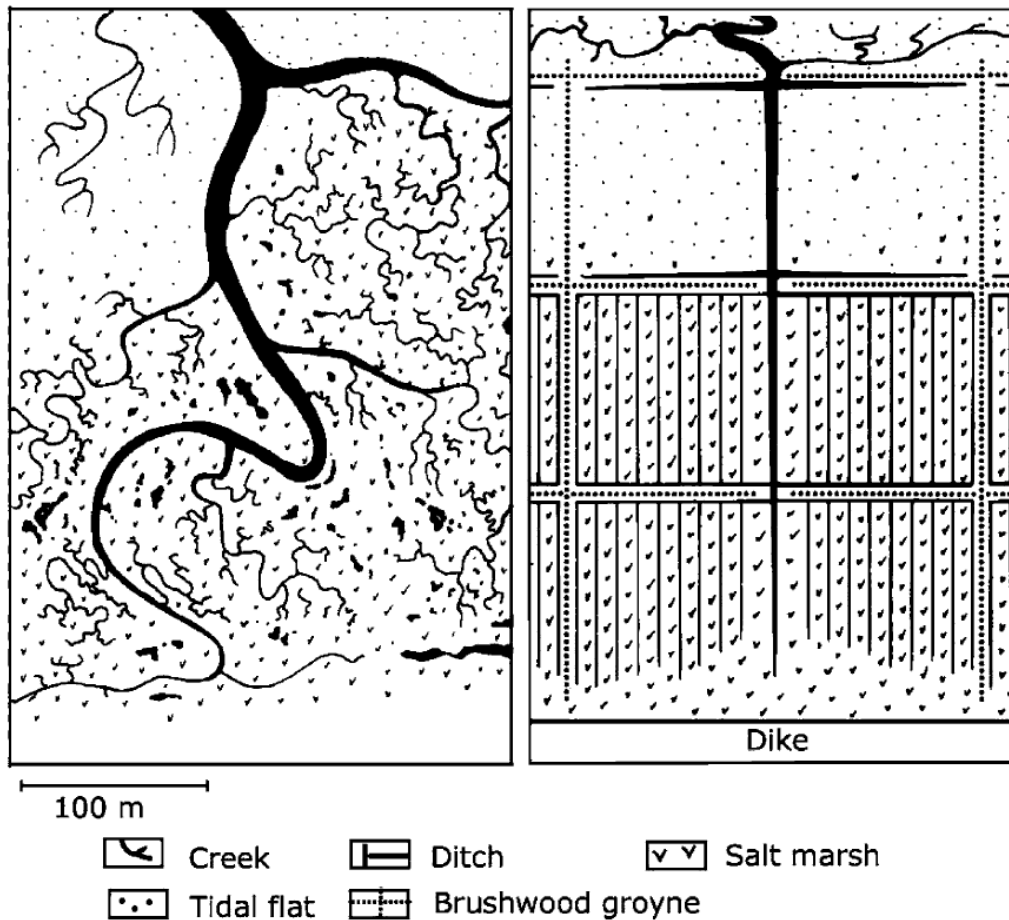


Figure 1.5 Natural salt marsh (left) and artificial salt marsh (right). In the Wadden Sea today, a transition from artificial high marshes to natural low marshes can be found frequently. Source: Reise 2005.

1.4 Salt marshes and SLR

Generally, salt marshes can cope with rising sea level as long as sea-level rise is lower than vertical marsh accretion (Nolte et al. 2013b). However, if coastal marshes cannot compensate for the future sea-level rise, they will be in danger of being submerged permanently when landward expansion is prevented by seawalls. Sediment deposition and accretion is mainly a result of complex bio-geomorphological interactions between marsh morphology (Brückner et al. 2019), vegetation (Cahoon et al. 2020) and sediment availability (Kirwan et al. 2010). Therefore, a sufficient sediment supply as well as sufficient sediment-deposition rates and vital salt-marsh vegetation are likely to be the factors allowing coastal marshes to adapt to increased sea-level rise, storminess, wave forcing, and flooding duration. However, global predictions

and observations of sedimentation and overall marsh development are highly challenging and lead to contrasting results (Wiberg et al. 2020). Some studies indicate a widespread global marsh loss (Crosby et al. 2016; Spencer et al. 2016; Thorne et al. 2018), whereas other studies predict low marsh losses and even marsh expansion (Kirwan et al. 2016; Schuerch et al. 2018; Ganju 2019). Globally, sediment availability and sediment deposition range from a high sediment availability and high sediment deposition rates (e.g. Wadden Sea marshes; minerogenic soil formation; Butzeck et al. 2015) to a lower sediment availability and lower sediment deposition rates (e.g. some marshes at the US east coast; organogenic soil formation; Peteet et al. 2018). Irrespective of sediment availability, it is well proven that salt marsh vegetation plays a crucial role in marsh survival by attenuating waves and water flows therefore allowing sediment to settle on the marsh surface (Cahoon et al. 2020).

1.5 Coastal protection by salt marsh vegetation

By modifying their physical environment through the reduction of hydrodynamic energy and the enhancement of sediment deposition, salt marsh plants act as ecosystem engineers (Peralta et al. 2008). The so-called biophysical plant properties play a key role in the capacity of marshes to dissipate wave height and energy (Möller et al. 2014; Paul et al. 2016; Rupprecht et al. 2017). Wave dissipation is a combined effect of bottom friction and vegetation which form an obstruction to uniform flow as well as to wave-induced oscillatory flow. The obstruction represented by salt marsh vegetation mostly depends on standing biomass, stem density and stem flexibility. Vegetation, in turn, experiences drag and re-orientation by wave forces (Mullarney and Henderson 2010). Salt marsh vegetation can attenuate waves even under storm surge conditions (Möller et al. 2014). Therefore, by reducing wave height and wave energy even under extreme conditions, salt marshes contribute to erosion protection, flood protection, the stabilisation of shores and dike safety (Keimer et al. 2021). As salt-marsh plants show a

wide variability in biophysical properties both within and among species, their canopies have different wave damping potentials on the one hand and a different resilience to physical damage by waves on the other hand (Rupprecht et al. 2015a; Tempest et al. 2015). For example, species with different stem flexibility also differ in their resilience to physical damages induced by waves (Vuik et al. 2018). Species with stiff stems are able to tolerate mechanical wave forcing leading to high wave attenuation rates but eventual stem breakage, whereas flexible species avoid mechanical stress by reconfiguration of the canopy. However, the growing body of studies on wave attenuation by vegetation only provides evidence for a specific setting of marsh plants for one point in time (Willemsen et al. 2020). As it is still poorly investigated how biophysical plant properties vary seasonally and along elevational within-marsh gradients, numerical and physical models on wave attenuation are still often limited due to simplifications of parameters (e.g. constant biophysical properties). The more temporal and spatial scales need to be considered in a model, the more the model simplifications increase (Fagherazzi et al. 2012; Wiberg et al. 2020). Overall, a lack of knowledge on the spatial and temporal variability of biophysical properties of salt marsh plants hampers realistic assessments of the wave attenuation capacity of salt marshes.

1.6 Effects of grazing and small-scale patterns of vegetation structure on sedimentation

As vegetation properties such as high stem densities, stiff canopies and high aboveground biomass were found to significantly decrease wave energy and flow velocity (Fagherazzi et al. 2012), a positive relationship between these properties and settling of sediment particles under vegetation-induced calmer hydrodynamic conditions can be assumed (Cahoon et al. 2020). The aboveground biomass, vegetation height and vegetation cover in salt marshes are, however, largely affected by human influences such as mowing or grazing for agricultural and nature conservation purposes (Esselink et al. 2000; Nolte et al. 2013a). Therefore, it can be

hypothesized that human influences highly alter hydrodynamic conditions and sedimentation rates in salt marshes. However, in Wadden Sea mainland marshes, where sediment deposition and accretion rates seem to be sufficient to compensate moderate levels of accelerated sea-level rise (Suchrow et al. 2012; Butzeck et al. 2015), no differences in sediment deposition and accretion between grazed and ungrazed areas were found (Elschot et al. 2013; Nolte et al. 2013a). As further studies on the influence of livestock grazing and salt-marsh vegetation on sedimentation in other marshes show contrasting results, it seems that it is not fully understood under which conditions vegetation promotes sediment deposition (Tinoco et al. 2020). It was recently discussed that effects of grazing and vegetation can eventually be masked by other factors influencing sediment deposition (Davidson et al. 2017). These factors can be the inundation frequency, the inundation duration (Temmerman et al. 2003a), the distance to the marsh edge or a creek (Temmerman et al. 2005), the overall sediment availability and the initial suspended sediment load in the floodwater (Butzeck et al. 2015). If, for example, the mineral sediment availability is as high as in the Wadden Sea mainland marshes, it is more likely that a potential effect of grazing is masked by high overall sediment deposition rates. Therefore, effects of grazing should be analysed in marshes with different settings from low to high sediment availability or from low to high inundation frequencies.

Vulnerable marshes with limited inundations and sediment availability are present on the northern Wadden Sea marsh islands (“Halligen”). On these Hallig islands, human alterations are more pronounced compared to mainland marshes (Schindler et al. 2014). Hydrodynamic and sedimentological processes are strongly affected by a set of human modifications such as so-called summer dikes and tide gates leading to a low inundation frequency and a limited sediment input. To date, it is still unclear how livestock grazing affects sediment deposition and accretion rates under these specific conditions with low inundation and a low sediment availability.

In summary, sedimentation in salt marshes is a highly context-dependent process (Davidson et al. 2017) and is still not fully understood. Each marsh system represents an individual setting of sediment availability, hydrodynamic conditions, vegetation properties, human modifications or presence or absence of grazing and mowing. Additionally, most of these factors are subject to temporal variability. For example, inundation frequency, height and duration are higher in autumn or winter compared to summer, whereas vegetation is fully developed from summer to autumn and degenerated from winter to spring. Furthermore, all of these factors vary spatially on scales from within-marsh differences to global differences. For a better understanding of the influence of vegetation (presence or absence, e.g. as a result of grazing) on sediment deposition, it requires investigations in as many different marsh settings as possible. This also includes the spatial positioning of vegetated and unvegetated patches and how this spatial arrangement affects sediment deposition and accretion on a within-marsh scale. Even on this scale and even without vegetation, sediment deposition would show spatial heterogeneous patterns as a large proportion of sediment is gravity-driven deposited at the first meters after inundation waters have entered the marsh platform, leading to high sedimentation rates at the marsh edge or the creek edge and to lower deposition in the marsh interior (Temmerman et al. 2003a). The presence of complex spatial vegetation patterns still hampers the understanding of small-scale sedimentation patterns and little is known about sedimentation patterns on a smaller scale of a few meters in vegetated and unvegetated salt marshes.

1.7 Aims and objectives

The main aims of this thesis were to (I) quantify the seasonal and spatial within-marsh differences of biophysical plant properties in a northern Wadden Sea mainland marsh, (II) to investigate the influence of livestock grazing on sediment deposition and accretion on a highly anthropogenically altered marsh island in the Wadden Sea with a limited inundation frequency

and (III) to analyse the effects of small-scale patterns of vegetation structure on suspended sediment concentration and sediment deposition in a Wadden Sea mainland salt marsh.

In the following sections, an overview of the objectives of the singles research papers, which are part of this thesis, is given:

Chapter 2: Seasonal and spatial within-marsh differences of biophysical plant properties: implications for wave attenuation capacity of salt marshes

In this chapter, the key morphological properties i.e. stem density, vegetation height and aboveground biomass as well as biomechanical properties such as stem flexibility of two salt-marsh grasses were quantified. These properties have implications for wave attenuation capacity of salt marshes. Three-point bending tests were used to determine stem flexibility parameters. The study was conducted in a Wadden Sea mainland marsh adjacent to the Elbe estuary.

Key objectives:

- Quantification of seasonal variability of biophysical properties of the salt-marsh grasses *Spartina anglica* and *Elymus athericus*
- Quantification of intraspecific differences in biophysical plant properties between seaward and landward-located marsh zones

Chapter 3: Livestock grazing reduces sediment deposition and accretion rates on a highly anthropogenically altered marsh island in the Wadden Sea

The aim of chapter 3 is to unravel the effect of livestock grazing on sediment deposition on a marsh island facing low inundation frequencies and a low sediment availability. Sediment deposition and suspended sediment concentration (SSC) were investigated on grazed plots adjacent to ungrazed plots at the marsh edge and in the marsh interior. The study was conducted on a Wadden Sea Hallig marsh island.

Key objectives:

- Comparison of total sediment deposition and accretion rates of grazed and ungrazed plots
- Comparison of SSC of grazed and ungrazed plots
- Comparison of total sediment deposition and accretion rates between the edge of the marsh island and interior located parts

Chapter 4: Effects of small-scale patterns of vegetation structure on suspended sediment concentration and sediment deposition in a salt marsh

This chapter addresses the determination of sediment deposition on a spatial scale of a few meters in vegetated and mown subplots adjacent to a major creek in a mainland salt marsh close to the Elbe estuary. The study was conducted over the course of several neap-spring cycles in winter and summer both in the low and the high marsh.

Key objectives:

- Determining differences of sediment deposition and SSC between tall and short vegetation
- Detecting potential effects of vegetation both in the low and the high marsh
- Determination of how spatial positioning of tall and short vegetation influences spatial patterns of sediment deposition and SSC on a small vegetation-patch scale of a few meters

2 Seasonal and spatial within-marsh differences of biophysical plant properties: implications for wave attenuation capacity of salt marshes

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Abstract

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

Introduction

Vegetation plays a vital role in the form, functioning and ecosystem service delivery of coastal salt marshes. Many salt-marsh plants act as ecosystem engineers by modifying their physical environment through the reduction of hydrodynamic energy and the enhancement of sediment deposition (Bouma et al. 2005, 2010; Peralta et al. 2008). If sufficient sediment is deposited, marshes can keep pace vertically with rising sea level (Nolte et al. 2013a, b). This ability implies that vegetated salt-marsh surfaces can be an important component of nature-based coastal protection schemes especially in times of climate change, accelerated sea-level rise and increased storm frequency (Koch et al. 2009; Narayan et al. 2016; Sutton-Grier et al. 2018). Recent studies have shown that biophysical properties of plants, which can be categorized as morphological (e.g. stem density, vegetation height and aboveground biomass) and biomechanical (e.g. stem flexibility), play a key role in the capacity of marshes to dissipate wave height and energy (Möller et al. 2014; Paul et al. 2016; Rupprecht et al. 2017). Wave dissipation is a combined effect of bottom friction and vegetation, which form an obstruction to wave-induced oscillatory flow. Vegetation induced obstruction depends both on standing biomass or stem density and stem flexibility. Vegetation, in turn, experiences drag and re-orientation by wave forces (Mullarney and Henderson 2010). Flexible plants move with the surrounding water and show an avoidance strategy to minimize the risk of folding and breakage under high drag forces. In contrast, stiff plants maximize the resistance to physical damage (tolerance strategy), thus leading to higher drag forces, higher flow resistance and an increased risk of breakage compared to flexible plants (Coops et al 1994; Puijalón et al. 2011). Apart from stem flexibility, aboveground biomass and stem density also play a crucial role in wave dissipation by vegetation (Bouma et al. 2005, 2010; Peralta et al. 2008; Widdows et al. 2008; Anderson and Smith 2014). For example, species with contrasting biomechanical plant properties can lead to a similar wave dissipation when regarded on a biomass basis (Bouma et al. 2010).

Salt-marsh plants show a wide variability in biophysical properties both within and among species, making their canopies structurally complex (Rupprecht et al. 2015a; Tempest et al. 2015). This structural complexity in combination with the unpredictable nature and high variability of hydrodynamic conditions make field measurements of the interaction between vegetation and hydrodynamics extremely challenging. Hence, many studies rely on numerical or physical modelling approaches (Tempest et al. 2015). A high model quality, however, is often hampered by limited data on biophysical properties of salt-marsh vegetation, especially regarding stem flexibility (Tempest et al. 2015). The majority of numerical wave dissipation models capture vegetation effects in a factor that consists of plant stem height, stem density, stem diameter and an empirical bulk drag coefficient C_D . (Mendez and Losada 2004; Paul and Amos 2011). Physical models often use plant mimics to simulate the effect of vegetation on currents and waves (e.g. Stewart 2006; Anderson and Smith 2014). However, insufficient data on plant biophysical properties lead to problems in reproducing salt-marsh plants realistically by plant mimics (see Anderson and Smith 2014; Tempest et al. 2015). Consequently, it would be valuable to assess the spatial and temporal variation in biophysical properties of salt-marsh species (Rupprecht et al. 2015a).

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

by seasonal climatic variation in temperate zones as previously found for helophytes (Coops and van der Velde 1996) or lake and river plants (Miler et al. 2014).

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

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

Methods

Species

Spartina anglica

The perennial grass *Spartina anglica* (hereafter referred to as *Spartina*) typically occurs in the salt marsh pioneer zone (below mean high tide level) and the low marsh, where it can form monospecific stands (Nehring and Adsersen 2006). In late fall, shoots die but largely remain as dead vegetation canopies while rhizome development increases (Nehring and Adsersen 2006). Throughout the last century, *Spartina* has spread from the south coast of the UK to salt marshes

all over Europe, both naturally and by deliberate transplantations (Nehring and Adersen 2006; Nehring and Hesse 2008). A reason for deliberate transplantations was its function to act as an ecosystem engineer by enhancing sedimentation through dense aboveground canopies and a dense root system (Chung 1993; Bouma et al. 2005, 2010; Van Hulzen et al. 2007).

Elymus athericus

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

Study site

Plant samples were obtained from a salt marsh on the mainland coast of Northern Frisia, German Wadden Sea (54.62°N, 8.84°E; Fig. 2.1 A). The studied salt marsh developed after the embankment of the adjacent Sönke-Nissen-Koog (SNK) polder and subsequent constructions of sedimentation fields in front of the dike (Kunz and Panten 1997; Mueller et al. 2019). As a salt marsh of anthropogenic origin with a thick clayish sediment layer and a regular system of creeks and drainage ditches, it can be considered representative for many salt marshes of North-West Europe. The tidal range is 3.4 m, the mean high tide is +1.59 m NHN (Normalhöhennull, which is comparable to mean sea level). Elevations within the salt marsh range from 0.9 m to 2.6 m NHN with a mean elevation of 2 m NHN (Müller et al. 2013). The marsh stretches from

the dike over 700 m to the tidal flats (Fig. 2.1B) and is predominantly covered by *Elymus* in the high marsh (Mueller et al. 2017) and by *Spartina* in the low marsh (according to own observations and the Trilateral Monitoring and Assessment Program, TMAP; Petersen et al. 2013).

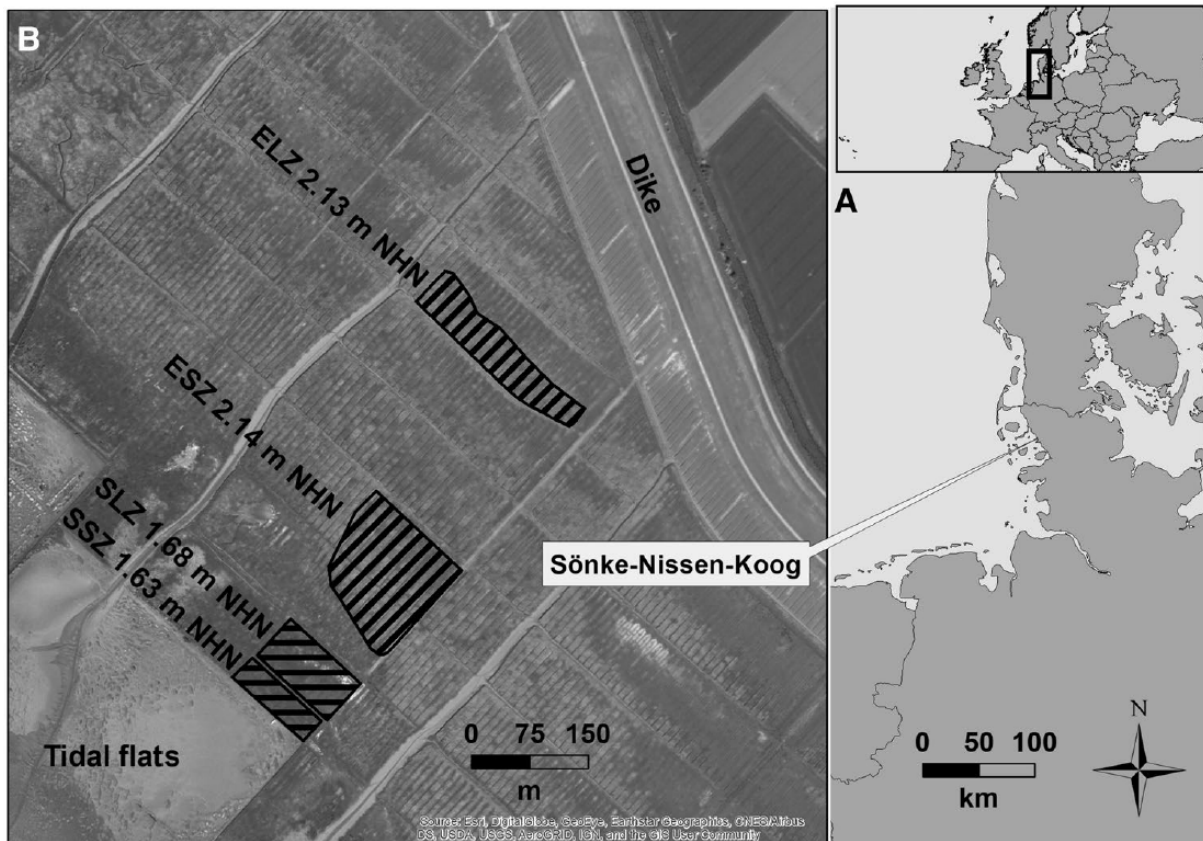


Figure 2.1 A) Location of the study site in the Wadden Sea National Park Schleswig-Holstein at the German North Sea coast. The black rectangle shows the position of the area in Europe. B) Satellite image of the study site with the sampling zones. Shown are the seaward and landward located *Elymus* (ESZ, ELZ; vertically hatched) and *Spartina* (SSZ, SLZ; diagonally hatched) sampling zones with respective mean elevations above NHN. The map was created using a base map in ArcGIS © Desktop: Release 10, ESRI 2014, Redlands, CA: Environmental Systems Research Institute.

Sampling design

Two sampling zones were chosen in the low marsh (dominated by *Spartina*) and in the high marsh (dominated by *Elymus*). One of the two sampling zones per vegetation type was set closer to the seaward marsh edge ('seawards'), and one closer to the landward marsh edge

(‘landwards’; Fig. 1B). The seaward-located *Spartina* zone (hereafter referred to as SSZ; inundation frequency: 182 times per year; total inundation time: 557.76 hours/year; F. Müller unpublished data) stretches 40 m perpendicular along the marsh towards the landward-located zone (hereafter referred to as SLZ; inundation frequency: 156 times per year; total inundation time: 452.88 hours/year). For *Elymus*, one zone was chosen towards the low marsh (ESZ; inundation frequency: 23 times per year; total inundation time: 62.64 hours/year) and one zone was chosen closer to the dike (ELZ; inundation frequency: 23 times per year; total inundation time: 64.32 hours/y). An area-based stratified random design was applied with 40 random sampling points (20 points for flexibility measurements; 20 points for aboveground biomass and stem density measurements) generated within each sampling zone of the *Spartina* and *Elymus* vegetation type using a random point tool of QGIS 2.0.1 Dufour (QGIS Development Team 2014). The elevation of each point was assessed using a Trimble LL500 precision laser and a Trimble HL 700 receiver as a levelling instrument (2.0 mm accuracy) and a known closely located benchmark. Data were used to calculate mean elevation per zone (Fig. 2.1B).

Measurements of plant stem flexibility

Three-point bending tests were performed to quantify plant stem flexibility under bending forces orthogonal to the plants stem. Plant samples were collected both in mid-March (before the onset of plant growth) and in late August. In the field, samples were excavated as small marsh blocks with a dimension of 10x10x10 cm and were packed in plastic bags to conduct measurements on fresh material. From each marsh block, a single adult and undamaged plant stem was chosen randomly and the stem length up to the inflorescence was measured and divided in four equal parts. A test section was defined as the beginning of the second quarter starting from the bottom end of the stem and was cut out with a razor blade. Test sections were consistently cylindrical. To minimize the effect of shear stress in bending tests, a stem diameter to stem length ratio (here stem length means the horizontal span of the tested stem section

between the two metal support bars, see Fig. 2.2) of 1:15 was chosen (see also Miler et al. 2012, 2014; Rupprecht et al. 2015a). The bending tests were performed with a Zwick/Roell testing machine (Type 1120.25, Nominal Force: max. 1 kN, using a 10 N load cell; initial load 0.01 N; Zwick GmbH & Co. KG, Ulm, Germany).

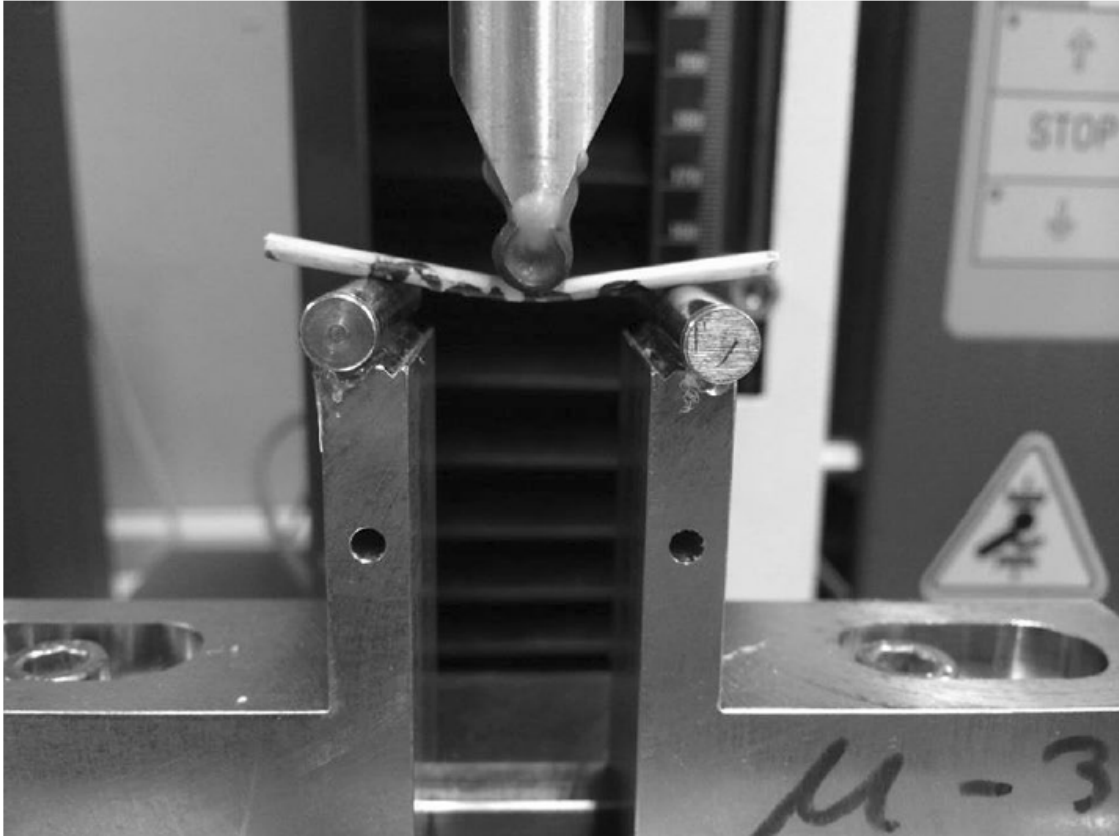


Figure 2.2 Three-point bending test with a stem section of *Elymus*.

For the measurements, a metal bar was lowered with a displacement rate of 10 mm min^{-1} . Then, the vertical deflection of the tested stem section and the applied force were recorded (see also Miler et al. 2012, 2014; Rupprecht et al. 2015a; Silinski et al. 2015, 2018). The slope was determined from the most linear part of the force-deflection curve. Furthermore, the diameter and the span of the stem between the two metal support bars were used to determine the following mechanical properties following Rupprecht et al. (2015a): (I) the second moment of area (I given in m^4) which describes the effect of stem morphology (considering stem diameter) on flexibility; (II) the Young's modulus (E given in Pa) which here describes the flexibility of

the plant stem tissue without considering stem morphology; (III) the flexural rigidity (EI given in Nm^2) which describes the overall stem flexibility considering stem tissue and morphological parameters. In this study, results on the Young's modulus and flexural rigidity are presented.

Biomass and stem density measurements

Aboveground biomass (hereafter referred to as biomass) was harvested twice in 2014; in early April and in mid-August in order to identify differences in morphological properties between spring and summer. All plants rooting inside a 50x50 cm frame were cut at the soil surface. Summer sampling was carried out within 1 m distance of the spring plots. Samples were dried for 48 hours at 65 °C to determine the dry biomass. Stem density was measured after the removal of litter by counting only the remaining stems that were still connected to a root. For *Elymus*, stem density was quantified on a 20x20 cm subplot due to large numbers of stems per area.

Statistical analysis

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

Results

Flexural rigidity

Flexural rigidity of *Spartina* differed significantly between seasons and zones (Fig. 2.3A; Table 2.1). However, the interaction between season and zone was also significant. Flexural rigidity was 5.0 times higher in summer compared to spring. In spring, *Spartina* stems of the SLZ were 4.0 times more rigid compared to the stems of the SSZ. In summer, stems of the SLZ showed a 2.8 times higher value compared to stems of the SSZ. For *Elymus*, flexural rigidity significantly differed between seasons (Fig. 2.3A; Table 2.1). Stems were 2.9 times more rigid in summer compared to spring. In both seasons, stems of the ESZ slightly, but not significantly, exceeded the rigidity of stems of the ELZ with a factor of 1.34 in spring and 1.14 in summer. For *Spartina*, a second order polynomial regression was found to best represent the positive relationship between stem diameter and flexural rigidity. For *Elymus*, we found a linear regression to best represent the positive relationship between stem diameter and flexural rigidity (Fig. 2.4).

Aboveground biomass

Biomass of *Spartina* differed significantly between spring and summer and between SSZ and SLZ (Fig. 2.3B; Table 2.1). Additionally, a significant interaction between season and zone was found. Compared to spring, biomass was 2.1 times higher in summer. SLZ exhibited 1.6 times more biomass compared to SSZ in spring and 1.5 times more biomass in summer. For *Elymus*, significant differences in biomass were only found between the seasons but not between the zones (Fig. 2.3B; Table 2.1). *Elymus* biomass was 1.3 times higher in summer compared to spring.

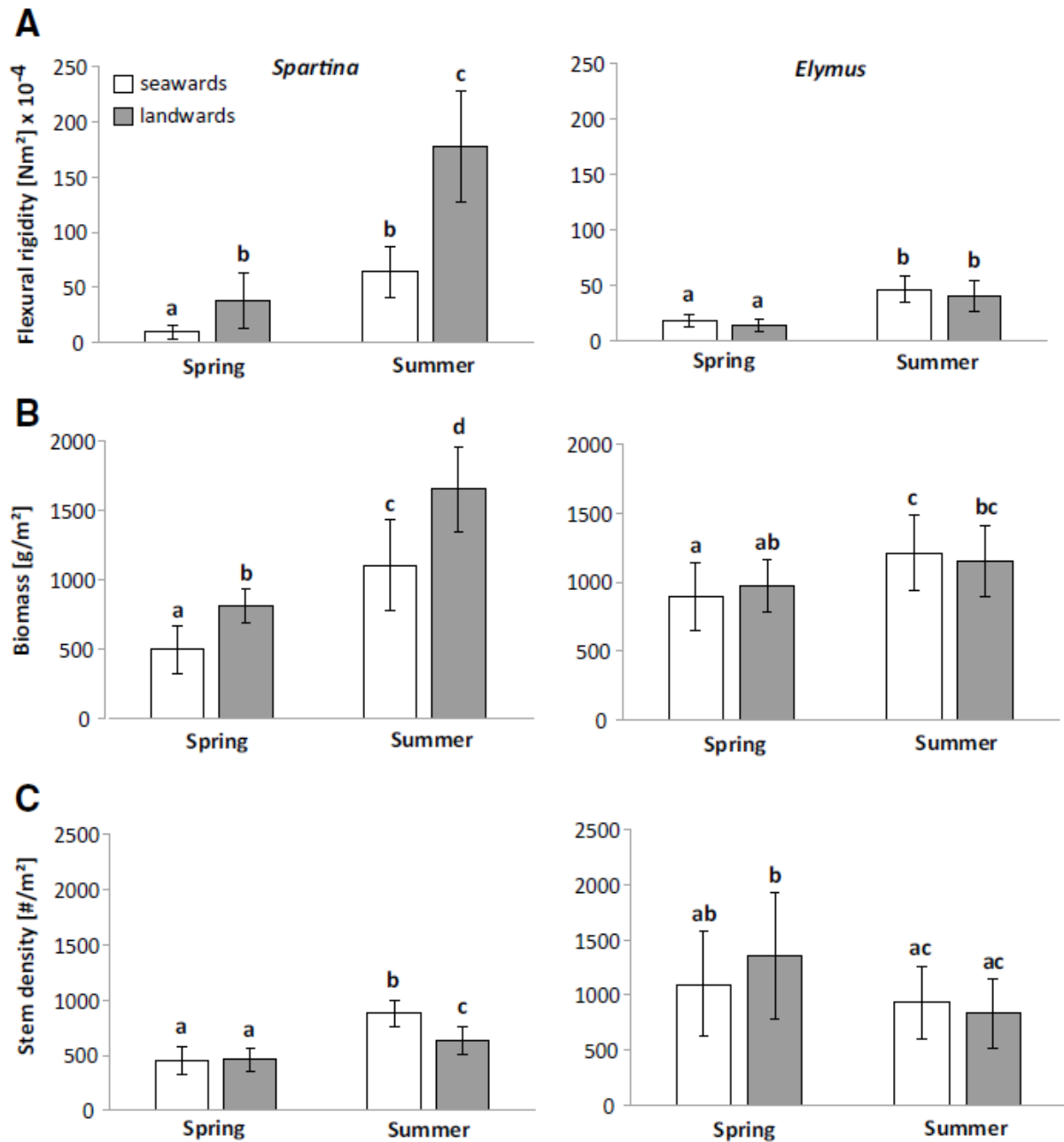


Figure 2.3 Flexural rigidity (A), biomass (B) and stem density (C) of *Spartina* and *Elymus* in spring and summer, respectively. Light bars show the zone directed seawards while dark bars show the zone directed landwards. Each bar represents 20 samples. Presented are mean values \pm standard deviations. Different lowercase letters indicate significant differences among the zones in both seasons. Interspecific differences have not been assessed.

Stem density

Stem density of *Spartina* significantly differed both between seasons and zones (Fig. 2.3C; Table 2.1). Furthermore, a significant interaction between season and zone was found. Stem density was 1.7 times higher in summer than in spring. While in spring no difference was detected between the two zones, in summer stem density was 1.4 times higher in SSZ than in SLZ. Stem densities in *Elymus* differed between seasons, but not between zones (Fig. 2.3C; Table 2.1). Stem density in spring was 1.4 times greater than in summer.

Table 2.1 ANOVA table of all biophysical parameters for *Spartina* and *Elymus* in spring and summer season in the landward and seaward-located zones. Given are F-values and p-values.

		Season		Zone		Season * Zone	
		F	p	F	p	F	p
Flexural rigidity	<i>Spartina</i>	192.39	< 0.01	103.65	< 0.01	36.50	< 0.01
	<i>Elymus</i>	145.81	< 0.01	5.01	< 0.05	0.81	0.78
Biomass	<i>Spartina</i>	163.46	< 0.01	57.30	< 0.01	4.33	< 0.05
	<i>Elymus</i>	19.26	< 0.01	0.02	0.90	1.60	0.21
Stem density	<i>Spartina</i>	120.31	< 0.01	17.59	< 0.01	21.58	< 0.01
	<i>Elymus</i>	11.63	< 0.05	0.61	0.44	3.04	0.08
Stem length	<i>Spartina</i>	48.39	< 0.01	54.77	< 0.01	1.40	0.24
	<i>Elymus</i>	380.31	< 0.01	2.06	0.16	0.08	0.78
Stem diameter	<i>Spartina</i>	136.60	< 0.01	58.19	< 0.01	0.81	0.37
	<i>Elymus</i>	65.42	< 0.01	0.62	0.43	2.42	0.12
Young's modulus	<i>Spartina</i>	2.26	0.14	6.23	< 0.05	0.37	0.54
	<i>Elymus</i>	1.26	0.27	2.07	0.15	4.54	< 0.05

Stem length, stem diameter, Young's Modulus

Spartina and *Elymus* stems were significantly longer in summer compared to spring in both zones (Fig. 2.5; Table 2.1). Furthermore, *Spartina* stems were significantly longer in the SLZ than in the SSZ in either season, whereas for *Elymus* no spatial differences were detected. Stem diameters show the same pattern with higher values in summer compared to spring for both species, and higher values in the landward zone only for *Spartina*. The least variability between the seasons and zones was detected for Young's modulus. Here, only *Spartina* stems showed

slightly but not significantly higher values in summer compared to spring and in the SLZ compared to the SSZ in either season. No differences for Young's modulus were detected in *Elymus* stems.

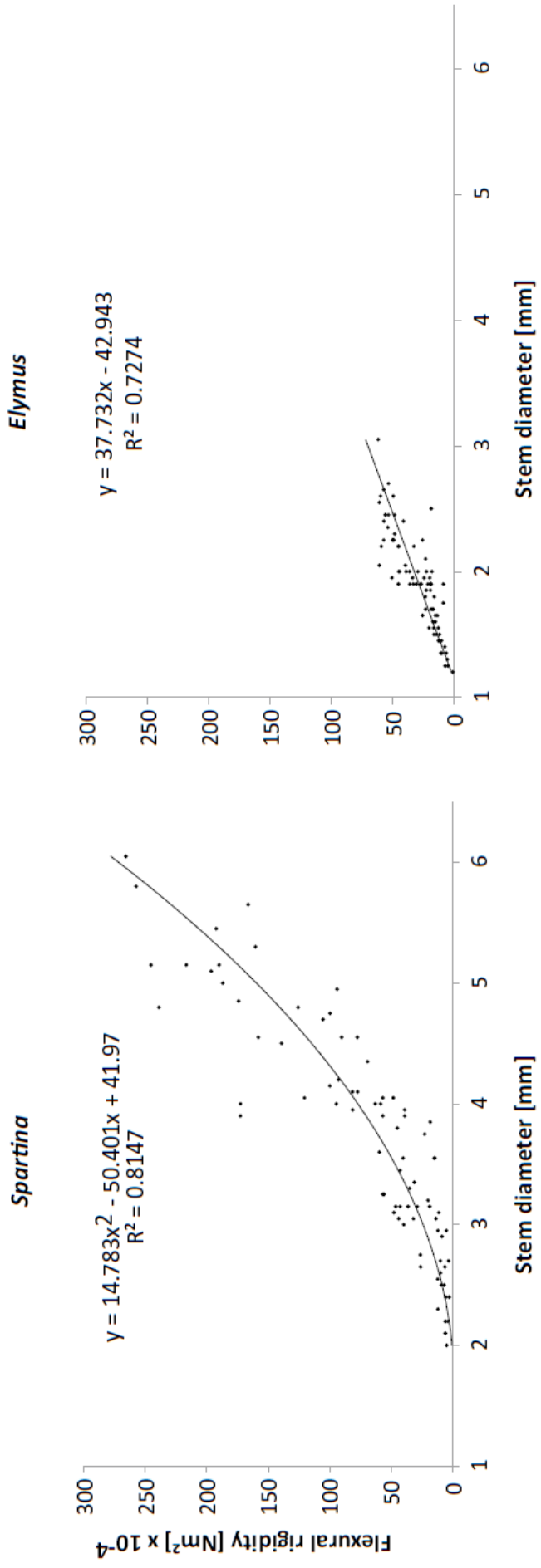


Figure 2.4 Best-fit polynomial regression and linear regression between stem diameter and flexural rigidity of *Spartina* and *Elymus* stems of both seasons and zones, respectively. Shown are equations and the coefficients of determination (R²).

Discussion

Stem flexibility

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

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

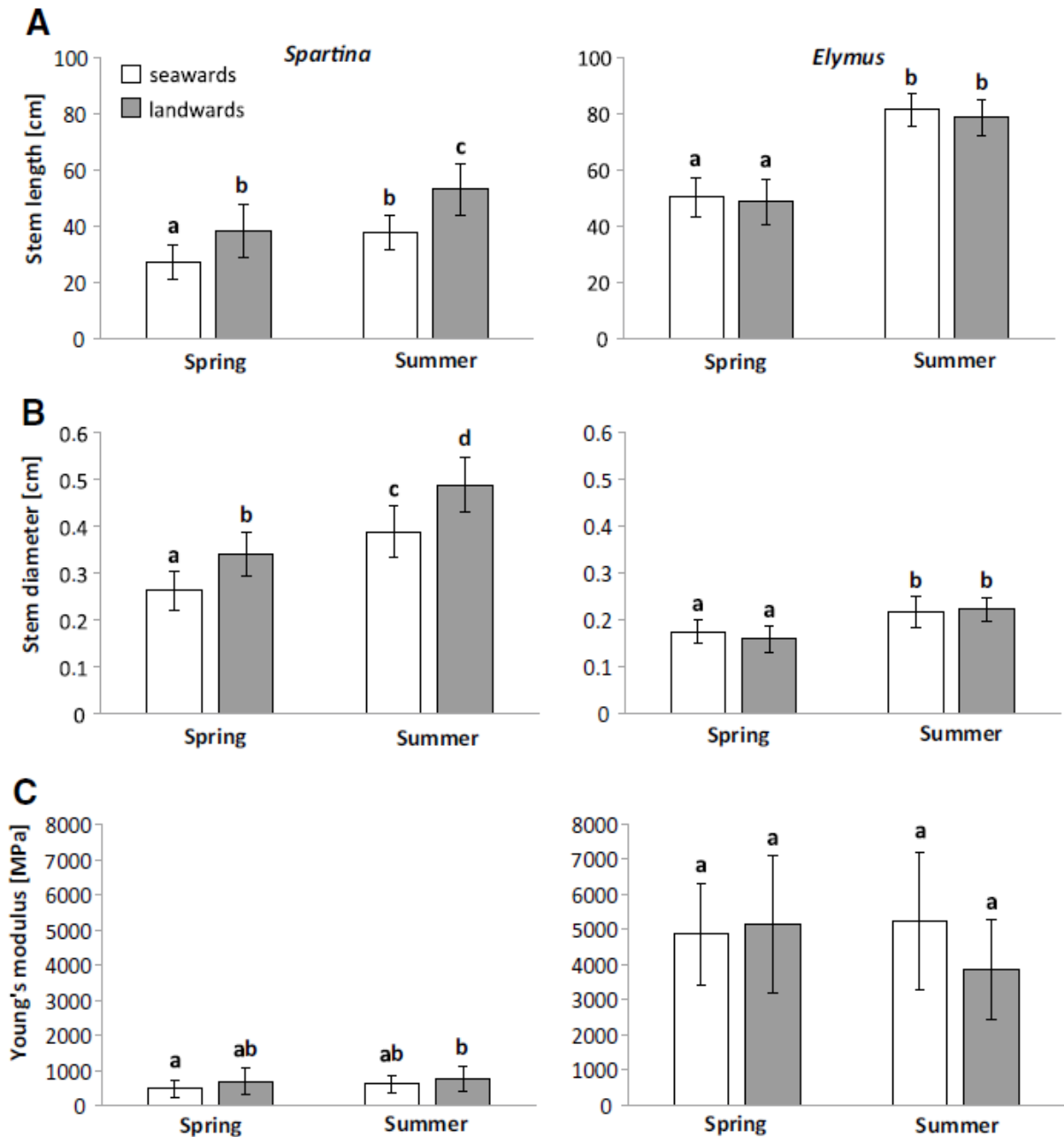


Fig. 2.5 Young's modulus (A), stem diameter (B) and stem length (C) of *Spartina* and *Elymus* in spring and summer, respectively. Light bars show the zone directed seawards while dark bars show the zone directed landwards. Each bar represents 20 samples. Presented are mean values \pm standard deviations. Different lowercase letters indicate significant differences among the zones in both seasons. Interspecific differences have not been assessed.

In contrast, Carus et al. (2016) found the opposite pattern for stems of *Bolboschoenus maritimus*, a typical species in the pioneer zone of European freshwater and brackish marshes along shorelines of estuaries where ship and wave induced wave forcing occurs. These findings suggest that species growing under harsh hydrodynamic conditions may develop different

biomechanical properties to either minimize physical stress (avoidance strategy; i.e. flexible stems, low flexural rigidity) from waves and currents or to withstand these mechanical forces (tolerance strategy; i.e. stiff stems, high flexural rigidity). Our results show an avoidance strategy of *Spartina* to increasing hydrodynamic forces and drag forces lower in the elevational gradient in salt marshes, as individuals in the SSZ were significantly smaller, thinner and more flexible than in the SLZ in both seasons. These characteristics should minimize the impact of hydrodynamic forces and the risk of plant breakage. However, it may also be possible that stem development in the SSZ is inhibited by constant wave action leading to thinner, smaller and more flexible stems.

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

Biomass

For both *Spartina* and *Elymus*, seasonal differences with higher biomass in summer than in spring were found which can be explained with the breakdown of canopies during the winter season in temperate zones (Bellis and Gaither 1985; Morris and Haskin 1990; Koch et al. 2009). In *Spartina*, we found up to two times higher biomass in summer compared to spring. Seasonal biomass changes in temperate zones have been found to affect wave dissipation in seagrass beds (Chen et al. 2007; Paul and Amos 2011), brackish marshes (Silinski et al. 2018; Schoutens et al. 2019) and salt marshes (Möller and Spencer 2002; Möller 2006). Accordingly, seasonal variability in *Spartina* biomass, as in our study, can be expected to affect wave dissipation capacity of the marsh with a higher contribution of vegetation to wave dissipation in summer

than in winter and spring (see Foster-Martinez et al. 2018). *Elymus*, by contrast, shows minor although significant seasonal differences in biomass, which suggests a more continuous contribution of *Elymus* biomass to wave dissipation throughout the year. Overall, wave attenuation and resulting coastal protection should be highest when the biomass of biotic structures is at its maximum (Coops et al. 1996; Chen et al. 2007; Koch et al. 2009).

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

Stem density

Significant seasonal differences in stem density were found for *Spartina* and *Elymus*. *Spartina* stem densities were higher in summer than in spring, whereas *Elymus* showed higher stem densities in spring compared to summer. The high stem densities in *Spartina* during summer correlate with high biomass amounts in summer. This pattern in *Spartina* biomass and stem density confirms results of Hill (1984) and Neumeier (2005). Carus et al. (2016) found lower

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

Implications of seasonal and spatial variability in biophysical properties

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

incorporate seasonal variability in plant biophysical properties, especially when simulating storm surge conditions that occur in the winter season when vegetation is degenerated. Future research should provide measurements of biophysical plant properties over the course of the year to get a better overall picture of the change of these properties.

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

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Supplementary material

Supplementary Table 2.1: Mean values \pm standard deviations for all biophysical parameters of *Elymus* and *Spartina* in both zones in spring and summer, respectively. Values followed by different lowercase letters are significantly different at $p < 0.05$ according to Tukey's test.

	Spring		Summer		Spring		Summer	
	Flex. rigidity [Nm ²]*10 ⁻⁴	Flex. rigidity [Nm ²]*10 ⁻⁴	Biomass [g/m ²]	Biomass [g/m ²]	Stem density [#/m ²]	Stem density [#/m ²]	Biomass [g/m ²]	Stem density [#/m ²]
<i>Spartina</i> seawards	9.62 \pm 05.74 a	64.15 \pm 22.98 b	493.86 \pm 173.32 a	1104.13 \pm 327.79 c	449.6 \pm 128.03 a	877.8 \pm 121.65 b		
<i>Spartina</i> landwards	38.45 \pm 24.70 b	177.17 \pm 50.18 c	806.82 \pm 120.73 b	1654.27 \pm 308.11 d	462.0 \pm 104.18 a	635.4 \pm 122.93 c		
<i>Elymus</i> seawards	17.67 \pm 5.28 a	46.06 \pm 11.72 b	895.87 \pm 245.61 a	1211.2 \pm 274.3 c	1097.50 \pm 473.21 ab	931.25 \pm 330.42 ac		
<i>Elymus</i> landwards	13.18 \pm 5.47 a	40.26 \pm 14.35 b	973.09 \pm 187.49 ab	1147.7 \pm 257.1 bc	1348.75 \pm 570.83 b	835.00 \pm 310.18 ac		
	Stem length [cm]	Stem length [cm]	Stem diameter [cm]	Stem diameter [cm]	Young's modulus [MPa]	Young's modulus [MPa]		
<i>Spartina</i> seawards	27.10 \pm 6.26 a	37.50 \pm 6.27 b	0.264 \pm 0.042 a	0.39 \pm 0.054 c	484.90 \pm 231.44 a	632.01 \pm 244.69 ab		
<i>Spartina</i> landwards	38.30 \pm 9.32 b	52.95 \pm 9.00 c	0.342 \pm 0.047 b	0.49 \pm 0.059 d	701.52 \pm 365.63 ab	763.67 \pm 346.62 b		
<i>Elymus</i> seawards	50.30 \pm 6.95 a	81.30 \pm 5.84 b	0.173 \pm 0.025 a	0.22 \pm 0.033 b	4851.68 \pm 1452.30 a	5122.95 \pm 1954.21 a		
<i>Elymus</i> landwards	48.50 \pm 7.95 a	78.06 \pm 6.40 b	0.158 \pm 0.03 a	0.22 \pm 0.026 b	5248.18 \pm 1951.59 a	3845.44 \pm 1411.73 a		

3 Livestock grazing reduces sediment deposition and accretion rates on a highly anthropogenically altered marsh island in the Wadden Sea

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Abstract

Coastal salt marshes and their provided ecosystem services are threatened by rising sea levels all over the world. In the Northern Wadden Sea region, a sea-level rise of 4 mm y^{-1} was recorded for recent years. Identifying and understanding factors that affect sediment deposition and determine vertical accretion of salt marshes is crucial for the management of these ecosystems. Even though major processes contributing to sedimentation and accretion have already been identified, the influence of reduced canopy heights due to livestock grazing is still debated. On a highly anthropogenically altered marsh island in the Wadden Sea, sediment deposition, accretion and suspended sediment concentration was analysed on grazed and adjacent ungrazed plots both at the marsh edge and at the marsh interior. Due to a low seawall (a so-called ‘summer dike’), flooding frequency on the island is reduced and flooding mainly takes place during storm surges. After five flooding events within a year, mean sediment deposition and accretion were found to be up to seven times higher on ungrazed plots compared to grazed plots, but only at the marsh edges. This result was not explained by the overmarsh suspended sediment concentration (SSC), which was found to be twice as high on grazed plots compared to ungrazed plots. It is concluded that grazing has a negative effect on sediment deposition and accretion on Wadden Sea marsh islands and areas with similar conditions (e.g. presence of a summer dike) by reducing the sediment trapping capacity of those marshes. Overall, vertical marsh accretion ranged from $0.11 \pm 0.09 \text{ mm y}^{-1}$ on a grazed plot at the marsh edge to $1.12 \pm 0.71 \text{ mm y}^{-1}$ on an ungrazed plot at the marsh edge. By increasing the discrepancy between accretion and sea-level rise, livestock grazing can lead to higher inundation levels and in turn to increased hydrodynamic forces acting on these anthropogenically altered marshes.

Introduction

Coastal salt marshes are vegetated ecosystems which form a transition zone between the sea and the land (Bakker 2014). They serve as habitats for specific plant and animal species adapted to salt stress and regular flooding. Furthermore, they provide several important ecosystem services such as climate regulation (McLeod et al. 2011; Mueller et al. 2019) and coastal protection (Temmerman et al. 2013; Spalding et al. 2014). However, the persistence of salt marshes around the world is threatened by global warming and associated sea-level rise (Crosby et al. 2016). Global-scale assessments of sea-level rise within recent years show average rates of approx. 3 mm yr⁻¹ (Chen et al. 2017; IPCC 2019). Nevertheless, varying regional conditions can lead to noticeable deviations from the global mean (Vermeersen et al. 2018). For northern parts of the Wadden Sea, Europe's largest area of salt marshes and mudflats, even higher sea-level-rise rates of up to 4 mm yr⁻¹ are described for recent years (Wahl et al. 2013). Thus far, mainland salt marshes in the Wadden Sea were able to keep pace with sea-level rise as sediment deposition and accretion are sufficient (Suchrow et al. 2012; Nolte et al. 2013a; Butzeck et al. 2015). However, places with limited inundations and sediment load, such as the Wadden sea marsh islands, are more vulnerable due to an increasing imbalance of accretion rates and rising sea level (Schindler et al. 2014).

Sediment deposition on marsh surfaces (usually specified as g m⁻² yr⁻¹) takes place during inundations and describes the process of sediments settling from the floodwater onto the soil surface (Nolte et al. 2013b). This process leads to a rise of elevation which then also affects plant colonization and vegetation succession (Olf et al. 1997). Established plants reduce hydrodynamic forces and flow velocity (Neumeier and Amos 2006; Peralta et al. 2008; Temmerman et al. 2012), leading to increased sediment deposition and consequently higher accretion rates (Van Hulzen et al. 2007). Accretion, describing vertical growth of the marsh platform by allochthonous sediment input and autochthonous organic production, also considers auto-compaction, compaction through trampling and erosion (Nolte et al. 2013b).

When sediment deposition and long-term accretion rates cannot keep pace with sea-level rise, coastal wetlands, including salt marshes, will be in danger of being submerged permanently (Crosby et al. 2016; Spencer et al. 2016). Therefore, to predict the stability and persistence of salt marshes and to possibly adapt coastal management activities, knowledge on the influence of site-specific management and characteristics on sediment deposition and accretion is crucial. The local elevation of the salt-marsh platform relative to the sea level determines the inundation parameters. Usually, more frequent inundations, longer flooding durations and higher water levels in low marshes compared to high marshes are related to higher sedimentation rates in low marshes (Temmerman et al. 2003a). Higher elevations and decreased flooding frequencies or lower water levels in turn lead to lower sedimentation rates in high marshes. Additionally, with increasing distance to a certain sediment source, such as the marsh edge or a creek, sedimentation rates were found to decrease as sediment is removed from the water continuously (Temmerman et al. 2003a; Moskalski and Summerfield 2012). The overmarsh SSC is another major factor influencing sediment deposition and accretion as it determines the mass of sediment which can be deposited on the marsh platform (Nolte et al. 2013b). Butzeck et al. (2015) found overmarsh SSC to be the main predictor for sediment deposition rates in freshwater marshes, brackish marshes and Wadden Sea mainland marshes. Thus, the question whether sediment deposition and accretion rates are sufficient in outpacing the rising sea level, largely depends on those local characteristics of the respective marshes.

Additionally, biophysical properties of marsh vegetation vary spatially (Schulze et al. 2019) and can therefore influence flow velocity, wave energy and sediment parameters such as SSC and sediment deposition to different degrees. For example, high stem densities, stiff canopies and high aboveground biomass (Peralta et al. 2008; Fagherazzi et al. 2012) were found to increase gravity-related sediment deposition on the marsh surface by slowing down flow velocities. Furthermore, suspended sediment particles can be intercepted by a dense vegetation and are likely to be deposited directly on parts of the canopy thus leading to potentially lower

SSC over ungrazed sites compared to grazed sites. This direct trapping effect of vegetation on sediment has been described before and depends, similar to sediment deposition processes, on biomass, stem density, surface roughness of the vegetation type and surface area of the whole foliage system (Yang et al. 2008; Li and Yang 2009; Schuerch et al. 2014; Fagherazzi et al. 2012; Kakeh et al. 2016).

The vegetation structure in many salt marshes, however, is largely affected by anthropogenic influences such as livestock grazing for agricultural and nature conservation purposes. Livestock grazing results in reduced aboveground biomass and shorter canopies (Esselink et al. 2000; Nolte et al. 2013a; 2015). Furthermore, livestock grazing can increase soil bulk density by trampling (Nolte et al. 2015) and thus potentially reduce accretion. Therefore, sedimentation and accretion rates are expected to be lower in grazed marshes. However, field studies on the effects of grazing and vegetation on sediment deposition and accretion rates are still scarce and show contradicting results with positive correlations between the presence of vegetation and sediment deposition on the one hand (e.g. Morris et al. 2002) and negative correlations (e.g. Silva et al. 2009) on the other hand. In Wadden Sea mainland salt marshes, Andresen et al. (1990) and Neuhaus et al. (1999) found sedimentation rates to be higher on ungrazed sites compared to grazed sites. More recently, Elschot et al. (2013) and Nolte et al. (2013a) did not find differences in accretion between grazed and ungrazed areas, albeit they found a trampling-driven higher soil bulk density in grazed marshes. However, these marshes show comparatively high sediment deposition, and it is unknown whether a grazing effect may potentially be more pronounced at sites with low rates of sediment deposition due to e.g. artificially reduced flooding frequencies.

Marshes with limited sediment input can be found on the so called 'Hallig' islands, which are remnants of the former mainland marshes of the Northern German Wadden Sea. The islands are largely consisting of salt marshes which have been used for livestock grazing for a long

time. Further human modifications, such as ‘summer dikes’ (comparatively low seawalls preventing marsh surfaces to be flooded during spring tides), ‘stone revetments’ of island margins (serving as erosion protection) and straightening of creeks for drainage, have turned the Hallig islands into highly anthropogenically altered marshes. Particularly due to the summer dike, which is still common in some parts of the North Sea area (Ahllhorn and Kunz, 2002), inundation does only occur during storm surges when the summer dike is overtopped. Therefore, the reduced inundation frequencies ranging between zero and 28 events per year have in turn led to low accretion rates (Schindler et al. 2014). Vulnerability of the specific Hallig marsh type results from the increasing discrepancy between sea-level rise and overall accretion, which over time results in higher inundation height and in turn goes along with increased hydrodynamic forces acting on the marsh surfaces (Schindler et al. 2014).

However, it is unknown how these already low sediment deposition and accretion rates are affected by livestock grazing and how this will affect their capability to keep up with sea-level rise in the long term. In this study, it was therefore aimed to investigate the effects of livestock grazing on sediment deposition and accretion rates on a marsh island in the Wadden Sea with a reduced flooding frequency and a reduced sediment input. It was hypothesized (I) that sediment deposition and accretion rates are higher on ungrazed plots than on grazed plots because of flow velocity reductions due to denser vegetation. It was also hypothesized (II) that SSC is lower over ungrazed marshes than over grazed marshes as suspended sediment is prone to be filtered out of the water by a dense vegetation canopy. Regarding the spatial distribution of sediment, it was hypothesized (III) that the total sediment deposition and accretion rates are higher at the edge of the marsh island compared to inner parts.

Methods

Study area

The study was conducted on the marsh island ‘Langeness’ in the Northern German Wadden Sea region. It is the largest island of the Hallig marsh-island group (9.2 km²) and is located off the mainland coast of the state of Schleswig-Holstein (Fig. 3.1A). All marsh islands in this area are remnants of the former mainland marshes and were separated by a severe storm surge event in 1634 (Ahrendt 2007). Today, they are part of the biosphere reserve ‘Schleswig-Holsteinisches Wattenmeer’. At the beginning of the 20th century, Langeness was encompassed by a stone revetment to prevent erosion of the island margins and by a summer dike with an average height of 1 m above mean high tide. In this way, flooding is mostly prevented from April to October when a large proportion of the marsh is used for cattle grazing by the permanent inhabitants of the island. The summer dike contains several tide gates connecting the marsh creeks to the Wadden Sea. These gates, however, automatically close during rising tides and prevent flooding of the island via the creeks. Tidal flooding thus only occurs as a sheet flow coming from the marsh edge and is induced by strong westerly winds and spring tides. The marsh topography is characterized by an elevational gradient from the higher elevated areas at the edges behind the summer dike towards the lower elevated inner parts of the marsh. Averagely, the marsh platform is elevated 0.17 m above mean high water (Schindler et al. 2014). Generally, the Hallig marshes mostly represent high marsh vegetation (Kleyer et al. 2003; Esselink et al. 2017).

Study sites and study design

To investigate the influence of livestock grazing (factor ‘treatment’) on sediment deposition, accretion and overmarsh SSC, two sites were chosen at the island marsh edge and two sites further inwards (factor ‘position’). Each site included a grazed and an ungrazed plot adjacent to each other, resulting in a total number of eight different plots (Fig. 3.1B). To test whether the

expected treatment and position effects are consistent over the entire island, one pair of sites (inner, edge) was positioned in the east and one pair in the west, reflecting the longitudinal shape of the island (factor ‘location’). On the grazed plots, the livestock grazing (i.e. cattle) takes place during the summer season. Grazing resulted in a vegetation which mainly consists of the *Festuca rubra* vegetation type (see also Kleyer et al. 2003). The ungrazed plots consist of monospecific dense stands of the *Elymus athericus* type and have not been exposed to either grazing or mowing for several years. In each of the eight plots, eight sampling points were randomly chosen using a random point tool of QGIS 2.10 Pisa (QGIS Development Team 2015). At these points, sediment deposition was recorded during every inundation between October 2015 and March 2016. In this period, five inundation events occurred, which is only half of the average number of inundation events between 2001 and 2010 with ten events per year (Schindler and Willim 2015).

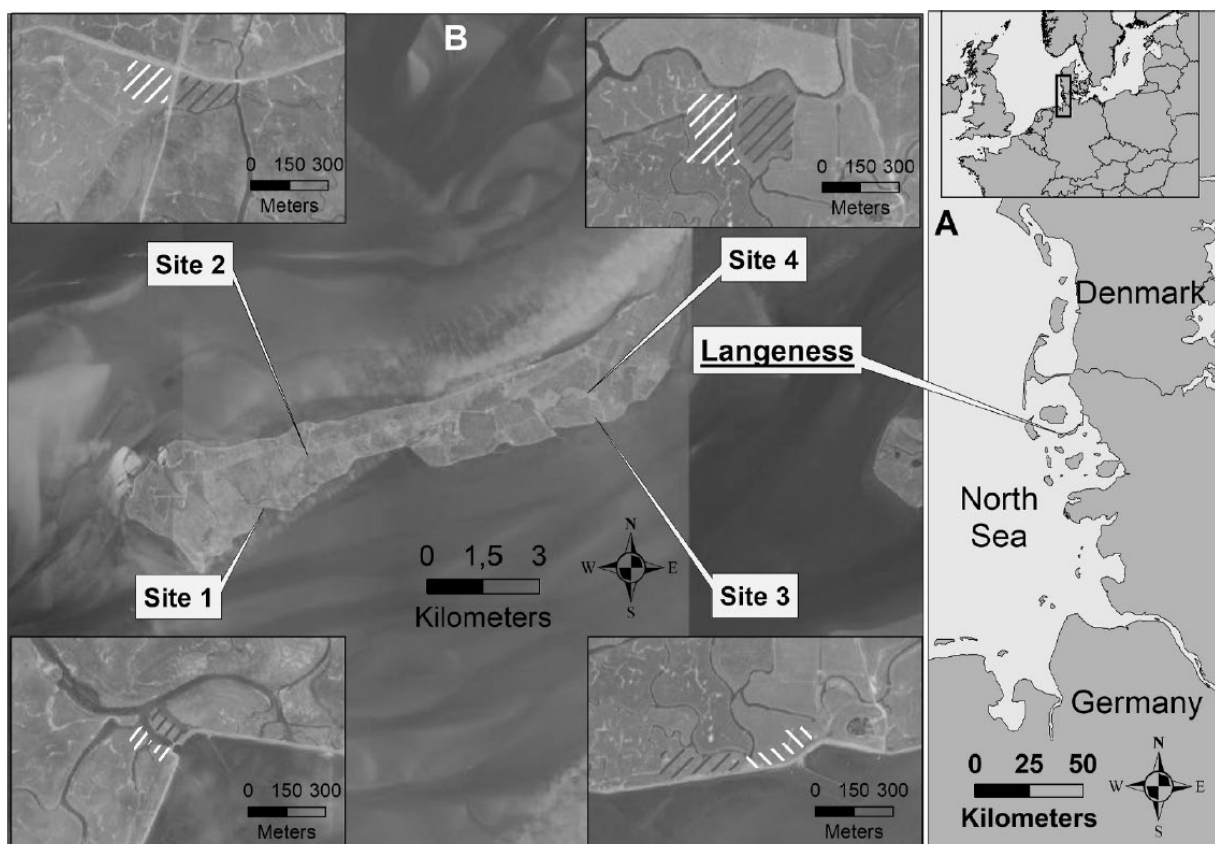


Figure 3.1 A) Location of the marsh island Langeness in the Northern Wadden Sea region. B) Satellite image of Langeness with the respective four study sites and the differently treated plots. Grazed plots are shown as white hatched whereas ungrazed plots are shown as dark grey hatched (ArcGIS ©).

Measurements of sediment deposition and suspended sediment concentration

At each of the 64 sampling points, which had a minimum distance of 3 m to each other, circular plastic plates (internal diameter: 19 cm; rim: 2.5 cm) were placed on the soil surface to trap the deposited sediment during inundations. The plates were attached to the ground with a plastic stick (1.5 m) and with metal wires. To prevent a washout of sediment by rain, every sediment trap was equipped with a floatable lid (Temmerman et al. 2003a; Butzeck et al. 2015; Nolte et al. 2019). After each inundation, the collected sediment was rinsed with freshwater, transferred to plastic bags and further processed in the laboratory. Samples were sieved (mesh size: 500 μm), washed with deionized water and oven dried at 100 $^{\circ}\text{C}$ until constant weight. The dry weight provided information on the sediment deposition (g m^{-2}) for each flooding event. To convert the sediment deposition into accretion rates, soil bulk density was determined by taking a soil sample using a 100 cm^3 steel cylinder next to each sampling point from the uppermost (0-6 cm) soil layer. Bulk density was calculated by dividing the mass of the oven dried soil sample by the core volume. Accretion rates are based on five flooding events in the storm surge season from the beginning of autumn 2015 to the end of spring 2016 and were calculated as follows:

$$\text{Accretion (cm yr}^{-1}\text{)} = \text{Sediment deposition (g cm}^{-2}\text{ yr}^{-1}\text{)} / \text{Bulk density (g cm}^{-3}\text{)} \quad [1]$$

Additionally, floodwater was collected to determine the suspended sediment concentration at each sampling point. For this purpose, plastic bottles (580 ml) with a 3 cm water inlet and a longer air outlet made of plastic tubes were buried at each sampling point. These bottles allowed a controlled water inflow 3 cm above the marsh surface (Butzeck et al. 2015). The filled bottles were replaced after each inundation event. To determine the suspended sediment concentration (g l^{-1}), water samples were resuspended and vacuum filtrated using cellulose nitrate filters (0.45 μm). Subsequently, samples were oven dried at 60 $^{\circ}\text{C}$ until constant weight.

Inundation and vegetation parameters

Elevation of each sampling point was measured in relation to the respective water gauges using a Trimble LL500 precision laser and a Trimble HL 700 receiver (2.0 mm accuracy). There was no significant difference in relative elevation between each of the corresponding plots. Information about inundation height, frequency and duration was obtained by installing a water gauge between the grazed and ungrazed plot at each of the four study sites, which allowed to determine absolute inundation levels above the plots. A slitted plastic pipe containing a water pressure sensor (Schlumberger Cera diver, accuracy of measuring water level: ± 1 cm), with a temporal resolution of five minutes, was inserted into the soil. An atmospheric pressure sensor (Baro Diver) was attached on one of the dwelling mounts on the island to compensate the water pressure measurements for the atmospheric pressure. The average canopy height for each plot was determined in late November by measuring the distance from the soil surface to a Styrofoam drop-disc (diameter: 30 cm) at four points around each sediment trap.

Statistical analysis

Three-factorial analysis of variance (e.g. sediment deposition \sim treatment*position*location) was used to test whether each of sediment deposition, accretion and suspended sediment concentration were affected by treatment (grazed, ungrazed), position (inner, edge) and geographical location (east, west). To determine differences between the groups, Tukey's HSD tests were applied when the ANOVA revealed a significant effect ($p < 0.05$). If necessary, data were log transformed to meet normality assumptions and to improve homogeneity of variances (applied on sediment deposition, accretion and SSC). Equal sample sizes in the study design assured robustness of parametric testing (McGuinness 2002). Following the protocol by Zuur et al. (2009), no spatial autocorrelation of either raw data within plots or of residuals across all sampling points was detected, and therefore it is concluded that the assumption of independence is met. For each site, differences in inundation level, vegetation height and soil bulk density

between grazed and ungrazed plots were analyzed with Bonferroni corrected t-tests for multiple testing. All analyses were performed using R version 3.5.3 (R Core Team 2019; base package).

Results

Overall, five complete inundations of the island were recorded between early October 2015 and late March 2016. The mean maximum inundation height was slightly, but not significantly, higher on the ungrazed plot at site 1 (west, edge; t-test, $p > 0.017$, Table 3.1). At site 2 (west, inner, minimal distance to marsh edge: 350 m), 3 (east, edge) and 4 (east, inner, minimal distance to marsh edge: 250 m), the inundation was slightly, but not significantly, higher on the grazed plot (t-test, $p > 0.017$, Table 3.1). Mean maximum inundation height ranged from 86.36 cm (site 3, east, edge, ungrazed) to 164.1 cm (site 1, west, edge, ungrazed). At each site, vegetation height was significantly higher in ungrazed compared to grazed plots ($p < 0.017$, t-test for every site, Table 3.1). Soil bulk density did not differ between grazed and ungrazed plots, neither at the edges nor in the inner parts both in the east and west (t-test, $p > 0.017$, Table 3.1).

Table 3.1: Mean maximum inundation heights, vegetation heights and soil bulk densities of the grazed and ungrazed plots at the islands marsh edges and the marsh interior in the east and west. After Bonferroni corrections for multiple testing, statistical significance was determined as $p < 0.017$. Different letters indicate significant differences among the treatments.

Site	Location	Position	Treatment	Mean max. inundation [cm]	Vegetation height [cm]	Soil bulk density [g/cm ³]
1	West	Edge	Grazed	137.62 a	5.69 a	0.66 a
			Ungrazed	164.12 a	12.56 b	0.75 a
2	West	Interior	Grazed	142.19 a	6.63 a	0.55 a
			Ungrazed	141.64 a	11.97 b	0.57 a
3	East	Edge	Grazed	87.86 a	4.81 a	0.82 a
			Ungrazed	86.36 a	12.56 b	0.83 a
4	East	Interior	Grazed	147.33 a	4.72 a	0.58 a
			Ungrazed	137.06 a	9.88 b	0.46 a

Highest mean sediment deposition occurred on the ungrazed plot at site 3 (east, edge; 189.35 g m⁻² yr⁻¹) while the lowest mean sediment deposition occurred at the grazed plot of site 1 (west,

edge; $13.75 \text{ g m}^{-2} \text{ yr}^{-1}$, Fig. 3.2). A significant interaction between the treatment and the position indicated that differences in sediment deposition between ungrazed and grazed plots were more pronounced at the island marsh edges (Fig 3.2; Table 3.2). At the marsh edges, sediment deposition was roughly 7 times (site 1, west, edge) and 5 times (site 3, east, edge) higher on the ungrazed plot compared to the grazed plot. The effect of the treatment and the position on sediment deposition was found both in the eastern and the western part of the island. Overall, sediment deposition was twice as high in the east as in the west and 60% higher at the marsh edge compared to the sites located further inwards. The mean accretion showed similar results as the sediment deposition rates with a significant interaction between treatment and position revealing that accretion was higher on ungrazed compared to grazed plots at the island marsh edges (Fig.3.3, Table 3.2). Overall, accretion was twice as high in the east as in the west. Furthermore, sediment deposition and accretion on at the edge positioned ungrazed plots was found to be slightly higher than on interior positioned ungrazed plots and vice versa for grazed plots (Figure 3.2, Figure 3.3, Supplementary Table S3.1).

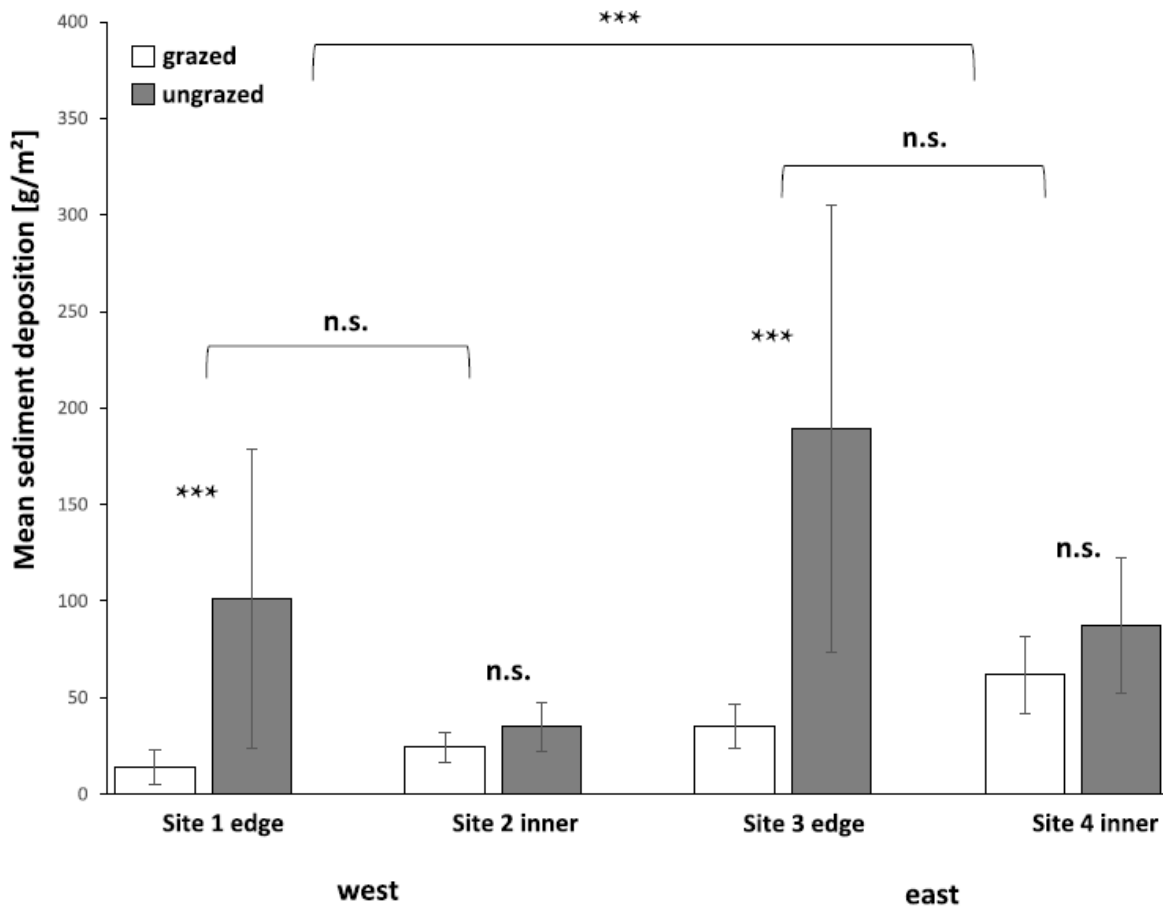


Figure 3.2 Mean sediment deposition on grazed and ungrazed plots at the marsh edges and marsh interior in the east and west of the island after five inundation events. Every bar represents the average of eight sampling points. Given are the mean and the standard deviation. For comparisons between sites, the grazed and ungrazed plot were combined. The difference between the eastern and western location was determined by comparing total sediment deposition in the east and in the west. Significant differences between treatments, sites and geographic locations are indicated as resulting from post-hoc tests following ANOVA (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

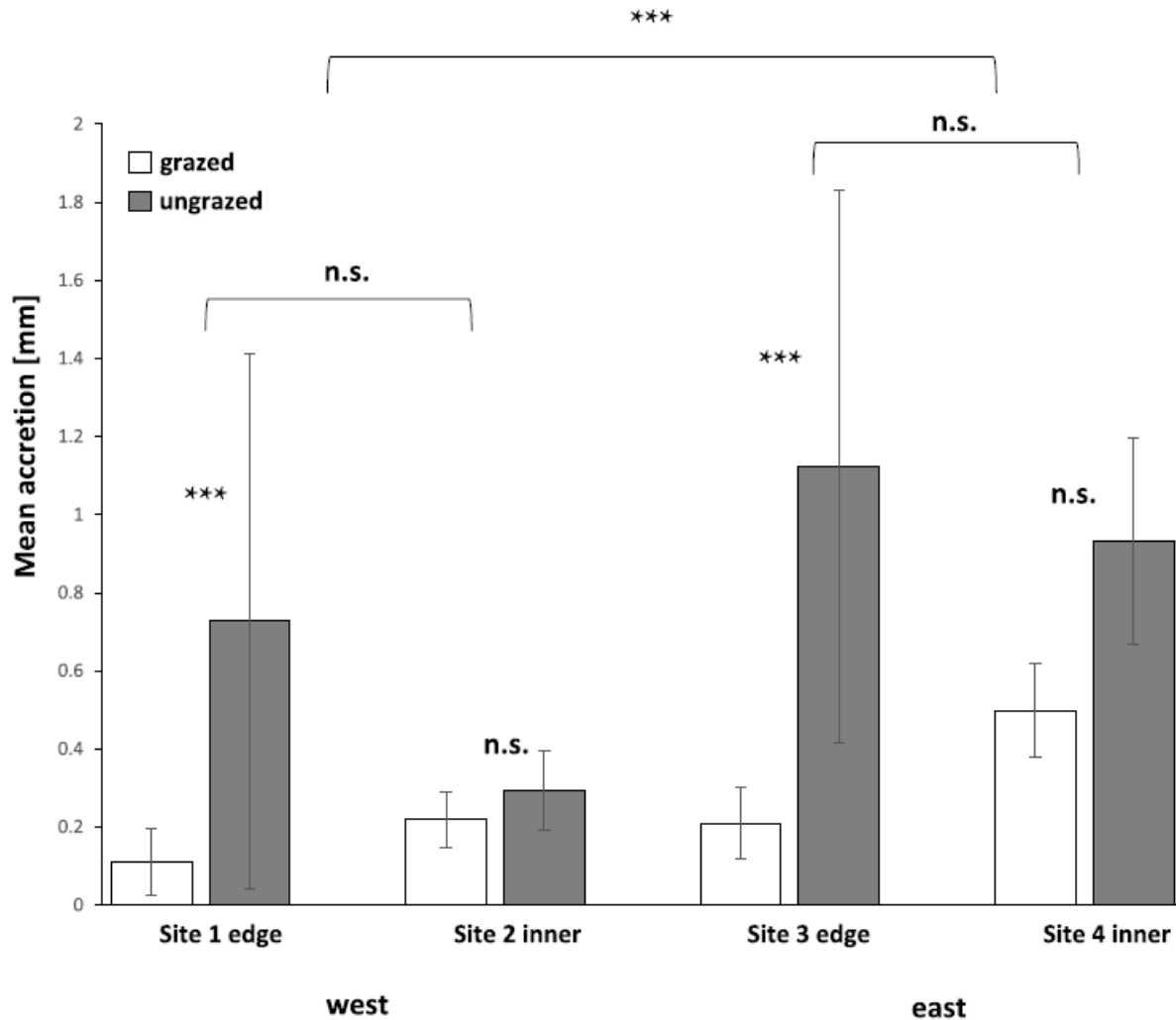


Figure 3.3 Mean annual accretion on grazed and ungrazed plots at the marsh edges and marsh interior in the east and west of the island. Every bar represents the average of eight sampling points. Given is the mean and the standard deviation. For comparisons between sites, the grazed and ungrazed plot were combined. The difference between the eastern and western location was determined by comparing total accretion in the east and in the west. Significant differences between plots, sites and geographic locations are indicated as resulting from post-hoc tests following ANOVA (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

SSC in the floodwater showed an opposite pattern to sediment deposition and accretion with higher concentrations over the grazed plots compared to the ungrazed plots. Highest SSC occurred over the grazed plot at site 3 (east, edge; $0.81 \text{ g liter}^{-1} \text{ yr}^{-1}$, Fig. 3.4) while lowest SSC occurred over the ungrazed plot at site 2 (west, inner; $0.15 \text{ g liter}^{-1} \text{ yr}^{-1}$, Fig. 3.4). SSC was found to be significantly affected by the interaction between treatment and location and between location and position (Table 3.2). The treatment effect was less pronounced in the west than in

the east as at site 1 (west, edge) SSC was only slightly, but not significantly, higher over the grazed than over the ungrazed plot. At site 2 (west, inner), 3 (east, edge) and 4 (east, inner), SSC was approx. twice as high over the grazed compared to the ungrazed plots. Differences in SSC between the island marsh edge and the marsh interior were more pronounced in the east than in the west with SSC being approx. 90% higher at the marsh edge compared to the marsh interior in the east. In the west, SSC was 40% higher at the marsh edge compared to the marsh interior. SSC was approx. 60 % higher in the east than in the west (Fig. 3.4).

Table 3.2: ANOVA table of the effects of treatment (grazed, ungrazed), position (marsh edge, marsh interior), location (east, west) and the respective interactions on sediment deposition, accretion rates and SSC rates. Given are F-values and p-values. Significant effects are symbolized as the following: *** p < 0.001, ** p < 0.01, * p < 0.05.

	Sediment deposition		SSC		Accretion	
	F	p	F	p	F	p
Treatment	60.75	***	106.01	***	54.83	***
Position	0.17	n.s.	78.13	***	4.22	*
Location	42.69	***	46.28	***	31.04	***
Treatment x Position	26.82	***	12.26	***	17.92	***
Position x Location	0.25	n.s.	3.65	n.s.	0.13	n.s.
Treatment x Location	1.05	n.s.	6.41	*	0.92	n.s.
Treatment x Position x Location	0.93	n.s.	4.22	*	0.22	n.s.

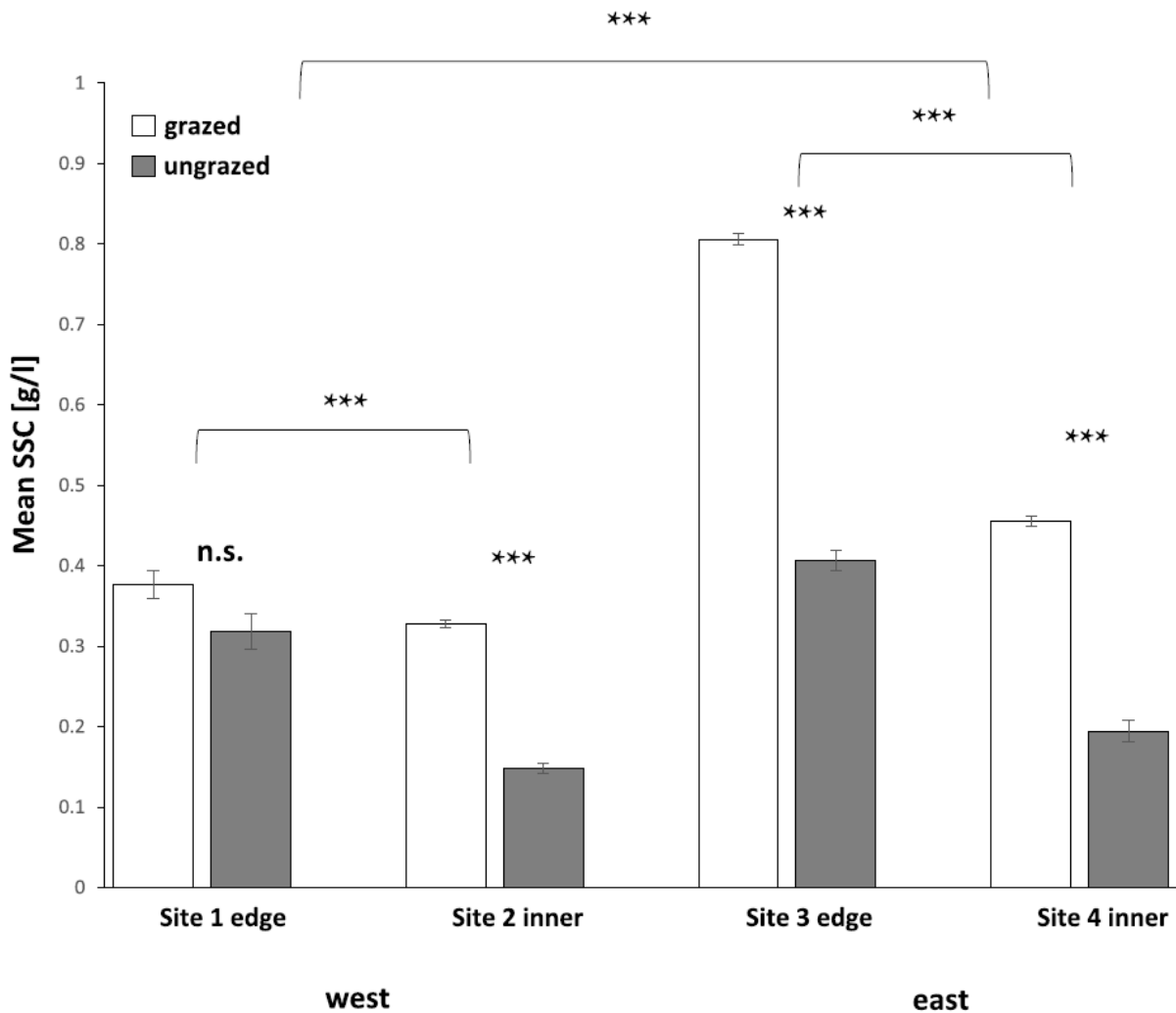


Figure 3.4 Mean suspended sediment concentration on grazed and ungrazed plots at the marsh edges and marsh interior in the east and west of the island after five inundation events. Every bar represents the average of eight sampling points. Given is the mean and the standard deviation. For comparisons between sites, the grazed and ungrazed plot were combined. The difference between the eastern and western location was determined by comparing the total SSC in the east and in the west. Significant differences between treatments, sites and geographic locations are indicated as resulting from post-hoc tests following ANOVA (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

Discussion

The results show a significant negative effect of livestock grazing on sediment deposition and accretion at the marsh edge with reduced sediment deposition and accretion on grazed plots compared to ungrazed plots, which is therefore in concordance with the first hypothesis. The same general, but non-significant, trend was found at the marsh interior. The suspended sediment concentration showed a contrasting pattern with lower SSC over ungrazed plots and

thus the results confirm the second hypothesis of high-marsh vegetation reducing overmarsh SSC. Furthermore, total sediment deposition and accretion rates were expected to be higher at the marsh edges compared to inner parts of the marsh but the results did not support this third hypothesis. The effects of grazing on sediment deposition, accretion and SSC were similar in the east and in the west of the island. Furthermore, the results confirm findings of Schindler et al. (2014) indicating low accretion on Langeness leading to an increasing discrepancy between sea-level rise and accretion, which over time likely results in higher inundations and in turn increased hydrodynamic forces acting on the marsh surfaces. High hydrodynamic forces were found to cause high folding and breakage rates for *Elymus* canopies (Möller et al. 2014; Rupprecht et al. 2017). As a consequence, losses in biomass and surface elevation might threaten the *Elymus* dominated ungrazed areas of the island.

Higher sedimentation and accretion rates on ungrazed plots compared to grazed plots at the island marsh edge, as found in this study, most likely indicate an interaction effect of vegetation and flow velocity. Vegetation characteristics such as high biomass, high stem densities and tall canopies of marsh vegetation have long been known to reduce flow velocity (Leonard and Croft 2006; Widdows et al. 2008) and to potentially increase sediment deposition and accretion on the marsh platform (Boorman et al. 1998; Morris et al. 2002). The findings of the study presented are supported by observations of Suchrow et al. (2012) who, probably as a result of lower sediment deposition, found a decreased surface-elevation change on grazed areas compared to ungrazed areas in high marshes of the Wadden Sea. Contrastingly, other studies on the influence of reduced canopy height (e.g. by grazing) on sediment deposition and accretion show no difference between non-manipulated areas and areas with decreased canopy height and biomass (Elschlot et al. 2013; Nolte et al. 2013a). Furthermore, Reef et al. (2018) found no effect of an experimentally reduced canopy height on the sediment budget in a south eastern British salt marsh and assume that the missing effect could have been caused by calm hydrodynamic conditions with inundation depths between 0.14 m and 0.54 m. A vegetation-

mediated sediment deposition thus may not become effective when flow velocities are low. This assumption is supported by Nolte et al. (2015) who only found an effect of vegetation structure on accretion in a study period with increased storminess (see also Schuerch et al. 2012). Neumeier and Ciavola (2004) even described a negative correlation between the presence and density of vegetation and sediment deposition rates during fair weather conditions which was explained by a smaller water volume and therefore lower sediment load above vegetated areas. On the contrary, Elschot et al. (2013) and Temmerman et al. (2005) expect vegetation structure to have no or only limited impact on sediment deposition when vegetation is overtopped by water. Under storm conditions and during high tides, sediment deposition can indeed be higher on unvegetated areas compared to fully vegetated areas as found by Silva et al. (2009). If the flow is relocated above the canopy as skimming flow, sediment deposition might be reduced (Neumeier and Amos 2006; Peralta et al. 2008). As average inundation levels in our study ranged between 0.86 m and 1.64 m and thus overtopped the canopy (Table 3.1), evidence for a positive effect of vegetation and accordingly a negative effect of grazing on sediment deposition and accretion under these conditions is provided.

Focusing on the investigation of the influence of grazing-driven different canopy heights (short, long) on SSC, it was hypothesized that SSC was lower over ungrazed plots compared to grazed plots. Indeed, SSC data show a significant trend of lower SSC over ungrazed plots compared to grazed plots. This result could be explained by a direct trapping effect of the *Elymus* vegetation on ungrazed plots as *Elymus* shows relatively high winter and spring biomass stocks of approx. 1 kg/m² (dry biomass) and high stem densities (>1000 stems/m²) in the Wadden Sea (Schulze et al. 2019). Additionally, resuspension of deposited sediment may be reduced on ungrazed plots, therefore leading to lower SSC in the water column over ungrazed plots (Yang et al. 2008). These observations are supported by Coulombier et al. (2012) who found SSC to be the highest when vegetation was minimal. A similar pattern was also found for a brackish marsh in Georgia, USA (Coleman and Kirwan 2019). As the amount of suspended sediment in

the floodwater as well as the amount that deposits, largely depends on the biophysical plant properties (Fagherazzi et al. 2012; Schuerch et al. 2014), these properties and their spatio-temporal variability should therefore be considered in studies investigating sedimentation patterns in salt marshes.

Contradicting the third hypothesis, total sediment deposition and accretion at the edges and the inner parts of the marsh did not differ significantly but still showed slightly higher rates at the edges. While sediment deposition and accretion on ungrazed plots was slightly higher at the edges than at the inner sites, which supports this hypothesis, the contrary was found for grazed plots. A similar pattern was found in a mowing experiment in the Scheldt Estuary (Schepers et al. 2019). In their study, fully vegetated plots close to the sediment source showed a higher sediment deposition compared to the interior located vegetated plots. In contrast, unvegetated plots nearby the sediment source showed less sediment deposition compared to interior located unvegetated plots. It was shown that sediment deposition not only depends on the treatment of the vegetation (e.g. grazed/ungrazed, mown/unmown) but also on the relative position of the plot to the source of the sediment and on respective flow velocities (see also Temmerman et al. 2012). At the Langeness study site, tide gates prevent flooding of the creeks resulting in water coming from the island edge being the only source for sediment. Already a small vegetation patch near the marsh edge can reduce flow velocities (Schepers et al. 2019) and therefore favour sediment deposition. Allowing for higher flow velocities, grazed areas at the marsh edge might thus lead to higher sediment transport rates to the inner parts where sediment can deposit.

Conclusion

The pattern of overmarsh SSC and sediment deposition rates observed in this study reveals the general complexity of sedimentation in salt marshes on the one hand, and the significant importance of vegetation for overmarsh SSC and sedimentation rates on the other hand. In contrast to the literature, sediment deposition in this study does not mainly depend on the SSC

recorded close to the sediment traps but rather on the management and characteristics of the plots and on the position of plots relative to the sediment source. Based on the data presented, it is shown that overall mean accretion of 0.5 mm yr⁻¹ (based on five inundations) is not sufficient to keep pace with sea-level rise. This result is supported by Schindler et al. (2014) who found similar accretion rates and suggest the removal of summer dikes to increase the number of flooding events and therefore accretion rates on this marsh island. Adding to this suggestion, this study moreover shows that non-grazing favours sediment deposition and accretion in salt marshes with low flooding frequencies. Comparing grazed and ungrazed plots of the marsh island, the results show an up to seven times higher sediment deposition and accretion on the ungrazed plots with accretion rates of up to 1.1 mm yr⁻¹. Therefore, a reduction or abandonment of grazing can increase accretion rates considerably and should be incorporated into future management plans for the studied island and for other similar areas in the Wadden Sea or elsewhere. Additionally, occasional mowing of the marsh edges could increase accretion rates in inner parts of the island by allowing higher suspended sediment concentrations in the floodwater reaching inner parts of the island.

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4 Effects of small-scale patterns of vegetation structure on suspended sediment concentration and sediment deposition in a salt marsh

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Abstract

Salt marshes contribute to coastal protection by attenuating waves and reducing flow velocities. Nevertheless, coastal salt marshes are threatened by rising sea levels. In order to keep pace with rising sea levels, salt marshes need to grow vertically by sediment input. Although major processes contributing to sediment deposition in salt marshes are known, there is still a lack of knowledge on the influence of reduced canopy height and reduced biomass on suspended sediment concentration and sediment deposition in Wadden Sea salt marshes. Furthermore, little is known on the role of small-scale patterns of vegetation structure on suspended sediment concentration and sediment deposition and on the spatial scale beyond which an influence of vegetation on sediment deposition comes into effect. We investigated the effects of small-scale patterns of vegetation on suspended sediment concentration and sediment deposition in a Wadden Sea mainland marsh. Partial mowing of the vegetation resulted in a pattern of mown subplots and control subplots with a size of 4 m² in various combinations adjacent to a creek. Based on the results, it can be concluded that on the spatial scale of 4 m², there is no effect of the vegetation on the waves and water flow to be expected since the sediment deposition between mown and control subplots did not differ neither in the upper nor in the lower marsh. Furthermore, a mown or a control subplot next to the creek had no influence on the sediment deposition on a mown or control subplot behind.

Introduction

Salt marshes are highly dynamic intertidal ecosystems at the coastlines in the world's temperate zones. They provide a unique habitat for many species and deliver important ecosystem services, such as coastal protection and carbon sequestration (Barbier et al. 2011). Because of their low elevation relative to the sea level, a major future threat for salt marshes is habitat loss due to an accelerated sea-level rise (Spencer et al. 2016). As salt marsh landward migration is often prevented by seawalls, persistence of these ecosystems relies on sedimentation and vertical marsh accretion (Kirwan et al. 2016). Accretion, defined as the vertical marsh growth including mineral sedimentation, organic matter production and erosion, is therefore a key parameter for salt marsh persistence in times of climate change (Fitzgerald and Hughes 2019; Fagherazzi et al. 2020). Generally, salt marshes can cope with rising sea level, when sea-level rise is lower than sedimentation rates and vertical marsh accretion (Nolte et al. 2013b). However, sedimentation processes are still not fully understood (Fagherazzi et al. 2020) as they are the result of complex bio-geomorphological interactions between marsh morphology (Brückner et al. 2019), sediment availability (Kirwan et al. 2010), hydrodynamics (Temmerman et al. 2005), vegetation (Cahoon et al. 2020) and even plant-animal interactions (Williams and Johnson 2021).

Many of these relevant factors can vary on a spatial scale from global to local and also within a single site (Cahoon et al. 2020). For example, on a global scale, North Sea salt marshes show a high sediment availability and are dominated by mineral sedimentation whereas US east coast marshes, which are dominated by organogenic accretion, face eventual sediment starvation in the future (Peteet et al. 2018). These differences can be explained by environmental drivers of sediment availability such as sea-level rise and tidal amplitude, which differ globally (Brown et al. 2016). Due to the spatial and temporal variability of these factors, estimates of marsh development by modelling studies, field measurements and combination of both are challenging. Consequently, global predictions and observations of sedimentation and overall

marsh development lead to contrasting results (Wiberg et al. 2020). Some studies indicate a widespread global marsh loss (Crosby et al. 2016; Spencer et al. 2016; Thorne et al. 2018), whereas other studies predict low marsh losses and even marsh expansion (Kirwan et al. 2016; Schuerch et al. 2018; Ganju 2019). Additionally, some factors, which are included in these predictions, also differ regionally, locally or are even within a single marsh, leading to difficulties in forecasts on future marsh developments. Marshes in the Wadden Sea region, for example, were found to be generally able to keep pace with a rising sea level mainly due to sufficient sedimentation rates (Suchrow et al. 2012), but within this region large local differences were described (e.g. Butzeck et al. 2015; Schulze et al. 2021). Even on a within-marsh scale, sedimentation is spatially heterogeneous. When flooding occurs via the marsh edge or a creek, a large proportion of sediment is gravity-driven deposited on the first meters leading to high sedimentation rates at the marsh edge or the creek edge and to lower deposition in the marsh interior (Temmerman et al. 2003a). While this pattern is generally accepted, it can interact with other processes defining spatial distribution of sediment on the marsh platform which are not fully understood (Marjoribanks et al. 2019; Wiberg et al. 2020). For example, understanding the role of complex vegetation-mediated sediment deposition still remains challenging (Fagherazzi et al. 2020).

Generally, it is assumed that vegetation enhances sediment deposition rates in minerogenic marshes by slowing down flow velocity as well as by directly trapping sediment particles on the plant surface (Li and Yang 2009; Fagherazzi et al. 2012; Kakeh et al. 2016). However, studies on this topic still show contrasting results and it is not fully understood under which conditions vegetation promotes sedimentation or might even cause erosion (i.e. “scouring”; Tinoco et al. 2020). Furthermore, results of field studies on the effects of salt marsh vegetation on sedimentation range from higher sedimentation rates in the presence of vegetation to higher sedimentation rates in the absence of vegetation (e.g. Morris et al. 2002; Silva et al. 2009; Reef et al. 2018). This simple question regarding presence or absence of vegetation is, however,

further complicated by complex spatial patterns within the vegetated marsh caused by e.g. marsh zonation. A vegetation zonation along an elevational gradient is a key characteristic in most marshes (Bakker 2014). This vegetation zonation is a spatial vegetation pattern consisting of coherent homogenous stands of single species or of a compound of different species with varying biophysical plant properties (Schulze et al. 2019; Zhu et al. 2019). These complex spatial patterns within the salt marsh vegetation further complicate the understanding of sedimentation (Fagherazzi et al. 2020).

Models and field studies often fail to incorporate the patterns and characteristics of salt marsh vegetation or tend to simplify vegetation properties (Wiberg et al. 2020). These limitations could explain the aforementioned contradicting results on sedimentation and overall marsh development on different scales. Therefore, understanding the effects of different plant species and the influence of within-marsh vegetation patterns on sediment transport and sediment deposition patterns is crucial for predictions of marsh development (Fagherazzi et al. 2020). However, predicting deposition on a vegetation-patch scale is difficult due to complex patch morphology and complex patch-flow interactions (Marjoribanks et al. 2019). In a recent field study on flow and sedimentation patterns, Schepers et al. (2019) found that vegetated plots positioned at a creek tended to show higher sedimentation rates compared to the vegetated plots located approximately 30 m further interior. Surprisingly, unvegetated plots close to the sediment source showed lower sedimentation rates compared to interior located unvegetated plots. Thus, the spatial positioning of vegetated and unvegetated patches seem to influence spatial patterns of sediment deposition and accretion on this within-marsh scale. However, little is known about patterns of sedimentation on a smaller scale of a few meters in vegetated and unvegetated plots. Yet, this is probably a very relevant scale, as most sediment is deposited on a distance of a few meters from a creek (Temmerman et al. 2003a). Additionally, it should be tested whether the effect of small-scale vegetation patterns on sedimentation can be found in

different salt marsh zones, as different plant species in these zones also differ in biophysical plant properties (Schulze et al. 2019).

We therefore conducted a mowing experiment adjacent to a tidal creek in a Wadden Sea low marsh and high marsh to answer the following questions: (I) Is the sediment deposition and suspended sediment concentration (hereafter referred to as SSC) generally higher in tall compared to short vegetation?; (II) Do we find these vegetation effects on sedimentation in both the low and the high marsh?; (III) How does the spatial positioning of tall and short vegetation influence spatial patterns of sediment deposition and SSC on a small vegetation-patch scale ?

Methods

Study site

The study was conducted on a mainland salt marsh in the Wadden Sea. The Wadden Sea is Europe's largest intertidal ecosystem complex and includes 4500 km² of tidal flats, as well as approximately 400 km² of salt marshes. Mainland salt marshes encompass around 60% of this area (Reise et al. 2010) and are often characterized by a long history of anthropogenic interventions such as brushwood groynes and drainage ditches to facilitate sedimentation. The studied salt marsh is located in front of the in 1935 embanked polder Dieksanderkoog (DSK) at 53.95°N, 8.89°E in Schleswig-Holstein, Germany (Fig 4.1). The tidal range is approximately 3 m with a mean high tide (MHT) at +1.62 m NHN. The marsh stretches ca. 1100 m from the seawall to the tidal flats. As an originally man-made landscape, the study site was used for livestock grazing, which was abandoned in the early 1990s. Additionally, the maintenance of an artificial drainage ditch system was abandoned at the same time (Stock et al. 2005). The marsh shows a clear vegetation zonation from pioneer zone to the high marsh and is predominantly covered by *Elymus athericus* in the high marsh and by *Spartina anglica* in the

pioneer zone (personal observations and the Trilateral Monitoring and Assessment Program, TMAP; Petersen et al. 2013).

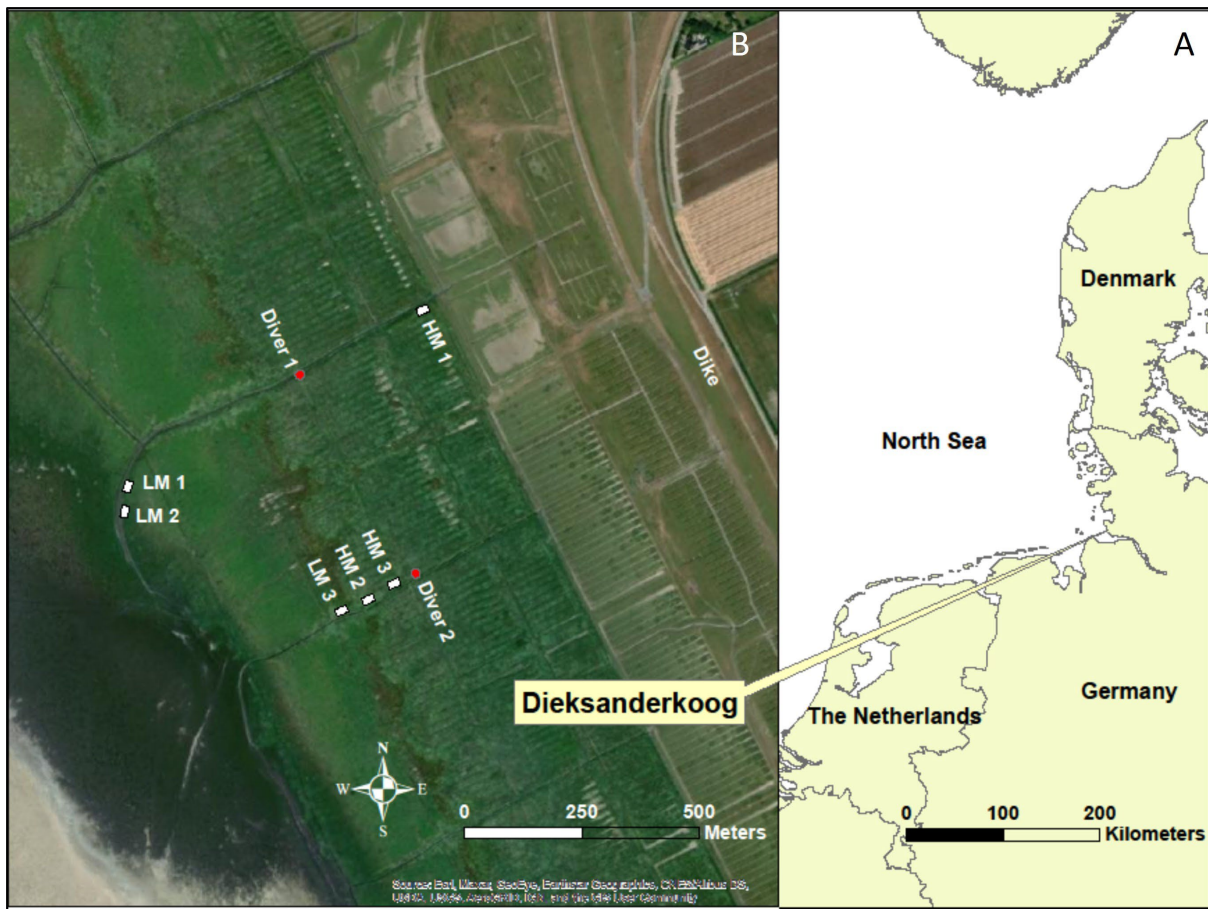


Figure 4.1 A) Location of the study site in the Wadden Sea National Park Schleswig–Holstein at the German North Sea coast B) Satellite image of the study site with the research plots. Shown are the high marsh plots (HM 1 – HM 3) and the low marsh plots (LM 1 – LM 3). The red dots show the locations of two divers. The map was created using a base map in ArcGIS © Desktop: Release 10, ESRI 2014, Redlands, CA: Environmental Systems.

Experimental design

To study how sediment deposition and suspended sediment concentration (SSC) is affected by a small-scale pattern of vegetation patches, a field experiment was established. Three replicate plots (4 m x 8 m) were placed in the low marsh dominated by *Spartina anglica* and three plots in the high marsh dominated by *Elymus athericus* (Fig. 4.2A) along a major creek. Each plot was subdivided into eight 2 m x 2 m subplots. One half of the subplots was situated next to the creek ('creek') and separated the inner half of the subplots ('inner') from the creek (Fig. 4.2B).

Subplots were either mown ('mown') or the vegetation was left intact ('control'). A full-factorial design with four different treatment-combinations (creek=mown/inner=mown, creek=mown/inner=control, creek=control/inner=mown and creek=control/inner=control) was randomly assigned to the six plots. Mowing was repeated several times in order to keep the vegetation as short as possible.

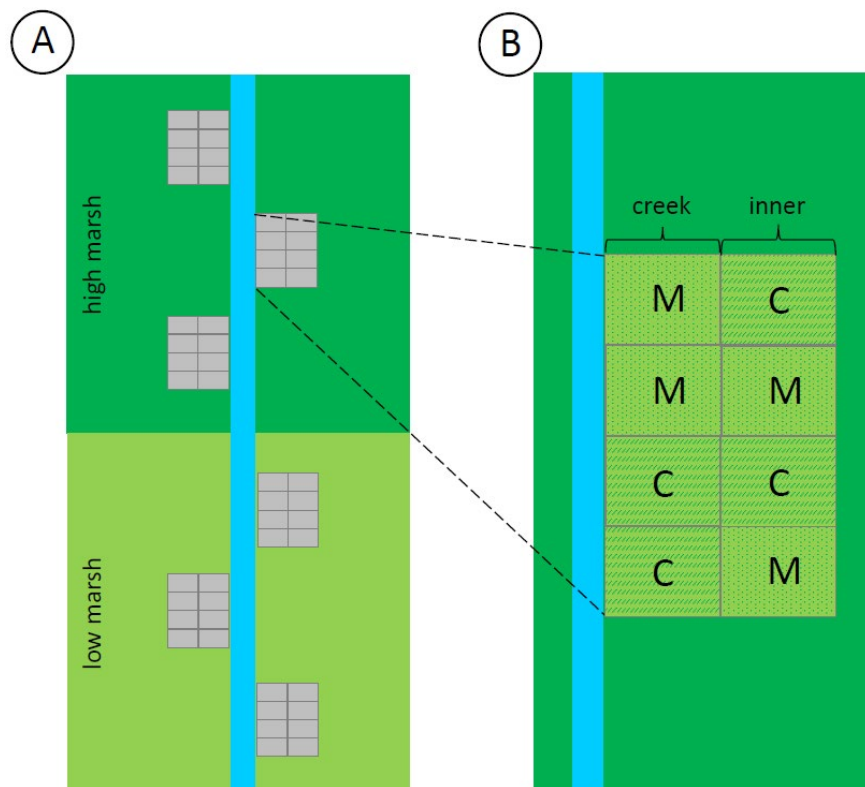


Figure 4.2 Experimental setup: **A)** Within the low and high marsh zone six experimental plots were established directly adjacent to the creek. **B)** Each experimental plot is subdivided into eight sub-plots with one half close to the creek ('creek') and the other further away from the creek ('inner'). The treatments mown ('M') and control ('C') are assigned to achieve a full factorial design within both zones.

We aimed to place all plots directly adjacent to a creek to ensure a comparable flooding regime for every plot. Additionally, plots were chosen which have a homogenous vegetation and flat topography at the start of the experiment. However, as marsh setting is variable in terms of e.g. microtopography, vegetation cover, species composition and levee formation, it was highly

challenging to find comparable conditions for every plot at one creek. We therefore had to choose plots at two adjacent creeks to ensure comparable microtopographic and vegetation-related conditions leading to an unbalanced design (Fig. 4.1).

Measurements of sediment deposition and SSC

Sediment deposition and SSC were assessed for one winter season (01/2017 to 03/2017) and one summer season (07/2017 to 10/2017). Within each subplot, we placed a circular plastic sediment trap (internal diameter: 19 cm; rim: 2.5 cm) with a floatable lid (Temmerman et al. 2003a; Nolte et al. 2019; Fig. 4.3A). The sediment traps were attached to the ground with a plastic stick (1.5 m) and with metal wires. On a biweekly basis, the sediment was collected from the traps after each spring-neap cycle. The collected deposited sediment was rinsed with freshwater, transferred to plastic bags and further processed in the laboratory. Samples were sieved (mesh size: 500 μm), washed with deionized water and oven dried at 100°C until constant weight. Additionally, floodwater was collected to determine SSC at each subplot. For this purpose, plastic bottles (580 ml) with a 3 cm water inlet and a longer air outlet made of plastic tubes were buried at each sampling point. These bottles allowed a controlled water inflow 3 cm above the marsh surface (Butzeck et al. 2015). The filled bottles were replaced after each spring-neap cycle. To determine SSC (g l^{-1}), water samples were resuspended and vacuum filtrated using cellulose nitrate filters (0.45 μm). Subsequently, samples were oven dried at 60°C until constant weight.

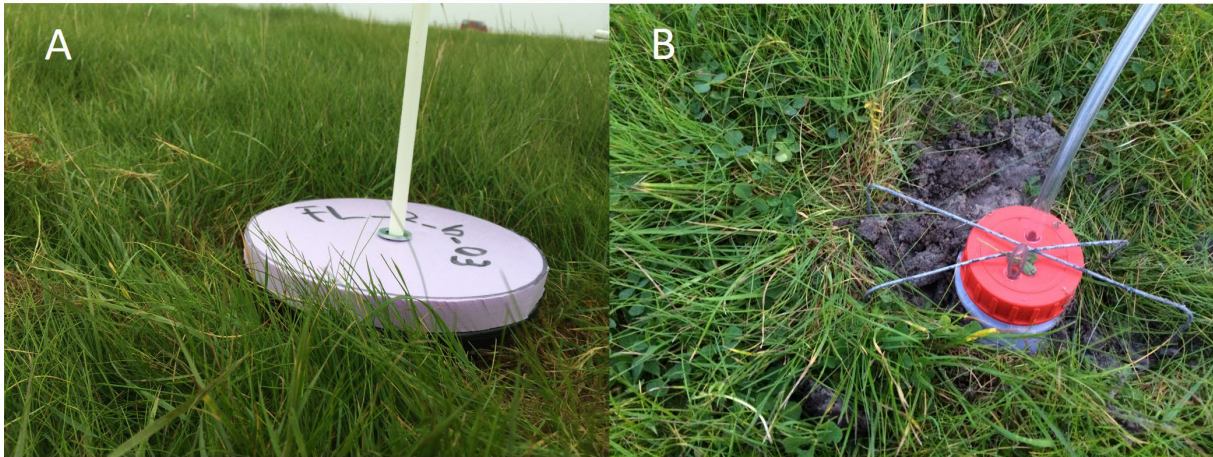


Figure 4.3 A) Sediment trap (internal diameter: 19 cm; rim: 2.5 cm) with floatable lid B) SSC bottle (580 ml; plastic water inlet and air outlet allowing for a controlled water inflow 3 cm above the marsh surface).

Inundation measurements

Inundation height, frequency and duration were measured by installing one water level gauge in each creek, which allowed to determine inundation levels above each subplot relative to the gauges. A slitted plastic pipe containing a water pressure sensor (Schlumberger Cera diver, accuracy of measuring water level: ± 1 cm) with a temporal resolution of 5 min was inserted into the soil. An atmospheric pressure sensor (Baro Diver) was installed in a close by location behind the dike to compensate the water pressure measurements for the atmospheric pressure. Elevation of each sampling point was measured in relation to the respective water gauges using a Trimble LL500 precision laser and a Trimble HL 700 receiver (2.0 mm accuracy).

Data processing and statistics

The raw data set included 480 data points (6 plots x 8 subplots x 10 measurements). From these, we calculated cumulative mean values of sediment deposition and SSC for each subplot, to compare overall effects of the treatments. We used two factorial analysis of variance with this cumulative sediment deposition as response variable and the interaction of the factors creek and marsh zone to test whether the unbalanced design (e.g. two high marsh plots at creek 1 and only one high marsh plot at creek 2) affected the results. As a significant interaction was found, we

split the dataset in a high marsh and a low marsh dataset to investigate treatment effects (sediment deposition ~ treatment) for each zone separately, thereby reducing unwanted creek effects in the model.

For each marsh zone, we first analysed the subplots adjacent to the creek ('creek') independently from the inner subplots to answer the question whether sediment deposition and SSC is generally higher in tall or short vegetation. We ran ANOVAs with sediment deposition or SSC as response variable and treatment as explanatory variable. To investigate how the spatial pattern of tall and short vegetation influences spatial patterns of sediment deposition and SSC, we analysed sedimentation in the 'inner' subplots. The ANOVA included both the treatment of the inner subplot and the treatment of the corresponding 'creek' subplot, as well as the interaction of both treatments. If necessary, data were log transformed to meet normality assumptions and to improve homogeneity of variances. Equal sample sizes in the study design assured robustness of parametric testing (McGuinness 2002). As a post hoc test, Tukey's-HSD (honest significant difference) test was applied to determine pairwise differences. Furthermore, to assess the effect of maximum inundation height on sediment deposition and SSC, linear regressions were used. All analyses were performed using R version 3.5.3 (R Core Team, 2019; base package).

Results

Inundation characteristics

Over the course of the experiment, the mean maximum inundation height over the creek subplots ranged from $0.55 \text{ m} \pm 0.13 \text{ m}$ (mean \pm standard deviation) in the high marsh to $0.80 \text{ m} \pm 0.1 \text{ m}$ in the low marsh. The mean maximum inundation height over inner located subplots ranged from $0.56 \text{ m} \pm 0.11 \text{ m}$ in the high marsh to $0.82 \text{ m} \pm 0.08$ in the low marsh. For subplots located at the creek, there were no differences in inundation height between the control

treatment and the mown treatment neither in the high marsh nor in the low marsh (HM control: $0.56 \text{ m} \pm 0.13 \text{ m}$ vs. HM mown: $0.55 \text{ m} \pm 0.13 \text{ m}$; LM control: $0.80 \text{ m} \pm 0.1 \text{ m}$ vs. LM mown: $0.79 \pm 0.1 \text{ m}$). Similar results were observed for the inner located subplots (HM control: $0.56 \text{ m} \pm 0.11 \text{ m}$ vs. HM mown: $0.56 \text{ m} \pm 0.11 \text{ m}$; LM control: $0.82 \text{ m} \pm 0.08 \text{ m}$ vs. LM mown: $0.81 \text{ m} \pm 0.08 \text{ m}$).

Sediment deposition and SSC

In both marsh zones, there was no consistent trend or significant difference in sediment deposition between the mown treatment and the untreated control for subplots located at the creek (Fig. 4.4, Table 4.1). The mowing treatment also had no significant effect on SSC (Fig.4.5, Table 4.1). However, in both zones SSC was slightly higher on mown subplots compared to the control subplots. In the high marsh, SSC was approximately 40% higher on mown subplots compared to control subplots whereas in the low marsh SSC was approximately 30% higher. For inner located subplots, there was no trend detectable across all treatment combinations indicating that treatment combination (control:control, mown:control, control:mown, mown:mown) had no significant effect on sediment deposition (Fig. 4.4, Table 1). SSC did not differ significantly but tended to be higher on mown inner subplots compared to control inner subplots (Fig. 4.5, Table 1). In the high marsh, SSC on mown subplots was approximately 45% higher compared to control subplots and in the low marsh SSC was 55% higher on mown subplots compared to control subplots.

Relationship between inundation and sedimentation

Regressions revealed a significant and strong positive linear relationship between maximum inundation height and sediment deposition (Fig. 4.6 A,B), as well as SSC (Fig. 4.6 C,D). However, on control subplots this correlation was slightly stronger compared to mown subplots for sediment deposition and SSC both in the high and low marsh. For sediment deposition, the strongest correlation with maximum inundation height occurred on control subplots in the high

marsh ($R^2=0.687$) while the lowest correlation occurred on mown subplots in the low marsh ($R^2=0.636$). For SSC, the strongest correlation with maximum inundation height occurred on control subplots in the high marsh ($R^2=0.782$) while the lowest correlation occurred on mown subplots in the low marsh ($R^2=0.602$).

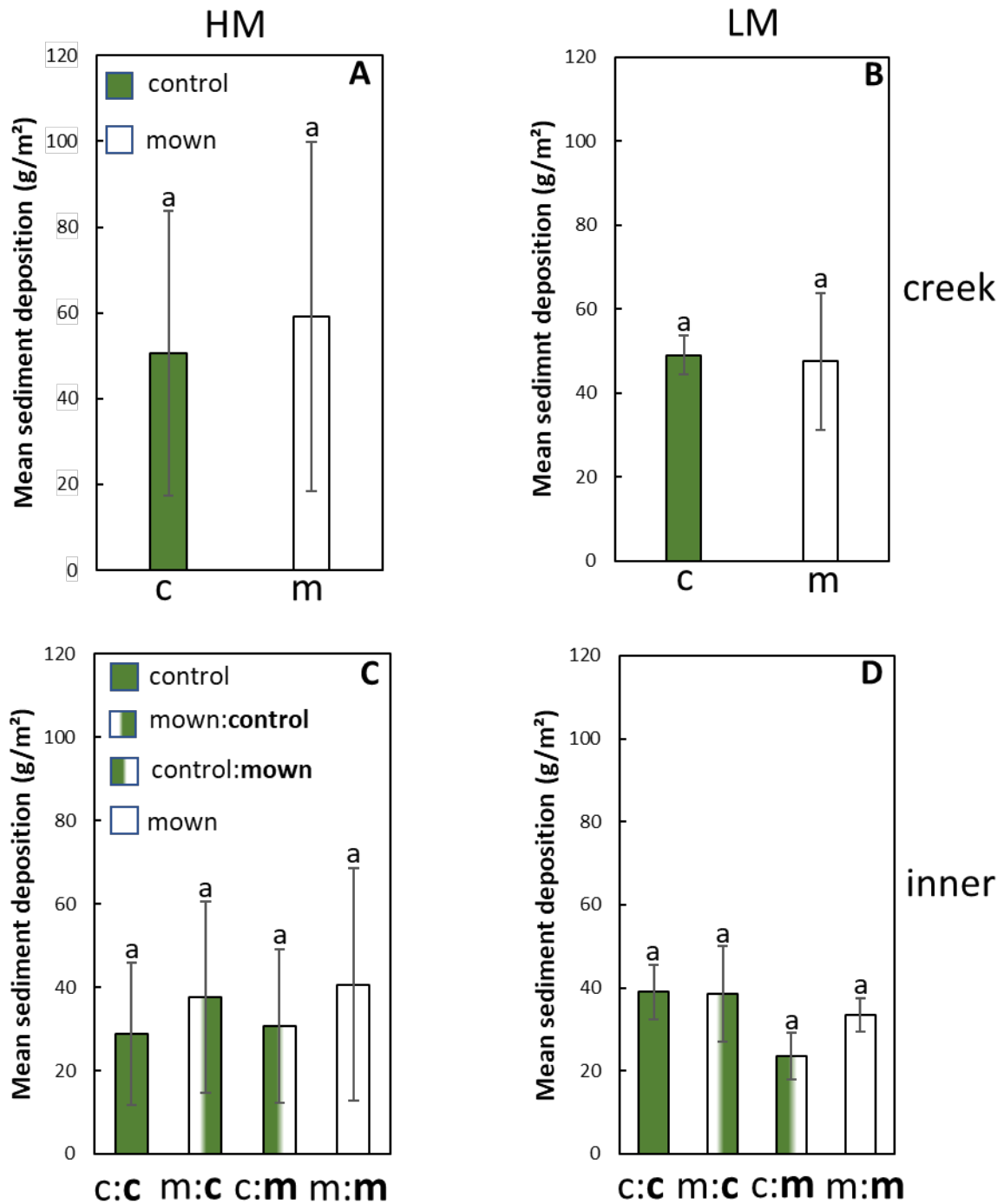


Figure 4.4 Sediment deposition at subplots located at the creek (panel A, B) and of inner located subplots (panel C, D) in the high (panel A, C) and low marsh (panel B, D). Green bars show control subplots, white bars show mown subplots. Bars with a colour shift from white to green show inner control subplots, which are located behind a mown subplot and bars with a colour shift from green to white show inner mown subplots, which are located behind a control subplot. Values are means and the error bars indicate standard deviation. Treatment and treatment combination of at the creek and inner located subplots had no effect on sediment deposition (illustrated by equal lowercase letters following ANOVA and Tukey's tests).

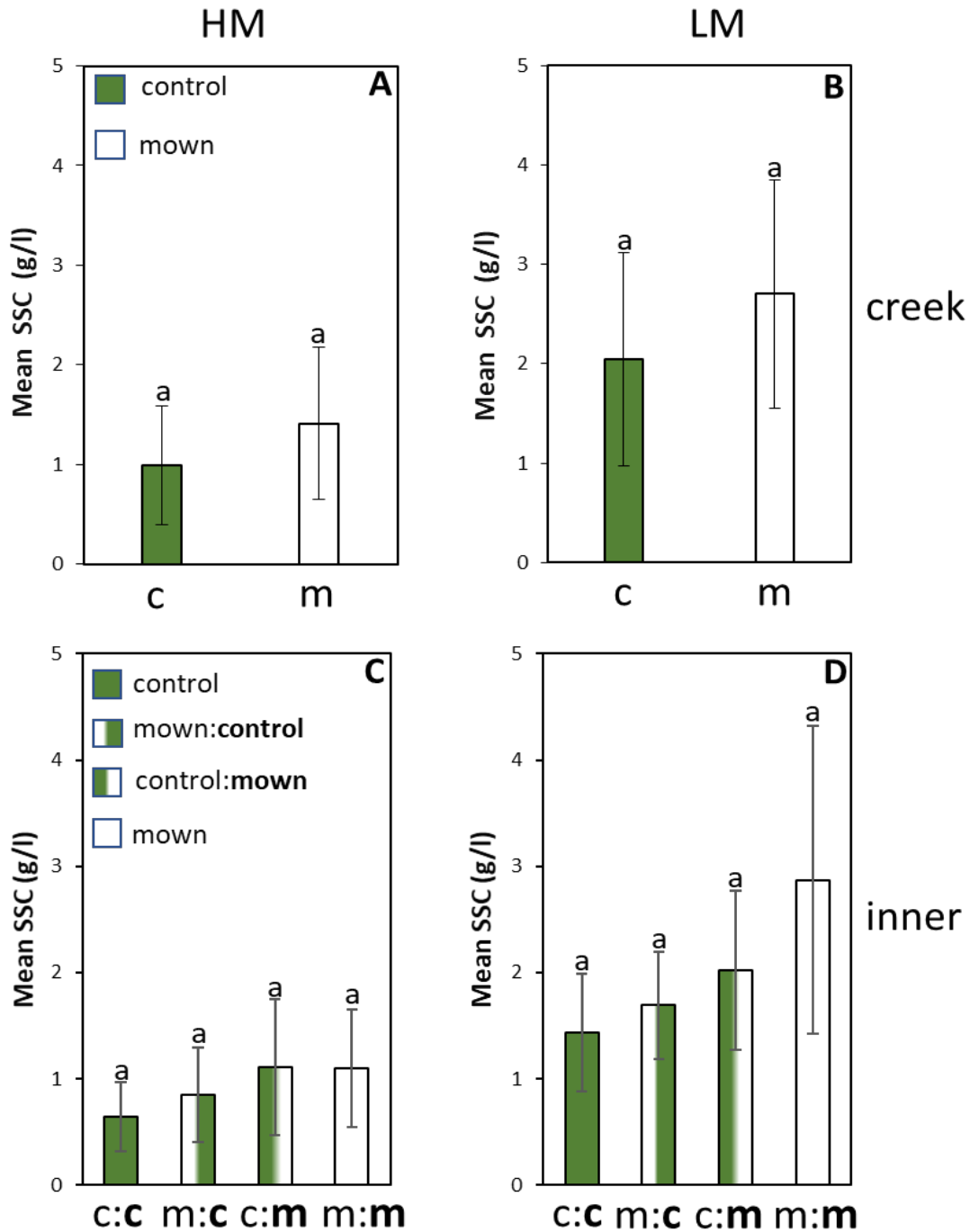


Figure 4.5 SSC of at the subplots located at the creek (panel **A**, **B**) and of inner located subplots (panel **C**, **D**) in the high (panel **A**, **C**) and low marsh (panel **B**, **D**). Green bars show control subplots, white bars show mown subplots. Bars with a colour shift from white to green show inner control subplots, which are located behind a mown subplot and bars with a colour shift from green to white show inner mown plots, which are located behind a control subplot. Values are means and the error bars indicate standard deviation. Treatment and treatment combination of at the creek and inner located subplots had no effect on SSC (illustrated by equal lowercase letters following ANOVA and Tukey's tests).

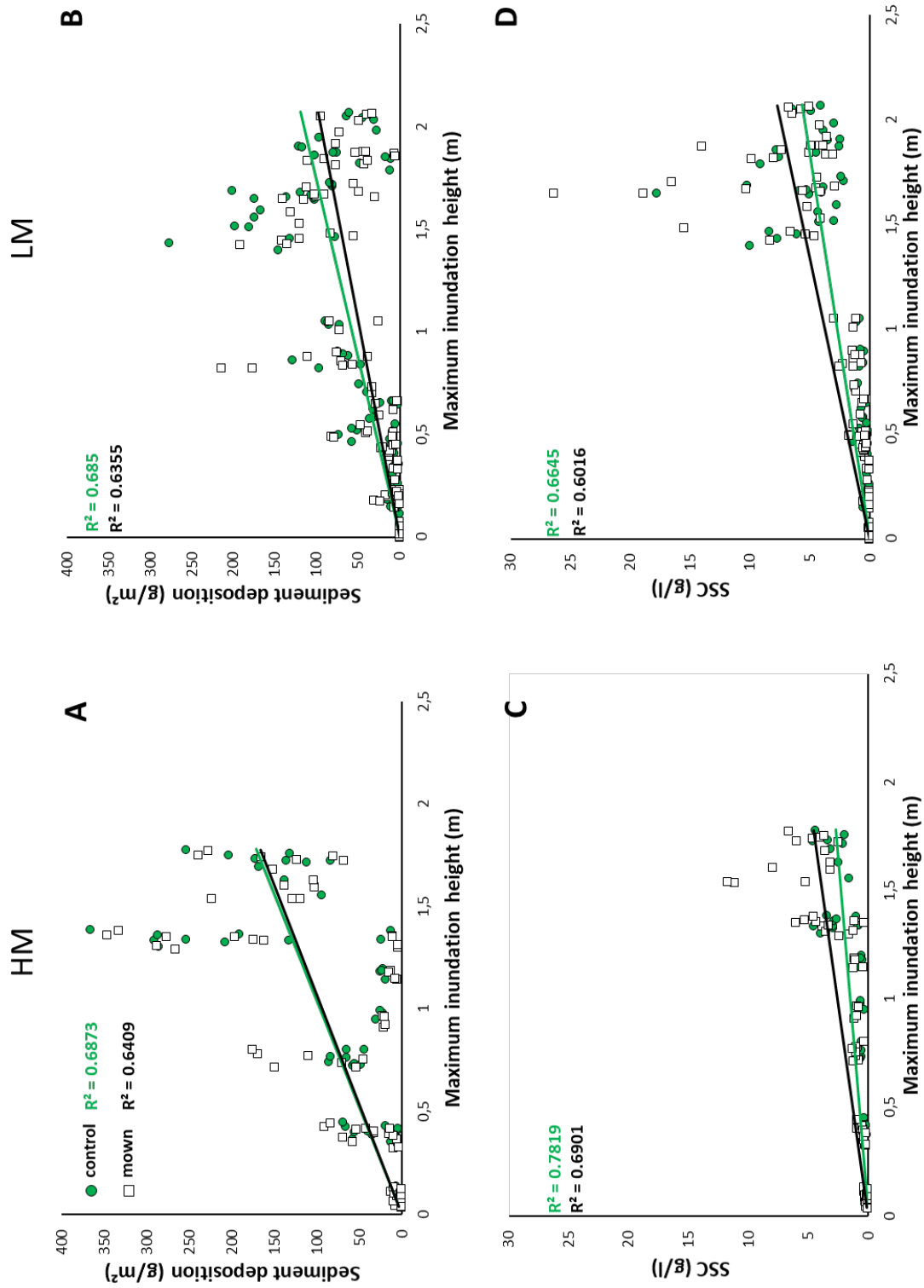


Figure 4.6 Sediment deposition (panel A, B) and SSC (panel C, D) as a function of maximum inundation height in the high (panel A, C) and low (panel B, D) marsh. White squares show mown subplots with a corresponding black regression line. Green circles show control plots with a corresponding green regression line. All relationships between maximum inundation height and SSC or sediment deposition are linear and significant.

Table 4.1 ANOVA table of the effects of treatment (mown, control) on sediment deposition and SSC on at the creek located subplots in the high and low marsh and of treatment combination on sediment deposition and SSC on inner located subplots in the high and low marsh. Given are F-values and p-values.

	Sediment deposition HM		Sediment deposition LM		SSC HM		SSC LM	
	F	p	F	p	F	p	F	p
Treatment	0.722	n.s.	0.043	n.s.	0.933	n.s.	0.862	n.s.
Treatment creek x Treatment inner	0.001	n.s.	0.883	n.s.	0.087	n.s.	0.311	n.s.
Treatment creek	0.364	n.s.	0.732	n.s.	0.076	n.s.	0.618	n.s.
Treatment inner	0.024	n.s.	3.440	n.s.	1.005	n.s.	1.694	n.s.

Discussion

Vegetation-induced sedimentation is an important factor for coastal marsh maintenance under sea-level rise (Baustian et al. 2012; Zhang et al. 2020). Yet, even though it is often assumed that vegetation has a positive effect on sedimentation, the relationship between sediment deposition and vegetation structure is not fully understood. Indeed, contrary to our expectations, there were no differences in sediment deposition and SSC between patches of control and mown vegetation in both the high marsh and the low marsh. We also did not find evidence for an influence of different spatial positioning of vegetated control and mown subplots on patterns of sediment deposition and SSC.

This study adds to a body of research showing contrasting results on the influence of tall and short marsh vegetation on sediment deposition and SSC (e.g. Morris et al. 2002; Neumeier and Ciavola 2004; Temmerman et al. 2005; Silva et al. 2009; Elschot et al. 2013; Nolte et al. 2013a; Reef et al. 2018; Schulze et al. 2021). Within a marsh, on a small vegetation-patch scale, it is assumed that a patch of vegetation represents an obstacle to the water flow, leading to altered hydrodynamic conditions within, between and around the vegetation patch. A vegetation patch adjacent to a creek or marsh edge experiences high drag forces (Bouma et al. 2010), dissipates

wave energy and reduces flow velocity causing lower hydrodynamic energy behind the patch and therefore protection and conditions for enhanced sediment deposition (Marjoribanks et al. 2019). However, these studies investigating flow-patch interactions mostly focus on isolated vegetated patches (i.e. tussocks) on an unvegetated tidal flat, which are not necessarily comparable to patches and patterns within a vegetation canopy. This might explain why this process seems not to come into effect on the chosen spatial scale in our study, as we do not find enhanced sediment deposition neither on at the creek located vegetated control subplots nor on inner located control subplots for none of the treatment combinations.

Previous studies have found, that a considerable amount of hydrodynamic energy (~40-50%) is effectively attenuated on the first five to ten meters of a vegetated marsh (Möller and Spencer 2002; Leonard and Croft 2006; Ysebaert et al. 2011), but it stays unclear what happens on shorter distances comparable to those studied here. Our results indicate that substantial attenuation of hydrodynamic energy and enhanced sediment deposition probably only takes place on coherent vegetation patches which are larger than 2x2 m or 4x4 m. In a salt marsh study on flow and sediment deposition patterns, it was shown that fully vegetated plots adjacent to the sediment source showed a higher sediment deposition compared to the 10 m interior located vegetated plots (Schepers et al. 2019). In contrast, unvegetated plots close to the sediment source showed less sediment deposition compared to interior located unvegetated plots. It was shown that sediment deposition not only depends on the treatment of the vegetation (e.g. grazed/ungrazed, mown/unmown) but also on the distance of the plot to the source of the sediment and on the spatial scale.

Interestingly, we found a consistent, but non-significant, trend of SSC being higher over mown subplots compared to control subplots, which could provide an additional explanation for the unexpected results on sediment deposition. The lower SSC over control subplots suggests that a certain amount of suspended sediment is directly trapped by the vegetation, which is a well

described process (e.g. Fagherazzi et al. 2012; Li et al. 2014; Kakeh et al. 2016). This active trapping mechanism, in contrast to the above-described passive deposition mechanism, is not reflected in our results as the lid of the sediment traps prevented uptake of sediment sticking to vegetation. During an inundation, the lid first moves up allowing sediment in the water column to settle and then shuts when water level moves down thus preventing washout of trapped sediment by rain (Nolte et al. 2019). However, during rainfalls, sediment sticking on the vegetation surface can be rinsed and accumulated on the marsh surface leading to underestimation of total sediment deposition on control subplots when using this type of sediment traps. We therefore suggest that considering this mechanism in future studies would substantially increase our knowledge on the influence of salt marsh vegetation on SSC and sediment deposition.

Furthermore, we found a linear relationship between inundation height and SSC as well as between inundation height and sediment deposition across treatments and thus conclude that inundation height seems to be the control mechanism for SSC and sediment deposition in this study. This is in line with previous studies showing a linear increase of initial floodwater SSC with increasing inundation height (Temmerman et al. 2003b). However, this correlation seems to be slightly, but consistently, more pronounced on control subplots (higher R^2 on control subplots compared to mown subplots). This underlines the lack of influence of vegetation on sediment deposition in this study, as sediment deposition is more strongly affected by inundation height on vegetated plots than on mown plots. Thus, there is less unexplained variability of sediment deposition left in the model for vegetated control subplots, indicating that a further explanation of the variability by vegetation is unlikely. If the relationship between inundation height and sediment deposition on control subplots had been weaker, more of the variability of sediment deposition on vegetated control subplots could have possibly been explained by the influence of vegetation in further models. We thus assume that on larger patches consisting of dense vegetation, more of the variability in sediment deposition can be

explained by the presence of vegetation. This would be in line with Schulze et al. (2021) who found a significantly higher sediment deposition on large ungrazed plots (>100 m²) compared to large grazed plots (>100 m²).

Based on the results of our study, it can be concluded that the presence of salt marsh vegetation not automatically leads to higher sediment deposition on vegetated patches compared to mown patches, which is also in line with Schepers et al. (2019). To provide comprehensive information on scale dependency of vegetation-mediated sediment deposition, future studies should include measurements of flow velocity, sediment transport, sediment deposition, resuspension of sediment as well as vegetation behaviour on patches of different sizes in order to find critical thresholds for effects of vegetation on sediment deposition (Fagherazzi et al. 2020). However, the fact that biophysical plant properties are highly variable spatially and seasonally (Schulze et al. 2019) and hydrodynamic attenuation follows non-linear relationships makes research in this field challenging and explains the scarcity of studies (Koch et al. 2009; Friess et al. 2012; Wiberg et al. 2020).

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5 Synthesis

This first section of the synthesis summarizes the key findings of my thesis chapter by chapter, including short conclusions. In the second section, I integrate and synthesise these key findings to reach the comprehensive overarching results of the thesis. In the last section, further implications based on my results are described.

Key findings

Chapter 1 – Seasonal and spatial within-marsh differences of biophysical plant properties: implications for wave attenuation capacity of salt marshes

1. Biophysical plant properties such as stem flexibility, biomass or stem density mostly showed a high seasonal variability in *Spartina anglica* and *Elymus athericus* with significantly higher values during summer.
2. More than 70% of the variability in stem flexibility was explained by the variability in stem diameter of *S. anglica* and *E. athericus* stems indicating the importance of considering plant morphology (here diameter) when describing plant stem flexibility. Plant tissue properties (characterized by the Young's modulus) did not vary significantly between spring and summer.
3. Small-scale spatial differences for biophysical plant properties were found for *S. anglica* with plant stem stiffness and aboveground biomass being significantly higher in a landward than in a seaward-located marsh zone. Small-scale spatial differences of biophysical properties were not found in *E. athericus*.
4. These results indicate the importance of considering variability in biophysical plant properties when describing or investigating wave attenuation and coastal protection potential of salt marshes.

Chapter 2 - Livestock grazing reduces sediment deposition and accretion rates on a highly anthropogenically altered marsh island in the Wadden Sea

1. Ungrazed plots showed significantly higher sediment deposition and accretions rates compared to grazed plots while suspended sediment concentration was higher under grazing.
2. Natural marsh vegetation is thought to have a considerable sediment trapping effect. As ungrazed plots were dominated by *E. athericus*, it can be concluded that monospecific stands of *E. athericus* have a high sediment trapping potential.
3. It seems that accretion rates of intensively grazed Wadden Sea marsh islands with reduced flooding frequencies cannot keep pace with rising sea levels.
4. Based on the results, it can be concluded that accretion rates can be considerably improved once monospecific *E. athericus* stands have established after abandonment of grazing.

Chapter 3 - Effects of small-scale patterns of vegetation structure on suspended sediment concentration and sediment deposition in a salt marsh

1. No differences in sediment deposition and SSC were found between patches of control and mown vegetation in both the high marsh and the low marsh. Furthermore, no evidence was found for an influence of different spatial positioning of vegetated control and mown subplots on patterns of sediment deposition and SSC.
2. Based on the results of this study, it can be concluded that the presence of salt marsh vegetation not automatically leads to higher sediment deposition on vegetated patches compared to mown patches.

Synthesis of key findings

Coastal protection by salt marshes and marsh survival to sea-level rise presupposes complex physical processes of which only some were further studied here. However, for a deeper understanding of the functioning of salt marshes we need to see them in a wider context of processes. When sediment-rich seawater moves over Wadden Sea mudflats, wave-action accumulates even more sediment by inducing shear stress onto the mudflats. Consequently, fine sediment particles are brought into suspension leading to a high suspended sediment concentration when floodwater arrives on the vegetated marsh platform (Brooks et al. 2021). The subsequent wave and flow attenuation on salt marshes mostly is a combined effect of bottom friction and vegetation, which form an obstruction to wave-induced oscillatory flow and to uniform flow (Mullarney and Henderson 2010). The wave attenuation and reduction of horizontal current velocities over vegetated marshes are controlled by the biophysical plant properties such as stem density, stem flexibility and aboveground biomass (Peralta et al. 2008; Widdows et al. 2008; Bouma et al. 2010). Furthermore, the water levels above the marsh surface and above the canopy play an important role (Temmerman et al. 2005). The influence of vegetation on hydrodynamic conditions over vegetated salt marshes are also accompanied by altered turbulences leading to a reduced within-canopy and bottom shear stress, which promotes sediment deposition (Fig. 5.1). Within a vegetation patch, the vegetation exerts drag on the water flow and is, in turn, exposed to drag forces from the flow therefore reducing flow velocity (Paul et al. 2016). In case of water levels reaching above the height of the canopy, flow velocity above the canopy is higher compared to the flow within the canopy. The drag forces acting on stiffer stems are higher (tolerance strategy: stiff stems; high flexural rigidity) compared to flexible stems (avoidance strategy: flexible stems; low flexural rigidity), which are more likely to reconfigure their shape in the water flow. Consequently, sediment particles are more likely to be gravity-driven deposited in vegetated canopies compared to bare mudflats. Therefore, salt marsh vegetation has a major impact on sedimentation processes by altering flow velocity and

wave energy. Vegetation patches consisting of species with high biomass, stem densities, stem lengths and flexural rigidity should lead to even higher sedimentation rates compared to mudflats or patches with lower biomass, stem lengths and flexural rigidity.

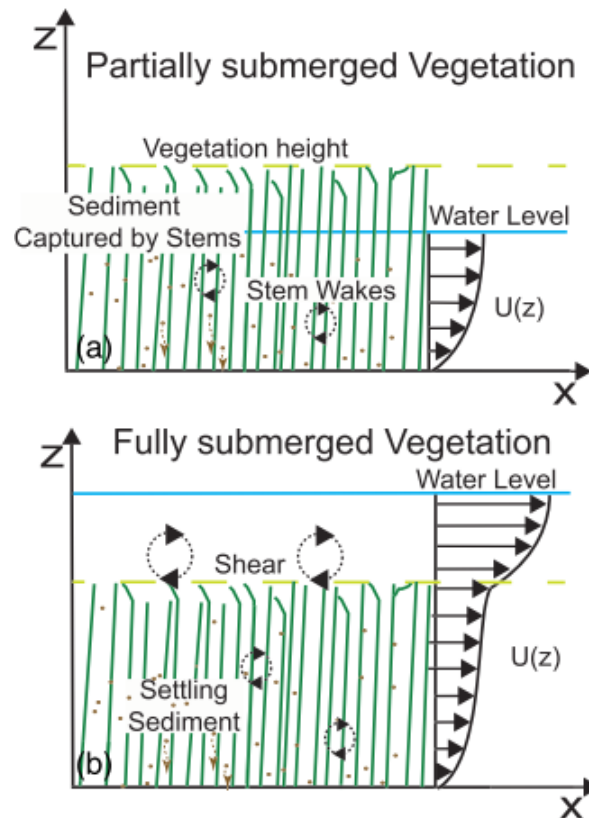


Figure 5.1 Scheme of the interaction of hydrodynamic forces, sedimentation processes and a (a) partially submerged canopy and a (b) fully submerged canopy. $U(z)$ symbolizes the reduction of flow velocity caused by vegetation-induced drag. Interactions are simplified and schematised. Reconfiguration of vegetation and vegetation movement is not considered. Source: Fagherazzi et al. 2020.

However, in temperate zones these processes neither take place steadily nor linearly (Koch et al. 2009). The breakdown of vegetation in winter leads to considerable seasonal differences in e.g. biomass between summer and winter or spring (Bellis and Gaither 1985; Morris and Haskin 1990). Therefore, the significantly reduced biomass, flexural rigidity or stem density for *Elymus* and *Spartina* in spring and winter compared to summer, as found in chapter 2, are associated with a lower contribution of salt marsh vegetation to wave attenuation from winter to spring.

This in turn reduces the capacity of plant-modulated sediment settling in a vegetated marsh (Fig. 5.2).

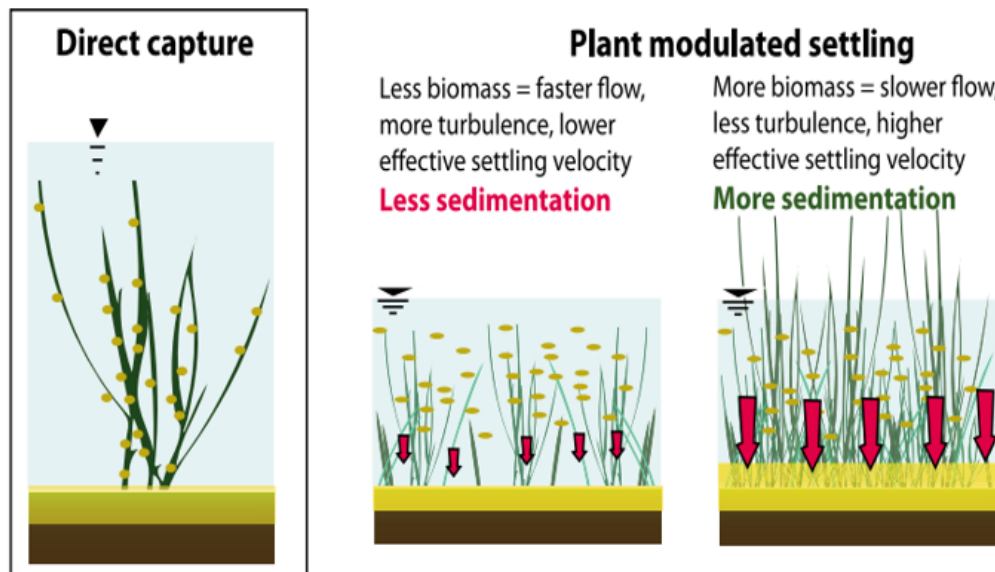


Figure 5.2 Influence of vegetation on sediment particle settling through direct trapping and plant-modulated settling. Source: Fagherazzi et al. 2012.

Based on these mechanisms, it is likely that in a marsh with year-round inundations, sedimentation rates are higher in summer when vegetation is fully developed. However, sedimentation rates in Wadden Sea salt marshes are higher in autumn and winter compared to summer when biomass is lower (Fig. 5.3; Fig. 5.4; Fig. 5.5; see also Butzeck et al. 2015). This fact is attributed to other factors influencing sediment deposition such as inundation height, which is a consequence of storms and higher hydrodynamic forcing in autumn and winter compared to summer. Increased hydrodynamic forcing also transfers more sediment into suspension through shear forces in autumn and winter leading to higher SSC, which is one of the main predictors for sediment deposition (Butzeck et al. 2015). Furthermore, differences in standing biomass between winter/spring and summer are indeed significant, but especially in ungrazed high marshes, still a high proportion of standing *Elymus* biomass remains on the marshes throughout the winter season (Chapter 2, Schulze et al. 2019). Therefore, *Elymus*

shows minor seasonal differences in biomass compared to e.g. *Spartina*, suggesting a more continuous contribution to wave energy reduction and to vegetation induced sediment deposition.



Figure 5.3 Experimental setup in chapter 4. **Figure 5.3A** shows the setup in its summer state with fully developed biomass in unmown subplots. **Figure 5.3B** shows the setup in its winter state with degenerated biomass.

Based on flume experiments on vegetation-wave interactions in salt marshes under storm surge conditions, Rupprecht et al. (2017) state that a vegetation control on orbital velocities and therefore on sediment transport and deposition is species-specific. Under low to medium wave energy and 1 m water level, a stiff *Elymus* canopy contributed more to the reduction of orbital flow and wave energy than a flexible *Puccinellia maritima* canopy (Rupprecht et al. 2017). As *Festuca rubra* is comparable to *Puccinellia maritima* in terms of its biophysical properties, this is another explanation for the significantly higher sediment deposition rates on *Elymus athericus* dominated ungrazed sites compared to *Festuca rubra* dominated grazed sites on Langeness (chapter 3). As there is yet only a limited number of studies investigating the influence of biophysical plant properties on sedimentation, it is important to consider different species, different marsh types (e.g. natural vs. man-made), different marsh zones, different

management types (e.g. grazing) and seasonal and spatial variability in further studies to better understand the influence of vegetation on sedimentation (see also Baaij et al. 2021).

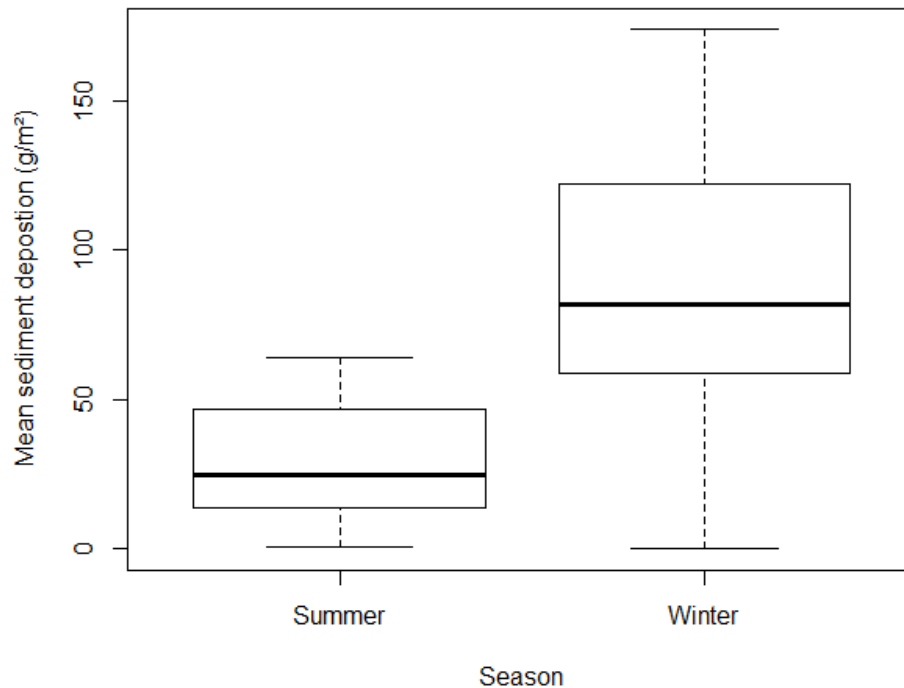


Figure 5.4 Mean sediment deposition in a mainland saltmarsh at Dieksanderkoog in summer and winter. Data were obtained in chapter 4 and are based on sediment samples from sediment traps in both the high and low marsh. Based on Mann-Whitney U testing, sediment deposition differs significantly between summer and winter ($p < 0.05$). Shown are medians, quartiles and ranges.

Furthermore, most studies were limited to a small number of plant species, with a predominant focus on *Spartina* species, rarely taking dominant high marsh species such as *Elymus athericus* into account (Shepard et al. 2011; Baaij et al. 2021). The results of my thesis suggest that *Spartina anglica* is perfectly adapted to high wave energy by showing a high overall stem stiffness (i.e. high flexural rigidity) and a soft plant tissue (i.e. low Young's modulus), which reduces the risk of stem folding under wave forcing. *Elymus athericus* in turn is exposed to lower wave forcing which allows for a stiffer plant tissue. Furthermore, *Elymus* shows high

stem densities and stem lengths which correlates positively with sedimentation (Bouma et al. 2005; Baaij et al. 2021).

Biophysical plant properties can furthermore and unsurprisingly be modified by livestock grazing, which is widely distributed in Wadden Sea salt marshes and leads to trampling and removal of vegetation by the animals as well as changes in vegetation composition (He and Silliman 2016). Sediment deposition, which takes place either by direct trapping on the plants surface or by deposition through plant-modulated flow reduction, is expected to be reduced under grazing pressure (Fig. 5.5).

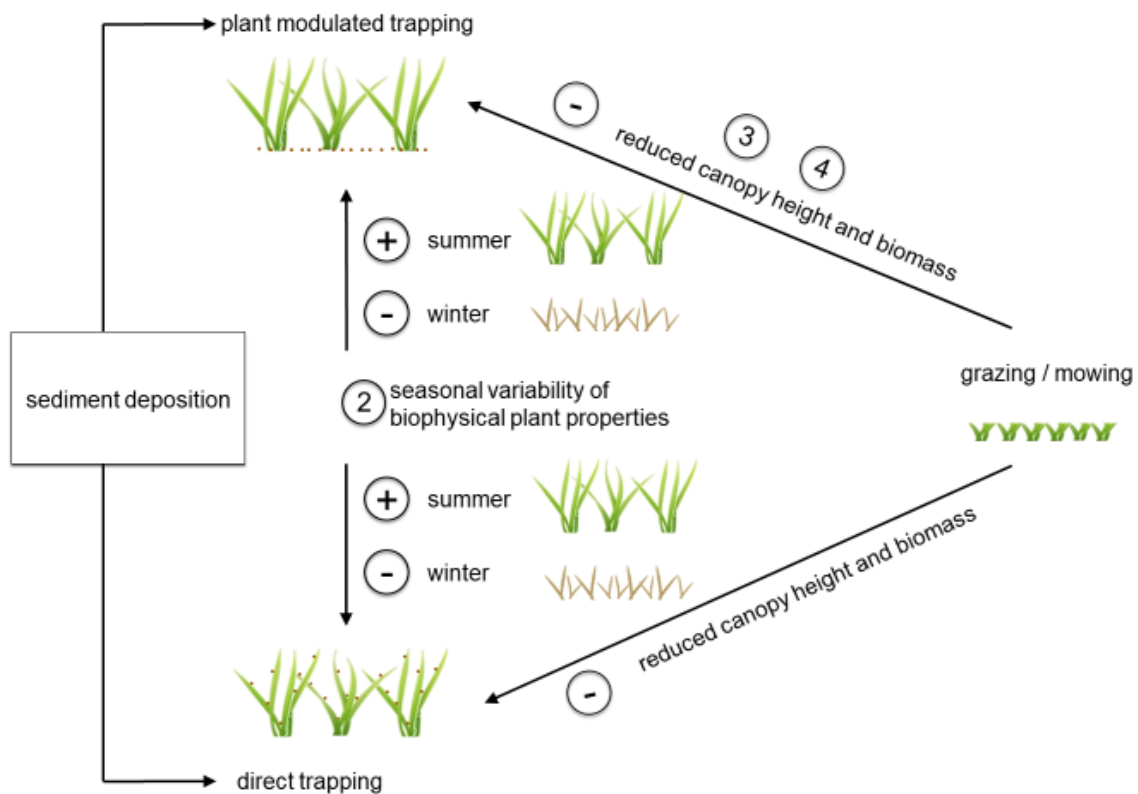


Figure 5.5 Graphical overview describing the connections of the chapters (numbers 2-4 in circles) in this thesis. The spatio-temporal variability of the biophysical plant properties quantified in chapter 2 influences the hydrodynamic conditions as well as the sediment deposition capacity of salt marshes. In chapter 3, the influence of a canopy reduced in height by grazing on sediment deposition was investigated. Chapter 4 considers the effects of spatial positioning of tall and short vegetation on spatial patterns of sediment deposition both in summer with high biomass, flexural rigidity and stem density and in winter with low biomass, flexural rigidity and stem density. The contribution of direct sediment trapping by salt-marsh plants to the overall sediment deposition remains unclear and needs to be systematically investigated in Wadden Sea salt marshes.

In high marshes for example, grazing sensitive *Elymus athericus* canopies, which have a high sediment trapping potential and biophysical properties associated with a high wave attenuation potential, are often replaced by low growing *Festuca rubra* under livestock grazing. Therefore, wave attenuation and sediment deposition are likely to be negatively influenced by livestock grazing in Wadden Sea high marshes. However, when sediment deposition is quantified via common sediment traps like in chapter 3 and 4 (see also Temmerman et al. 2003a; Nolte et al. 2019), I strongly suspect that sediment deposition rates are highly underestimated as direct trapping is not considered by this method. The suspended sediment particles are intercepted by a dense vegetation and are likely to be deposited directly on parts of the plants. The particles stick on the plants through adherence (Fig. 5.6; Li and Yang 2009; Fagherazzi et al. 2012; Kakeh et al. 2016). This direct trapping effect was already described 40 years ago in a study in which sediment on *Spartina* plants accounted for 50% of a suspended sediment lost during a spring tide (Stumpf 1983). However, systematic investigations on this effect in Wadden Sea marshes are lacking. I assume that sediment deposition rates in chapter 3 and 4 were highly underestimated as during rainfalls sediment sticking on the vegetation can be rinsed off and would have accumulated on the marsh surface. Due to the greater surface area of the foliage system of ungrazed canopies compared to grazed canopies, this effect is likely to be more distinct in ungrazed marshes. Instead of circular plastic traps with lids, artificial grass mats (e.g. AstroTurf) could be used in order to mimic vegetation (Nolte et al. 2019; Fig. 5.7). Due to the higher surface roughness of AstroTurf mats compared to plastic plates, small-scale sedimentation patterns probably can be recorded more realistically. However, in ungrazed parts of marshes with high biomass and vegetation heights >50 cm, typical AstroTurf mats with low vegetation surrogate heights do not represent real vegetation sufficiently (Nolte et al. 2019). In a study investigating AstroTurf as surrogates for vegetation, it was found that flow velocity over AstroTurf and real vegetation differed significantly due to insufficient rotational movement by the AstroTurf vegetation surrogates (Wilson et al. 2005).

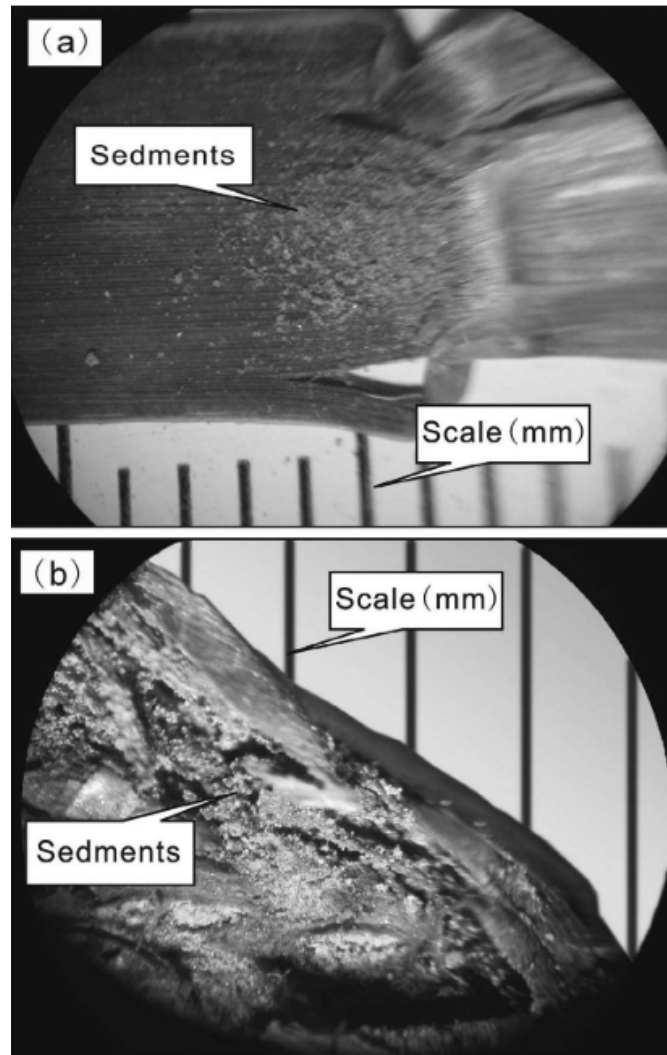


Figure 5.6 Small sediment particles sticking on a leaf and stem of *Spartina alterniflora* (a) and a fruit of *Spartina mariqueter* (b). Source: Li and Yang 2009.

Furthermore, heavy rainfalls can rinse the trapped sediment particles from the AstroTurf mats onto the marsh surface leading to underestimation of sediment deposition when using AstroTurf mats. Circular sediment traps made of plastic and covered by lids prevent sediment particles from being washed out of the sediment trap (Fig. 5.7). The advantage of floor mats over circular sediment traps by mimicking vegetation on a small scale is not of consequence, as the conclusion of chapter 3 and 4 is that flow velocity is rather reduced on a scale of coherent spacious vegetation canopies ($>50 \text{ m}^2$) and not on a spatial scale of a sediment trap ($\sim 400 \text{ cm}^2$). This means that sediment deposition is induced when a moving body of water is slowed down to a certain point by large coherent compound of vegetation and by the marsh surface.

One conclusion of the insights of chapter 3 and 4 is that future research should aim to identify the threshold for the spatial scale beyond which an influence of vegetation on sediment deposition comes into effect. On large coherent vegetation patches, vegetation had a clear effect on sediment deposition (chapter 3), whereas on small vegetation patches of 2x2 m (chapter 4), vegetation had no effect on sediment deposition.

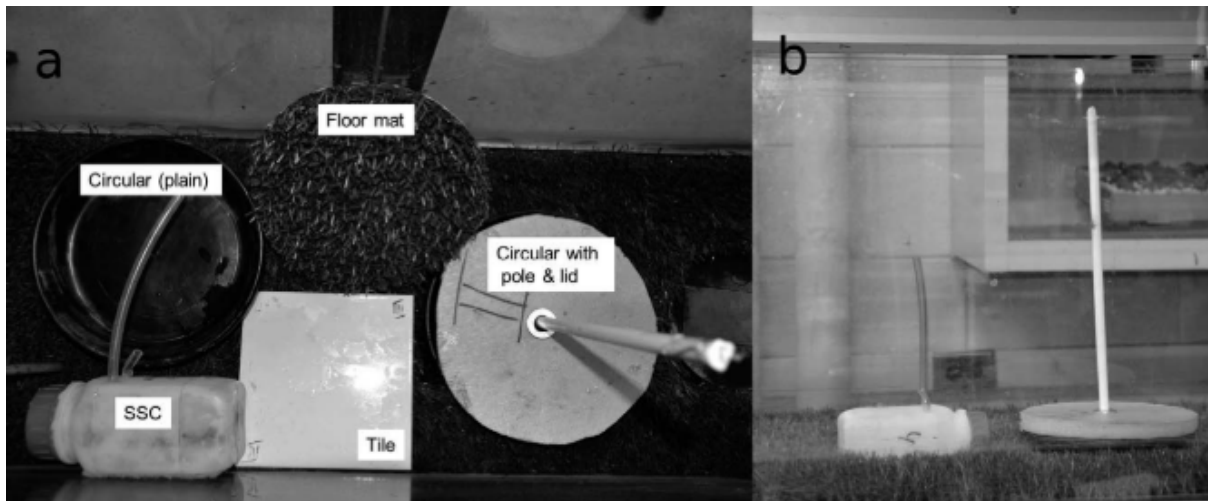


Figure 5.7 a) Different sediment traps including a floor mat (AstroTurf) and a circular plastic sediment trap with lid. **b)** Combination of SSC bottle to quantify suspended sediment concentration and circular sediment trap with lid to measure sediment deposition. This combination was used in chapter 3 and 4. Source: Nolte et al. 2019.

However, as the above-mentioned direct sediment trapping was not considered in these studies, this could be a further explanation for the missing influence of vegetation on sediment deposition in chapter 4. If direct trapping of vegetation on unmown subplots had been included in this study, the results possibly would have revealed a vegetation effect with higher sediment deposition on unmown subplots compared to mown subplots. The vegetation effect, therefore, would have been masked by not considering the directly trapped sediment. This effect probably is more important in high marshes than in low marshes: sediment grain size decreases with distance to the marsh edge or creek due to a reduced flow velocity. High marshes are predominantly reached by smaller sediment particles, whereas low marshes experience sediment deposition by larger and heavier particles (Baaij et al. 2021). As mostly small

sediment particles stick on the plants surface (Kretz et al. 2020; 2021a), investigating the effect of direct sediment trapping thus becomes particularly important in high marshes.

Based on the literature and on the insights of chapter 2-4, it can be stated that more research on sediment transport and sediment deposition behaviour is needed in order to obtain a better understanding of suspended sediment dynamic and sediment deposition patterns over different vegetation zones and differently managed parts of the marsh (e.g. grazed/ungrazed/). Turbidity sensors (e.g. optical backscatter sensors) could help to achieve higher temporal resolution of suspended sediment concentrations compared to SSC bottles, therefore enabling for SSC measurements of initial flooding, during an inundation and of water running off the marshes (Fig. 5.8; Shao and Maa 2017; Hache et al. 2019). Recently, an autonomous working turbidity measurement network was installed at and around the marsh island Langeness (Hache et al. 2019; 2020; 2021). Following these examples, a combination of OBS sensors and sediment traps placed on ungrazed and grazed sites would lead to a high spatial and temporal resolution of measurements, which can help to better understand sediment deposition patterns on differently managed sites of the marsh. This approach, for example, could reveal how much of the sediment remains in suspension during an inundation and how much sediment is transported back to the creeks without being deposited on the marsh surface. The low sediment deposition rates on grazed sites of the marsh island Langeness (chapter 3) are probably caused by a quick drainage of the sites and a runoff of water and suspended sediment towards the creeks, thus preventing sediment deposition. On ungrazed sites, attenuation of hydrodynamics through vegetation and adherence of suspended sediment particles onto the vegetation surfaces probably leads to a quicker and thus higher sediment deposition. Furthermore, a potential prevention of resuspension of fine sediment by the dense vegetation on ungrazed sites could be recorded and proven with turbidity sensors. These techniques and measurements also can be used in order to better understand the effects of each plant species or composition of species on hydrodynamics, sediment transport and sediment deposition in salt marshes (Fagherazzi et al. 2020). Regarding

the direct trapping of sediments by salt marsh vegetation, I suggest to investigate the effects of plant traits and plant biophysical properties on sediment trapping systematically in flume and field studies. Flume studies on the direct sediment trapping of floodplain vegetation, for example, found that sedimentation can be driven by leaf area and leaf hair density (Kretz et al. 2020) or by biomass (Kretz et al. 2021a, b). Furthermore, it was found that single species largely differed in terms of their sediment trapping capacity (Kretz et al. 2021b).



Figure 5.8 Optical backscatter sensors placed in a mainland salt marsh close to creek in order to obtain data on suspended sediment concentrations.

Implications

The findings of chapter 2 provide first data on the variability of biophysical plant properties in Wadden Sea salt marshes which help to assess wave attenuation in this region in the future. Based on the findings of chapter 2, any experiments investigating plant-wave interaction and wave attenuation in the temperate zone need to consider especially the seasonal variability of

the biophysical plant properties in salt marshes in order to describe wave dissipation processes more realistically. If only “one point in time” measurements are possible, I suggest using degenerated vegetation with corresponding biophysical properties of vegetation in the winter or early spring state. As storm surges mostly occur outside the vegetation period from autumn to spring (van Loon-Steensma et al. 2016), information on wave attenuation in these seasons are highly valuable. When using plant mimics in a wave flume for physical models on wave attenuation from autumn to early spring, properties of the mimics should be based on degenerated vegetation (e.g. reduced stem stiffness, reduced biomass, reduced stem density and reduced vegetation height). Furthermore, the findings of chapter 2 showed that *Spartina* shows excellent properties related to wave attenuation such as a high overall stiffness accompanied by a relatively soft plant tissue or a high biomass. This assumption is supported by a recent study on the wave attenuation potential of different Wadden Sea plant species (Baaij et al. 2021). In this study, a *Spartina* vegetation type showed the strongest wave attenuation compared to a *Salicornia* type, *Atriplex* type and *Limonium* type.

The findings of chapter 3 clearly show that operations of storm surge measures (e.g. summer dike, stone revetment, tide gates) can lead to reduced sediment deposition and accretion rates on a marsh island in the Wadden Sea compared to Wadden Sea mainland marshes. Schindler et al. (2014) and more recently Hache et al. (2019; 2020; 2021) already discussed that the above-mentioned coastal protection structures lead to a decreased flooding frequency and therefore to limited sediment deposition rates. According to Hache et al. (2019; 2020), suspended sediment concentrations based on turbidity measurements on the tidal flats adjacent to the marsh island show sufficient concentrations, whereas concentrations on the marsh decreased distinctly showing that the transport of suspended sediments onto the marshes is hampered. Therefore, the considerations of adapting the coastal protection measures towards a more ecosystem-based coastal defence (Temmerman et al. 2013) seem to be reasonable, but in this context probably also depend on defence against marsh edge erosion. I strongly suggest to also take the influence

of grazing on sediment deposition into account when discussing measures with the aim of increasing flooding frequency or flooding duration. When sufficient sediment loads reach the island accompanied by an increased flooding frequency through e.g. a removed summer dike, grazing still can lead to relatively low accretion rates as long as the flooding duration is not increased. On grazed plots on Langeness, a relatively high SSC and low sediment deposition rate indicate that the floodwater including suspended sediments has drained off before sediment particles settled onto the marsh surface. A management of the tide gates as discussed in Hache et al. (2021) could help to increase the flooding duration (e.g. opening tide gates before the island is flooded and closing of tide gates when the island is flooded). If these measures are not feasible, an abandonment of grazing could help to increase sediment deposition. A partly abandonment of grazing with a grazed ring at the marsh edge around the island could be advantageous over a complete abandonment of grazing. Consequently, lesser sediment is filtered out by tall vegetation at the marsh edge allowing higher suspended sediment concentrations in the floodwater reaching inner parts of the island. On the inner parts, suspended sediment is more likely to be deposited on ungrazed parts compared to grazed parts. The vegetation height and biomass at the edges should be kept low either by grazing or by mowing. By increasing the flooding frequency and duration and by a partly abandonment of grazing, a further degradation of the marshland can be prevented. Furthermore, grazed parts adjacent to ungrazed parts of the marsh can increase species and habitat diversity (Wanner et al. 2014).

The more general implications for future research based on the findings of chapter 4, indicate that the spatial scale matters not only for biodiversity studies (Wanner et al. 2014) in the Wadden Sea, but also for studies on sediment deposition. More research is needed to understand the effect of salt marsh vegetation on sediment deposition and to determine the spatial scale beyond which this process comes into effect. Furthermore, more studies on the effects of single salt marsh species on flow reduction, sediment transport and sediment deposition, also considering the spatial scale, are needed (see also Fagherazzi et al. 2020).

To summarise, I can draw these key conclusions based on the studies presented in my thesis. Firstly, it was shown that biophysical properties of salt marsh plants are highly variable seasonally and spatially. These findings need to be considered in studies on wave attenuation by salt marshes (Chapter 2). Secondly, I found that livestock grazing can have a striking effect on sediment deposition in salt marshes via the reduction of aboveground biomass (Chapter 3). Managers and authorities can incorporate findings of chapter 2 and 3 in order to better assess the vulnerability of salt marshes on Wadden Sea marsh islands and in Wadden Sea mainland marshes. However, I also conclude that effects of salt marsh vegetation properties on sediment deposition are scale dependent (Chapter 4). The spatial scale beyond which an influence of salt marsh vegetation on sediment deposition comes into effect needs to be determined in further studies.

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Summary

Salt marshes are tidal ecosystems that form a transition area between the land and the sea. A central ecosystem service of the vegetation adapted to salt- and flooding-stress is the wave attenuation potential. By attenuating the waves, salt marsh vegetation significantly contributes to coastal protection. The extent of the wave attenuation depends on the biophysical properties of the salt marsh vegetation and generally correlates positively with the shoot density, the rigidity of the stems, the height of the vegetation, and the biomass. When calculating and investigating the wave attenuation over salt marshes with numerical models or physical laboratory models, the biophysical plant properties must be taken into account. To date, only a few studies have quantified the biophysical properties of salt marsh plants. The temporal and spatial variability has not been considered adequately and was not taken into account for all biophysical properties. Salt marsh vegetation also contributes substantially to sediment deposition and therefore to the vertical accretion of salt marshes. On the one hand, the vegetation-induced wave attenuation and reduction of flow velocity leads to faster gravity-induced deposition of suspended sediment particles from the water column onto the marsh surface. On the other hand, suspended sediments are deposited directly on plant surfaces. Livestock grazing leads to massive alterations of the vegetation such as a reduced biomass or vegetation height. Consequently, grazing has the potential to cause considerable changes in biophysical plant properties and thus in the vegetation's influence on sediment deposition. This thesis aims to improve the database and the understanding of the spatial and temporal variability of biophysical plant properties in Wadden Sea salt marshes. Furthermore, it aims to investigate and understand the influence of grazing and vegetation structure (short vs. high vegetation) on sediment deposition.

This thesis consists of five chapters. A general introduction (Chapter 1) is followed by three manuscripts (Chapters 2-4) and a synthesis (Chapter 5) discussing the overall context and links

between the manuscripts. Furthermore, this chapter derives concrete implications from the research results presented in the three manuscripts.

Chapter 2 deals with the seasonal and spatial variability of the biophysical properties of *Spartina anglica* (pioneer zone/low marsh) and *Elymus athericus* (high marsh) within a mainland marsh in Northern Frisia. A pronounced seasonal variability of the biophysical properties (e.g. biomass, stem density and stem flexibility) with significant intraspecific differences was found in this study. Compared to *Elymus athericus*, *Spartina anglica* showed a greater seasonal variability. Also, with regard to the spatial variability, *Spartina anglica* showed clear differences in biophysical properties between a seaward and a landward-located zone.

Chapter 3 investigates the influence of livestock grazing on sediment deposition and accretion on the marsh island Hallig Langeness in the Wadden Sea. The results show significantly reduced sediment deposition and accretion on grazed areas compared to adjacent non-grazed areas. This difference was more pronounced at the marsh edges adjacent to the mudflats compared to areas in the interior of the marsh island.

Chapter 4 presents the results of a study on the influence of small-scale vegetation patterns on the suspended sediment concentration and on the sediment deposition in a mainland salt marsh in Dithmarschen. Partial mowing of the vegetation resulted in a pattern of mown subplots and control subplots with a size of 4 m² in various combinations adjacent to a creek. Based on the results, it can be concluded that on the spatial scale of 4 m², there is no effect of the vegetation on the waves and water flow to be expected since the sediment deposition between mown and control subplots did not differ neither in the high nor in the low marsh. Furthermore, a mown or a control subplot next to the creek had no influence on the sediment deposition on a mown or control subplot behind.

Zusammenfassung

Salzmarschen sind tidebeeinflusste Ökosysteme, die einen Übergangsbereich zwischen Land und Meer bilden. Eine zentrale Ökosystemleistung der an Salzstress und Überflutungsstress angepassten Vegetation ist das Wellendämpfungspotential. Durch die Wellendämpfung trägt Salzmarschvegetation wesentlich zum Küstenschutz bei. Das Ausmaß der Wellendämpfung hängt dabei von den biophysikalischen Eigenschaften der Salzmarschvegetation ab und korreliert grundsätzlich positiv mit der Sprossdichte, der Starrheit der Halme, der Vegetationshöhe und der Biomasse. Beim Prognostizieren und Untersuchen der Wellendämpfung über Salzmarschen mit numerischen Modellen oder physikalischen Labormodellen müssen folglich die biophysikalischen Pflanzeigenschaften berücksichtigt werden. Bisher haben nur wenige Studien die biophysikalischen Eigenschaften von Salzmarschpflanzen quantifiziert. Die zeitliche und räumliche Variabilität wurde dabei bisher nicht ausreichend erfasst und nicht für alle biophysikalischen Eigenschaften berücksichtigt. Weiterhin trägt Salzmarschvegetation wesentlich zur Sedimentdeposition und somit zum vertikalen Wachstum der Salzmarsch bei. Einerseits werden durch die Vegetation Wellen gedämpft und Strömungsgeschwindigkeiten reduziert, wodurch die im Wasser gelösten Sedimente schneller absinken können. Andererseits werden im Wasser gelöste Sedimente direkt auf der Pflanzenoberfläche abgelagert. Die in Wattenmeer Salzmarschen häufig verbreitete Beweidung führt zu massiven Veränderungen der Vegetation wie beispielsweise verringerter Biomasse und Vegetationshöhe. Dadurch werden sowohl die biophysikalischen Pflanzeigenschaften verändert als auch der Einfluss der Vegetation auf die Sedimentdeposition. Diese Arbeit zielt darauf ab, die Datenlage und das Verständnis zu räumlicher und zeitlicher Variabilität von biophysikalischen Pflanzeigenschaften in Wattenmeer Salzmarschen zu verbessern und weiterhin den Einfluss von Beweidung bzw. Vegetationsstruktur (kurze vs. hohe Vegetation) auf die Sedimentdeposition zu erfassen und zu verstehen.

Die Arbeit setzt sich aus insgesamt fünf Kapiteln zusammen. Einer allgemeinen Einleitung (Kapitel 1) schließen sich im Hauptteil drei Manuskripte an (Kapitel 2-4), deren inhaltlicher Zusammenhang in einer Synthese (Kapitel 5) dargestellt wird. Weiterhin werden in diesem letzten Kapitel konkrete Implikationen aus den in den Manuskripten dargestellten Forschungsergebnissen abgeleitet.

Kapitel 2 befasst sich mit der saisonalen und räumlichen Variabilität der biophysikalischen Eigenschaften von *Spartina anglica* (Pionierzone/untere Marsch) und *Elymus athericus* (obere Marsch) innerhalb einer Festlandsalzmarsch in Nordfriesland. Es wurde gezeigt, dass vor allem eine ausgeprägte saisonale Variabilität der biophysikalischen Eigenschaften (z.B. Biomasse, Sprossdichte, Sprossflexibilität) mit signifikanten innerartlichen Unterschieden vorliegt. *Spartina anglica* zeigte im Vergleich zu *Elymus athericus* eine ausgeprägtere Variabilität. Auch bezüglich der räumlichen Variabilität zeigte vor allem *Spartina anglica* deutliche Unterschiede in den biophysikalischen Eigenschaften zwischen einer seewärts und landwärts gelegenen Zone.

Kapitel 3 untersucht den Einfluss von Beweidung auf die Sedimentdeposition und Akkretion auf der Marschinsel Hallig Langeness im Wattenmeer. Die Ergebnisse zeigen eine deutlich verringerte Sedimentdeposition und Akkretion auf beweideten Flächen im Vergleich zu angrenzenden unbeweideten Flächen. Dieser Unterschied zeigte sich deutlicher an den an Wattflächen angrenzenden Marschflächen im Vergleich zu weiter im Inselinneren gelegenen Marschflächen.

Kapitel 4 stellt die Ergebnisse einer Studie zum Einfluss kleinräumlicher Vegetationsmuster auf die im Wasser gelöste Sedimentfracht und auf die Sedimentdeposition in einer Festlandsalzmarsch in Dithmarschen dar. Durch ein teilweises Abmähen der Vegetation entstand ein Muster aus aneinandergrenzenden gemähten und ungemähten Subplots einer Größe von 4 m² in verschiedenen Kombinationen neben einem Priel. Die Ergebnisse lassen den

Schluss zu, dass auf dieser räumlichen Skala von 4 m² noch kein signifikanter Effekt der Vegetation auf die Reduzierung der Strömung oder auf die Dämpfung der Wellen zu erwarten ist, da sich die Sedimentdeposition zwischen gemähten und ungemähten Subplots weder in der oberen noch in der unteren Marsch unterschied. Weiterhin hatten sowohl am Priel liegende gemähte als auch ungemähte Subplots hinsichtlich der Sedimentdeposition keinen Einfluss auf dahinterliegende Subplots mit gemähter oder ungemähter Vegetation.

Author contributions

Chapter 1 D. Schulze wrote this chapter.

Chapter 2 D. Schulze and F. Rupprecht designed the field study. D. Schulze set up the field study, conducted the field work and the lab work, analysed the data and wrote the initial manuscript. F. Rupprecht, S. Nolte and K. Jensen contributed to the manuscript by commenting and editing the manuscript.

Chapter 3 D. Schulze, S. Nolte and K. Jensen designed the field study. D. Schulze set up the field study, conducted the field work and the lab work, analysed the data and wrote the initial manuscript. S. Nolte and K. Jensen contributed to the manuscript by commenting and editing the manuscript.

Chapter 4 S. Nolte and K. Jensen designed the field study. D. Schulze analysed the data and wrote the initial manuscript. S. Nolte and K. Jensen contributed to the manuscript by commenting and editing the manuscript.

Chapter 5 D. Schulze wrote this chapter.

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Information on published chapters

Chapter 2

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

Published in: **Aquatic Sciences**

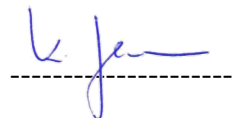
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Signature

Prof. Dr. Kai Jensen (first advisor)

Chapter 3

Livestock grazing reduces sediment deposition and accretion rates on a highly anthropogenically altered marsh island in the Wadden Sea

Published in: **Estuarine, Coastal and Shelf Science**

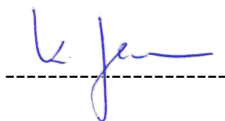
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Prof. Dr. Kai Jensen (first advisor)

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den 20.01.2022

Unterschrift (D.Schulze)

D. Schulze