Vegetation succession
and coastal protection by wave dissipation
in salt marshes of North-West Europe

Dissertation

zur Erlangung der Würde des Doktors der Naturwissenschaften
des Fachbereichs Biologie der Fakultät für Mathematik, Informatik und
Naturwissenschaften der Universität Hamburg

vorgelegt von
Franziska Rupprecht

aus Nürnberg

Hamburg 2015

Erstgutachter: Prof. Dr. Kai Jensen

Zweitgutachterin: Dr. Iris Möller

Tag der Disputation: 25.09.2015

This thesis is based on three papers and one unpublished manuscript:

1) Rupprecht, F., Wanner, A., Stock, M. & Jensen, K. 2015. Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage. *Applied Vegetation Science* 18:86–98.

2) Rupprecht, F., Möller, I., Evans, B., Spencer, T. & Jensen, K. 2015. Biophysical properties of salt marsh canopies – Quantifying plant stem flexibility and above ground biomass. *Coastal Engineering* 100:48–57.

3) Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience* 7:727–731.

4) Rupprecht, F., Möller, I., Paul, M., Kudella, M., Jensen, K., Bouma, T. J., Van Wesenbeeck, B. K., Wolters, G., Spencer, T., Miranda-Lange, M. & Schimmels, S. (Manuscript). Vegetation-wave interactions in salt marshes under storm surge conditions.

The three papers were reprinted with kind permission of John Wiley & Sons (paper 1), Elsevier (paper 2) and Macmillan Publishers (paper 3).

For consistency throughout this thesis, the figures and tables of all manuscripts were renumbered and all references were summarised at the end of the thesis.

Contents

1

General Introduction

Franziska Rupprecht

Salt marshes

Salt marshes are intertidal ecosystems that form at shallow tidal coasts under conditions of low water currents and continuous sedimentation and are characterised by a low species diversity and a high primary productivity (Adam 1993). To match the coastal environments they inhabit, salt marshes are highly dynamic ecosystems with periods of areal extension and contraction. These dynamics in salt marsh formation and erosion stability are thought to result both from bio-geomorphic feedback processes between plant growth, water flow and sediment transport (Van de Koppel et al. 2005; Bouma et al. 2013) but can also be affected by anthropogenic impact (Pringle 1995) and global change (IPCC 2007).

As intertidal ecosystems, salt marshes are subject to frequent flooding with saline water and mechanical stresses due to currents, wave action and ice scour. Salt marshes constitute precious and irreplaceable habitat for a wide range of plant and animal species adapted to these stresses. Additionally coastal marshes are essential breeding, foraging and resting habitat for a large number of bird species (Zedler and Kercher 2005).

Globally salt marshes are estimated to cover between 22,000 and 400,000 km^2 (McLeod etal. 2011). In Europe salt marshes cover at least 2,300 km^2. Dijkema (1987) proposed a classification of European coastal marshes based on the origin of the marsh substrate, geological development and marsh geomorphology. According to this classification the majority of European salt marshes belong to the group of 'foreland' salt marshes with minerogenic, allochthonous substrate (i.e. substrate deposited by marine or fluvial transport) which developed in front of seawalls along the mainland coast in locations where sheltered conditions allowed the deposition of clay-rich sediments. Often European 'foreland salt marshes' (hereafter referred to as mainland salt marshes) were developed artificially by the help of man-made sedimentation fields and drainage structures (Dijkema 1987).

The vegetation composition and tidal regime of salt marshes along the European coast differs between the North Atlantic, the South Atlantic, the Mediterranean and the Baltic and Boreal regions (Adam 1993). Salt marshes in North-West Europe can be considered to belong to the North Atlantic region. They are mostly exposed to large tidal amplitudes with a tidal range >2 m (meso- to macro-tidal regime), have fewer plant species than e.g. South Atlantic or Mediterranean marshes and a vegetation structure influenced by vegetation die-off during the winter season (Adam 1993).

Vegetation zonation and succession in salt marshes

The vegetation composition of salt marshes is determined both by abiotic factors such as elevation, salinity, flooding, and nutrient availability (Mitsch and Gosselink 2008) as well as biotic processes such as competition (Pennings and Callaway 1992) and facilitation (Hacker and Bertness 1995) among plants and herbivorous grazers (Silliman and Bertness 2002; Silliman et al. 2005).

Salt marsh plant communities often show striking zonation patterns that are strongly related to gradients in elevation (Olff et al. 1997). The daily flooded pioneer zone extends down to 40 cm below MHT, and is followed at its landward end by the low marsh (100–400 inundations a year) and the high marsh (less than 100 inundations a year) (Bakker 2005). In salt marshes of North-West Europe, typical species occurring in the pioneer zone are *Salicornia europaea* and *Spartina anglica*. Plant communities of the low marsh are frequently characterized by *Puccinellia maritima*, *Atriplex portulacoides*, *Aster tripolium* and *Suaeda maritima*, the high marsh is often dominated by *Elymus athericus*, *Festuca rubra, Agrostis stolonifera*, *Atriplex prostrata* and *Phragmites australis* (Adam 1993).

Following the natural dynamic of salt marshes, salt marsh vegetation is subject to succession. Succession starts with species from the pioneer zone that colonise bare tidal flats and stabilise the substrate. The presence of plants promotes sediment deposition and accretion, leading to increased surface elevation and soil aeration that enable the establishment of low marsh species. Finally, late-successional species, characterising the high marsh plant communities, can establish.

Vegetation succession in salt marshes is governed by inundation frequency, sediment deposition, soil aeration, nutrient status and salinity, all factors being directly related to elevation (Adam 1993), as well as by competitive interactions between plant species (Pennings and Callaway 1992; Bockelmann and Neuhaus 1999; Bockelmann et al. 2002). The pace of salt marsh succession depends on drainage conditions and sedimentation rates in relation to inundation frequency and sea level rise (Leendertse et al. 1997; Olff et al. 1997; Schröder et al. 2002). Progressive succession from early- to late-successional plant species or vegetation types is favoured by high sedimentation rates and low inundation frequencies, while water logging and high inundation frequencies lead to retardation of succession or retrogressive succession from late- to early-successional plant species (Rupprecht et al. 2015a).

Ecosystem services of salt marshes

Ecosystem services represent the benefits that human populations derive from the interactions between ecosystem structure and processes and can be classified into provisioning, regulating, cultural and amenity services as well as supporting services (MEA 2005). Salt marshes contribute to human well-being in many ways:

They provide food, shelter and nursery areas for numerous species (Zedler and Kercher 2005) (provisioning services), play an important role in mitigating effects of climate change by sequestering enormous amounts of carbon (McLeod et al. 2011) and contribute to coastal protection as a buffer zone between land and see (Möller et al. 1999; Duarte et al. 2013) (regulating services). Tourism and recreation represent cultural and amenity services and primary production and nutrient cycling important supporting services provided by salt marshes (MEA 2005).

In an attempt to estimate the value of the world’s ecosystem services, coastal ecosystems such as salt marshes have been ranked among the most valuable ecosystems on Earth (Costanza et al. 1998). The valuing of ecosystem services is increasingly recognised as a decision-making strategy in case of conflicting interests in ecosystem use. Nature conservation uses the concept of ecosystem services in order to justify the maintenance of natural ecosystems in healthy, productive and resilient conditions (Costanza et al. 1998; Barbier et al. 2008; Barbier et al. 2011). Especially management decisions in densely populated coastal areas are often concerned with how much natural habitat to preserve and how much to allocate to human development activities (Barbier et al. 2008). Yet assessing the actual value of coastal ecosystems and the services they provide remains challenging, as the ecological functions underlying ecosystem are often non-linear and highly variable through space and time (Barbier et al. 2008; Koch et al. 2009; Gedan et al. 2011). For instance the wave attenuation function of salt marshes is nonlinearly and negatively correlated with traverse distance from the sea ward marsh edge (Gedan et al. 2011), which implies that even small salt marsh areas can considerably contribute to coastal protection. A thorough investigation and understanding of the interrelationship of ecosystem structure, function, and economic value is hence critical to coastal management decisions and may allow to reconcile contrasting interests of ecosystem use (Barbier et al. 2008).

Environmental threats to salt marshes

As coastal ecosystems, salt marshes are among the most heavily used and threatened natural systems on earth (Lotze et al. 2006; Kirwan and Megonigal 2013). The global loss rate for salt marshes is estimated at a minimum of 1–2% yr^{-1} and equals that of mangroves (1–3% yr^{-1}), while being about half the loss rate of seagrass meadows (2–5% yr^{-1}) (Duarte et al. 2008).

Sea level rise is one of the main future threats to low lying coastal areas (IPCC 2007). To survive sea level rise, salt marshes must build soil elevation by the help of positive bio-geomorphic feedbacks between plant growth and sediment accretion at a rate equal to or faster than the rate of sea level rise. Recent findings on the stability of coastal wetlands under sea level rise suggest that marshes can survive increasing rates of sea level rise by the help of the increasing flooding frequencies which allows them to build elevation by mineral and organic matter at progressively faster rates until flooding surpasses a critical level, vegetation dies-off and stabilising bio-geomorphic feedbacks are lost (Morris et al. 2002; Kirwan et al. 2010; Kirwan and Megonigal 2013). As the organic contribution to elevation gain decreases with the rate of sea level rise, the threshold rate of sea level rise beyond which marshes will drown is thought to be a function of sediment availability (Kirwan and Megonigal 2013). This makes the rate of sea level rise beyond which marshes tend to drown highly site-specific and heavily influenced by human impact.

Humans alter sediment delivery to coastal areas by the construction of river dams and reservoirs in many parts of the world. The most rapid loss of salt marshes has been reported for sediment-deficient areas such as the Gulf of Mexico, Chesapeake Bay or the Venice Lagoon (Kirwan and Megonigal 2013). Salt marshes of North-West Europe are less threatened by sea level rise. For instance in salt marshes of the Wadden Sea coast, accretion rates range from 11–16 mm yr^{-1} in the Netherlands, 6–26 mm yr^{-1} in Schleswig-Holstein, northern Germany and 10 mm yr^{-1} in Denmark (Dittmann and Wilhelmsen 2004; Suchrow et al. 2012; Nolte et al. 2013) are expected to compensate for sea level rise (4.4–8.8 mm yr^{-1} until 2100) (Gönnert et al. 2010) in the forthcoming decades.

Apart from sea level rise and restricted sediment supply, elevated atmospheric CO_2 concentrations, increased temperature and eutrophication represent further indirect human impacts that may affect salt marsh stability. While in marshes dominated by C_3-plants elevated CO_2 may result in enhanced production of above and below ground biomass and thus positively affect salt marsh stability, in marshes dominated by C_4-plants it is likely to have no effect on marsh stability. Like elevated CO_2 in C_3-dominated systems, rising temperatures are thought to cause an increase of marsh productivity and stability (Kirwan and Megonigal 2013). In the long-term, however, rising temperatures may induce a shift in plant species composition of salt marshes (Gedan et al. 2011) leading to more complex responses of salt marshes to warming (Kirwan and Megonigal 2013). Similar to elevated CO_2, eutrophication of salt marshes may induce a shift in vegetation composition following an alteration of competitive hierarchies of salt marsh plants (Levine et al. 1998). Since most salt marsh plants are nitrogen (N) limited under natural conditions, anthropogenically elevated N levels favour highly competitive species with high above ground biomass production such as *E. athericus* and *P. australis* and enable them to outcompete smaller plants in competition for light. In sediment-rich systems, the higher rates of plant growth are likely to enhance elevation while in low-sediment environments and peat forming marshes both elevation gain and loss have been observed in response to N and phosphorus (P) enrichment (Kirwan and Megonigal 2013).

Apart from the above mentioned physical stresses, direct human modification such as shoreline development and embankment of salt marshes for agricultural and industrial uses (land claim) is considered to be the major cause of both historical and contemporary salt marsh loss. In Europe and the United States the importance of salt marshes has been increasingly recognised over the past decades by the public and governments resulting in a decreasing rate of salt marsh loss (Gedan et al. 2009; Kirwan and Megonigal 2013).

In China by contrast reclamation of salt marshes has been accelerating due to rapid urbanisation and economic development. Between 2000 and 2010 the reclamation rate has increased from 24,000 ha yr^{-1} to 40,000 ha yr^{-1} and is expected to further increase to 60,000 ha yr^{-1} during 2010–2020. The massive coastal reclamation has severely reduced biodiversity and associated ecosystem services and many coastal wetlands converted from sinks to sources of pollutants (Ma et al. 2014). This development is unlikely to slow-down unless effective measures against the deterioration of coastal wetlands are taken such as strict and clear legislation binding to both the central government and local government agencies and the establishment of mechanisms to charge government authorities for ecological losses (Ma et al. 2014).

Besides embankment as a cause for salt marsh loss, hydrological alterations in salt marshes such as ditching for soil drainage and mosquito control can affect marsh stability. In many man-made salt marshes of North-West Europe, artificial drainage structures persist even decades after their abandonment. The well drained conditions have been related to shifts in vegetation cover (e.g. expansion of high marsh species such as *E. athericus* or *P. australis*) that may alter marsh stability by changing the morphological plant traits involved in bio-geomorphic feedbacks. In North-American coastal regions near Orleans and Louisiana but also in the Venice Lagoon (Italy) subsidence caused by artificial drainage and ground water extraction threatens the existence of salt marshes (Törnqvist et al. 2008).

Another reason for salt marsh loss are engineering structures built as a measure for land claim and coastal defence, such as seawalls. Because salt marshes lie between seawalls and the sea, they contribute to salt marsh loss through 'coastal squeeze', in which erosion removes salt marsh area at its seaward margin and the seawalls prevent offset of these areal losses by landward migration of salt marshes (Kirwan and Megonigal 2013).

Salt marsh management in the Wadden Sea

History of human alterations to the coastline

The Wadden Sea – Europes's largest intertidal ecosystem complex – includes around 400 km^2 (20%) of the European salt marshes and extends along the shallow tidal coast of the North Sea from Esbjerg (Denmark) to Den Helder (Dijkema and Heydemann 1984). From a geological point of view, the Wadden Sea is a comparably young system since it formed during and after the last two ice ages (Ahrendt 2006). Human settlement in the salt marshes of the Wadden Sea is first known from the Early Iron Age (8th–5th century BC; Bazelmans et al. 2012), but it was not until the 11th century AD that people started the construction of seawalls to protect settlements, and agricultural areas. In the following centuries, the increasing land use pressure like cutting of peat and drainage of agricultural land resulted in a marked reduction of water storage capacity of the coastal landscape and land subsidence (Bantelmann 1960). Along the coast of Northern Frisia two devastating storm surges (Marcellus strom surge in 1362 'Grote Mandränke' and Burchardy strom surge in 1634 'zweite Grote Mandränke') led to the loss of around 1300 km^2 marsh land and changed the coastline in a way that the western Geest edge became the new coastline (Behre 2002). In the following centuries, people started to reclaim the lost land. To enhance vertical growth of tidal flats, sedimentation fields (regularly shaped, artificial low-energy environments surrounded by groynes made from brushwood or stones) were constructed in front of the seawall (Hofstede 2003). In addition dredging of furrows was used to drain the sediments and promote the establishment of pioneer plant species (Hofstede 2003). Once a salt marsh had developed, a new seawall was constructed. After some years of desalination, the newly embanked area could be used as farm land.

Salt marsh management and vegetation succession in the Wadden Sea mainland salt marshes

Today mainland salt marshes, which have been artificially developed with the help of the accretion enhancement techniques described above, encompass around 60% of the Wadden Sea salt marshes (Esselink et al. 2009) and can be considered as representative for many salt marshes in North-West Europe. The Wadden Sea mainland salt marshes have traditionally been used as grazing ground for domestic livestock such as sheep or cattle since more than 2600 years (Esselink 2000) with a strong intensification from the early 19th century onwards. The palatability of salt marsh plants to grazers, as well as tolerance to grazing-induced biomass losses, soil compaction and water logging, decreases from early- to late successional stages (Summers et al. 1993; Kiehl et al. 1996; Levine et al. 1998). Consequently, intensive sheep grazing (>10 sheep per ha) resulted in a retardation of succession. Low and high marsh were dominated by a short turf of palatable grass species like *P. maritima* and *F. rubra*. From the early 1990s onwards, grazing was reduced and the artificial drainage system was abandoned in many of the Wadden Sea mainland salt marshes due to the establishment of national parks and nature reserves aiming at re-introducing natural dynamics in the ecosystem. To assess trends in the development of the Wadden Sea ecosystem, including salt marshes, across the whole Wadden Sea region, the Trilateral Monitoring and Assessment Program (TMAP; Bakker et al. 1997) was established by the three Wadden Sea countries (Denmark, Germany and The Netherlands).

Initially the change in salt marsh management led to an increase in plant species richness and structural diversity of salt marshes (Kiehl et al. 1996; Schröder et al. 2002). Studies over longer time periods (≥10 yrs) suggested an increase of progressive succession towards plant species sensitive to grazing and water logging, such as the dwarf shrub *A. portulacoides* (low marsh) and the tall grass *E. athericus* (high marsh; Kiehl et al. 1996; Bos et al. 2002; Schröder et al. 2002; Bakker et al. 2003; Esselink et al. 2009) in many of the Wadden Sea mainland salt marshes.

The spread and formation of large monospecific stands of grazing-sensitve species such as *E. athericus* resulted in a scientific debate on the advantages and disadvantages of grazing in the Wadden Sea salt marshes with respect to species diversity (Esselink et al. 2002; Bakker et al. 2003; Wanner et al. 2014). In Denmark and the Netherlands, where maintenance of a high biodiversity is a primary management objective for salt marshes, grazing has been reintroduced as a management tool. The majority of mainland salt marshes within the German Wadden Sea National Parks of Schleswig-Holstein, Hamburg and Lower Saxony however remained abandoned to allow for the undisturbed course of natural processes, which is the major aim of National Parks in Germany according to legislation regulations.

Some authors hypothesised that a local-scale increase of progressive succession after abandonment of grazing and drainage in salt marshes could be compensated at the landscape-scale by the occurrence of retrogressive succession in lowlying parts of abandoned salt marshes, following increased waterlogging and a decline in soil aeration (Stock and Kiehl 2000; Esselink et al. 2002). Moreover environmental gradients such as an increase of inundation frequency and salinity from the central to the northern Wadden Sea region (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer und Umweltbundesamt 1998; Kappenberg and Fanger 2007) are supposed to cause differences in the course of succession at different locations (Crain et al. 2008). However, following the lack of large scale (>100 km spatial extent) and long-term studies, main trends in vegetation succession at the landscape-scale remained unclear.

In this thesis large-scale and long-term trends of vegetation succession after abandonment of grazing and artificial drainage were investigated in mainland salt marshes of the Wadden Sea National Park of Schleswig-Holstein, Germany, that encompasses around 45% of the Wadden Sea mainland salt marshes (chapter 2; Wanner et al. 2014).

Apart from plant species composition, the course of vegetation succession in salt marshes affects primary productivity as well as biophysical properties of the vegetation canopy such as density, height and flexibility. In this way succession influences many ecosystem processes and functions such as e.g. carbon storage, silica delivery and coastal protection by wave dissipation (Valéry et al. 2004; Möller 2006; Müller et al. 2013). Canopy density, canopy height and plant flexibility are a key controls in the coastal protection service provided by salt marshes through dissipation of wave energy and shoreline stabilisation (Möller 2006; Gedan et al. 2011). As these biophysical characteristics of salt marsh canopies are likely to vary between plant species belonging to different successional stages (Möller 2006; Feagin et al. 2011) an improved understanding of vegetation succession is critical in assessing and predicting the contribution of salt marshes to coastal protection.

Coastal protection by salt marshes

The ongoing increase of population densities and resource requirements in coastal areas (Seto 2011) alongside physical pressure imposed on coastal margins by sea level rise and increased storminess (Donat et al. 2011; Young et al. 2011), calls for an improvement of coastal defence at many of the world’s coastlines. Salt marshes can contribute significantly to the reduction of wave height and energy (wave dissipation), the stabilisation of shorelines and the reduction of flood surge propagation and hence act as a valuable natural component in coastal defence schemes (Borsje et al. 2010; Gedan et al. 2011; Arkema et al. 2013; Temmerman et al. 2013). Hence in areas where seawalls are fronted by salt marshes, this may allow for a reduction in e.g. seawall height which would considerably reduce the cost of building (King and Lester 1995; Möller et al. 2001).

Despite that the sea-defence value of salt marshes is increasingly recognised, the actual incorporation of salt marshes into quantitative flood or erosion risk assessments and coastal protection schemes remains challenging. One important caveat in building intertidal ecosystems such as salt marshes into coastal protection schemes is the limited understanding and predictive ability of their long-term persistence (Bouma et al. 2014). The long-term persistence of salt marshes depends on both inherent ecosystem dynamics such as positive feedbacks between sediment accretion and plant growth (Van de Koppel et al. 2005) and the ecosystem response to disturbance caused by changes in the environmental setting e.g. sea level rise or enhanced storminess or changes in salt marsh management (Bouma et al. 2014). Assessing the sensitivity of salt marshes to disturbance regimes is highly complicated as salt marshes (and many other coastal ecosystems) exhibit 'alternative stable state behavior'. This means that the ecosystem can exist in different stable states (e.g. different degrees of vegetation cover) under the same environmental conditions and responds to disturbance in a non-linear way. Once a critical disturbance threshold is surpassed, this can lead to a collapse of the ecosystem (Scheffer et al. 2001; Van de Koppel et al. 2005; Van Wesenbeeck et al. 2008).

Process based studies describing mechanisms involved in passing such thresholds and identifying reliable indicators to predict salt marsh stability and the risk of collapse, are still a matter of research. Hence, as best practice to judge salt marsh stability, it has been suggested to rely on currently available knowledge on the dynamics of salt marsh ecosystems and to allocate sufficient space to coastal ecosystems, to account for natural dynamics while maintaining the minimal area needed for coastal defence (Bouma et al. 2014).

Another important knowledge gap hampering application of salt marshes in coastal protection is the lack of empirical evidence for their capacity to act as wave dissipaters under extreme water level and wave conditions i.e. when most disturbance occurs and their coastal protection service is most required (Feagin et al. 2010; Gedan et al. 2011; Shepard et al. 2011). Moreover a quantitative understanding of their ability to survive those types of conditions is required (Fagherazzi et al. 2013; Mariotti and Fagherazzi 2013; Bouma et al. 2014).

Wave dissipation over vegetated salt marsh surfaces

Most plant species in intertidal areas are able to act as ecosystem engineers i.e. to reduce physical stress levels by modifying their environment through the interaction of their shoots with hydrodynamics (Jones et al. 1994; Peralta et al. 2008). The vegetation of salt marshes contributes to wave dissipation and shoreline stabilisation directly, via plant-flow interactions and stabilisation of the soil substrate, and indirectly, through causing spatially varying sediment accretion and thus the formation of topographic roughness (Gedan et al. 2011; Duarte et al. 2013; Möller et al. 2014). Many studies have reported that wave dissipation across vegetated salt marsh surfaces is significantly higher than over unvegetated sand or mudflats which underlines the important role of vegetation-wave interactions in the wave dissipation capacity of salt marshes, as opposed to the effect of the topographic roughness of intertidal surfaces alone (Gedan et al. 2011). When waves advance over a vegetated marsh surface, vegetation interacts with the flow by forming an obstruction and hence provides flow resistance. In return plants experience a drag force (corresponding to the amount of flow resistance) and re-orientation by wave forces (Mullarney and Henderson 2010). The flow resistance provided by plants reduces wave orbital velocities and associated turbulence resulting in a reduction of wave height and energy.

Wave dissipation by vegetation is a highly variable and complex process. It is a function of both biophysical vegetation characteristics such as plant flexibility, buoyancy, density, height of the canopy and of hydrodynamic conditions, such as water depth and incident wave energy (Anderson et al. 2011). In addition local-scale topography (e.g. cliff versus ramped transitions between salt marsh and adjacent tidal flats) determine the degree to which wave energy is dissipated across salt marsh surfaces (Möller and Spencer 2002). With respect to the effect of plant properties, plant flexibility has been identified as a key control of vegetation-wave interactions and vegetation-induced flow and wave dissipation, as it determines how much and in what way plants move under wave orbital flow, i.e. the amount of flow resistance they provide (Mullarney and Henderson 2010; Paul et al. 2012). Plant flexibility plays also an important role in susceptibility of folding and breakage and hence in the physical damage occurring to vegetation under wave forcing (Bouma et al. 2005). However, field studies providing quantitative data on the flexibility of salt marsh plants are still very scarce and limited to only a few species (Feagin et al. 2011). The density an height of salt marsh canopies represent further important controls of flow resistance provided by vegetation and the wave dissipation capacity of salt marshes (Bouma et al. 2005; Möller 2006). Above ground biomass varies with volume and density of plant material present and can be regarded as a useful proxy for such more complex structural canopy bulk properties, if not necessarily for flexibility and buoyancy. At the scale of plant stands, a positive correlation between canopy density, above ground biomass and wave dissipation has been observed (Koch and Gust 1999; Bouma et al. 2005; Möller 2006).

For waves passing over a flooded marsh surface, the amount of orbital water motion being affected by the submerged canopy decreases with increasing water depth and with decreasing incident wave energy (i.e. decreasing wave heights and wave periods). Consequently, it seems reasonable that hydrodynamic conditions may exist beyond which marshes lose their wave dissipating effect. Under deep submergence or very low wave energy, orbital wave motion may no longer reach the canopy and hence vegetation is likely to have a minor effect on wave dissipation. Under shallow water depths or extreme incident wave energy, high forces imparted by the flow could damage the vegetation canopy and the marsh surface and in this way reduce the wave dissipation capacity of the marsh.

The hydrodynamic conditions controlling transitions from regimes of energy reduction (due to flow obstruction by vegetation) to regimes of energy transmission (through either vegetation ‘overtopping’ or vegetation flexing and breakage), however, have not yet been identified for various reasons: (i) Following the unpredictable nature and high temporal variability of wave conditions, a detailed and systematic study of plant behavior over a wide range of wave conditions in the field is challenging (Anderson and Smith 2014). (ii) Laboratory flume studies under controlled wave conditions are often performed in relatively small and narrow flumes and deal with scaling problems and edge effects, which hinders the applicability of results to situations encountered in the field (Fonseca and Cahalan 1992; Mendez and Losada 2004). Furthermore, flume studies often use simplified plant surrogates. The high complexity and variability of real salt marsh canopies in biophysical properties and a lack of quantitative data on this, make it questionable, whether plant surrogates can realistically represent the behaviour of salt marsh canopies under wave forcing. (iii) In the absence of suitably representative field or flume calibration data, numerical models of wave dissipation suffer from the difficulty of realistically representing vegetation as well as its effect on orbital flow (Wolters et al. under review).

The goal of successfully incorporating salt marshes into coastal protection schemes requires a full exploration and understanding of their wave dissipation capacity. The quantification of biophysical characteristics of salt marsh canopies with application to wave dissipation and the evaluation of methodologies to do so (see chapter 3 of this thesis) are important steps to achieve this goal. An enhanced database on biophysical plant properties will allow for the production and use of more realistic plant mimics in flume studies and can contribute to a more accurate representation of vegetation-induced flow resistance in numerical models of wave dissipation.

Moreover, obtaining fundamental knowledge on the wave dissipation process over vegetation under controlled conditions, in a scale-appropriate setting is critical. A unique flume experiment conducted by Möller et al. (2014) in one of the world’s largest wave flumes allowed for the first time a detailed study of vegetation-induced flow and wave dissipation in real salt marsh plant canopies (i.e. field-excavated salt marsh vegetation) under average up to extreme levels of wave energy and near-field-scale conditions. Insights into the wave dissipation capacity and erosion stability of salt marshes under extreme storm surge conditions as well as into the ability of vegetation to reduce wave orbital flow and physical damage occurring to the vegetation canopy under rising wave forces, are reported in chapter 4 and chapter 5 of this thesis.

Objective and chapter outline

The overall aims of this thesis were (1) to analyse large-scale and long-term patterns in vegetation succession after abandonment of grazing and drainage in mainland salt marshes of the Wadden Sea and to identify the major environmental drivers, (2) to quantify biophysical vegetation characteristics with application to wave dissipation in canopies of four plant species typically occurring in salt marshes of the Wadden Sea and North-West Europe, (3) to measure wave dissipation, erosion stability of the marsh surface and physical damage occurring to the vegetation canopy in these salt marshes under average up to storm surge wave conditions, and (4) to analyse the effect of vegetation on wave orbital flow and susceptibility of plants to breakage under rising wave forces in canopies of two salt marsh plant with different flexibility and height.

Chapter 2: Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage

Main successional pathways of vegetation characterized by *Puccinellia maritima* and *Festuca rubra*, two grasses that dominate low and high marsh areas under intensive grazing, were analysed, using vegetation monitoring data covering around half of the Wadden Sea mainland salt marshes over a 18 year time period (1988–2006). Drivers of succession were identified with classification tree models, a non- parametric vegetation modeling technique.

The study had three key aims:

(i) to analyse long-term and large-scale trends of vegetation succession in low and high marsh since the abandonment of grazing and drainage in many mainland salt marshes
(ii) to identify the major drivers of main successional pathways
(iii) investigate whether the pace of succession varies along large-scale environmental gradients

Rupprecht, F., Wanner, A., Stock, M. & Jensen, K. 2015. Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage. *Applied Vegetation Science* 18:86–98.

Chapter 3: Biophysical properties of salt marsh canopies – Quantifying plant stem flexibility and above ground biomass

Two key biophysical properties of salt marsh canopies with application to wave dissipation were considered, above ground biomass and plant flexibility. Furthermore, we evaluated two methodologies to assess above ground biomass as a proxy for more complex canopy bulk properties such as canopy structure and density: Side-on photography of vegetation (photo-method) and the measurement of light availability in the canopy.

The study had two key aims:

(i) to quantify stem flexibility as well as stem diameter and stem length of *Spartina anglica*, *Puccinellia maritima* and *Elymus athericus,* three grasses that form large stands in many salt marshes of North-West Europe
(ii) to compare the performance of the photo-method with measurements of light availability for non-destructive assessment of above ground biomass in canopies of two salt marsh species with different canopy structure: *Atriplex portulacoides*, a dense low growing dwarf shrub and *Elymus athericus*, a tall upright growing grass

Rupprecht, F., Möller, I., Evans, B., Spencer, T. & Jensen, K. 2015. Biophysical properties of salt marsh canopies – Quantifying plant stem flexibility and above ground biomass. *Coastal Engineering* 100:48–57.

Chapter 4: Wave attenuation over coastal salt marshes under storm surge conditions

Wave dissipation by salt marshes and the erosion stability of the marsh surface was experimentally assessed under average up to extreme hydrodynamic conditions in a 300-metre-long wave flume tank that contained a transplanted section of natural salt marsh, excavated from the Wadden Sea.

The study had three key aims:

(i) to explore the dissipation of waves over a vegetated marsh canopy under storm conditions
(ii) to quantify the effect of vegetation on wave attenuation compared with the effects of a mowed platform
(iii) to quantify the response of marsh vegetation and soil surface to incident wave energy

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience* 7:727–731.

Chapter 5: Vegetation-wave interactions in salt marshes under storm surge conditions

Canopy movement, wave orbital velocity and physical damage occurring to vegetation under rising wave forces were studied in the framework of the large-scale flume experiment described in chapter 4, within the canopy of *Puccinellia maritima*, low-growing grass, flexible grass and *Elymus athericus*, a tall grass with relative stems, in comparison to *Puccinellia maritima*.

The study had two key aims:

(i) to analyse how different vegetation (flexible and low-growing vs stiff and tall) affects wave orbital flow under low, medium and high levels of wave energy
(ii) to analyse whether physical damage occurring to vegetation differs between flexible, low-growing and tall, stiff canopies and if so – under which level of wave energy differences in plant susceptibility to folding and breakage become apparent

Rupprecht, F., Möller, I., Paul, M., Kudella, M., Jensen, K., Bouma, T. J., Van Wesenbeeck, B. K., Wolters, G., Spencer, T., Miranda-Lange, M. & Schimmels, S. (Manuscript). Vegetation-wave interactions in salt marshes under storm surge conditions.

2

Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage

Franziska Rupprecht, Antonia Wanner, Martin Stock and Kai Jensen

Applied Vegetation Science 18 (2015) 86–98

Abstract

Questions: In the early 1990s, grazing and drainage have been abandoned in many artificially created mainland salt marshes of the Wadden Sea to increase their natural character and heterogeneity of vegetation composition. We asked: How did vegetation succession in low and high marsh respond to this change in management from a large-scale and long-term perspective and what were the major drivers of successional change?

Location: Wadden Sea coast, Schleswig-Holstein, Germany

Methods: We used vegetation data from the Trilateral Monitoring and Assessment Program (TMAP) for around half of the Wadden Sea mainland salt marshes to identify main successional pathways of the TMAP vegetation types *Puccinellia maritima* and *Festuca rubra*, dominating low and high marsh areas, respectively, prior to the change in management. Drivers of succession were analysed using Classification and Regression Tree Models (CART), a non-parametric vegetation modeling technique.

Results: Since the abandonment of grazing and drainage, progressive succession towards the TMAP vegetation types *Atriplex portulacoides* and *Elymus athericus* strongly increased and mostly occurred in abandoned areas at medium to high elevation. Retarded and retrogressive succession decreased and mostly occurred in grazed and low lying areas. Persistance of the early successional vegetation type *Puccinellia maritima* in the salt marshes of the northern Wadden Sea suggests that large-scale gradients of salinity, inundation frequency and sedimentation lead to geographical variation in the pace of succession.

Conlusions: Considered from a large-scale and long-term perspective, abandonmnent of grazing and drainage caused spread of grazing sensitive plant species from mid and late-successional stages. This change in vegetation composition affects species diversity and ecosystem functions of the Wadden Sea mainland salt marshes. Grazing-regime and elevation were found to be the most important drivers of succession. To achieve and maintain large-scale heterogeneity in vegetation composition, we recommend management to maintain a mosaic of grazed and ungrazed areas and to consider the role of large-scale gradients of environmental factors driving succession.

Nomenclature: Wisskirchen & Haeupler (1998)

Keywords: Classification tree model; *Festuca rubra*; *Puccinellia maritima*; Salt marsh management; TMAP vegetation monitoring; Wadden Sea

Introduction

Understanding the process of vegetation succession is essential to predict the effects of anthropogenic disturbance, climate change and invasive species on biodiversity, functioning and services of the world's ecosystems (Loreau et al. 2001; Isbell et al. 2011; Prach & Walker 2011). Current theory for vegetation succession specifies three major causes for temporal patterns of vegetation change (successional pathways) including differences in species performance and availability of species and sites (Pickett et al. 1987; Pickett et al. 2009). Changing the disturbance regime and thereby manipulating site availability, is an opportunity to intervene in vegetation succession and conserve ecosystems (Hobbs et al. 2007; Pickett et al. 2009; Prach & Walker 2011).

Recent concern about salt marsh losses following sea level rise and growing anthropogenic pressure on coastal areas has increased the interest in salt marsh conservation and in effects of grazing on vegetation succession and species diversity (Adam 2002; Clausen et al. 2013; Kirwan and Megonigal 2013). Salt marshes develop at shallow tidal coasts under conditions of low water currents and continuous sedimentation (Adam 1993). The sediment is first colonised by pioneer species, which are replaced by plant species from mid- and late-successional stages in low and the high marsh.

The pace of salt marsh succession depends on drainage conditions and sedimentation rates in relation to inundation frequency and sea level rise (Leendertse et al. 1997; Olff et al. 1997; Schröder et al. 2002). Progressive succession from early- to late-successional plant species or vegetation types is favoured by high sedimentation rates and low inundation frequencies, while waterlogging and high inundation frequencies lead to retardation of succession or retrogressive succession from late- to early-successional plant species.

In addition to abiotic factors, herbivory also affects the pace of succession (Davidson 1993; Kiehl et al. 1996; Cingolani et al. 2005). Palatability of salt marsh plants to grazers, as well as tolerance to biomass losses, soil compaction and waterlogging, decreases from early- to late successional stages (Summers et al. 1993; Kiehl et al. 1996; Levine et al. 1998). In salt marshes of Northern Europe, intensive livestock grazing (≥1 livestock unit per ha) leads to retardation of succession and dominance of palatable grass species like *Puccinellia maritima* and *Festuca rubra* from early- to mid- successional stages in the low and in the high marsh. Abandonment of grazing induces secondary succession on previously grazed areas (Kleyer et al. 2003).

The Wadden Sea – Europe's largest intertidal ecosystem complex – includes around 400 km^2 of salt marshes (Reise et al. 2010). Mainland salt marshes, which have been artificially created with the help of accretion enhancement techniques, encompass around 60% of this area. Wadden Sea mainland salt marshes have traditionally been used for livestock grazing and mowing (Bakker et al. 2002). In recent decades, agricultural economic interest has decreased. To achieve a large-scale heterogeneity in soil conditions and vegetation composition intensive livestock grazing and the artificial drainage system were abandoned in many mainland salt marshes (Bakker et al. 2003; Esselink et al. 2009).

Small-scale studies investigating vegetation dynamics shortly after grazing and drainage abandonment have reported an increase in plant species richness and structural diversity of salt marshes (Kiehl et al. 1996; Schröder et al. 2002). Results from the few available studies conducted at larger scales (20–600 ha) or over longer time periods (≥10 yrs), suggest an increase of progressive succession from *Puccinellia maritima* and *Festuca rubra* towards plant species sensitive to grazing and waterlogging, such as the dwarf shrub *Atriplex portulacoides* (low marsh) and the tall grass *Elymus athericus* (high marsh; Bos et al. 2002; Bakker et al. 2003; Esselink et al. 2009). Both *A. portulacoides* and *E. athericus* form almost monospecific vegetation types with a low plant and structural diversity (Esselink et al. 2009). Whether increase of progressive succession across this landscape represents a large-scale and long-term trend that might decrease of species diversity and affect ecosystem functions of salt marshes, such as e.g. carbon sequestration and silica delivery, has been widely discussed (Valéry et al. 2004; Esselink et al. 2009; Ford et al. 2013; Müller et al. 2013; Veeneklaas et al. 2013; Wanner et al. 2014).

It has been hypothesized that a local-scale increase of progressive succession after abandonment of grazing and drainage could be compensated at the landscape scale by the occurrence of retrogressive succession in low-lying parts of abandoned salt marshes, following increased waterlogging and a decline in soil aeration (Stock & Kiehl 2000; Esselink et al. 2002). Furthermore, the pace of succession in the Wadden Sea region might vary across large-scale gradients of environmental factors such as salinity and inundation frequency (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer und Umweltbundesamt 1998; Kappenberg & Fanger 2007).

To assess long-term and large-scale trends in the development of salt marshes, the Trilateral Monitoring and Assessment Program (TMAP; Bakker et al. 1997) has been established by the three Wadden Sea countries (Denmark, Germany and The Netherlands). In the framework of TMAP, vegetation composition of salt marshes as well as land use and management of salt marshes are recorded in the entire Wadden Sea region every five years. In this paper, we present the first study of vegetation succession since the change in management in the early 1990s based on the large-scale TMAP vegetation surveys.

The primary objectives of the present study were: (i) to analyze long-term and large-scale trends of vegetation succession in low and high marsh since the abandonment of grazing and drainage in many mainland salt marshes (ii) to identify the major drivers of main successional pathways and (iii) to investigate whether the pace of succession varies along large-scale environmental gradients.

Methods

Study area

The study area extends from the central to the northern Wadden Sea region (Fig. 2.1). It encompasses the mainland salt marshes along the German North Sea coast in the federal state of Schleswig-Holstein (approx. 55°N to 54°N and 8°E to 9°E; Fig. 2.1).

Nearly all mainland salt marshes in the study area are of anthropogenic origin (Esselink et al. 2009) and are characterized by a thick clayish sediment layer and a regular system of creeks and drainage ditches. Their overall area increased from 6747 ha in 1988 to 8861 ha in 2006 (the latter corresponding to around 45% of all the Wadden Sea mainland salt marshes in 2006; Wanner et al. 2014). The salinity of inundation water decreases from about 25–32 practical salinity units (psu) at the northern to about 10–12 psu at the southern end of the study area (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer und Umweltbundesamt 1998). Vertical accretion rates are generally described to be in the range of 6–10 mm yr^{-1} (Esselink et al. 2009; Stock 2011; Suchrow et al. 2012). In the wide mainland salt marshes within the study area (marsh width around 2 km), vertical accretion rates and thus marsh elevation often decrease landward (Stock 2011).

After the establishment of the Wadden Sea National Park of Schleswig Holstein in 1985, the percentage of the study area with intensive sheep grazing (>10 sheep per ha) as former predominant land use, decreased from 89% in the early 1990s to about 49% in 1996, finally falling down to 41% in 2006 (Stock et al. 2005; updated). In 2006, about 6% of the study area was moderately grazed (≤3 sheep per ha, Fig. 2.1).

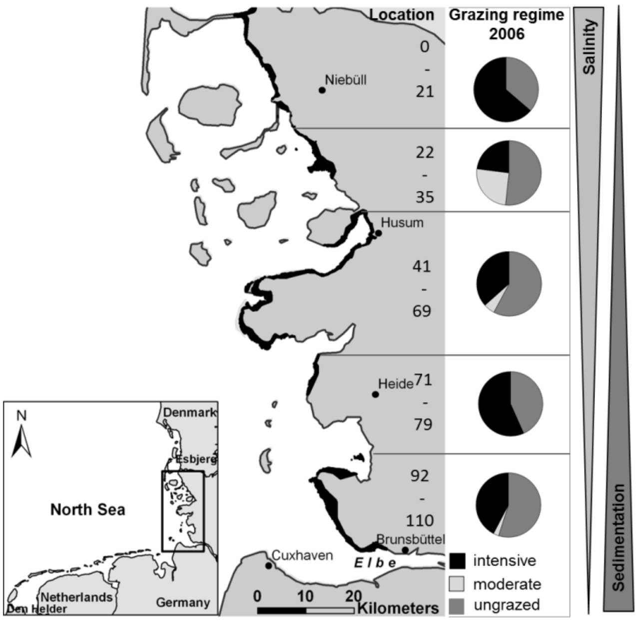


Figure 2.1. Study site locations of mainland salt marshes (shaded in black) along the North Sea coast of the Wadden Sea, Schleswig-Holstein, Germany. The location index (calculated from values of latitude) indicates the position of salt marshes, pie charts indictate sheep grazing regimes in 2006 (intensive, moderate, ungrazed).

The TMAP vegetation data

Data from four digital vegetation maps of the study area were analyzed, resulting from TMAP vegetation surveys in 1988, 1996, 2001 and 2006. All of the vegetation surveys took place in the summer between July and September. The maps show the spatial distribution of vegetation type patches at a scale of 1:5000 that corresponds to a minimum mapping unit during the vegetation surveys of 25 m x 25 m.

In the standardized TMAP typology for the nomenclature of vegetation types (Petersen et al. 2013), salt marsh plant communities are aggregated to 25 vegetation types defined by the occurrence and cover percentage of dominant or characteristic plant species. The following TMAP vegetation types were considered in the present study: Pioneer zone and low marsh: '*Spartina anglica*' (*Spartina*), '*Puccinellia maritima*' (*Puccinellia*), '*Atriplex portulacoides*' (*Atriplex*); high marsh: '*Festuca rubra*' (*Festuca*), '*Elymus athericus*' (*Elymus*; Table 2.1).

Table 2.1. Salt marsh vegetation types used in field and mapping following standardized TMAP typology.

Vegetation type	Abbreviation	Successional stage	Characterizing species (cover %)	Associated species and remarks
Spartina anglica	*Spartina*	early	*Spartina anglica* (>10)	*Salicornia stricta, Salicornia ramossisima*
Puccinellia maritima	*Puccinellia*	early to middle	*Puccinellia maritima* (>10)	*Suaeda maritima, Salicornia ramossisima, Plantago maritima, Trigochin maritimum, Festuca rubra*
Atriplex portulacoides	*Atriplex*	middle	*Atriplex portulacoides* (>35)	
Festuca rubra	*Festuca*	middle	No characterizing species	Only mapped when characterizing species from all other vegetatipn types are absent and *F. rubra* >35% cover
Elymus athericus	*Elymus*	late	*Elymus athericus* (>30)	

Analysis of successional pathways

In 1988, the predomiant vegetation type was *Puccinellia* in the low marsh and *Festuca* in the high marsh. Both vegetation types covered together approximately 65% of the study area (Stock et al. 2005). To find the main successional pathways of these vegetation types between 1988 and 2006, we analyzed digital vegetation maps from 1988 through 2006 in three time steps: 1988 vs 1996 (TS 1), 1996 vs 2001 (TS 2) and 2001 vs 2006 (TS 3). Each pair of maps representing a time step was overlain using the geographic information system (GIS) software ArcGIS (ESRI; Environmental Systems Research Institute, Redlands, CA, US). In the GIS data overlay, the vegetation type at the beginning and end of the time step was specified for each of the patch fragment types (hereafter referred to as 'polygons'). We selected polygons that belonged to either *Puccinellia* or *Festuca* at the beginning of the respective time step (e.g., 1988 in time step 1). Subsequently, we recorded the type and area of the vegetation type at the end of the time step (e.g., 1996 in TS 1) and noted the successional pathway.

Vegetation changes of more than 5% of the area in *Puccinellia* or *Festuca* in at least two time steps were considered as main successional pathways and taken into account in the classification tree analysis. Main successional pathways were attributed to retrogressive, retarded or progressive succession according to the stages of succession represented by the vegetation types involved in the pathway (see Table 2.1). Thus, a change from *Puccinellia* to *Spartina* or from *Festuca* to *Puccinellia* was called 'retrogressive succession'. No change in *Puccinellia* or *Festuca* was called 'retarded succession'. A change from *Puccinellia* to *Atriplex*, *Puccinellia* to *Festuca*, *Puccinellia* to *Elymus* or *Festuca* to *Elymus* was called 'progressive succession' following the hierarchical system of the TMAP vegetation classification (Bakker et al. 1997). Although the successional pathway from *Puccinellia* to *Elymus* was <5% of the area in *Puccinellia* or *Festuca* in TS 1 and TS 2 it was included due to the relevance of *Elymus* for the understanding of current vegetation dynamics in Wadden Sea salt marshes (see Introduction).

Sampling strategy to build data sets for classification tree models

In each time step, all polygons representing main successional pathways of *Puccinellia* or *Festuca* were sampled once within the GIS. Sampling took place randomly throughout the study area, but with a minimum distance of 25 m between two sampling points required in both *x* and *y* directions. The distance of 25 m between the sampling points was chosen both because of information from previous investigations of spatial autocorrelation in multinomial regression models of successional pathways in the study area (unpubl. data), as well as the fact that the level of sampling intensity matched the spatial resolution of TMAP vegetation surveys of 25 m x 25 m. In total, six data sets were built from which the classification tree models were calculated, in each time step one for the successional pathways of *Puccinellia* and one for the successional pathways of *Festuca*.

Environmental factors

Several environmental factors were considered as predictors for successional pathways in the classification tree models (Table 2.2). Values of the environmental factors were attributed to the sampling points within the GIS and corresponded to the respective environmental condition at the beginning of the considered time step. Elevation and the distance to next main creek were exceptions to this rule for reasons of data availability (see below).

Elevation (ELEV) of each sampling point was derived from a digital terrain model calculated after an aerial laserscan survey (LiDAR) in the study area in 2005 (digital terrain model ATKIS-DGM2, Innenministerium of Schleswig-Holstein, Referat IV 28 – Vermessungswesen und Geoinformation, Kiel, Germany). Elevation is indicated in metres above sea level (m a. s. l.), as currently information on elevation in relation to mean high tide is not available for the whole study area. Values of ELEV vary from 0.25 m to 3.50 m with a mean of 1.90 ± 0.33 m (±SD).

In the following, elevation ≤1.60 m is referred to as low, 1.6 m < X ≤2.10 m as medium and >2.10 m as high elevation. The distance to marsh edge (MARSH_DIST) and the distance to main creeks in 2006 were calculated for each sampling point using GIS. We used the location of sampling points along the north–south extent of the study area as a proxy for large-scale environmental gradients of salinity and inundation frequency, because no area wide data base of these variables was available. The location index (LOC) was calculated from the latitude value of sampling points (Fig. 2.1). For both *Puccinellia* and *Festuca* patches a shape index was calculated according to the method described by Lang and Blaschke (2007). The distance to and the area of neighboring patches of all considered vegetation types (e.g. Dist_Atriplex*,* Area_Atriplex*,* etc.) were calculated using the *near* function in ArcGIS (ESRI). To build the predictor grazing (GRAZ) we combined assessment of land use in the field during the TMAP vegetation surveys (Stock et al. 2005, updated) with information from GIS data of the Administration of the Wadden Sea National Park Schleswig-Holstein, Tönning, Germany, based on lease contracts. GRAZ contained five categories of grazing regime (A–E), indicating the stocking density or time passed since abandonment of livestock grazing for each sampling point (Table 2.3).

Table 2.2. Descriptions and abbreviations of environmental variables considered as predictors in classification tree models of successional pathways of the *Puccinellia* and the *Festuca* vegetation type in TS 1–TS 3 (TS 1, TS 2 and TS 3, respectively). For each predictor the number of times it occurs in the respective classification tree models is indicated. The following predictors were selected in none of the classification tree models and are therefore not listed in the table: distance to the next creek; shape of *Puccinellia* and *Festuca* patches; distance to and the area of the next *Spartina*, *Puccinellia* or *Festuca* patch; and area of next *Atriplex* or *Elymus* patch.

Predictors (Abbreviation)	**Description**	**Unit**	***Puccinellia***			***Festuca***		
			TS 1	**TS 2**	**TS 3**	**TS 1**	**TS 2**	**TS 3**
ELEV	Elevation	m	2	3	3	–	3	3
MARSH_DIST	Distance to marsh edge	m	2	–	1	1	–	–
LOC*	Sampling point location relative to the north-south extent of the study area		1	–	3	1	–	4
Dist_Atripl.	Distance to next *Atriplex* patch	m	–	–	1	–	–	–
Dist_Elymus	Distance to next *Elymus* patch	m	–	–	–	2	1	–
GRAZ†	Type and history of grazing regime		2	3	2	1	1	3

* see Fig. 2.1; †Five categories of grazing regime, see Table 2.3.

Classification tree models

Classification and regression tree analyses CART (Breiman et al. 1984; De'ath & Fabricius 2000) were used to predict the main successional pathways of *Puccinellia* and *Festuca* (response variables) from environmental factors (hereafter referred to as predictors).

One classification tree model per time step was calculated in order to track a potential change in the driving factors of successional pathways over time.

Table 2.3. Categories of the predictor grazing regime (GRAZ) in the classification tree models. The categories indicate stocking density (category A, D) or time passed since the abandonment of sheep grazing (category B, C, E) in case of abandoned sites.

Category	Description
A	Intensive grazing (>10 sheep per ha) from 1988 to 2006
B	Intensive grazing until 2001, later abandoned
C	Intensive grazing unti 1996, later abandoned
D	Moderate grazing (≤3 sheep per ha)
E	Abandoned since latest 1996

The basic principle of CART, a non-parametric approach to vegetation modeling, is the recursive partitioning (or splitting) of the response variable data set into increasingly homogeneous subsets (nodes). Classification trees were calculated using the party package (Hothorn et al. 2006) from the statistical and programming language R, v 2.1.2.2 (R Foundation for Statistical Computing, Vienna, AT). We specified a minimum split value of 100, a maximum depth of four split levels and the Bonferroni test type for multiplicity adjusted p-values.

The predictive accuracy of each tree model was assessed with an independent evaluation data set that was built by random sampling without replacement from the original data pool, thus splitting the response variable into 70% of sampling points for model calibration and 30% for model evaluation. For both the model using the calibration and the model using the evaluation data set, the proportion of correct predictions (correct classification rate) in each successional pathway was calculated. In the case of the *Festuca* tree model in time step 1, no independent model evaluation could be performed due to limited sample size.

Results

Main successional pathways and driving environmental factors

Our findings indicate a strong increase of progressive succession towards *Atriplex* and *Elymus* and a decrease of retarded or retrogressive succession since the abandonment of grazing in the early 1990s (Table 2.4).

Elevation (ELEV), grazing regime (GRAZ) and location of vegetation type patches along the north–south extent of the study area (LOC) were the most important predictors and thus the primary determinants of succession (Table 2.2). Distance to the marsh edge (MARSH_DIST) and to patches of *Atriplex* and *Elymus* (Dist_Atriplex, Dist_Elymus) were of minor importance for the explanation of successional pathways (Table 2.2).

Predictive accuracy of classification tree models

Classification tree models showed average to good model quality with an increase in model accuracy from TS 1 to TS 3 for *Puccinellia* (Table 2.5), and *Festuca* (Table 2.6), respectively.

Small differences in correct classification rate values for the calibration and the evaluation data sets in any successional pathway and time step indicate statistical robustness. In TS 1 and TS 2, classification tree models had difficulty in discriminating successional pathways from *Puccinellia* to *Festuca* and from *Festuca* to *Puccinellia* with no change in vegetation type (Tables 2.5, 2.6). This might be due to the fact that in grazed areas, *Puccinellia* and *Festuca* often occur closely together, which hampers accurate mapping of boundaries between both vegetation types. In the *Puccinellia* tree models, the successional pathway from *Puccinellia* to *Atriplex* was frequently misclassified as *Puccinellia* to *Spartina* in TS 1 and vice versa in TS 3, presumably because of the small number of sampling points in both pathways (Table 2.5). The successional pathway from *Festuca* to *Elymus* reached the highest correct classification rate, with more than 70% in TS 2 and TS 3 (Table 2.6).

Classification tree models of the *Puccinellia* vegetation type

Retarded succession (i.e., persistence of *Puccinellia*) or retrogressive succession from *Puccinellia* to *Spartina* occurred from 1988 to 1996 (TS 1) mainly at medium to low elevations (node 1, ELEV ≤1.96 m; Fig. 2.2a). Succession to *Spartina* was found mainly close to the seaward marsh edge (node 2, MARSH_DIST ≤206.13 m; node 13 MARSH_DIST ≤304.06 m). Progressive successional pathways were found at medium to high elevation (node 1, ELEV >1.96 m), but these pathways were rare at the northernmost end of the study area (node 9, LOC ≤27.97).

From 1996 to 2001 (TS 2), progressive succession from *Puccinellia* to *Atriplex* occurred almost exclusively in moderately grazed areas (Fig. 2.2b). At medium to low elevations, no change in *Puccinellia* and progressive succession to *Festuca* occurred in intensively grazed areas, while the retrogressive pathway to *Spartina* was found both in grazed and abandoned areas (node 5, GRAZ = A; node 8, GRAZ = C, E). At high elevation (node 3, ELEV >2.15 m), progressive succession to *Festuca* occurred mostly in intensively grazed areas (node 11, GRAZ = A, C) and to *Elymus* in abandoned areas (node 11, GRAZ = E).

From 2001 to 2006 (TS 3), persistence of *Puccinellia* was mainly restricted to intensively grazed areas especially in the northern part of the study area (node 11, LOC ≤67.57; Fig. 2.4a). Progressive succession to *Festuca* occurred in intensively grazed areas, mostly in the southern part of the study area (node 11, LOC >68). Different types of progressive successional pathways were found in moderately grazed or abandoned areas depending on elevation. The pathway to *Atriplex* occurred at medium to low elevation (node 2, ELEV ≤2.06) and that to *Elymus* at medium to high elevation (node 2, ELEV >2.06).

Table 2.4. Main successional pathways of the *Puccinellia* and the *Festuca* vegetation type from 1988 to 1996 (time step 1), 1996 to 2001 (time step 2) and 2001 to 2006 (time step 3).

	1988–1996		**1996–2001**		**2001–2006**	
Successional pathway	**Area [ha]**	**Sampling points**	**Area [ha]**	**Sampling points**	**Area [ha]**	**Sampling points**
Puccinellia						
to *Spartina* (PS)	273	903	157	554	54	243
to *Puccinellia* (no change; PP)	1960	729	1113	723	809	883
to *Atriplex* (PA)	82	130	134	380	222	597
to *Festuca* (PF)	623	651	356	734	196	700
to *Elymus* (PE)	55	190	70	326	91	621
to other	437	–	862	–	277	–
Total	3430	2603	2692	2717	1649	3044
Festuca						
to *Puccinellia* (FP)	269	446	172	609	189	689
to Festuca (no change; FF)	578	173	644	498	436	560
to *Elymus* (FE)	27	75	137	468	295	579
to other	182	–	509	–	282	–
Total	1056	694	1462	1575	1202	1828

Table 2.5. Predictions of classification tree models for successional pathways of the *Puccinellia* vegetation type in TS 1 (1988–1996), TS 2 (1996–2001) and TS 3 (2001–2006). The proportion of correctly predicted cases of each successional pathway (correct classification rate; e.g., the proportion of sampling points from the category PS (succession from *Puccinellia* to *Spartina*) predicted as PS) is shaded in grey. Results from the evaluation data set are indicated in brackets.

		Classification tree model predictions [% of sampling points]				
Successional pathways	**Sampling points**	**PS**	**PP**	**PA**	**PF**	**PE**
TS 1						
PS	903	81.5 (76.7)	11.0 (12.2)	–	6.5 (9.2)	0.9 (1.8)
PP	729	42.7 (40.5)	28.3 (29.0)	–	24.6 (26.7)	4.3 (3.7)
PA	130	81.5 (82.1)	4.3 (5.1)	–	14.1 (12.8)	–
PF	651	34.2 (28.6)	9.6 (13.3)	–	48.7 (48.5)	7.4 (9.7)
PE	190	34.3 (41.4)	–	–	34.3 (25.9)	30.6 (32.7)
Total	2603					
TS 2						
PS	554	71.6 (74.7)	20.6 (18.0)	1.8 (1.8)	1.8 (0.7)	4.6 (3.6)
PP	723	26.6 (25.7)	60.7 (62.8)	3.5 (5.0)	5.7 (5.0)	3.3 (1.4)
PA	380	47.9 (43.0)	13.8 (12.3)	27.7 (30.7)	0.3 (0.0)	10.1 (14.0)
PF	734	25.0 (30.4)	43.6 (37.7)	3.3 (4.5)	16.4 (15.9)	11.7 (11.4)
PE	326	28.2 (36.0)	5.2 (3.0)	9.2 (7.2)	14.0 (13.4)	43.2 (40.2)
Total	2717					
TS 3						
PS	243	–	32.3 (25.7)	58.8 (56.7)	4.7 (12.2)	4.1 (5.4)
PP	883	–	63.2 (64.9)	15.3 (12.0)	19.0 (21.5)	2.4 1.5)
PA	597	–	20.8 (21.8)	68.0 (66.5)	2.1 (2.2)	9.0 (9.4)
PF	700	–	24.5 (27.6)	13.0 (13.8)	59.3 (54.8)	3.0 (3.8)
PE	621	–	10.6 (11.8)	29.3 (27.4)	16.1 (17.7)	43.9 (43.0)
Total	3044					

Table 2.6. Classification tree model predictions of successional pathways of the *Festuca* vegetation type in TS 1 (1988–1996), TS 2 (1996–2001) and TS 3 (2001–2006). The proportion of correctly predicted cases of each successional pathway (correct classification rate; e.g., the proportion of sampling points from the category FP (succession from *Festuca* to *Puccinellia*) predicted as FP) is shaded in grey. Results from the evaluation data set are indicated in brackets.

		Classification tree model predictions [% of sampling points]		
Successional pathways	**Sampling points**	**FP**	**FF**	**FE**
TS 1				
FP	446	98.2	–	1.8
FF	173	96.0	–	4.0
FE	75	56.7	–	43.2
Total	694			
TS 2				
FP	609	81.7 (83.6)	–	18.3 (16.4)
FF	498	67.3 (64.0)	–	32.7 (36.0)
FE	468	14.0 (15.0)	–	85.9 (85.0)
Total	1575			
TS 3				
FP	689	63.0 (60.3)	21.7 (26.0)	15.3 (13.5)
FF	560	32.4 (32.1)	46.5 (42.2)	21.0 (25.6)
FE	579	6.0 (5.7)	19.5 (24.7)	74.5 (69.5)
Total	1828			

Classification tree models of the *Festuca* vegetation type

In 1988 to 1996 (TS 1), progressive succession from *Festuca* to *Elymus* occurred almost exclusively in abandoned areas and was facilitated by close distances between patches of both vegetation types (node 7, Dist_Elymus ≤155.08 m; Fig. 2.3a). Retarded succession (i.e., persistence of *Festuca*) or retrogressive succession to *Puccinellia* was mostly found in areas under intensive or moderate grazing. In addition, the successional pathway to *Puccinellia* occurred more often in the the northern part of the study area (node 2, LOC ≤65.15).

In 1996 to 2001 (TS 2), successional pathways were controlled by the grazing regime, elevation and distance to patches of *Elymus* (Fig. 2.3b). Retrogressive succession from *Festuca* to *Puccinellia* was mainly found in grazed areas, but the persistence of *Festuca* could not be attributed to environmental conditions such as grazing or elevation or location within the study area. Progressive succession from *Festuca* to *Elymus* occured mainly in abandoned areas at medium to high elevation, especially in proximity to patches of *Elymus* (node 8, Dist_Elymus ≤99 m). In 2001 to 2006 (TS 3), persistence of *Festuca* or retrogressive succession to Puccinellia was found mainly at medium to low elevations (≤2.16 m; Fig. 2.4b). In addition, persistence of *Festuca* occurred in the southern part of the study area, in both grazed and abandoned areas (node 3, LOC >96.67; node 10, LOC >69; node 19 LOC >70.97). Progressive succession to *Elymus* occurred mainly at medium to high elevation (>2.16 m), mostly in abandoned or moderately grazed areas.

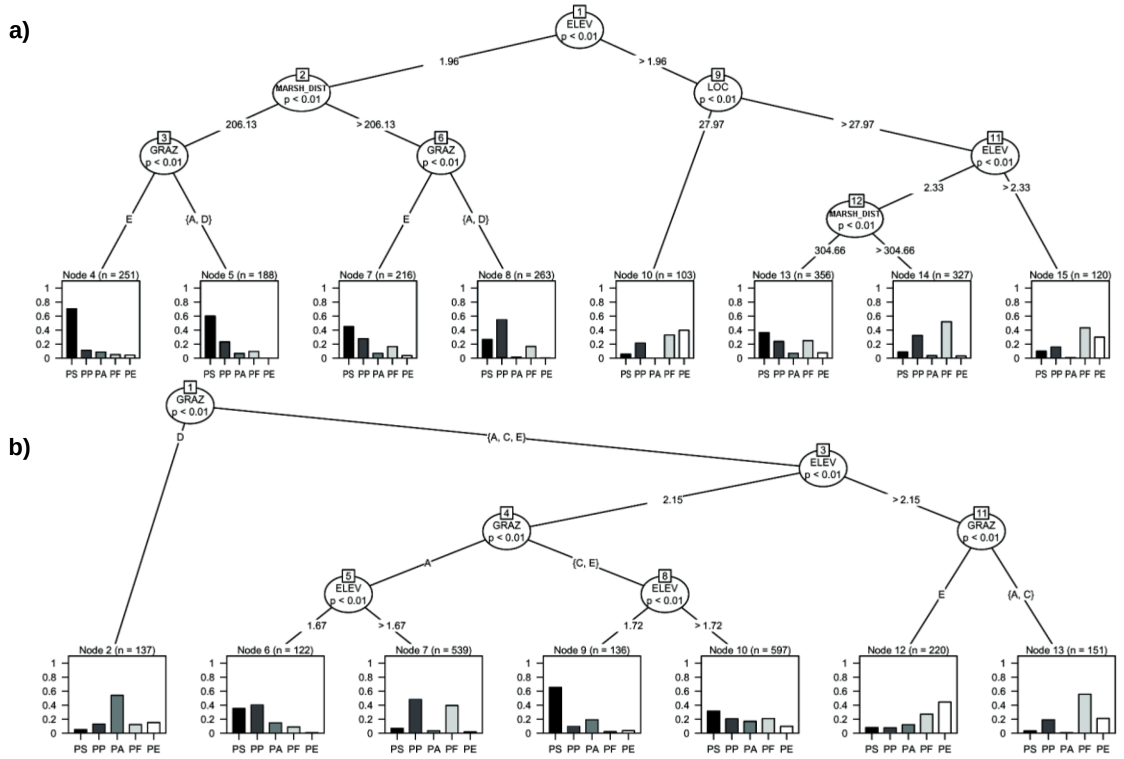


Figure 2.2. Classification tree (calculated from classification and regression tree analysis; CART) of successional pathways of the *Puccinellia* vegetation type in time step 1 (1988–1996; **a)** and time step 2 (1996–2001; **b)**. The predictors and the point along their distribution of values, at which a split was made, are written as labels on the branches of the trees. Circles represent internal subsets of successional pathways of *Puccinellia* (internal 'nodes') and rectangles terminal nodes. Histograms indicate the proportion of sampling points of successional pathways within each terminal node. Successional pathways: PS = Puccinellia to Spartina, PP = Puccinellia to Puccinellia (no change), PF = Puccinellia to Festuca, PE = Puccinellia to Elymus. Predictors: ELEV = Elevation [m], MARSH_DIST = Distance to marsh edge [m], LOC = Location relative to north-south extent of study area (see Fig. 2.1), GRAZ = razing regime; A: intensive grazing, C: intensive grazing until 1996, later abandoned, D: moderate grazing, E: abandoned since 1996.

Discussion

Large-scale and long-term trends of vegetation succession are of vital importance to assess the consequences of changes in management for species diversity, ecosystem functions and conservation of salt marshes (Adam 2002; Prach & Walker 2011). Matching long-term predictions of contemporary models on the effect of grazing abandonment on vegetation in highly productive ecosystems (Cingolani et al. 2005), our results show an increase of progressive succession after abandonment of grazing and drainage in salt marshes of the Wadden Sea. Previous studies conducted at smaller scales and at species level have had similar conclusions (Bos et al. 2002; Bakker et al. 2003; Kleyer et al. 2003). However, the geographical variation in the pace of succession observed in our study points to an influence of large-scale environmental gradients on the course of succession.

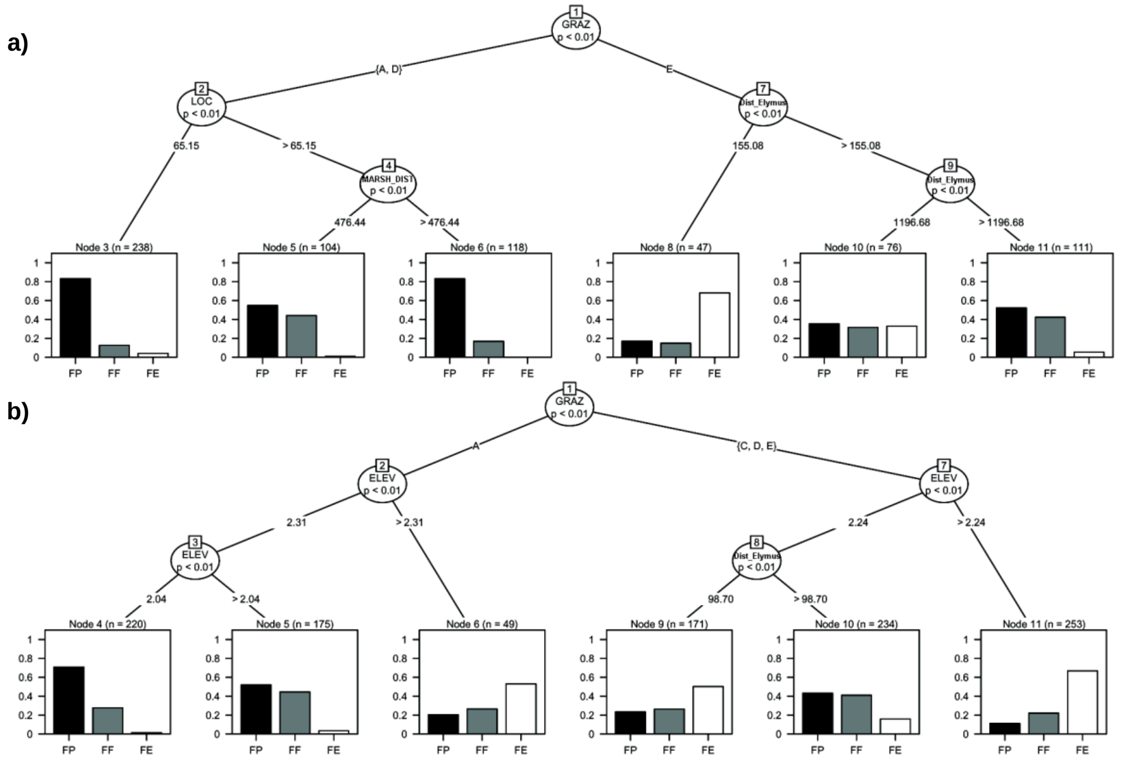


Figure 2.3. Classification tree (CART) of successional pathways of the *Festuca* vegetation type in time step 1 (1988–1996; **a)** and time step 2 (1996 –2001; **b)**. The predictors and the point along their distribution of values, at which a split was made, are written as labels on the branches of the trees. Circles represent internal subsets of successional pathways of *Festuca* (internal 'nodes') and rectangles terminal nodes. Histograms indicate the proportion of sampling points of successional pathways within each terminal node. Successional pathways: FP = Festuca to Puccinellia, FF = Festuca to Festuca (no change), FE = Festuca to Elymus. Predictors: ELEV = Elevation [m], MARSH_DIST = Distance to marsh edge [m], Dist_Elymus = Distance to next Elymus patch [m], GRAZ = Grazing regime; A: intensive grazing, C: intensive grazing until 1996, later abandoned, D: moderate grazing, E: abandoned since 1996.

Abiotic conditions, related to elevation, large-scale environmental gradients of salinity, inundation frequency and vertical accretion and the grazing regime were the major drivers of successional pathways over both the short and long term. Pathways towards *Atriplex* and *Elymus* were facilitated by proximity of patches of these vegetation types. Their characteristic plant species *A. portulacoides* and *E. athericus* which reproduce both clonally and by seeds, were rare during the time of intensive sheep grazing in these salt marshes. Consequently, the spatial distribution of remnant populations may have been important in their spread after grazing abandonment (see also Rand 2000; Lanta and Leps 2009).

Pathways of retarded and retrogressive succession

Pathways of retarded and retrogressive succession decreased over the entire study period (1988–2006) and were mainly found at medium to low elevation. One reason for the decline of retrogressive succession may be the reduction of grazing-induced soil compaction and waterlogging after abandonment. Soil compaction and waterlogging favour early successional species of the low marsh, also at comparatively high elevation.

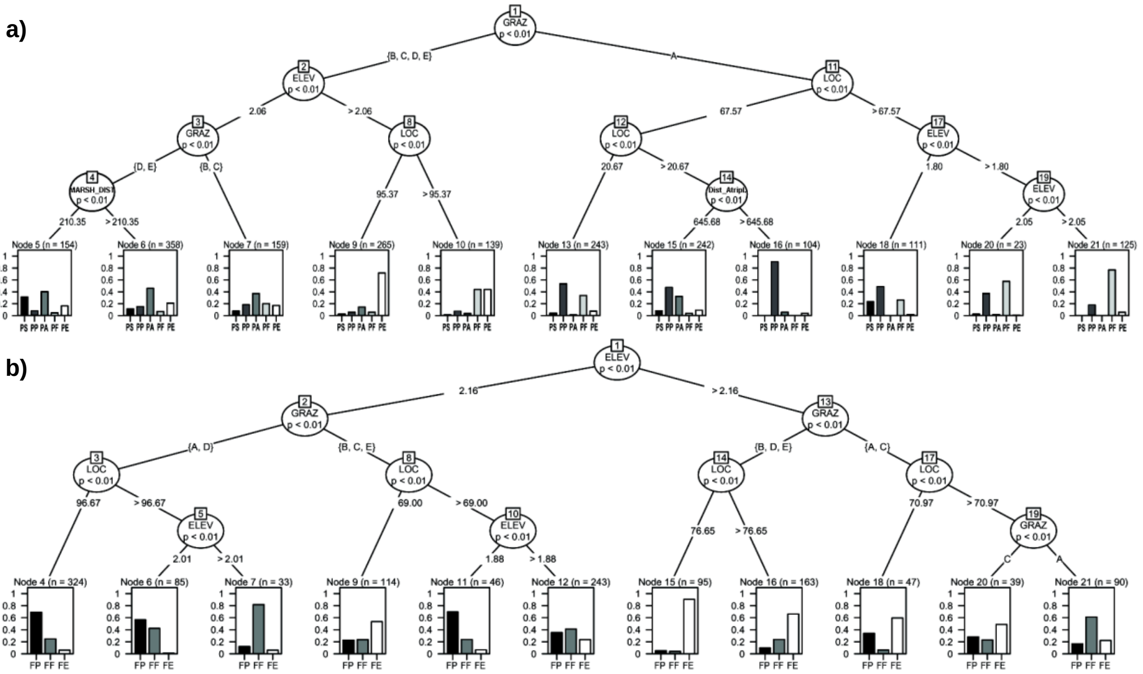


Figure 2.4. Classification tree (CART) of successional pathways of the *Puccinellia* vegetation type **(a)** and the *Festuca* vegetation type **(b)** in time step 3 (2001–2006). The predictors and the point along their distribution of values, at which a split was made, are written as labels on the branches of the trees. Circles represent internal subsets of successional pathways of *Puccinellia* or *Festuca* (internal 'nodes') and rectangles terminal nodes. Histograms indicate the proportion of sampling points of successional pathways within each terminal node. Successional pathways: PS = Puccinellia to Spartina, PP = Puccinellia to Puccinellia (no change), PF = Puccinellia to Festuca, PE = Puccinellia to Elymus, FP = Festuca to Puccinellia, FF = Festuca to Festuca (no change), FE = Festuca to Elymus. Predictors: ELEV = Elevation [m], MARSH_DIST = Distance to marsh edge [m], LOC = Location relative to north-south extent of study area (see Fig. 2.1), Dist_Atripl. = Distance to next Atriplex patch [m], GRAZ = Grazing regime; A: intensive grazing, B: intensive grazing until 2001, later abandoned, C: intensive grazing until 1996, later ungrazed D: moderate grazing, E: abandoned since 1996.

Abandonment of grazing thus induces a downward shift of the low marsh zone along the elevational gradient and a decrease of its areal extent (Bakker 1989; Kiehl et al. 1997). Furthermore, our results show that retarded or retrogressive succession mainly occurred in grazed marshes. Conversely, this suggests that in most of the areas where grazing was abandoned, the concurrent neglect of the drainage system did not lead to a degree of rewetting favouring the occurrence of retarded or retrogressive succession in wet depressions. Presumably this is due to the flat topography of artificially created marshes and the fact that the dense drainage system promotes soil aeration even nearly two decades after abandonment. However, our findings contrast with a study by Esselink et al. (2002), reporting a decline of soil aeration and the formation of wet depressions after abandonment of the drainage system in salt marshes of the Dollard Estuary (southern Wadden Sea). Such contradictory results ask for separating the effects of abandonment of grazing and of drainage, in order to detect the mechanisms behind the changes observed in the present study.

Progressive successional pathways

Progressive succession towards *Atriplex* and *Elymus* strongly increased from 1988 to 2006 and occurred mainly in abandoned areas and at medium to high elevation.

The spread of *Elymus* represents one of the most significant changes in plant communities of European salt marshes during the last decades (Bockelmann et al. 2002). Besides the species ability for both sexual and clonal reproduction, rapid colonisation of salt marshes has been related to abandonment of grazing, vertical accretion rates and marsh age (Bakker et al. 1993; Bockelmann et al. 2002; Bockelmann et al. 2011; Veeneklaas et al. 2013). In artificial mainland salt marshes the spread of *Elymus* may be additionally favoured by enhanced soil aeration due to the dense drainage system.

Both *Atriplex* and *Elymus* are usually species-poor and of low structural diversity (Esselink et al. 2009). Apart from negative effects on the diversity of plant species and several arthropod species, the increase in cover of these vegetation types may negatively affect several endangered species: waterbirds and waders preferring breeding and foraging habitats with spatial variation in canopy height (Verhulst et al. 2011; Mandema et al. 2013; Van Klink et al. 2013).

With respect to salt marsh functions, the spread of *Elymus* is likely to increase carbon trapping within salt marshes (Valéry et al. 2004). Enhanced export of dissolved silica after abandonment of salt marshes may stabilise marine food webs (Müller et al. 2013).

Geographical variation in the pace of succession

The recovery time of salt marsh vegetation from disturbance varies along landscape-scale gradients and increases under harsh environmental conditions (Crain et al. 2008). Persistance of *Puccinellia* implies retardation of succession in salt marshes at the northern end of the study area (northern Wadden Sea) in comparison to the rest of the study area. However, this might be caused both by the decreasing salinity and inundation frequency from the northern to the central Wadden Sea region (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer und Umweltbundesamt 1998) as well as by the slightly higher percentage of grazed salt marsh areas in the northern Wadden Sea.

Despite high inundation frequencies, salt marshes at the northern end of the study area are narrow in comparison to those at its southern end near the Elbe estuary (central Wadden Sea). Here, marshes experience high growth rates of the pioneer zone and show extended low and high marsh zones (Esselink et al. 2009). One reason for the spatial differences in marsh width may be a deficit in sedimentation in the northern Wadden Sea, as discussed by CPSL (2005), Reise (2005), Ahrendt (2007) and Andersen et al. (2010). Such a deficit in sedimentation might contribute to the geographical variation in the pace of succession, in addition to landscape-scale stress gradients. In order to learn whether the spatial patterns in succession found in our study will maintain, diverge or converge in the future, continuation of the large-scale TMAP vegetation monitoring is of vital importance.

Implications for future salt marsh management

The Wadden Sea Plan, a trilateral agreement between Denmark, The Netherlands and Germany, seeks to increase the area, stability and 'naturalness' as part of the main aims for salt marsh conservation in the Wadden Sea region (CWSS 2010). Naturally formed salt marshes show a large-scale heterogeneity in soil conditions and vegetation composition. However, in the artificial mainland salt marshes investigated here, long-term and large-scale trends of succession point to an increase of progressive succession and dominance of late-successional, species-poor plant communities.

To achieve and maintain a large-scale heterogeneity in vegetation composition in artificial mainland salt marshes, consideration of large-scale gradients of salinity, inundation frequency and sedimentation in management schemes may be helpful. Similar ideas have been proposed by Esselink et al. (2009) and Wanner et al. (2014), who suggest that, in salt marshes with low sedimentation rates (1–3 mm yr^{-1}), abandonment of grazing and drainage is an appropriate measure to achieve a large-scale heterogeneity in vegetation composition. In salt marshes with high sedimentation rates, however, a mosaic of grazed and ungrazed areas and active measures to reinforce rewetting might be needed to prevent dominance of species from late-successional stages.

Acknowledgements

We thank Boris Schröder and Torsten Hothorn for statistical advice, Iris Möller for language editing and two anonymous reviewers for helpful comments of earlier drafts of the manuscript. We also thank the administration of the Wadden Sea National Park for providing TMAP vegetation data and the 'Innenministerium of Schleswig-Holstein, Referat IV 28 - Vermessungswesen und Geoinformation' for providing the digital elevation model. This work was part of the project BASSIA (Biodiversity, Management and Ecoystem functions of Saltmarshes in the Wadden Sea National Park of Schleswig-Holstein) funded by the Bauer-Hollmann foundation and the University of Hamburg.

3

Biophysical properties of salt marsh canopies - Quantifying plant stem flexibility and above ground biomass

Franziska Rupprecht, Iris Möller, Ben Evans, Tom Spencer and Kai Jensen

Coastal Engineering 100 (2015) 48–57

CHAPTER 3

Abstract

The three-dimensional structure of salt marsh plant canopies, amongst other marsh surface characteristics, is of critical importance to the functioning and persistence of coastal salt marshes. Together with plant flexibility it controls the contribution of vegetation to the tidal flow and wave energy dissipation potential of marshes. However detailed information on these two key biophysical properties of salt marsh canopies is scarce.

In this paper we present biophysical properties of four plants commonly occurring in NW European salt marshes. We measured stem flexibility, diameter and height of the grasses *Spartina anglica*, *Puccinellia maritima* and *Elymus athericus* and above ground biomass and canopy height in stands of *Elymus athericus* and the dwarf shrub *Atriplex portulacoides*. Further we compared the performance of two methods for the non-destructive assessment of above ground biomass, such that they may be used during field assessments of marsh surface vegetation structure (i) Measurement of light availability within the canopy and (ii) side-on photography of vegetation. All data were collected on a salt marsh on the Dengie Peninsula, eastern England, UK, in summer (July).

We found significant differences in stem flexibility both between species and between the different parts of their stems. *P. maritima* was found to be the species with the most flexible stems, and, as a result of their relatively large stem diameter, *S. anglica* the species with the stiffest stems. Above ground biomass and hence potential canopy resistance to water flow could be estimated more accurately by side-on photography of vegetation than from measurement of light availability within the canopy.

Our results extend the existing knowledge base on plant properties with relevance to studies of habitat structure and ecosystem functioning as well as wave energy dissipation in salt marsh environments and can be used for the development of a more realistic representation of vegetation in numerical models and laboratory flume studies of plant-flow interactions.

Key words: Wave attenuation; Vegetation structure; Drag; Flexural rigidity; Young's bending modulus

Introduction

Vegetation is an important factor affecting both the functioning and form of salt marsh ecosystems at the coast. The often structurally complex plant canopies provide a key habitat and food source for a wide range of bird and arthropod species as well as contributing to the dissipation of wave energy and tidal flow over salt marsh surfaces directly, via plant-flow interactions, and indirectly, through causing spatially varying sediment accumulation and thus the formation of topographic roughness (Zedler and Kercher 2004; Gedan et al. 2011; Duarte et al. 2013; Möller et al. 2014). Under wave motion, and when water depths are low enough to allow wave-induced orbital flow to penetrate into the canopy layer, vegetation interacts with this flow by forming an obstruction. In return it experiences drag and re-orientation by wave forces (Mullarney and Henderson 2010). At the scale of the vegetated landform (e.g. a coastal salt marsh), these plant-flow interactions have been shown to be affected by the spatial configuration of vegetation patches as well as by the ratio of water depth to canopy height (Kirwan and Murray 2007; Vandenbruwaene et al. 2011). At the scale of individual plants, however, the magnitude of flow resistance provided, and drag force experienced, is governed by plant architecture and by mechanical characteristics such as stem flexibility and buoyancy (Paul et al. 2014a).

The flexibility of plant stems, often reported as Young's bending modulus or flexural rigidity (see also Methods section 'Measurements of plant stem flexibility'), is critical for plant behaviour and flow resistance provided under wave-generated orbital flow as well as being a potentially important ecological adaptation mechanism linked to ecosystem resilience. While highly flexible stems bend and take a flattened posture for part of the wave cycle, less flexible stems tend to remain in an upright posture and the flow must travel through, rather than over, the canopy. Peralta et al. (2008) have shown that for a specific range of stem spacings, the capacity of plant canopies to provide flow resistance and dissipate hydrodynamic energy increases with decreasing stem flexibility. A more recent flume study of the salt marsh grasses *Elymus athericus* and *Puccinellia maritima* also highlighted the importance of plant flexibility for wave dissipation during storm surge conditions (2 m water depth above the marsh surface and waves of 40–80 cm in height) (Möller et al. 2014).

While the importance of plant stem flexibility has begun to be recognized through the studies mentioned above, field studies on plant stem flexibility are still scarce and limited to only a few species (see, for example, Feagin et al.'s 2011 study on *Spartina alterniflora*). Laboratory flume studies providing a controlled environment to investigate vegetation-induced flow and wave dissipation often use artificial plant mimics instead of real plants. Quantitative data on plant flexibility can aid to develop more realistic plant mimics and hence a more realistic representation the interaction between vegetation and hydrodynamics in flume studies.

A realistic representation of the interactions between flow and vegetation is also needed for accurately modelling coastal hydrodynamics. While some models approximate vegetation with higher bottom friction factors (Möller et al. 1999, Augustin et al. 2009), the majority of numerical models capture vegetation effects in a vegetation factor that consists of e.g. plant stem height, stem density and diameter and a empirical bulk drag coefficient C_D e.g. (Kobayashi et al. 1993; Mendez and Losada 2004; Paul and Amos 2011; Möller et al. 2014). C_D is a function of both flow regime and plant characteristics and accounts for the ignorance of varying responses of different plant species to hydrodynamic forcing, that means it can be calibrated to different plant architecture or flexibility. The inclusion of a vertical layer schematization for the vegetation as proposed by Suzuki et al. (2011), enables the calibration of C_D for vertical variations in canopy density. In general the value of C_D reflects the flow resistance provided by vegetation, for example canopies composed of flexible plants with low amounts of above ground biomass can be expected to yield lower values of C_D than stiff plants and large amounts of above ground biomass.

Salt marshes present a great diversity in plant architecture and a significant degree of flow resistance might be achieved by branching upper stems and their leaves in addition to the basal stems (Möller and Spencer 2002; Möller 2006; Paul et al. 2014a). As above ground biomass varies with volume and density of plant material present, it can be regarded as a useful proxy for these more complex structural canopy bulk properties, if not necessarily for flexibility and buoyancy. At the scale of plant stands, a positive correlation between canopy density, above ground biomass and wave dissipation has been observed (Koch and Gust 1999; Bouma et al. 2005; Möller 2006). As branches and leaves can constitute a significant proportion of the overall plant above ground biomass (Russell et al. 1990), these non-stem components may contribute significantly to wave dissipation. Canopies with the same total above ground biomass, however, can differ in stem flexibility, buoyancy, canopy architecture and the amount of biomass present at different levels within the canopy. Apart from affecting the canopy’s flow- and wave-dissipation capacity above ground biomass and the arrangement of plant elements within the canopy (canopy structure) also play an important role for sediment dynamics and carbon stocks in salt marshes and constitutes an important habitat factor for arthropod and breeding-bird communities (Mandema et al. 2013; Temmerman et al. 2005; Van Klink et al. 2013;).

The dependence of a range of ecosystem services (e.g. coastal protection, carbon stocks and habitat provisioning) on a complex set of salt marsh vegetation canopy attributes calls for a critical assessment of methods that can be used to measure not only above ground biomass but also canopy structure, and the vertical distribution of both, which cannot be captured as such by traditional biomass harvesting methods (Neumeier 2005).

As a method of capturing the more complex structure of vegetation canopies in non-destructive ways, side-on photography of vegetation (Zehm et al. 2003; Möller 2006), hereafter referred to as the photo-method), has been trialled. Observed wave and flow dissipation by simple salt marsh canopies composed of *Salicornia europaea*, *Suaeda maritima* and *Spartina anglica* has been found to reflect variations in both above ground biomass and projected surface area of the canopy as determined by the photo-method (Möller 2006).

A difficulty of this methodology is that flow resistance by dense canopies could be underestimated. Beyond a critical threshold value of biomass, plant elements may shade one another and a further increase of biomass may thus no longer be reflected in an increase in the projected surface area. The relationship between projected surface area and biomass, however, has not yet been established for a wider range of canopy densities and for different types of canopy architecture.

Furthermore, there has so far been no comparison between the photo-method and other non-destructive ways of assessing above ground biomass and canopy structure such as the measuring of light availability in the canopy (Schrautzer and Jensen 2006). The light measurement approach originates from the field of agricultural science, where it has been used to estimate crop yields (Webb et al. 2008). In comparison to the photo-method, measurements of light availability offer several advantages. The above ground biomass estimates are derived by analysing a larger surface area and can be calculated directly from the light availability recorded, while the photo-method requires the complex processing of vegetation photographs that can be affected by subjective interpretation (Neumeier 2005). Moreover, damage to the vegetation is minimized as the slim light measuring probe can be easily inserted into even the densest canopies.

In this study we consider plant flexibility and above ground biomass, two biophysical properties of salt marsh canopies that both need to feed into wave dissipation models, if the predictive capacity of such models is to be improved; furthermore we evaluate two methodologies to assess above ground biomass as a proxy for more complex canopy bulk properties such as canopy structure and density:

(i) we present field observations of stem flexibility as well as stem diameter and stem length of *S. anglica*, *Puccinellia maritima* and *E. athericus,* three grasses that form large stands in many salt marshes of NW Europe; and

(ii) we compare the performance of the photo-method with that using measurements of light availability for non-destructive assessment of above ground biomass in canopies of two salt marsh species with different canopy structure: *Atriplex portulacoides*, a dense low growing dwarf shrub and *E. athericus*, a tall upright growing grass.

Our study thus presents the first data set with systematically collected information on biophysical properties of salt marsh canopies acquired by using a series of alternative methodologies. In this way it provides critical input not only for the study of the ecological importance of canopy structure but also for a greater insight into the reasons why an approximation of hydrodynamic drag based solely on incident flow regime and plant stem density, diameter and height, remains elusive.

Methods

Study site

Field measurements were undertaken in a macro-tidal (MSTR = 4.8 m; Reed 1988) salt marsh of the UK east coast (Southern North Sea), near Tillingham on the Dengie Peninsula in Essex (Fig. 3.1). The Dengie marshes lie between the estuaries of the Rivers Blackwater and Crouch and form a narrow belt with a maximum of 700 m in marsh width between low lying agricultural land and extensive intertidal mudflats. Over the past 100–150 years the marshes have experienced several phases of advance and retreat (Harmsworth and Long 1986; Pye 2000). Marsh surfaces are composed of clayey silts and are approximately horizontal, with elevations of between 2.4–2.7 m ODN (Ordnance Datum Newlyn, which approximates to mean sea level; Fig. 3.1b, 3.1c). Current rates of relative sea level rise for the Dengie Peninsula have been estimated at 2–3 mm a^{-1} (Burningham and French 2011). The vegetation of the Dengie marshes is typical of UK east coast salt marshes (Adam 1988). Marsh edge erosion has all but removed the low marsh communities near Tillingham, but near the seaward marsh edge, plant communities occur at elevations ≤2.5 m ODN; Fig. 3.1b, 3.1c) and are characterized by *Aster tripolium*, *S. anglica, Suaeda maritima* and pioneer *Salicornia europaea*. Mid to high marsh plant communities occur at elevations >2.5 m ODN (Fig. 3.1b, 3.1c) and are characterized by a canopy of *P. maritima* and *A. portulacoides* with *E. athericus* occurring on levees along creek margins. These species form mixed canopies but also exist in distinct mono-specific patches of several square metres in size, such that approximately uniform vegetation types can be found in close proximity to each other. Over an annual time scale, offshore wave heights have been estimated as averaging 1.09 m (on Long Sand Head, 42 km NE of Tillingham), while winter (January) mean monthly maxima reach 1.45–1.70 m (Herman 1999). Over the vegetated marsh edge (at an elevation of 2.4 m ODN) at Tillingham (Fig. 3.1b, 3.1c), water depths have been observed to vary between 0.12 and 0.84 m (mean of 0.43 m) over 236 tidal inundations recorded within one year. For the same tides and time period, significant wave heights were less than 0.87 m on all occasions over the tidal mudflat (Möller and Spencer 2002).

Species

S. anglica C.E. Hubbard

S. anglica is a perennial grass typically occurring in the pioneer zone and the low marsh (Adam 1993). Throughout the last century, *S. anglica* has spread from its original site (southern coast of UK), both naturally and through deliberate transplantation, to salt marshes all over Europe. The main reason for the planting of *S. anglica* was the perceived stabilization of mudflats as a precursor to land claim or for coastal protection.

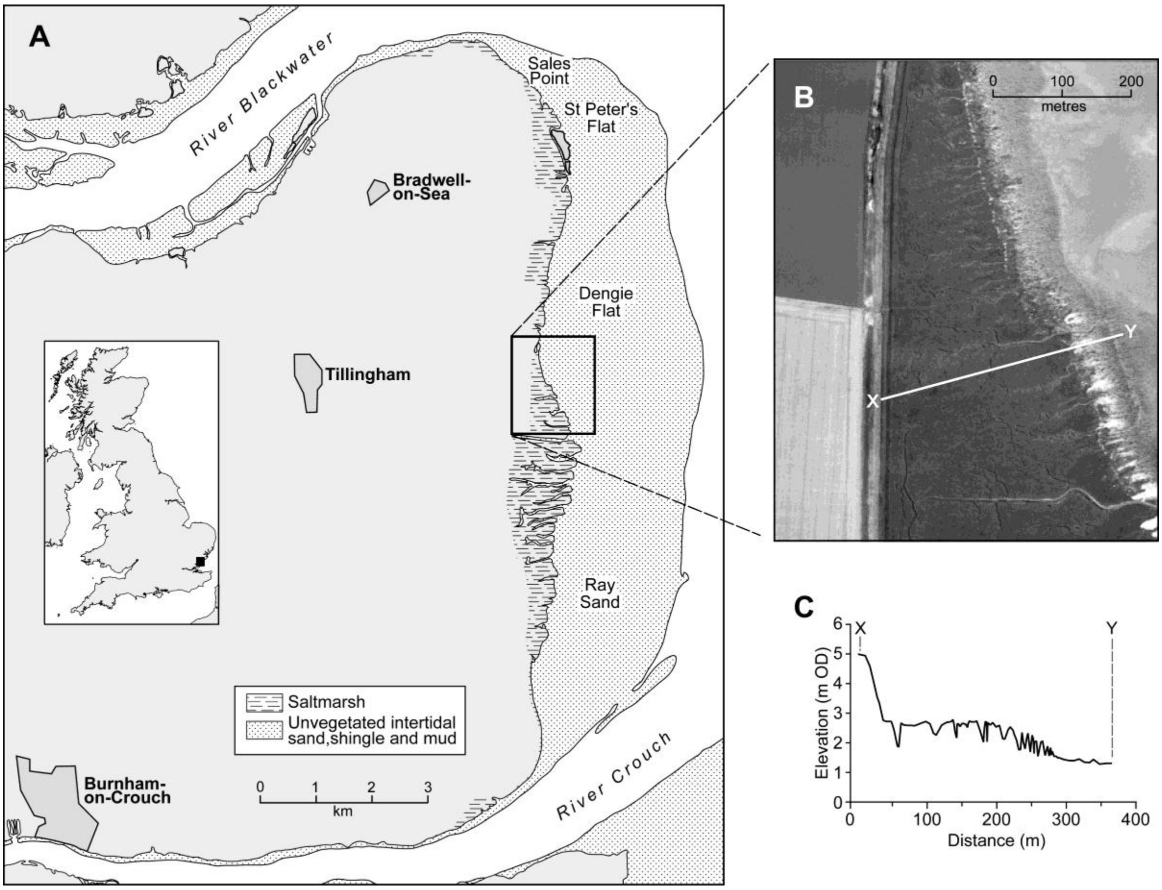


Figure 3.1. Study site at the Dengie marshes, Essex, England, UK. Along the transect from X (sea defenceboundary) to Y (intertidal mudflat) across the marsh platform mid marsh plant communities occur at elevations >2.4 m ODN (Ordnance Datum Newlyn, which approximates mean sea level) and low marsh and pioneer plant communities at elevations ≤2.4 m ODN.

P. maritima Huds. Parl.

The perennial grass *P. maritima* has its typical habitat in the low marsh, although at Tillingham, it extends into the mid marsh and in salt marshes with sandy substrates it can also be found in the pioneer zone. *P. maritima* is a common grass of European salt marshes and especially of grazed salt marshes, as the species is tolerant to trampling, biomass loss and waterlogging.

A. portulacoides (L.) [syn. Halimione portulacoides Aellen, Obione portulacoides (L.) Moq.]

A. portulacoides is a perennial dwarf shrub occurring in European salt marshes, but also in salt marshes along the coasts of North Africa and South-West Asia (Redondo-Gomez et al. 2007). The distribution of *A. portulacoides* within salt marshes depends on soil drainage as the species is lacking aerenchyma and needs aerated substrates. It thus often colonizes creek bank levees on mid- to upper marshes (Cott et al. 2013). In salt marshes of the Wadden Sea on the Eastern fringes of the North Sea *A. portulacoides* often forms monospecific stands in the low marsh. Moreover, the species is sensitive to grazing and trampling.

E. athericus (L.)

The tall grass *E. athericus* occurs in European salt marshes from northern Portugal to southern Denmark and along the southern and south eastern coasts of the British Isles (Veeneklaas et al. 2013). Like *A. portulacoides, E. athericus* needs aerated substrates and is sensitive to grazing. In recent decades *E. athericus* has rapidly colonized mainland salt marshes along the North Sea coast, its expansion being related to the abandonment of grazing, high vertical accretion rates and high marsh age (Rupprecht et al. 2015a).

Measurements of plant stem flexibility

To study plant stem flexibility under bending forces orthogonal to the plant stem, as occurs in vegetation canopies under wave forcing, we conducted three-point-bending tests with bottom, middle and top stem sections of *S. anglica*, *P. maritima* and *E. athericus*. These tests yielded information on Young's bending modulus, E, a measure describing how much force has to be applied to bend the stem to a defined displacement. The higher the value for E, the less flexible the plant stem. The second moment of area I describes the effect of stem morphology (considering stem diameter) on its flexibility. The value of I increases with stem diameter. The product of E and I, known as flexural rigidity, gives a measure of overall stem flexibility. High values of flexural rigidity indicate low stem flexibility.

Samples were collected in the study area in July 2013. For each plant species a small salt marsh section (around 25 cm^2) was excavated, placed in a bucket and transferred to the laboratory. The three-point-bending tests (hereafter referred to as bending tests) were conducted within 14 days of excavating the plants and soil base in the field. Within this time period, plants were kept outside and watered with fresh water.

In total 15 stems of each species were harvested and used for bending tests. Prior to performing the tests, stem length up to the onset of the youngest leaf was measured and stems were divided into three equal parts (bottom, middle, top). The test section was cut from the middle of each part. To minimize the effect of shear stress, a maximum stem-diameter-to-length ratio of 1:15 was chosen. At each end of the stem sections, two diameters were measured with an electronic caliper (precision ± 0.5 mm). Bending tests of *S. anglica* were conducted with a standardized stem section length of 50 mm and, for *P. maritima* and *E. athericus*, a length of 36 mm.

The bending tests were performed with an INSTRON 5544 mechanical testing machine (precision ± 0.5%) using a 100 N load cell (INSTRON Corporation, Canton, MA, USA). The stem test section was placed centrally onto two support bars and a metal bar was lowered from above at a displacement rate of 10 mm min^{-1} (Fig. 3.2). The vertical deflection of the stem, D, and the corresponding force, F, were recorded. Flexural rigidity was calculated from the slope of the force deflection curve F/D as $EI = (s^3F)/(48D)$, where s is the horizontal span of the stem between the two support bars (Fig. 3.3) (Usherwood et al. 1997).

The second moment of area was calculated as

$$I_c = \pi d^4/64 \qquad [3.1]$$

for circular cross sections (*S. anglica*, *P. maritima* and *E. athericus*) and as

$$I_{ch} = \pi(d^4_{\text{outer}} - d^4_{\text{inner}})/64 \qquad [3.2]$$

for circular hollow cross sections (as occurring for some bottom stem sections of *S. anglica*), where *d* = stem diameter (Niklas 1992). From the flexural rigidity, *EI,* and the second moment of area, *I*, the Young's bending modulus, *E*, was calculated as

$$E=EI/I_c = (4\, s^3 F)/3D\pi\, d^4) \qquad [3.3]$$

for stem sections with a circular cross section and as

$$E=EI/I_{ch} \qquad [3.4]$$

for stem sections with a circular hollow cross sections. To analyse the differences in flexural rigidity between species and between stem sections within each species, Kruskall-Wallis tests were performed using R software version 3.1.0 (R Development Core Team, Vienna, AT) as the data did not meet the assumptions required for an Analysis of Variance (ANOVA).

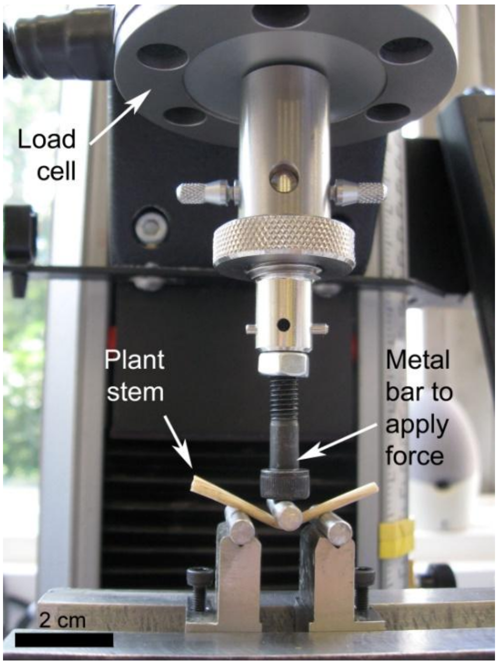


Figure 3.2. Three-point-bending test apparatus and bending test of a stem section of *Elymus athericus*.

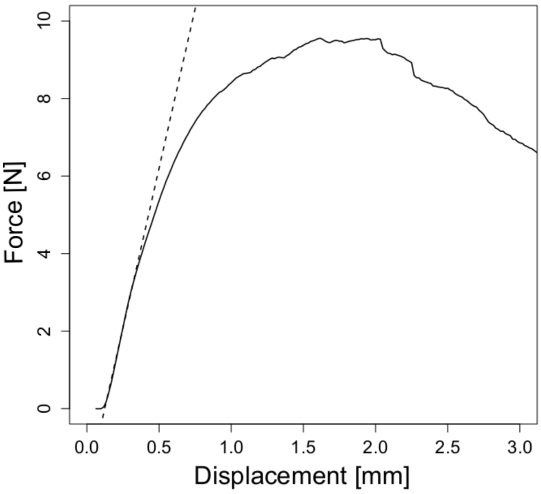


Figure 3.3. Force-displacement curve (solid line) from a middle part of a stem of *Elymus athericus.* Young's bending modulus and flexural rigidity were calculated from the slope of the initial linear part (dotted line). The curve shape is representative for all species and stem parts in this study.

Non-destructive assessment of above ground biomass by the photo-method and by measurements of light availability

Field measurements were undertaken in July 2013. In both stands of *A. portulacoides* (hereafter referred to as *Atriplex*) and *E. athericus* (hereafter referred to as *Elymus*) 10 plots of 1 x 1 m size were chosen to represent a range of various canopy densities. Canopy height was measured at 10 randomly chosen locations within each plot using a folding rule. In the case of *Elymus*, the stem length was recorded whilst for *Atriplex* the height of the youngest leaf or branch tip was measured. At each plot, light availability in the canopy was recorded initially, followed by the application of the photo-method as described below. To calibrate both methods by identifying the relationship between light availability and dry above ground biomass (hereafter referred to as biomass) as well as between canopy density on the photograph and biomass, the vegetation contained in the plot sections used for the photo-method (0.6 m x 0.2 m) was harvested and the dry biomass determined, after drying for 48 h at 60^{o}C.

Measurement of light availability

Light availability in the canopy was recorded by measuring photosynthetically active radiation (PAR) with a Sunscan Canopy Analysis System (Delta T Devices Ltd. Cambridge, UK). The method uses a 0.015 m x 1 m probe containing 64 photodiodes that is inserted into the canopy (Fig. 3.4a). Light conditions were clouded skies at noon. On each of the 1 m^2 plots five measurements were taken in the *x*- and five in the *z*-dimension of the plot. All measurements were taken on the soil surface above the litter layer. PAR measurements were expressed as relative irradiance (*RI*) which characterizes the light intensity within the canopy relative to that existing above the canopy. PAR above the canopy was measured with a incident solar radiation sensor mounted on a tripod immediately above the canopy. *RI* decreases with increasing canopy density from the top of the canopy towards the soil surface. For a better comparability of *RI* with results of the photo-method, we converted the *RI*-values into values of '*RI absorbed*' (*RIA*) where *RIA* = 100 - *RI*.

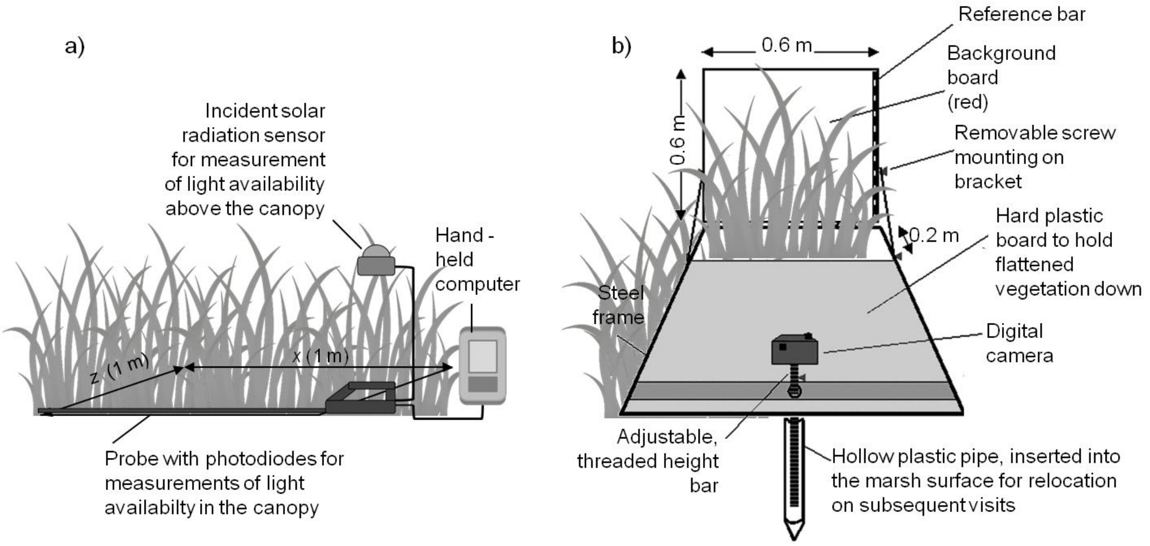


Figure 3.4. a) Sun scan canopy analysis system used to measure light availability in and above the canopy; **b)** portable digital photograph frame used to capture side-on photographs of salt marsh vegetation.

Photo-method

On each plot a digital photograph of a 0.6 m wide by 0.2 m deep strip of salt marsh vegetation was taken against a red background board using a portable photo-frame (Fig. 3.4b).

The digital images were processed using Erdas Imagine 10.1 image processing software and a series of programme routines written in Matlab R2012a software to achieve:

1) Rectification and cropping of the image to the size of the background board, thus excluding all other elements besides vegetation and background from the digital photograph (Matlab);

2) Unsupervised classification of each image into 20 classes and subsequent manual class attribution to two classes, yielding binary images with the two classes 'vegetation' (0, black pixels) and 'background' (1, white pixels). Figure 3.5 shows a binary picture of the *Atriplex* and the *Elymus* canopy (Erdas Imagine);

3) Further analysis to provide detail on the projected surface area of vegetation expressed as the overall area of vegetation pixels (m^2) per m horizontal image dimension or *vegetation pixel density* (Matlab).

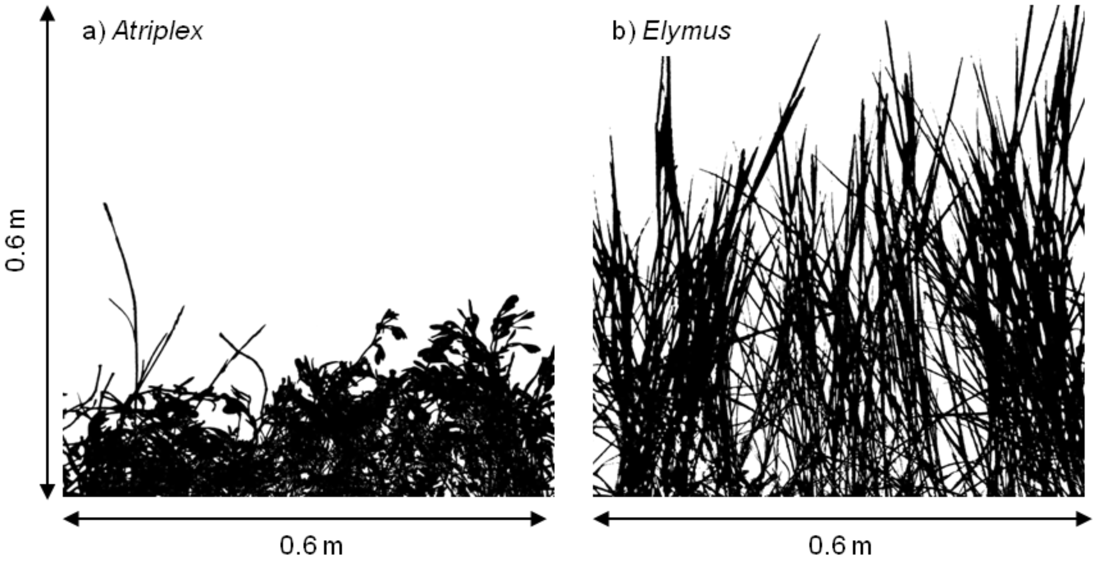


Figure 3.5. Classified binary black and white digital images of the canopy of **a)** *Atriplex portulacoides* and **b)** *Elymus athericus* used to estimate above ground biomass from vegetation pixel density from side-on photographs of vegetation.

Non-destructive assessment of vertical distribution of biomass

In *Elymus* we also applied measurements of light availability and the photo-method to estimate the vertical distribution of biomass within the canopy (hereafter referred to as vertical biomass distribution). Three 1 m^2 plots of *Elymus* similar in canopy density, height (around 0.6 m) and above ground biomass (0.6 ± 0.01 kg/m^2) were chosen. At these plots, light availability was recorded as described in Methods section 'Measurement of light availability', on top of the litter layer and at two further canopy heights, 0.2 m and 0.4 m above the litter layer respectively. Subsequently, the photo-method was applied as described in Methods section 'Photo-method' three times on each plot. Vegetation pixel density was calculated separately for the vertical canopy layers >0.4–0.6 m (top layer), >0.2–0.4 m (middle layer) and 0–0.2 m (bottom layer; 0 m refers to the top of the litter layer, approximately 5 cm above the soil surface). To identify the relationship between light availability and the vertical biomass distribution as well as between vegetation pixel density and vertical biomass distribution, the vegetation contained in the top, middle and bottom canopy layer of the photographed sections of each plot was harvested, transferred to the laboratory, dried for 48 h at 60°C and weighed.

Results

Plant stem flexibility

Measurements of stem length and diameter (Table 3.1) showed that *S. anglica* and *P. maritim*a were comparable in stem length. The stem length of *E. athericus* exceeded that of *S. anglica* and *P. maritima* by a factor of 2. The stem diameter of *P. maritima* and *E. athericus* was on average around half that of the stem diameter of *S. anglica*.

Flexural rigidity of the three salt marsh grasses under investigation ranged from 0.17 x 10^{-3} Nm^2 (*P. maritima* top stem part) to 3.51 x 10^{-3} Nm^2 (*S. anglica* bottom stem part; Fig. 3.6, Table 3.1).

Flexural rigidity was significantly different between all three species (Kruskall-Wallis test, H = 59.33, 2 d.f., $p < 0.01$) and decreased from the bottom to the top of plant stems. In all three species a significant difference was found between the top third and the rest of the stem (Kruskall-Wallis test: *S. anglica*, H = 22.50, 2 d.f. 2, $p < 0.01$; *P. maritima* H = 24.60, 2 d.f. 2, $p < 0.05$; *E. athericus* H = 13.12, 2 d.f. 2, $p < 0.01$).

Values of the Young's bending modulus *E* ranged from 118.28 MPa (*S. anglica* bottom stem part) to 4081.79 MPa (*E. athericus*, bottom stem part; Table 3.1).

Table 3.1. Mean values (±1 SD) for biomechanical properties of three salt marsh grasses.

	Stem diameter [cm]	**Stem length [cm]**	**Flexural rigidity [x10^{-3} Nm^2]**	**Young's bending modulus [MPa]**	**Sample size n**
S. anglica		27.87 ± 4.66			15
Bottom	0.45 ± 0.06		3.51 ± 0.58	118.28 ± 49.94	15
Middle	0.48 ± 0.05		3.29 ± 1.14	122.90 ± 36.05	15
Top	0.23 ± 0.07		0.69 ± 1.10	310.86 ± 136.93	15
P. maritima		23.93 ± 6.94			15
Bottom	0.14 ± 0.01		0.40 ± 0.14	1995.35 ± 648.70	15
Middle	0.15 ± 0.02		0.45 ± 0.17	1764.90 ± 354.44	15
Top	0.15 ± 0.02		0.17 ± 0.07	736.54 ± 280.60	15
E. athericus		46.00 ± 12.30			15
Bottom	0.16 ± 0.02		1.23 ± 0.64	4081.79 ± 1386.30	15
Middle	0.17 ± 0.02		1.01 ± 0.42	2755.09 ± 694.03	15
Top	0.16 ± 0.02		0.61 ± 0.32	1952.07 ± 667.63	15

Assessment of biomass with measurements of light availability and the photo-method

Total biomass

The canopy types under investigation, *Atriplex* and *Elymus*, varied in mean biomass and height. The biomass of *Atriplex* was 1.2 ± 0.5 kg/m^2 with a mean canopy height of 33.1 ± 6.5 cm. Mean biomass of E*lymus* was 0.6 ± 0.2 kg / m^2, corresponding to around half the biomass of *Atriplex* while the canopy height of *Elymu*s (70.8 ± 7.5 cm) exeeded that of *Atriplex* by a factor of 2.

Results from the calibration of measurements of light availability revealed that in both the *Atriplex* and the *Elymus* canopy biomass increased with *RIA* in a non-linear way. A clear relationship between *RIA* and biomass could not be identified. In dense stands of vegetation a further increase of biomass resulted only in minor increases in *RIA* (Fig. 3.7a, 3.7b).

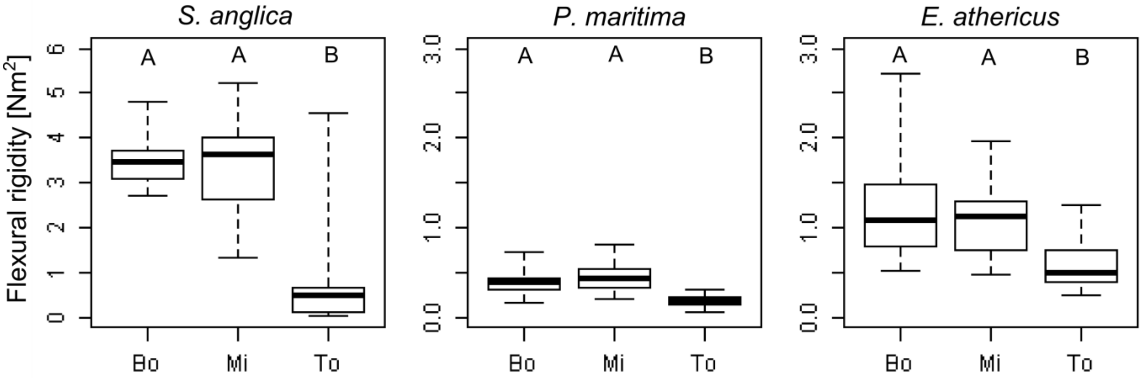


Figure 3.6. Median and variability in flexural rigidity for bottom (Bo), middle (Mi) and top (To) stem parts of three salt marsh grasses. The bottom and top of the box represent the first and third quartiles, ends of whiskers represent the minimum and maximum values. Flexural rigidity was significantly different between all species (Kruskall–Wallis-test, H = 59.33, p <0.01, d.f. = 2). Significant differences in flexural rigidity between bottom (Bo), middle (Mi) and top (To) stem parts of *S. anglica*, *P. maritima* and *E. athericus* are marked with A and B.

In the canopy of *Atriplex*, the amount of biomass beyond which no further increase in biomass could be detected (hereafter referred to as biomass threshold value) was well below the mean biomass of *Atriplex,* at around 0.85 kg/m^2. In the *Elymus* canopy, the biomass threshold value was around 0.68 kg/m^2, close to the mean biomass (0.6 kg/m^2). In both the *Atriplex* and the *Elymus* canopies, values of *RIA* showed high standard deviations (± 5–12%) when biomass was equal or less than 0.6 kg/m^2.

Results from the calibration of the photo-method showed an exponential relationship vegetation pixel density (area of vegetation pixels in m^2 per m horizontal image dimension) and biomass, in the *Atriplex* and *Elymus* canopy, although in *Atriplex* this relationship was somewhat less clear when biomass exceeded 1.0 kg m^{-2} (Fig. 3.7c, 3.7d). In both the canopy of *Atriplex* and *Elymus* the biomass threshold value, beyond which a further increase of biomass would no longer result in an increase of vegetation pixel density, does not appear to have been reached in this study.

Vertical biomass distribution

Our results suggest an exponential relationship between *RIA* in the Elymus canopy at heights above the ground of 0.4 m, 0.2 m and on top of the litter layer (0 m) and the amount of biomass in the top canopy layer, the top and the middle canopy layer and of the whole canopy (Fig. 3.8a). Rates of increase in RIA became smaller with an increase in biomass and conversely with a decrease in height above the ground within the canopy. Measurements of light availability at a defined canopy height represent the cumulative amount of irradiation absorbed by the canopy above. Hence it remains unclear whether this pattern was caused by increase in biomass weight per unit volume or by an increase of canopy density and shading effects.

By contrast the photo-method allowed analysis of vegetation pixel density and biomass in the top, middle and bottom canopy layer alone. We found an exponential relationship between both variables (Fig 3.8b). This suggests that there was an increase in biomass weight per unit volume with decreasing height within the canopy of *Elymus*.

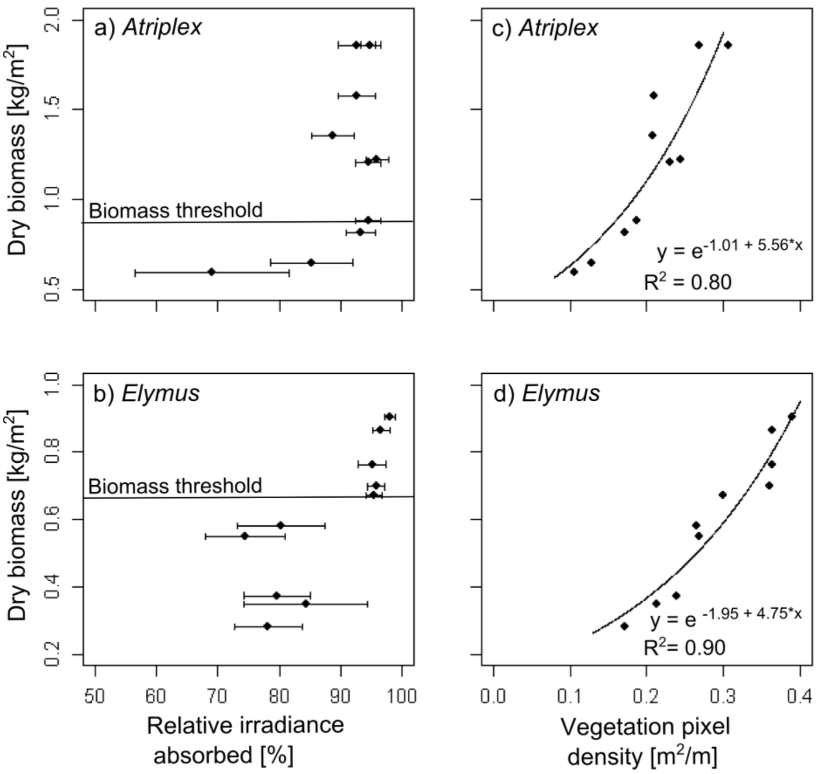


Fig. 3.7. Relationship between light availability (expressed as mean ± 1 SD of relative irradiance absorbed by the canopy) in the canopy of **a)** *Atriplex* and **b)** *Elymus* and above ground biomass (dry weight), the horizontal black line indicates the threshold beyond which a further increase of biomass did not result in an increase of irradiance absorbed. Relationship between density of vegetation pixels as derived from side-on photography of vegetation in stands of **c)** *Atriplex* and **d)** *Elymus* and above ground biomass (dry weight).

Discussion

Plant stem flexibility

This study presents the first quantitative data of stem flexibility for the common salt marsh grasses *S. anglica, P. maritima* and *E. athericus,* building on a previous study of a single related species, *Spartina alterniflora* (Feagin et al. 2011). Except for the very flexible species *P. maritima* (with low values of flexural rigidity), the flexural rigidity values of salt marsh grasses recorded in this study were one to four orders of magnitude higher than those described for seagrasses or

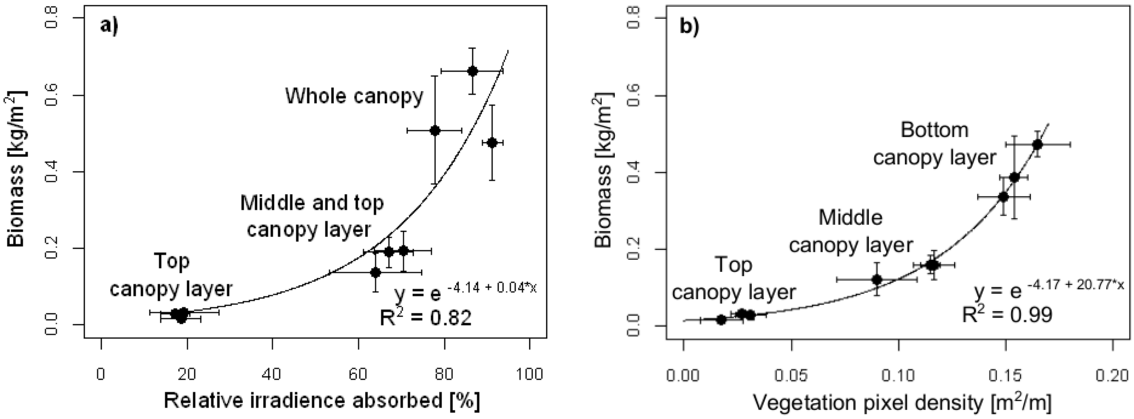


Figure 3.8. Assessment of vertical biomass distribution in the canopy of *Elymus*. **a)** Relationship between light availability (expressed as relative irradiance absorbed by the canopy) at heights of 0.4 m (top canopy layer), 0.2 m (top and middle canopy layer) and 0 m (whole canopy) and the cumulative amount of above ground biomass present at the corresponding canopy heights. **b)** Relationship between vegetation pixel density derived from the analysis of side-on photographs for the top (>0.4 m–0.6 m), the middle >0.2–0.4 m) and the bottom canopy layer (0–0.2 m) and biomass of the respective canopy layers. All values represent mean ± 1 SD from measurements on three plots with a similar amount of above ground biomass (0.6 ± 0.01 kg/m^2).

freshwater plants (Fonseca and Koehl 2006; Miler et al. 2012). Flexural rigidity of bottom and middle stem sections of *S. anglica* and *E. athericus* were within an order of magnitude of flexural rigidity found in stems of brown macroalgae (Paul et al. 2014b).

The fact that flexural rigidity of all three species shows high variability (Fig. 3.6) may be attributed to differences in the stage of life cycle or vitality of plant stems. Environmental factors as a cause for intraspecific variability may be of minor importance in this study, as all analysed plant stems were harvested from one turf of 25 x 25 cm in size. Very high intraspecific variability of flexural rigidity has also been reported for freshwater plants (Miler et al. 2012) and, independent of sample size, for brown macroalgae (Paul et al. 2014b).

Values of Young's bending modulus, *E*, were much higher than those reported so far for aquatic plants (Table 3.2). *S. anglica* yielded the smallest values of *E*, in spite of the fact that the species is known for its stiff and upright growing shoots (Bouma et al. 2005). The high values of flexural rigidity which identify *S. anglica* as the stiffest of the considered plant species, result from high values of the second moment of area *I*, i.e. the large stem diameter. This highlights the importance of considering plant size and morphology (here stem diameter) when determining plant biomechanical characteristics (Niklas 1992). For the related species *S. alterniflora*, Feagin et al. (2011) derived values of *E* of 1410 ± 710 MPa which is five to ten times higher than the values reported here for *S. anglica*. However, Feagin et al. (2011) measured *E* with an improvised 3-point-bending test apparatus and, thus their data may not be strictly comparable to the results from this study.

Biophysical properties of salt marsh plants such as stem flexibility, biomass and vegetation density are key parameters controlling their capacity to dissipate wave and tidal flow energy and hence their ability to establish and grow in coastal environments (Bouma et al. 2005; Bouma et al. 2010). Considering stem flexibility alone, *S. anglica*, the species with the strongest and stiffest shoots of all species investigated here, would be expected to be more effective in dissipation of wave energy than species with very thin and flexible stems such as *P. maritima*. Bouma et al. (2010) compared *S. anglica* and *P. maritima* in their ability to dissipate wave energy and found both species to be equally effective due to much higher values for stem density in stands of *P. maritima*. The fact that stem density may compensate for stiffness illustrates that trade-offs between different biophysical properties needs to be considered when estimating the capacity of marsh surface plant canopies to dissipate wave energy.

Future research should focus on plant movement and breakage in response to various wave conditions as a function of stem flexibility, stem density and biomass. Moreover the values of plant biophysical properties reported here refer to the summer season. Further studies are needed to quantify their seasonal as well as geographical variability.

Non-destructive assessment of biomass

Our results suggest that the non-destructive assessment of biomass as a proxy for the relative degree of canopy resistance to water flow is possible both with measurements of light availability and the photo-method, albeit with a required species-specific calibration and within set biomass limits.

Table 3.2. Young's bending modulus and flexural rigidity (mean ±1 SD) of selected species from seagrass, brown macroalgae, freshwater and salt marsh plants.

	Flexural rigidity [x10^{-3} Nm^2]	**Young's bending modulus [MPa]**	**Source**
Seagrass			
Zostera marina	0.00018		Fonseca and Koehl (2006)
Brown macro algae (stems)			
Aliaria esculenta	2.46 ± 0.62	16 ± 4	Paul et al. (2014b)
Fucus serratus	2.89 ± 0.89	11 ± 4	Paul et al. (2014b)
Laminaria digitata	1.95 ± 0.70	29 ± 13	Paul et al. (2014b)
Freshwater plants			
Glyceria fluitans	0.68 ± 0.27	90 ± 33	Miler et al. (2012)
Myriophyllum alternifolium	0.025 ± 0.11	89 ± 38	Miler et al. (2012)
Ranunculus penicillatus	0.022 ± 0.14	12 ± 7	Miler et al. (2012)
Salt marsh plants			
Spartina alterniflora		1410 ± 710	Feagin et al. (2011)

The non-linear relationship between light availability (expressed as percentage of relative irradiation absorbed by the canopy (*RIA*)) and biomass reported here is in accordance with results of Schrautzer and Jensen (2006), who estimated biomass of fen grasslands by measuring light availability. The high standard deviations of light availability in the canopies of *Atriplex* and *Elymus* when biomass was equal or less than 0.6 kg/m^2 suggest that the position of the irradiation measuring probe had a great effect on records of light availability if the canopy density was low. With respect to the photo-method, the clear exponential relationship between projected surface area of vegetation (expressed as vegetation pixel density) and biomass apparent in the *Elymus* canopy, supports the findings of Möller (2006) who estimated biomass with the photo-method at various canopy densities in stands of *S. anglica* (Fig. 3.7d). In the structurally complex *Atriplex* vegetation type, more samples are needed to verify the exponential increase of biomass with vegetation pixel density (Fig. 3.7c).

Two main reasons account for the non-linear trend between absorbed relative irradiation and biomass as well as vegetation pixel density and biomass reported here. First, when canopy density increases plant elements in the different horizontal and vertical canopy layers may shade one another, causing saturation in absorbed relative irradiation and in vegetation pixel density. According to our results, measurements of light availability are more sensitive to saturation and an underestimation of biomass due to shading effects than the photo-method.

Second, the space occupied by a plant element in the canopy is not directly related to its weight per volume unit (Neumeier 2005). Consequently, an increase of biomass due to an increase of woody plant elements is not necessarily reflected by a decrease in light availability or an increase in vegetation pixel density. This applies particularly to assessments of the vertical biomass distribution in the canopy, as in stands of many plant species the percentage of woody plant elements increases near the soil surface.

Our results suggest that the photo-method is more appropriate to assess the vertical distribution of biomass in the canopy than measurements of light availability at different heights within the canopy. Light availability recorded at a defined height within the canopy represents the cumulative absorption of relative irradiation by the canopy layers above. Light penetration from one canopy layer through to the next is strongly affected by variation in spatial arrangement and orientation of plant elements within the canopy. Consequently, it is difficult to establish a relationship between the amount of irradiation absorbed by the top, middle and bottom canopy layer alone and the biomass present in the respective layers.

By contrast, the photo-method allowed for the analysis of vegetation pixel density and biomass in the bottom, middle and top canopy layer. The increase in biomass weight per unit volume with decreasing height in the canopy found in this study implies an increase of lignifications and stiffness of *Elymus* stems near the soil surface – an assumption that is confirmed by the results of the stem flexibility measurements reported in this paper.

Future studies that aim to quantify vegetation canopy resistance to water flow must also address the complication that arises when the submergence of the canopy results in a vertical biomass distribution within the canopy that differs from that measured when the canopy is dry. Once again, the need to consider such canopy buoyancy effects may be species specific, with stiff and upright growing species, such as *Spartina* spp., being less affected than species with more flexible stems, such as *Puccinellia* spp. or *Elymus* spp..

Conclusions

This study is the first to provide systematically acquired information on biophysical properties with application to wave dissipation of four typical plant species of NW European salt marshes. It is also the first to compare the performance of two methods for the non-destructive assessment of biomass in salt marshes. Our results show significant differences in stem flexibility, both between different species and between the different stem parts of specimens of one species. This underlines the fact that biomechanical properties often vary not only between, but also within, the individuals of a plant species (Feagin et al. 2011; Miler et al. 2012; Paul et al. 2014b). Flexibility of plant stems and its vertical distribution affects the bending angle and re-orientation of stems under wave forcing (Feagin et al. 2011).

The comparison of methods for the non-destructive assessment of biomass and canopy structure showed that the photo-method is a more appropriate technique than the measurement of light availability. While measurements of light availability showed saturation at low biomass values, analysis of digital photographs of vegetation allowed for the estimation of biomass over the whole range of biomass values and in both types of canopy architecture tested. Moreover, it was more suitable for the estimation of vertical biomass distribution and, given that it measures the area of the vegetation elements projected into horizontal flow (rather than obstruction to light coming from above), could be considered a more meaningful parameter in relation to flow and wave dissipation.

Our study suggests a way forward for the measurement/quantification of biophysical properties of salt marsh canopies with high relevance to studies of habitat structure and ecosystem functioning as well as flow and wave energy dissipation in salt marsh environments. Considering the application of our findings in numerical models dealing with the interaction between flow and vegetation, data on canopy biomass and structure as well as plant flexibility should now be combined with measurements of flow regime and wave dissipation, to investigate whether it is possible to quantify the currently empirically derived relationship between flow regime, plant spacing (height and diameter), drag, and wave dissipation, a priori. This would mean that models for wave dissipation over such structurally complex canopies could be applied without the requirement for empirical calibration of drag against observed dissipation.

Acknowledgements

This study was carried out with the financial support of the German Academic Exchange Service (DAAD; grant number D/12/44810), while the first author was a visitor at the Cambridge Coastal Research Unit, University of Cambridge. We thank Dr. Michelle Oyen, Anne Bahnweg, Len Howlett and Alan Heaver, Department of Engineering, University of Cambridge, for advice and assistance provided in the measurements of plant stem flexibility.


5
6
7
8
9
10

4

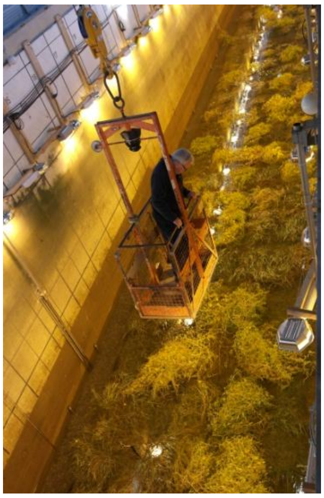
Wave attenuation over coastal salt marshes under storm surge conditions

Iris Möller, Matthias Kudella, Franziska Rupprecht, Tom Spencer, Maike Paul,
Bregje K. van Wesenbeeck, Guido Wolters, Kai Jensen, Tjeerd J. Bouma,
Martin Miranda-Lange and Stefan Schimmels

Nature Geoscience 7 (2014) 727–731

Abstract

Coastal communities around the world face an increasing risk from flooding as a result of rising sea level, increasing storminess and land subsidence (Woodruff et al. 2013; Wong 2014). Salt marshes can act as natural buffer zones, providing protection from waves during storms (Koch et al. 2009; Loder et al. 2009; Gedan et al. 2011; Shepard et al. 2011; Temmerman et al. 2013). However, the effectiveness of marshes in protecting the coastline during extreme events when water levels are at a maximum and waves are highest is poorly understood (Kirwan and Megonigal 2013; Bouma et al. 2014). Here we experimentally assess wave dissipation under storm surge conditions in a 300-metre-long wave flume tank that contains a transplanted section of natural salt marsh. We find that the presence of marsh vegetation causes considerable wave attenuation, even when water levels and waves are highest. From a comparison with experiments without vegetation, we estimate that up to 60% of observed wave reduction is attributed to vegetation. We also find that although waves progressively flatten and break vegetation stems and thereby reduce dissipation, the marsh substrate remained stable and resistant to surface erosion under all conditions. The effectiveness of storm wave dissipation and the resilience of tidal marshes even at extreme conditions suggest that salt marsh ecosystems can be a valuable component of coastal protection schemes.



Coastal margins are experiencing increased pressure from both physical environmental (sea-level rise, increased storminess; Jones et al. 2012) and human use (increased population densities, resource requirements; Kabat et al. 2009) perspectives. This has resulted in a re-evaluation of coastal flood and erosion risk reduction methods (Shepard et al. 2011). Natural coastal landforms, including sand dunes, mudflats and salt marshes, are now widely recognized as potential barriers to wave and tidal flow or as wave/tidal energy buffers (Kabat et al. 2009; Barbier et al. 2011; Temmerman et al. 2013; USACE 2013). The inclusion of such natural features into quantitative flood risk assessments, however, has been hampered by a lack of: empirical evidence for their capacity to act as wave dissipaters under extreme water level and wave conditions (when their coastal protection service is most required); and a quantitative understanding of their ability to survive those types of conditions (Fagherazzi et al. 2006; Mariotti and Fagherazzi 2013; Bouma et al. 2014; Spalding et al. 2014).

Previous studies have suggested that wave dissipation over submerged salt marsh canopies is dependent on water depth and incident wave energy, and that hydrodynamic conditions may exist beyond which marshes lose their wave dissipating effect (Möller et al. 1999; Gedan et al. 2011; Yang et al. 2012). The existence of such conditions makes intuitive sense, as the orbital wave motion that is affected by the submerged vegetation canopy decreases with increasing depth and decreasing incident wave energy. Existing empirical studies of wave reduction over vegetated canopies have, however, been limited to low water depths (<1 m) and low wave heights (<0.3 m) (Möller and Spencer 2002; Yang et al. 2012).

Salt marsh resistance to wave impact is intricately connected to wave dissipation over salt marsh surfaces (Duarte et al. 2013). Under high energy conditions, dissipation of wave energy may be achieved by wave shoaling/breaking as well as removal of material (both plant and soil) from the marsh edge/surface, rather than only by drag from the vegetation canopy (Möller and Spencer 2002). Existing evidence points to the stabilizing effect of organic matter with respect to resistance of the marsh surface to erosion by waves from above (with contrasting evidence for roots increasing erosion on exposed marsh margins; Feagin et al. 2009). Little is known, however, about the response of the marsh soil to extreme levels of wave impact, as might be experienced during a storm surge. The stability of the marsh surface under such conditions is critical to any assessment of its usefulness as part of coastal flood risk reduction schemes.

Here we present results of a unique large-scale flume experiment with three key aims: to explore the dissipation of waves over a vegetated marsh canopy under storm conditions; to quantify the effect of vegetation on wave attenuation compared with the effects of a mowed platform; and to quantify the response of marsh vegetation and soil surface to incident wave energy.

Waves were generated in a 300-m-long, 5-m-wide and 7-m-deep flume over a test section of almost 40 m length consisting of a coherent patchwork of marsh blocks (Fig. 4.1a). Blocks were characterized by a mixed canopy of *Elymus athericus*, *Puccinellia maritima*, and

Atriplex prostrata, typical of mid to high southern North Sea marsh communities (Fig. 4.1b–d). Whereas incident wave heights on salt marsh margins are limited by shallow inshore water depths and thus are generally low (<0.3 m), above-marsh water depths are known to reach or exceed 2 m, accompanied by wave heights (H_s) in excess of 0.8 m, during storms (Möller and Spencer 2002). Tests were thus conducted for regular and irregular non-breaking waves of heights up to 0.9 m in 2 m water depth above the vegetated bed. There was no statistical difference between flume and field soil bulk density, stem diameter and plant stem flexibility (Young's modulus; t-test; p >0.05; see Table 4.1 and Supplementary Information for detail).

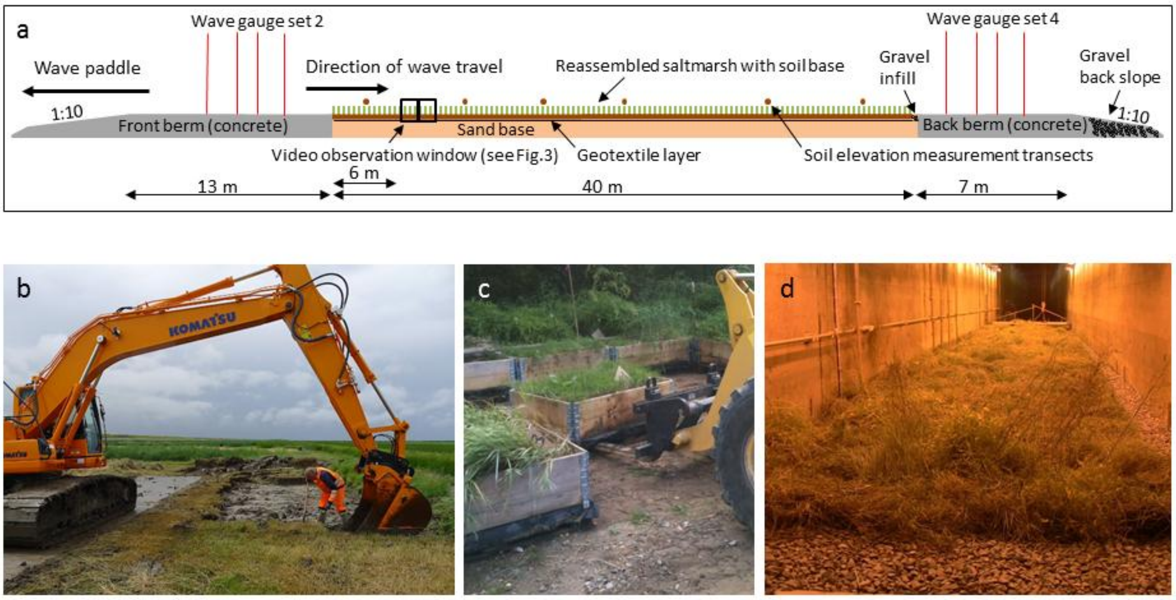


Figure 4.1. Experimental set-up and photographs of excavation. **a**, General experimental set-up in the wave flume, with position of recording equipment relevant to reported results. **b**, Excavation of marsh blocks, northern German Wadden Sea (53° 42.7540' N, 7° 52.9630' E). **c**, Marsh blocks with *Elymus* vegetation cover before positioning in the flume test section. **d**, Reassembled salt marsh inside the 5-m-wide flume, looking towards the wave generator; lamps are mounted at about 3 m above the soil surface.

Table 4.1. Plant stem flexibility (Young's modulus), height, density and diameter and soil bulk density at the field site where marsh blocks were extracted and in the flume immediately before the experimental runs (means ± 1 SD).

	Stem flexibility Young's bending modulus [MPa]		**Stem height [mm]**	**Stem diameter [mm]**		**Stem density [number per 20 x 20 cm quadrat]**		**Dry soil bulk density [g cm^{-3}]**	
	Mean	**N**	**Mean**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**
***Puccinellia* (Flume)**	111.6 ± 66.3	17	220 ± 30	1.1 ± 0.3	17	-	-	0.6 ± 0.3	10
***Puccinellia* (Field)**	284.5 ± 369.1	17	-	1.2 ± 0.2	17	-	-	0.7 ± 0.5	20
***Elymus* (Flume)**	2,696.3 ± 1,963.8	18	700 ± 10	1.3 ± 0.3	18	49 ± 23	10	0.7 ± 1.0	20
***Elymus* (Field)**	2,514.6 ± 2,977.1	18	-	1.7 ± 0.4	18	68 ± 8	10	0.8 ± 0.7	20

Results show a clear dissipation pattern, remarkably consistent between regular and irregular waves. For regular waves, wave energy dissipation over the 40 m distance increased linearly from no dissipation in the case of waves with H = 0.1 m and T = 1.5 s to 19.5 % reduction for H = 0.3 m and T = 3.6 s (Fig. 4.2a). For irregular waves, dissipation between 11.9 and 17.9% occurred for $H_{rms,0}$ of 0.2–0.4 m (Fig. 4.2b). When incident wave heights increased beyond these levels, dissipation reduced to 13.8% for regular (H = 0.6 m, T = 3.6 s, Fig. 4.2a) and to 14.7% for irregular waves ($H_{rms,0}$ = 0.6 m, T_p =4.0 s, Fig. 4.2b), before increasing to 16.9% for the largest regular waves (H = 0.7 and 0.9 m; T = 5.1 and 4.1 s) and to 16.9% for the largest irregular waves ($H_{rms,0}$ =0.7 m, T_p = 6.2 s).

Dissipation over the mowed surface was significantly lower in all regular wave tests (t-test, $p < 0.05$; Fig. 4.2a) and irregular wave tests (Fig. 4.2b). At (or just after) the point of maximum wave dissipation (H and $H_{rms,0}$ = 0.2–0.4 m), wave height reduction over the mowed section was lower than over the section with intact vegetation by a factor of 0.4. Thus, it can be stated that the vegetation cover alone accounted for 60% of wave height reduction (Fig. 4.2a,b). However, when $\mathrm{H}_{\mathrm{rms},0}$ increased towards 0.6 m, the vegetation cover accounted for only 40% of wave height dissipation (Fig. 4.2b).

Models of wave dissipation by vegetated beds commonly rely on knowledge of the drag coefficient C_D incorporated into a friction factor that takes account of vegetation stem density, height and diameter. The complex nature of salt marsh vegetation precludes the a priori determination of C_D from simple plant metrics. Nevertheless, an exponential decay relationship between the stem Reynolds number Re_V and C_D of the form $C_D = \mathrm{a} + (\mathrm{b}/Re_V)^{\mathrm{c}}$ has been found to exist for other vegetation types (Kobayashi et al. 1993; Mendez et al. 1999; Paul and Amos 2011). Here, Re_V is a function of wave orbital velocity and the vegetation stem diameter. We initially used our vegetation metrics (Table 4.1) and the C_D–Re_V relationship developed for seagrasses to predict dissipation for our experimental conditions (Paul and Amos 2011). Figure 4.2a,b clearly shows that our observed dissipation exceeded that predicted by a factor of 1.5–2.2 for regular and 2.6–3.2 for irregular waves. We then calculated C_D for each experimental run from observed dissipation and plant metrics. C_D decreased with increasing Reynolds numbers Re_V, confirming the established exponential relationship between Re_V and C_D ($r^2 \geq 0.97$), but with coefficients a, b and c that differ from those of previous studies (Supplementary Information).

Analysis of video footage showed that the reduction in dissipation for regular waves exceeding 0.3 m in height was accompanied by a change in behaviour of the marsh vegetation. Under relatively low incident waves (H <0.3 m; T <3.6 s), the plants swayed and interacted with wave motion throughout the wave cycle (Fig. 4.2a, 4.3a). For larger waves (stronger currents), however, stems bent over to angles >50° during the forward wave motion, allowing the flow for part of the wave cycle to skim over, rather than travel through the vegetation, thus retaining energy and reducing dissipation (Fig. 4.2a, 4.3b).

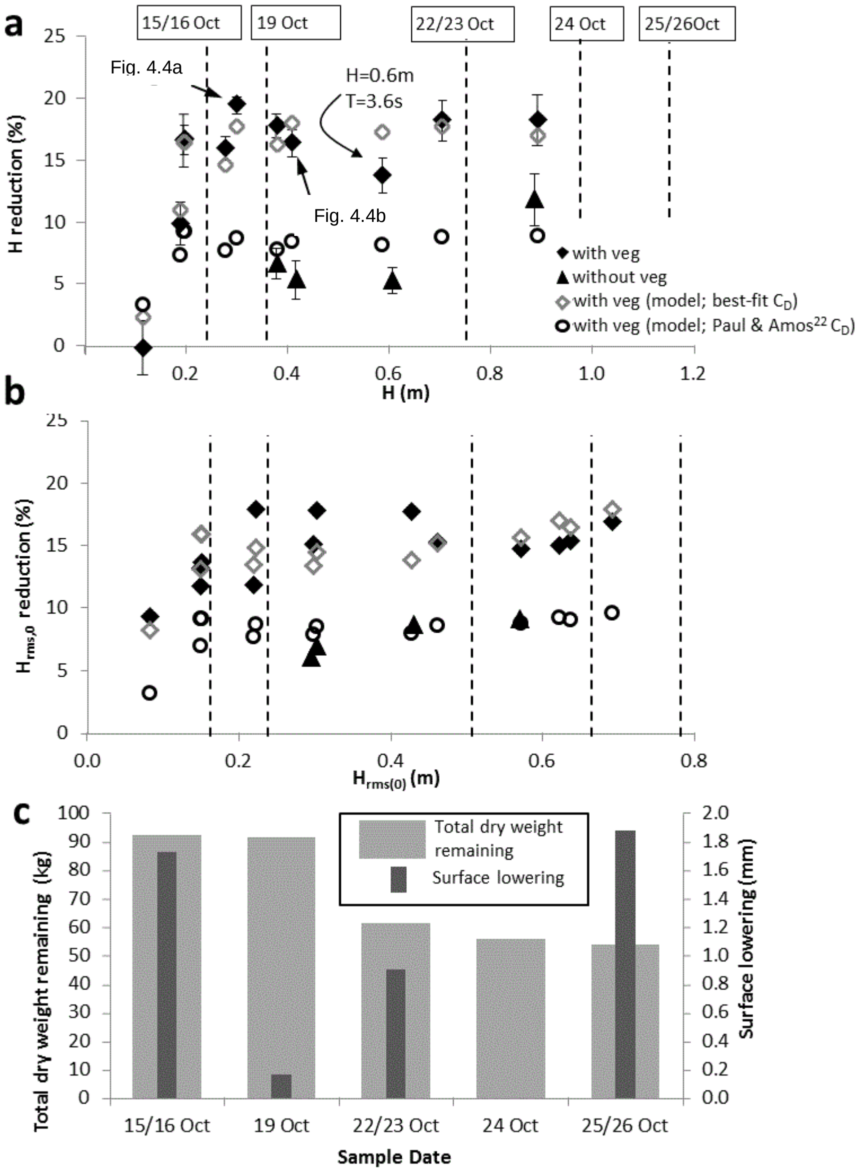


Figure 4.2. Wave dissipation across 40m of vegetated and mowed salt marsh. **a**,**b**, Percentage reduction for regular waves (**a**; *H*) and irregular waves (**b**; $H_{rms,0}$); error bars in **a** refer to the mean ± 1 s.d.; filled diamonds/triangles refer to observed vegetated/mowed conditions, open diamonds and circles refer to modelled vegetated conditions using best-fit and Paul et al. (2011). C_D values respectively, vertical lines mark times of soil elevation and floating debris measurement (Fig. 4.2c). **c**, Plant biomass (light thick bars) remaining and mean surface elevation lowering (dark thin bars; standard error of ± 10.4 mm not shown).

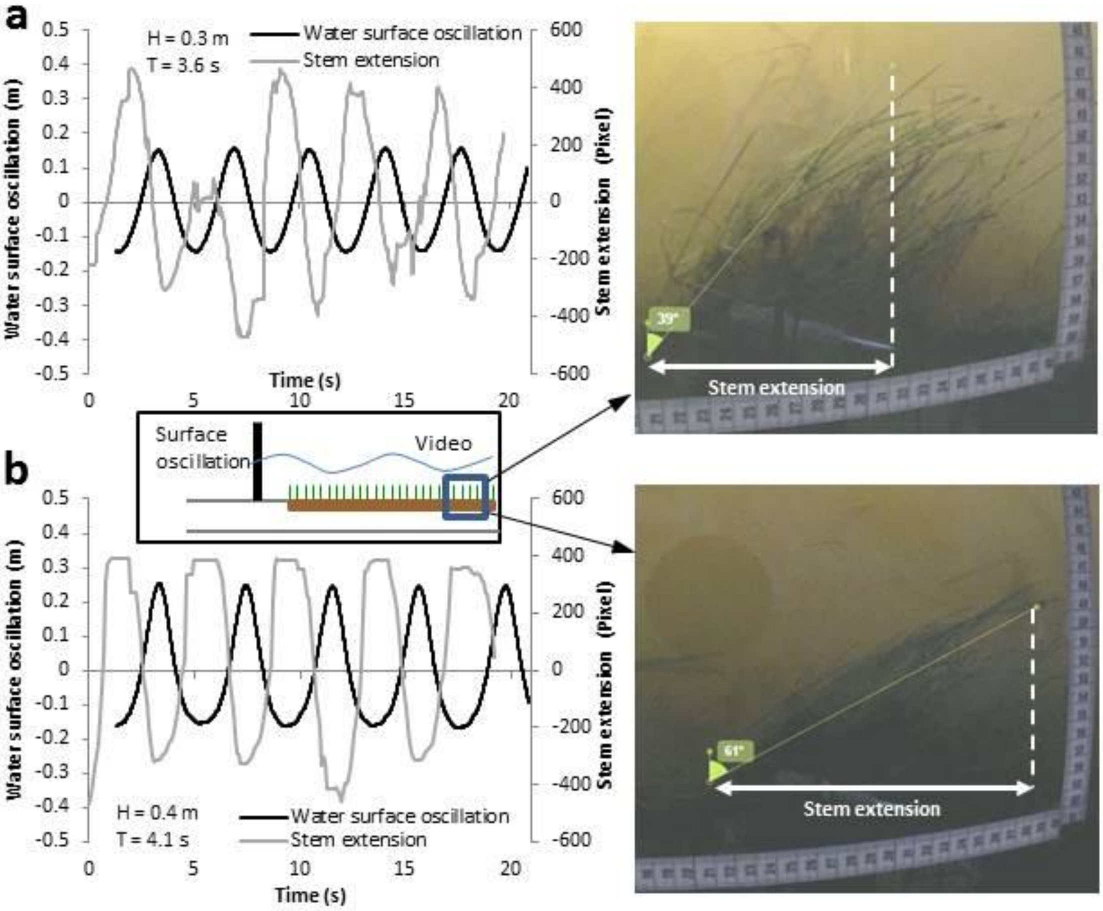


Figure 4.3. *Puccinellia* plant canopy movement during wave motion. **a**,**b**,Water level excursion (*y* axis) and time trace of horizontal stem extension (video pixel units; positive values in the direction of wave motion (white arrow in photographs) under waves experiencing maximum dissipation (Fig. 4.2a) (**a**) and waves of greater height and period but experiencing lower dissipation (Fig. 4.2a) (**b**). A phase shift results from water level measurement occurring approximately 10 m forward of video observations (see also experimental set-up in Fig. 4.1a). Lack of visibility in highly turbid water precluded analysis of conditions at *H* = 0.6 m, *T* = 3.6 s (Fig. 4.2a).

Video observations confirmed that this flattening of the plants preceded the tendency for plant stems to fracture along lines of weakness that formed when stems folded over to high bending angles. Cumulatively, this breakage resulted in a loss of 31% (30 kg) of the total 98 kg of biomass after two days of runs under higher energy conditions (Fig. 4.2c). Such loss of plant material may then have contributed to the reduced dissipation (Fig. 4.2a, 4.2b). The soil surface remained remarkably stable, with an average lowering that was not significantly different from zero (4.4 ± 10.4 mm over the entire experiment). The trend for average surface lowering from one surface exposure to the next was greatest during the test runs with the largest waves, rather than during the test runs that resulted in the largest release of plant biomass (Fig. 4.3.2c).

Wave attenuation of >80% has been reported in the literature for distances of about 160 m under low energy conditions (Möller and Spencer 2002). The spatially nonlinear nature of wave dissipation means that a conversion of this figure to units of per cent per metre makes little sense (Koch et al. 2009), but the evidence presented here shows that non-breaking wave dissipation can still reach 20% over a 40 m distance even in water depths typically found during storm conditions. This contribution is generated not only by the marsh platform but also, and significantly, by the vegetation canopy. Moreover, we identify process transitions in wave dissipation across the submerged salt marsh surface, associated with specific incident wave energy levels. The spatio-temporal nonlinearity in wave dissipation over coastal wetlands has been linked to, amongst other factors, variability in the characteristics of the vegetation cover (for example, flexibility; Mullarney and Henderson 2010). The established general nature of the relationship between Re_V and C_D seems robust, even for storm conditions, but the coefficients describing this relationship in our experiment differ markedly from those established for lower energy conditions and different vegetation types (Kobayashi et al. 1993; Mendez et al. 1999; Paul and Amos 2011). For regular waves of around 0.6 m height (Re_V of around 640), however, the model based on the empirical Re_V–C_D relationship leads to an over-prediction of dissipation (Fig. 4.2a) that warrants further investigation. We thus call for a re-evaluation of existing wave dissipation models and urge the scientific community to develop more appropriate methods for the a priori quantification of vegetation-induced drag for a broader range of plant species and wave conditions. Ideally, such methods should be able to quantify drag directly from plant metrics and knowledge of the incident flow field. Furthermore, the high bending angle and repeated bending of vegetation under energetic conditions lead to plant breakage along lines of weakness and a loss of biomass, a process that needs to be adequately represented in models of marsh canopy growth/recovery after storm incidence.

The higher than expected rates of storm wave dissipation and the fact that marsh surfaces are able to withstand larger wave forces without substantial erosion effects increase their reliability as part of coastal defence schemes and shifts debates about marsh stability and resilience to those locations where the marsh profile is exposed. In such settings, lateral retreat (for example, cliff undercutting/collapse on marsh fronts and channel widening) (Allen 2000; Howes et al. 2010; Fagherazzi et al. 2013) may be enhanced by the presence of vegetation, for example, when roots become exposed to wave impact (Feagin et al. 2009). The long-term balance between vertical and lateral marsh dynamics thus becomes a key area for further study (Kirwan and Megonigal 2013; Bouma et al. 2014).

The evidence presented here can serve as a validation data set for a new and improved representation of drag and friction effects in numerical models of wave dissipation and vegetation movement under storm conditions. It also supports the incorporation of salt marshes into coastal protection schemes, such as the Dutch ‘building with nature’ approach (Kabat et al. 2009; Shepard et al. 2011; Duarte et al. 2013). Any such schemes must carefully consider incident wave heights and water depths, alongside wave dissipation requirements and the ecological conditions necessary for the maintenance of a healthy vegetation canopy.

Methods

Experimental set-up

Experiments were conducted in the Large Wave Flume (Grosser Wellenkanal, GWK) of Forschungszentrum Küste (FZK) in Hannover, Germany. The flume is the largest freely accessible wave tank in the world; it is 310 m long, 5 m wide and 7 m deep. The vegetated test section of 39.44 m length (about 180 m^2) consisted of vegetated marsh blocks of 1.2 m length, 0.8 m width and 0.3 m depth, cut from a natural marsh on the mainland coast in Eastern Frisia, German Wadden Sea. The vegetated section was positioned on a 1.2-m-high sand base covered in geotextile at a distance of 108 m from the wave paddle and illuminated to prevent plant deterioration when exposed. Adjacent to the front and rear end of the vegetated test section, a flat concrete surface and ramped concrete slope allowed waves to shoal (Fig. 4.1a).

Wave conditions and inundation schedule

The flume was filled with fresh water to 2.0 m water depth above the vegetated soil surface and seven wave heights (H_0 : 0.1, 0.2, 0.3, 0.4, 0.6, 0.7 and 0.9 m) were simulated. Irregular waves (N ≥1,000) were generated using a JONSWAP spectrum with a peak enhancement factor of 3.3, followed by a regular wave run (N ≥100). After each two days of tests, the flume was drained and exposed for at least 12 h to allow plants to acquire oxygen. Tests were conducted with initially intact and then mowed vegetation to determine the effect of the vegetation as opposed to the topographic effect of the soil base.

Wave measurements

Sixteen wire wave gauges were deployed in sets of four (to enable reflection analysis at each location). Here we report analysed wave parameters from sets 2 and 4 that relate to the changes in wave characteristics over the full 40 m of the vegetated section (Fig. 4.1a, 4.1d). Wave gauges within each set were separated in the direction of wave travel by 2.07 m (front two gauges), 1.55 m (middle two), and 1.58 m (back two).

Wave analysis

For the regular wave tests, the first 11 fully developed waves were found to be entirely unaffected by reflection from the flume end and were used to determine average wave height (H, from min–max water surface elevations) and period (T, from zero-upcrossing points). For irregular wave tests, the root-mean-square wave height in front of ($H_{rms,0}$) and behind ($H_{rms,1}$) the vegetated section was calculated after reflection analysis, as described in the Supplementary Information. Dissipation was analysed by comparing values at the last gauge of set 2 (3.02 m in front of the vegetated section) and the first of set 4 (2.2 m behind the vegetated section) and expressed as a positive percentage of the wave height at the start of the section. If present, error bars indicate the standard deviation of the difference between the wave heights.

Wave dissipation model

Dalrymple et al.'s model (Dalrymple et al. 1984) was used to compute the dissipation of regular waves and Mendez and Losadas' model (Mendez and Losada 2004) was applied to irregular waves over the 40-m-long vegetated section x with H_0 ($H_{rms,0}$) incident wave height and H_1 ($H_{rms,1}$) damped wave height behind the section:

$$\frac{\mathrm{H_0-H_1}}{\mathrm{H_0}}=\frac{\alpha x}{1+\alpha x}\ (\text{reg. waves}),\ \frac{\mathrm{H_{rms,0}-H_{rms,1}}}{\mathrm{H_{rms,0}}}=\frac{\alpha x}{1+\alpha x}\ (\text{irreg. waves}) \qquad [4.1]$$

in which

$$\alpha=\mathrm{A}\frac{\mathrm{S_D}}{\mathrm{S_S^2}}\mathrm{C_D}\mathrm{k}\left[\frac{\sinh^3\mathrm{kS_H}+3\sinh\mathrm{kS_H}}{\sinh\mathrm{kh}(\sinh 2\mathrm{kh}+2\mathrm{kh})}\right] \qquad [4.2]$$

$\mathrm{A}=4/(9\pi)\,\mathrm{H_0}$ for regular waves and $\mathrm{A}=2/(3\sqrt{\pi})\,\mathrm{H_{rms,0}}$ for irregular waves, $\mathrm{k}=2\pi/\mathrm{L}$ (L = wave length of peak period T_p), h = water depth, S_D = stem diameter, S_S = stem spacing, S_H = stem height as measured on the test section for *Elymus*, the dominant species (h = 2 m, S_D = 1.3 mm, S_S = 28.6 mm, S_H = 700 mm; Table 4.1).

The drag coefficient C_D was determined as a function of the Reynolds Number Re_v (Paul and Amos 2011):

$$\mathrm{C_D}=-0.046+\left(\frac{305.5}{\mathrm{Re_v}}\right)^{0.977}\ \text{(regular waves; } r^2 = 0.97\text{)} \qquad [4.3]$$

$$\mathrm{C_D}=0.159+\left(\frac{227.3}{\mathrm{Re_v}}\right)^{1.615}\ \text{(irregular waves; } r^2 = 0.99\text{)} \qquad [4.4]$$

with

$$\mathrm{Re_v}=\mathrm{U_{max}}\,\frac{\mathrm{S_D}}{\mathrm{v_k}} \qquad [4.5]$$

Where v_k is the kinematic viscosity (1 x 10^{-6} m^2s^{-1}) and U_{max} = f(H_0 or $H_{rms,0}$ resp. and T_p) the orbital velocity at the bottom in front of the vegetated section based on linear wave theory. For further details on field site, test section construction, wave analysis and methods used to analyse vegetation behaviour and damage as well as soil elevation change, refer to the Supplementary Information.

Acknowledgements

We thank all of the staff at the Grosser Wellenkanal as well as B. Evans, J. Tempest, K. Milonidis and C. Edwards, Cambridge University, and D. Schulze, Hamburg University, for their invaluable logistical assistance, Fitzwilliam College for supporting the research time of I.M., and C. Rolfe, Cambridge University, for the soil analysis. The work described in this publication was supported by the European Community's 7th Framework Programme through the grant to the budget of the Integrating Activity HYDRALAB IV, Contract no. 261529 and a grant from The Isaac Newton Trust, Trinity College, Cambridge.

Author contributions

IM, BvW, GW, TS, TB, SS, MK, MML, MP, and KJ designed the experiment. IM, FR, MK, MML, MP, TS, GW, and SS participated in the construction and running of the experiment. IM and MK conducted the wave data analysis with FR processing biomass and video information. IM processed the soil elevation data and wrote the initial manuscript. All authors contributed to and approved the final manuscript.

Supplementary Information

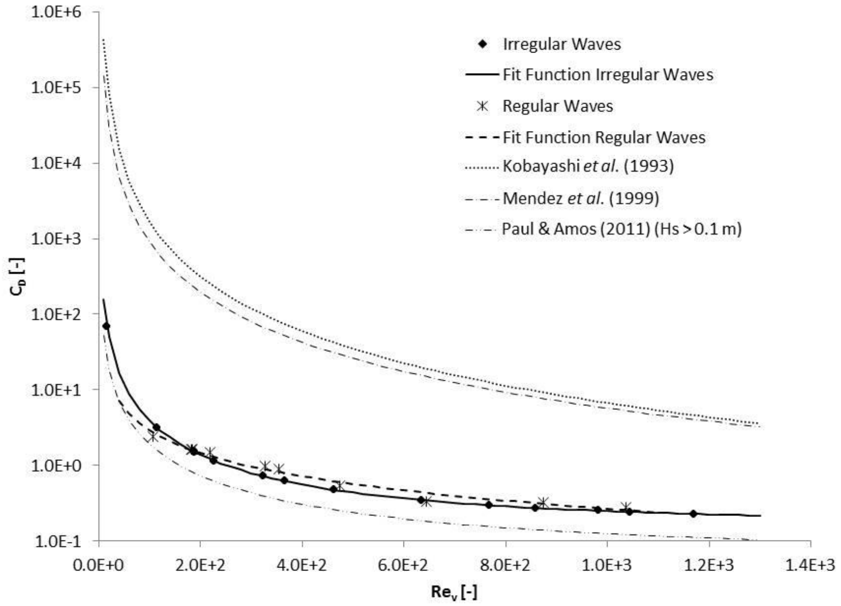


Figure 4.4. Relationship between C_D and vegetation Reynolds number Re_V and best fit for regular and irregular waves. Also shown are the best fit lines of Kobayashi et al. (1993), Mendez et al. (1999), and Paul and Amos (2011). For best fit line equation and coefficients, see Methods and Table 4.2.

Table 4.2. Coefficients of the exponential decay function relating C_D to Re_V as determined in previous studies and this experiment.

Study	Vegetation type	a	b	c
Kobayashi et al. (1993) (data from Asano et al. (1988))	Kelp	0.08	2200	2.40
Mendez et al. (1999)	Kelp (rigid)	0.08	2200	2.20
	Kelp (swaying)	0.40	4600	2.90
Paul and Amos (2011)	Seagrass	0.06	153	1.45
This experiment	Salt marsh (regular waves)	-0.05	306	0.98
	Salt marsh (irregular waves)	0.16	227	1.62

Supplementary Methods

Field site

The vegetated marsh blocks were cut from a natural marsh on the mainland coast in Eastern Frisia, German Wadden Sea (53°42.754 N; 07°52.963 E) in June 2012. Blocks were lifted mechanically and placed on a wooden pallet, lined with a plastic sheet covered by a layer of geotextile. The experiment could not be scheduled prior to autumn 2013 and marsh blocks were stored outdoors in appropriate temperature/moisture conditions and with fences to control for herbivory for 14 months. For marsh construction in the flume, individual blocks were separated from their wooden base, lowered into position and keyed to neighbouring blocks using a marsh clay sealant.

Experimental test section illumination

Illumination of plants on the test section was achieved by 60 flume wall-mounted lamps (GE 750W 400V PSL or equivalent).

Wave analysis

For irregular wave tests, time-series of water level fluctuations were used to determine incident and reflected waves using the standard three-gauge method of Mansard and Funke (Mansard and Funke 1980). After applying a low pass filter at 3.3 f_p (with f_p = peak frequency) and a high pass filter at $f_p/2.1$, incident spectra were used to compute the peak wave period (T_p). After a reverse *FFT* of the incident spectrum the root-mean-square wave height in front of ($H_{rms,0}$) and behind ($H_{rms,1}$) the vegetated section was calculated according to

$$H_{rms} = \sqrt{\frac{1}{N}\sum_{i=1}^{N} H_i^2} \qquad [4.6]$$

where N is the number of incident waves and H_i the individual waves in the time series of incident waves.

Vegetation behaviour and damage

The Youngs' modulus was measured according to the method described in Miler et al. (2012). Bending tests were performed with a ZWICK 1120 mechanical testing machine using a 100 N load cell (resolution 0.012 N) and a 1000 N load cell (resolution 0.12 N); Zwick GmbH & Co. KG, Ulm, Germany). Videography from behind lateral observation windows was used to record plant movement at a frequency of 10 Hz (Fig. 4.1a). Movement of plant stems was analysed using frame-by-frame tracking of stems (Mendez et al. 1999), using 'Kinovea' video analysis software. All floating organic debris was removed using a net (1 cm mesh size) when necessary and total dry weight was determined.

Soil elevation measurements

Soil elevation was measured from an access platform, lowered into six cross-flume positions, whenever the vegetated section was drained (Fig. 4.1a). The surface of the platform was approximately 30 cm above the soil base and temporarily locked into fixed basal slots, to within 1 mm accuracy. Soil surface elevations were determined with respect to a horizontal bar fixed to the platform. Pins were lowered vertically onto the soil surface every 20 cm along the bar to determine soil surface elevation to millimetre accuracy.

5

Vegetation-wave interactions in salt marshes under storm surge conditions

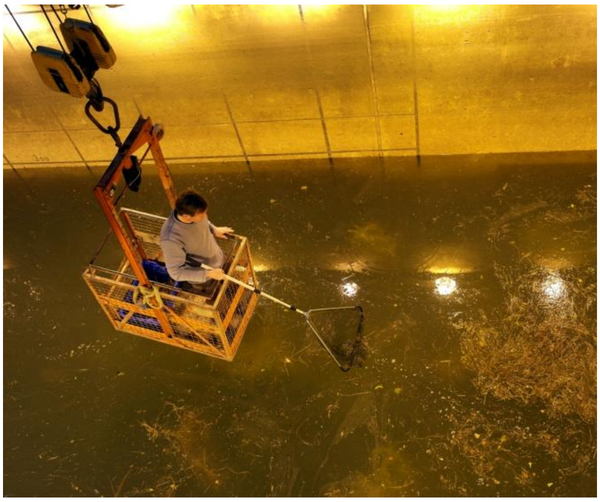
Franziska Rupprecht, Iris Möller, Maike Paul, Matthias Kudella, Kai Jensen, Tjeerd J. Bouma, Bregje K. van Wesenbeeck, Guido Wolters, Tom Spencer, Martin Miranda-Lange and Stefan Schimmels

CHAPTER 5

Abstract

Vegetation-wave interactions are critical in determining the capacity of coastal salt marshes to dissipate wave orbital flow and energy, enhance sedimentation and protect the shoreline from erosion. While vegetation-induced wave dissipation is increasingly recognised in low-energy environments, little is known on: i) the effect of vegetation on wave orbital flow under higher wave energy and water levels during storms, when coastal protection by marshes matters most; and ii) the ability of different plant species to reduce orbital flow and survive under such conditions. Experiments undertaken in one of the world's largest wave flumes, allowed for the first time to study vegetation-wave interactions at near-field scale under low up to extreme wave forcing in canopies of two salt marsh grasses from NW Europe: *Puccinellia maritima* (*Puccinellia*) and *Elymus athericus* (*Elymus*). Results indicate that plant flexibility and height, as well as wave and water depth conditions, play an important role in determining how salt marsh vegetation interacts with orbital flow. Under medium wave energy (wave height = 0.4 m), the effect of *Puccinellia* and *Elymus* on orbital flow varied with water depth. Under low water level (1 m) the rather stiff, tall *Elymus* had a higher ability to reduce maximum orbital velocity near the bed than the flexible, low-growing, *Puccinellia*. Under high water level (2 m) by contrast, deflection and folding of *Elymus* stems caused relocation of orbital flow on top of the vegetation and an increase of orbital velocity, while within *Puccinellia* maximum orbital velocity was reduced by 20–40%. Under high wave energy (wave height ≥0.6 m), an increase of flow velocity was observed in both canopies. Stem folding and breakage in *Elymus* under wave heights ≥0.4 m coincided with a leveling-off in the marsh wave dissipation capacity, while *Puccinellia* survived even extreme wave forces without physical damage. These findings suggest a species-specific control of flow and wave dissipation by salt marshes and can inform predictions of marsh wave dissipation capacity and resilience to storm surge conditions.

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



Introduction

Important ecosystem services provided by coastal salt marshes such as protecting the shoreline from wave energy and erosion as well as enhancing sediment deposition are related to the capacity of the vegetation to reduce water flow and turbulence (Möller et al. 1999; Temmerman et al. 2005; Gedan et al. 2011). When waves advance over a vegetated marsh surface, vegetation interacts with the flow and imposes a drag force counter to the direction of water motion (Mullarney and Henderson 2010). The flow resistance or drag by plants reduces wave orbital velocities resulting in a reduction of wave height and wave energy. Apart from being an important control of the wave dissipation capacity of salt marshes, changes in flow velocity and flow structure due to the presence of vegetation have a significant influence on sediment dynamics, geochemical exchanges in the water column and biological processes such as the dispersal of seeds and larvae (Fingerut et al. 2003; Neumeier and Amos 2006a; Chang et al. 2008).

Most knowledge on flow dynamics in and around salt marsh canopies has been acquired through field and flume studies under unidirectional flow and average hydrodynamic conditions. These studies have shown that flow reduction within plant canopies can lead to a decline in bed shear stress and erosion and promote sedimentation (Neumeier and Amos 2006a; Peralta et al. 2008). Little is known by contrast on the effect of salt marsh canopies on the velocity of wave orbital flow, especially during storms when the wave energy is high, large amounts of sediment are mobilised and currents and waves have a high erosion potential (Stumpf 1983; Cahoon 2006; Turner et al. 2006). Detailed insights into how salt marsh canopies affect wave orbital-velocities are of major importance for the generation of reliable predictions of the marsh wave dissipation capacity over a wide range of wave conditions and thus for the successful incorporation of marshes into coastal defence and management schemes (Anderson and Smith 2014; Bouma et al. 2014; Möller et al. 2014).

Vegetation-wave interactions and the resulting retardation effect that plant canopies exert on orbital flow are a function of biophysical plant properties such as canopy architecture, flexibility, buoyancy and density as well as hydrodynamic conditions such as incident wave height, wave period and water depth (Anderson et al. 2011). With respect to the effect of plant properties on vegetation-wave interactions, plant flexibility has been identified as a key control as it determines how much and in what way plants move under wave orbital flow (Mullarney and Henderson 2010; Paul et al. 2012). While stems of high or intermediate stiffness typically show an oscillatory swaying movement throughout the wave cycle, highly flexible plants bend to wide angles in the dominant direction of flow (in general the direction of wave travel) resulting in flattening of the canopy and a loss of flow resistance for part of the wave cycle (whip-like canopy movement). A transition from swaying to whip-like movement can occur when wave forcing increases, with the point of transition depending on the stiffness of the plant (Manca 2010; Paul et al. 2012). Stresses experienced by plants under wave forcing are inversely related to their flexibility: flexible plants avoid high drag forces imparted by the flow and the risk of physical damage due to stem folding and breakage through reconfiguration in the flow; in stiff, brittle plants the risk of folding and breakage increases with rising orbital velocities and wave energy (Bouma et al. 2005). For plants with swaying movement, a positive correlation between stem stiffness and the capacity of vegetation to dissipate wave energy has been observed (Bouma et al. 2010). When comparing two salt marsh grasses with different stem flexibility and stem density, Bouma et al. (2010) found that an increase in stem density and biomass can counteract the reduced energy dissipation capacity of flexible plants.

Apart from stem flexibility and density, the flow reduction and wave dissipation capacity of salt marsh canopies is affected by the ratio of water depth to canopy height (submergence ratio) (Yang et al. 2012). The effectiveness of vegetation in dissipating waves has been shown to increase with the percentage of the water column it occupies (Augustin et al. 2009; Paul et al. 2012). In a modelling study, Chen et al. (2007) showed that the upper depth limit for wave dissipation by submerged vegetation depends on the incident hydrodynamic forcing. In water depths too deep for orbital wave motion to reach the bed, but shallow enough to interact with the canopy, orbital velocities and wave period become important controls of vegetation-wave interactions and vegetation-induced wave dissipation.

It is generally agreed that relationships between vegetation properties (flexibility, density, biomass, height) and physical parameters (wave height, wave period, water depth, and observed wave dissipation are non-linear (Koch et al. 2009). This implies that beyond a critical level of wave energy and water depth, changes in type and magnitude of vegetation-wave interactions are likely to result in a significant alteration of vegetation-induced reduction of orbital flow velocity and wave dissipation. The existence of hydrodynamic thresholds determining the transition from wave regimes with vegetation-induced flow modification and wave dissipation to regimes characterised by a decline in flow resistance by vegetation due to flexing, folding or breakage of plants has been suggested by various authors (Möller et al. 1999; Gedan et al. 2011; Yang et al. 2012), but remains to be demonstrated.

The quantification of such hydrodynamic thresholds either by field studies, flume experiments or by numerical modelling, is however extremely challenging. Detailed and systematic field studies of plant behavior under increasing wave forces are hampered by the unpredictable nature and high temporal variability of wave conditions, and the difficulties and risks involved in deploying instrumentation under higher energy wave events. Laboratory flume studies offer controlled wave conditions, but are often hampered by scale effects as water depths and waves that can be generated within flumes are often limited in depth and energy which hinders the applicability of results to situations encountered in the field (Fonseca and Cahalan 1992; Mendez and Losada 2004). Furthermore, flume studies often use highly simplified plant surrogates. Real salt marsh canopies by contrast show a high complexity and high variability in biophysical properties making it questionable whether plant surrogates can realistically represent the behaviour of salt marsh canopies under wave forcing. Finally, numerical models of wave dissipation can simulate a wide range of wave conditions but, in the absence of suitably representative flume or field calibration data, suffer from the difficulty of realistically representing vegetation as well as its effect on orbital flow (i.e. vegetation-wave interactions).

A unique experiment conducted by Möller et al. (2014) in one of the world's largest wave flumes allowed for the first time a detailed study of vegetation-induced flow and wave dissipation in real salt marsh plant canopies (i.e. field-excavated salt marsh vegetation) over a wide range of average to extreme wave conditions under near-field-scale conditions. In this paper, we analysed video material on canopy movement and measurements of orbital flow velocity as well as physical damage occurring to vegetation, recorded for two plant canopies with different biophysical properties to answer the following questions:

How does different vegetation (flexible and low-growing vs tall and stiff) affect wave orbital flow under low, medium and high levels of wave energy?

Does physical damage to vegetation under rising wave forces differ between flexible and low-growing and tall, stiff canopies and if so – under which level of wave energy do differences in plant susceptibility to folding and breakage become apparent?

Methods

Study species and biophysical properties

In our study we investigated two grasses commonly occurring in salt marshes of NW Europe, *Puccinellia maritima* (Hudson) Parl. (*Puccinellia*) and *Elymus athericus L.* (*Elymus*). *Puccinellia* has its typical habitat in the low and mid marsh, in salt marshes with sandy soils it can also be found in the pioneer zone. *Puccinellia* is also a characteristic species of grazed salt marshes, as the species is tolerant to trampling, biomass loss and waterlogging. In contrast to *Puccinellia, Elymus* needs aerated soils and is sensitive to grazing. In recent decades, *Elymus* has rapidly colonised mainland salt marshes along the North Sea coast, its expansion being related to the abandonment of grazing, high vertical accretion rates and marsh age (Veeneklaas et al. 2013; Rupprecht et al. 2015a).

Puccinellia and *Elymus* differ with respect to biophysical properties, such as plant stem flexibility, stem density and stem height, which have relevance for flow and wave dissipation. In comparison to *Elymus*, *Puccinellia* is characterised by a high stem flexibility (as indicated by low values of Young's bending modulus and flexural rigidity), high stem density and low canopy height (Table 5.1).

We compared stem flexibility and stem height of the *Puccinellia* and the *Elymus* canopy between the flume and at the field site where the salt marsh for the flume experiment was excavated. In addition, stem density was compared in *Elymus* canopies between the flume and the field. As measures of stem flexibility, the Young's bending modulus and flexural rigidity of *Puccinellia* and *Elymus* stems were determined according to the methodology described in Rupprecht et al. (2015b). Stem height was measured with a folding rule for 30 randomly chosen stems. Stem density of *Elymus* was measured by counting the number of stems in 15 quadrats of a size of 20 x 20 cm in the flume and in the field. For each species, differences in biophysical properties between the flume and the field site were analysed with t-tests calculated in R 3.1.0 (R Foundation for Statistical Computing, Vienna, AT).

Table 5.1. Biophysical properties (mean values ± 1 SD) of the *Puccinellia* and *Elymus* canopy. Plant stem flexibility, stem diameter, stem height and biomass were measured at the test section in the flume and at the field site where the marsh blocks for the flume experiment were excavated.

	Stem flexibility Young's bending Modulus [MPa]	**Stem flexibility** Flexural rigidity [Nm^2 x 10^{-5}]		**Stem diameter** [mm]		**Stem height** [mm]		**Stem density** [number per 10 x 10 cm quadrat]	**Stem density** [number per 20 x 20 cm quadrat]	
	Mean	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**Mean**	**N**
Puccinellia (Flume)	111.6 ± 66.3	0.7 ± 0.2	17	1.1 ± 0.3	17	220 ± 30	30	–	–	–
Puccinellia (Field)	284.5 ± 369.1	2.1± 1.7	17	1.2 ± 0.2	17	180 ± 30	30	–	–	–
Elymus (Flume)	2696.3 ± 1963.8	29.9 ± 18.4	18	1.3 ± 0.3	18	700 ± 10	30	29 ± 6	49 ±23	10
Elymus (Field)	2514.7 ± 2977.1	56.9 ± 20.7	18	1.7 ± 0.4	18	800 ± 10	30	28 ± 8	68 ±8	10

Experimental set-up

The effect of *Puccinellia* and *Elymus* on wave orbital flow and physical damage occurring to both canopies under hydrodynamic forcing was measured during a flume experiment on wave dissipation over salt marshes (Möller et al. (2014). The experiment ran from September to November 2013 in the Large Wave Flume (GWK) of the Forschungszentrum Küste (FZK) in Hannover, Germany, one of the world's largest wave flumes.

To provide the vegetation for the experiment, approximately 210 m^2 of salt marsh was cut by spade and mechanical digger into 1.2 x 0.8 m blocks to a depth of around. 0.3 m from a site in Eastern Frisia, German Wadden Sea (53°42.754 N; 07°52.963 E) in June 2012. The vegetation of the excavated marsh section was typical for mid to high marsh plant communities in NW Europe and consisted of the grasses *Puccinellia* and *Elymus* and the herbaceous forb *Atriplex prostrata* (*Atriplex*). Prior to the start of the experiment, the excavated marsh blocks were stored and cultivated outdoors at the wave flume location for 14 months and watered with salt water.

In the flume with a width of 4.5 m, the 204 individual marsh blocks were reassembled to a vegetated test section of 39.44 m length (ca. 180 m^2) on top of a 1.2 m high sand base covered by a layer of geotextile. At its front and rear end, a flat concrete surface followed by a ramped concrete slope was built to allow the waves to shoal and/or break, as would be the case in a natural shallow water marsh setting (Fig. 5.1a). The vegetated test bed was divided into two sections. In the first (front) section, marsh blocks vegetated with *Puccinellia*, *Elymus* and *Atriplex* were placed parallel to each other, over a length of approximately 6 m (i.e. five marsh blocks deep). Behind this front set of 6 x 5 marsh blocks, the remaining 174 blocks were arranged in a chequerboard pattern to simulate a mixed marsh community. An underwater observation window in the flume wall at a distance of about 6 m from the front edge of the vegetated test section allowed the video capture of individual *Elymus* and *Puccinellia* movement during the experiment. Two 2D-Electromagnetic current meters (EMCs) were positioned on both sides of the underwater observation window approximately 15 cm above the bed, one in the canopy of *Puccinellia* and one in the canopy of *Elymus* (Fig. 5.1b). During wave tests, EMCs recorded the flow velocity in the direction of wave travel and perpendicular to it with a frequency of 100 Hz and a precision of ± 10 cm s^{-1}. In the immediate vicinity of the EMCs, water pressure oscillation was recorded with a pressure wave gauge. A detailed description of the excavation of the salt marsh and its installation within the flume, the experimental set-up and the employed instrumentation to measure wave dissipation is given in Möller et al. (2014).

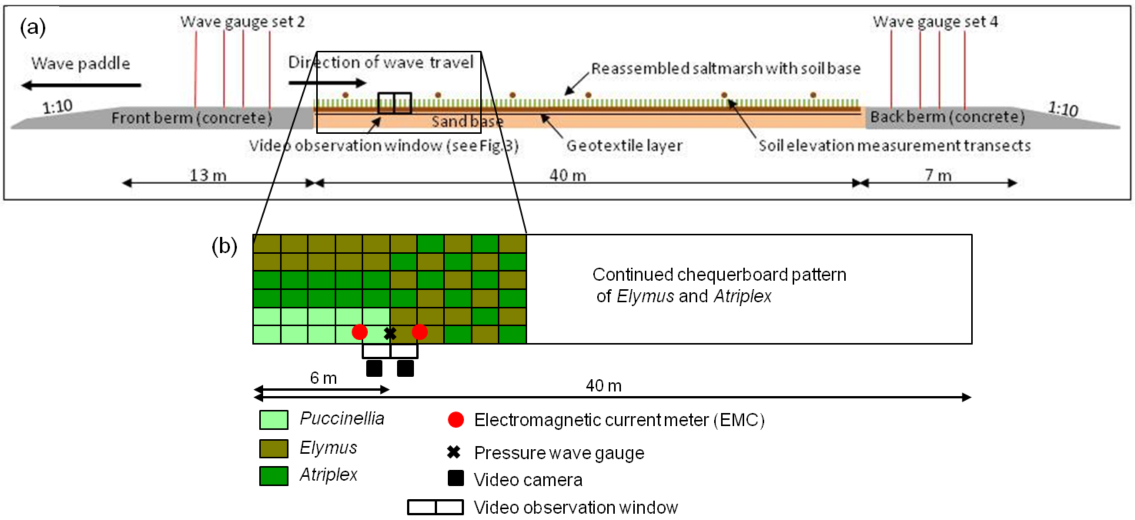


Figure 5.1. Large scale flume experiment conducted by Möller et al. (2014). **(a)** General experimental setup in the GWK (Großer Wellenkanal Hannover) wave flume (taken from Möller et al. 2014), **(b)** top view of the front vegetated test section where the electromagnetic current meters in *Puccinellia* and *Elymus* were deployed.

Experimental programme

Conditions with wave heights (*H*) ranging from 0.1–1.1 m and wave periods (*T*) of 1.5– 6.2 s were simulated in two different water depths (*h*) of 1 m and 2 m above the vegetated soil surface. For each hydrodynamic condition tested, irregular waves (N = 1000) were generated first using a JONSWAP spectrum with a peak enhancement factor of 3.3, followed by a regular wave run (N = 100). In our study, we used only data from wave tests with regular non-breaking waves (Table 5.2) to analyse the effect of the two different (*Elymus* vs *Puccinellia*) plant canopies on orbital flow.

In order to categorise the wave tests with respect to the level of hydrodynamic energy and drag imparted by the waves on the vegetation, we calculated for each test the wave energy flux per meter crest length (*P,* equation 5.2) and the maximum orbital velocity 15 cm above the bed (matching the height at which orbital flow velocity was recorded within plant canopies) according to linear wave theory ($U_{max\ pred}$, equation 5.5) from wave parameters recorded by the wave gauge deployed immediately in front of the vegetated test section. The first 11 fully developed waves were found to be entirely unaffected by reflection from the flume end and were used to determine average wave height (*H*, from min-max water surface elevations) and period (*T*, from zero-upcrossing points). Wave length (*L*) was calculated with the formula

$$L = \frac{gT^2}{2\pi}\ tanh\left(\frac{2\pi h}{L}\right) \qquad [5.1]$$

The following formulae were used to calculate *P* and $U_{max\ pred}$:

$$P = CgE \qquad [5.2]$$

in which

$$Cg = \frac{1}{2}\left[1 + \frac{4\pi h/L}{\sinh(\frac{4\pi h}{L})}\right]\frac{L}{T} \qquad [5.3]$$

and

$$E = \frac{1}{8}\rho g H^2 \qquad [5.4]$$

$$U_{\max pred} = \frac{\frac{H\,\pi}{T}}{Sinh\left(2\pi\frac{h}{L}\right)} \qquad [5.5]$$

where *Cg* = group wave celerity, *E* = wave energy, *H* = wave height, *T*= wave period, *L* = wave length, *h* = water depth, *ρ* = water density, *g* = acceleration by gravity

In the following, conditions with *P* ≤0.36 kW m^{-1} (corresponding to $U_{max\ pred}$ 28.8–31.4 cms^{-1}) are referred to as ‘low wave energy’; P ≥0.47 and ≤0.71 kW m^{-1} (corresponding to $U_{max\ pred}$ 41.6–62.7 cms^{-1}) as ‘medium wave energy’ and P ≥1.36 kW m^{-1} (corresponding to $U_{max\ pred}$ 56.6–90.9 cms^{-1}) as ‘high wave energy’ (Table 5.2).

After each two days of submergence for wave tests, the flume was drained and exposed for at least 12 hours to allow plants to acquire regular gas exchange. To determine the effect of the vegetation canopy on wave dissipation as opposed to the topographic effect of the soil base, a number of tests were conducted with initially intact and then removed (mowed) vegetation. During the course of the experiment the entire vegetated test section was illuminated for the benefit of the plants, at least whenever these were emergent between wave tests, by a total of 60 lamps (GE 750W 400V PSL or equivalent) mounted along the sides of the flume.

Table 5.2. Hydrodynamic conditions simulated with regular non-breaking waves in the flume experiment. Wave height (*H*), water depth above the marsh platform (*h*), wave period (*T*), energy flux per meter crest length (*P*), maximum orbital velocity at the bed predicted from wave parameters ($U_{max\ pred}$) and maxima/minima of orbital velocity in/counter the direction of wave travel (U_{max}, U_{min}) recorded within canopies of *Puccinellia* and *Elymus*. Wave tests which were repeated after mowing of the marsh platform are shaded in grey. Statistical significance of differences between U_{max} and U_{min} in *Puccinellia* and *Elymus* was verified with t-tests, significant differences are marked with $p < 0.05$.

Date	**Energy level**	***h*** **[m]**	***P*** **[kW m^{-1}]**	***H*** **[m]**	***T*** **[s]**	**$U_{max\ pred}$ [cm s^{-1}]**	**U_{max} [cm s^{-1}] (mean ± 1 SD)**		**t-test (2-tailed)**	**U_{min} [cm s^{-1}] (mean ± 1 SD)**		**t-test (2-tailed)**
							Puccinellia	***Elymus***		***Puccinellia***	***Elymus***	
Wave tests with vegetated marsh platform												
18 Oct	Low	1	0.07	0.2	2.1	23.7	17.2 ± 1.0	21.9 ± 1.2	p<0.05	-19.8 ± 1.1	18.9 ± 1.2	p<0.05
18 Oct	Low/ Medium	1	0.12	0.2	2.9	31.4	25.1 ± 1.4	30.1 ± 2.4	p<0.05	-21.5 ± 1.5	24.4 ± 2.6	p<0.05
22 Oct	Medium	1	0.47	0.4	2.9	62.7	74.2 ± 6.5	48.2 ± 8.7	p<0.05	-41.5 ± 2.9	50.5 ± 8.7	p<0.05
25 Oct	Medium/ High	1	0.65	0.5	3.3	74.3	98.5 ± 16.8	83.5 ± 9.2	p<0.05	-50.5 ± 9.2	48.2 ± 9.2	p>0.05
15 Oct	Low	2	0.02	0.1	1.5	1.8	1.9 ± 0.6	2.3 ± 0.6	p<0.05	-2.8 ± 0.6	2.2 ± 0.5	p<0.05
15 Oct	Low	2	0.08	0.2	2.1	10.0	8.9 ± 0.7	9.1 ± 0.6	p<0.05	-10.4 ± 0.7	9.6 ± 0.7	p<0.05
15 Oct	Low	2	0.13	0.2	2.9	16.2	15.2 ± 0.8	15.5 ± 0.9	p<0.05	-15.9 ± 1.0	14.6 ± 0.9	p<0.05
17 Oct	Low	2	0.13	0.2	2.9	16.4	16.0 ± 0.9	15.5 ± 0.8	p<0.05	-15.9 ± 1.1	13.5 ± 1.4	p<0.05
17 Oct	Low	2	0.22	0.3	2.5	19.8	16.5 ± 0.8	20.5 ± 1.6	p<0.05	-17.7 ± 1.1	18.2 ± 2.1	p<0.05
17 Oct	Low/ Medium	2	0.36	0.3	3.6	28.8	24.2 ±1.2	32.6 ± 3.2	p<0.05	-20.5 ± 1.5	24.1 ± 3.5	p<0.05
21 Oct	Medium	2	0.48	0.4	2.9	31.6	27.2 ± 3.1	32.9 ± 3.3	p<0.05	-30.5 ± 2.1	24.5 ± 2.5	p<0.05
21 Oct	Medium	2	0.71	0.4	4.1	41.6	29.4 ± 1.7	47.9 ± 7.3	p<0.05	-34.1 ± 1.8	38.9 ± 5.4	p<0.05
21 Oct	High	2	1.36	0.6	3.6	56.6	63.2 ± 6.7	64.3 ± 11.5	p>0.05	-48.6 ± 2.4	46.7 ± 9.4	p>0.05
22 Oct	High	2	2.31	0.7	5.1	76.2	101.4 ± 7.0	83.2 ± 17.1	p<0.05	-41.0 ± 3.1	37.2 ± 10.1	p<0.05
24 Oct	High	2	3.39	0.9	4.1	90.9	100.9 ± 12.6	95.4 ± 9.8	p<0.05	-73.7 ± 4.4	62.8 ± 9.5	p<0.05
Wave tests with mowed marsh platform												
31 Oct	Low	1	0.08	0.2	2.1	24.7	21.0 ± 1.8	19.5 ± 1.3	–	19.7 ± 1.6	20.2 ± 1.2	–
31 Oct	Medium/ High	1	0.46	0.4	2.9	61.9	61.4 ± 3.5	55.3 ± 5.0	–	40.7 ± 4.3	48.7 ± 3.4	–
29 Oct	Medium	2	0.48	0.4	2.9	31.6	33.6 ± 3.1	27.2 ± 1.5	–	30.5 ± 2.1	24.5 ± 2.5	–
29 Oct	Medium	2	0.74	0.4	4.1	42.3	45.6 ± 2.0	43.5 ± 3.7	–	38.0 ± 1.8	41.1 ± 2.5	–
31 Oct	High	2	1.45	0.6	3.6	58.3	64.4 ± 3.6	57.2 ± 4.5	–	51.5 ± 3.4	50.7 ± 3.0	–
31 Oct	High	2	3.34	0.9	4.1	90.1	96.0 ± 5.6	78.9 ± 4.9	–	74.1 ± 4.5	65.8 ± 6.6	–

Videography of plant movement and video processing

Video cameras were installed behind the lateral observation window 6.0 m from the front end of the vegetated test section. These cameras recorded the movement of *Puccinellia* and *Elymus* at bed level simultaneously to the records of flow velocity in both canopies. Images were continuously acquired at a frequency of 10 Hz. Plant movement was analysed through frame-by-frame tracking of individual plant stems by using ‘Kinovea’ video analysis software (Kinovea 0.8.15, © 2006 - 2011 - Joan Charmant & Contrib.). In ‘Kinovea’ tracking of objects (here plant stems) is a semi-automatic process. After manually choosing a well distinguishable point on a plant stem, the point location is computed automatically by recording x (horizontal) and y (vertical) coordinates in pixels. The tracking process can be interrupted and adjusted at any time. In each wave test, we recorded stem movement for an interval of 10–20 s at the same location in the canopy. In tests with medium to high wave energy, fast canopy movement and high water turbidity, the point location needed to be manually adjusted several times during the tracking process. This may have caused a lower precision of the video analysis in these wave tests. In addition to the analysis of plant movement, we measured the maximum bending angle of stems in and counter to the direction of wave travel by the help of the ‘angle measurement tool’ in ‘Kinovea’.

Plant behaviour characteristics for swaying and whip-like movement under wave motion have been reported elsewhere (Bradley and Houser 2009; Manca 2010) and are illustrated in Fig. 5.2. However, it should be noted that many transitional states exist between these two main types of plant movement. Under swaying-movement, plants bend to similar angles in and counter to the direction of wave travel (Fig. 5.2a). Thus, plants and orbital flow interact throughout the whole wave cycle. Here, flow reduction and wave dissipation are achieved by transfer of kinetic energy from the waves to the plants and by turbulence generated around and between the plant elements that interfere with the flow. Under whip-like movement, plants bend to much wider angles in the direction of wave travel than counter to the direction of wave travel (Fig. 5.2b). For part of the wave cycle (wave ‘forward’ motion in the direction of wave travel), the flow passes unimpeded over the flattened canopy resulting in a lower vegetation-induced flow reduction and wave dissipation.

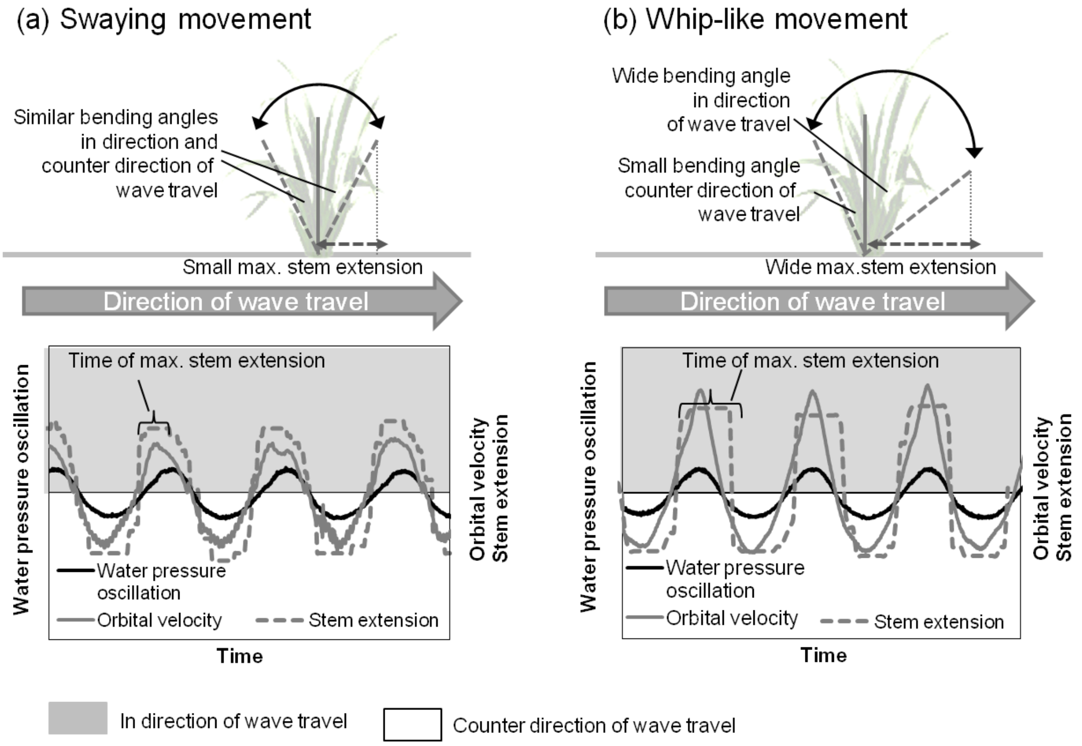


Figure 5.2. Plant movement under wave motion. **(a)** Bending angles, stem extension and orbital flow velocity under swaying movement characteristic for low to medium wave energy, **(b)** bending angles, stem extension and orbital flow velocity under whip-like movement characteristic for high wave energy.

Calculation of flow velocity

Time-series data of orbital velocity under regular non-breaking waves were used to evaluate the effect of canopy movement of *Puccinellia* and *Elymus* (observed with the video cameras) on orbital flow velocity near the bed. The mean maximum orbital velocities in the direction of wave travel (U_{max}) and counter to the direction of wave travel (U_{min}) were calculated from the horizontal velocity component (component in direction of wave travel) recorded with the EMCs at height of 15 cm above the bed within canopies of *Puccinellia* and *Elymus*: for each wave cycle within the time series, the minimum and maximum values were identified and then averaged over all waves in the record.

In shallow water environments, wave shape changes with increasing wave height and wave period from a symmetric sinusoidal pattern to an asymmetric trochoidal shape with steep wave crests and shallower wave troughs. Hence, orbital velocity in the direction of wave travel (wave forward motion/wave crest) determines vegetation-wave interactions characteristic of a specific level of wave energy or drag imparted by waves on the vegetation canopy. For this reason, we focused on U_{max} recorded within canopies of *Puccinellia* and *Elymus* when comparing the responses of the different canopies to wave forcing in terms of movement and their capacities to slow-down orbital flow.

To assess the effect of the presence of *Puccinellia* and *Elymus* on orbital velocities as opposed to unvegetated conditions, we compared U_{max} measured within both canopies with U_{max} when the canopies were mowed as well as with $U_{max\ pred}$, the maximum orbital velocity predicted from wave parameters only, i.e. in the absence of a vegetated marsh surface. Differences in orbital velocities between *Puccinellia* and *Elymus* as well as between vegetated and mowed conditions were analysed with t-tests calculated in R 3.1.0 (R Foundation for Statistical Computing, Vienna, AT).

Assessment of physical damage to the vegetation canopy

To assess the overall physical damage to the vegetation canopy due to plant folding and subsequent breakage, all floating biomass was removed from the water surface using a net (1 cm mesh size) when necessary. Removal of biomass was carried out after each test (or set of tests) which produced visible floating debris. Biomass was dried and bagged for the determination of total dry weight as an indicator of damage occurring to the vegetation canopy in relation to incident hydrodynamic energy level.

To assess the physical damage occurring to the *Elymus* canopy under rising wave energy, the number of *Elymus* stems was counted at 18 quadrats of 10 x 10 cm each time the flume was drained and plants exposed. The quadrats were distributed in sets of three from the front to the rear end of the vegetated test section and located within a distance of 0.7 m into the vegetated test section from the northern flume wall. They were accessible via a small walkway along the northern flume wall. Very high stem density of the *Puccinellia* make stem counts an inappropriate method to assess physical damage occurring to the *Puccinellia* canopy.

For this purpose we took photographs of the *Puccinellia* canopy close to the location where the EMCs in *Puccinellia* was deployed, each time when the flume was drained and stem counts in *Elymus* were carried out.

Results

Biophysical properties of *Puccinellia* and *Elymus* canopies in the flume and in the field

Neither in *Puccinellia* nor in *Elymus* were significant differences between flume and field site found for the Young's bending modulus of stems (N = 17), indicating a similar flexibility of stem tissue in the flume and at the field site (t-test: *Puccinellia*, t = 1.90, df = 32, p = 0.06; *Elymus*, t = -0.21, df = 34, p = 0.83; Table 5.1). However, flexural rigidity of *Puccinellia* and *Elymus* stems (N=15) was significantly lower in the flume than in the field (t-test: *Puccinellia*, t = 3.37, df = 32, p <0.01; *Elymus*, t = 4.14, df = 34, p <0.01). This indicates that, accounting for varying stem diameter, stems of *Puccinellia* and *Elymus* in the flume were more flexible than stems at the field site. Stem height of *Puccinellia* (N = 30) was significantly higher in the flume (220 mm; Table 5.1) than in the field (180 mm) (t-test: t = -2.41, df = 18, p <0.05). For *Elymus,* no significant differences of stem height (N = 30) (t-test: t = 1.64, df = 16, p = 0.11) and stem density (N = 15) (t-test: t = 1.95, df = 26, p = 0.06) were found between the flume and the field site.

Canopy movement and orbital velocity in *Puccinellia* and *Elymus* under rising wave energy

Under low wave energy ($P \leq 0.36$ kW m^{-1}), both canopies showed a swaying movement alongside similar absolute values of U_{max} and U_{min} (Table 5.2). When wave energy increased, larger differences in U_{max} occurred between *Puccinellia* and *Elymus* both under 1 m and 2 m water depth.

Under a water depth of 1 m and medium wave energy ($P = 0.47$ kW m^{-1}), U_{max} in *Elymus* was lower than in *Puccinellia* (35%; 26 cm s^{-1}) (Fig. 5.3, Table 5.2). Here, different types of canopy movement occurred in *Puccinellia* and *Elymus*. *Puccinellia* moved in a whip-like fashion as indicated by wide bending angles of plant stems in the direction of wave travel (50–60°) and smaller bending angles counter to the direction of wave travel (30–40°) and a long time of maximum stem extension (approximately 1.5 s) that allowed the flow to pass unimpeded over the deflected canopy for a large part of the wave cycle (Fig. 5.4a). In contrast, *Elymus* showed a swaying movement with symmetric bending angles (35–45°) of the bottom stem parts in and counter to the direction of wave travel (Fig. 5.4b). The upper stem parts, however, bent to much wider angles causing folding of *Elymus* stems around 5 cm above the bed. Maximum stem extension in *Elymus* lasted 0.5–1 s.

Under a water depth of 1 m and high wave energy (P = 0.65 kW m^{-1}), high values of U_{max} indicated whip-like movement and very low flow resistance provided by both *Puccinellia* and *Elymus*. However, U_{max} in *Elymus* was still lower than U_{max} in *Puccinellia* by 15% (15 cm s^{-1}) (Fig. 5.3, Table 5.2).

Under a water depth of 2 m, U_{max} in *Puccinellia* and *Elymus* greatly differed in the two tests with medium to high wave energy and long wave periods (T = 4.1 s and T = 5.1 s; Fig. 5.6): under medium wave energy (P = 0.71 kW m^{-1}) and T = 4.1 s, U_{max} in *Elymus* was 60% (18 cm s^{-1}) higher than in *Puccinellia*. However, video material of this wave test revealed, that both *Puccinellia* and *Elymus* exhibited a swaying movement with symmetric bending angles in and counter to the direction of wave travel (Fig. 5.5a, 5.5b). In *Elymus*, the bottom stem parts bent to small angles (30–40°) while the upper more flexible stem parts folded over, resulting in a wide bending angle (80–90°) of the *Elymus* canopy as a whole in comparison to the bending angle of *Puccinellia* (40–50°). Time trace analysis of plant stem movement indicated a similar time of maximum stem extension in *Puccinellia* and *Elymus* and a phase difference of around 20–40° between canopy movement and wave motion in both canopies (Fig. 5.5a, 5.5b).

Under high wave energy (P = 2.31 kW m^{-1}) and T = 5.1 s, U_{max} in *Puccinellia* exceeded U_{max} in *Elymus* by 20% (18 cm s^{-1}). According to video observations, both *Puccinellia* and *Elymus* exhibited a whip-like movement with wide bending angles (60–90°) in the direction of wave travel and smaller bending angles (25–55°) counter to the direction of wave travel (Fig. 5.6a, 5.6b). In the *Elymus* canopy, the wide bending angles resulted in folding and finally breakage of stems. The time of maximum stem extension and hence the time of a flattened canopy posture lasted in *Puccinellia* around 1.5–2 s and in *Elymus* 1–2 s. Due to the wide bending angles during wave forward motion, both canopies were in a flattened posture for part of the wave cycle and provided low flow obstruction. Both in *Puccinellia* and *Elymus*, a phase difference occurred between canopy movement and wave motion, in *Elymus* the phase difference was much larger (around 90°) than in *Puccinellia* (around 30–40°).

Maximum orbital velocity (U_{max}) in *Puccinellia* and *Elymus* under vegetated and mowed conditions

Under low wave energy and 1 m water depth (P = 0.07 kW m^{-1}) both within the *Puccinellia* and *Elmyus* canopy differences between U_{max}, U_{max} under mowed conditions and $U_{max\,pred}$ were small (± 1–6 cm s^{-1}; 7–27%) (Fig. 5.7, Table 5.2).

Under medium wave energy ($P \geq 0.47 \leq 0.71$ kW m^{-1}), the effect of *Puccinellia* and *Elymus* on U_{max} varied between water depths of 1 m and 2 m: under 1 m water depth, the presence of the *Puccinellia* canopy led to an increase of U_{max} both compared to mowed conditions (+20%; 12 cm s^{-1}) and $U_{max\,pred}$ (+18%; 11 cm s^{-1}) (Fig. 5.7a, Table 5.2). Presence of the *Elymus* canopy caused a reduction of U_{max} compared to mowed conditions (-10%; 7 cm s^{-1}) and $U_{max\,pred}$ (-23%; 14 cm s^{-1}) (Fig. 5.7b, Table 5.2).

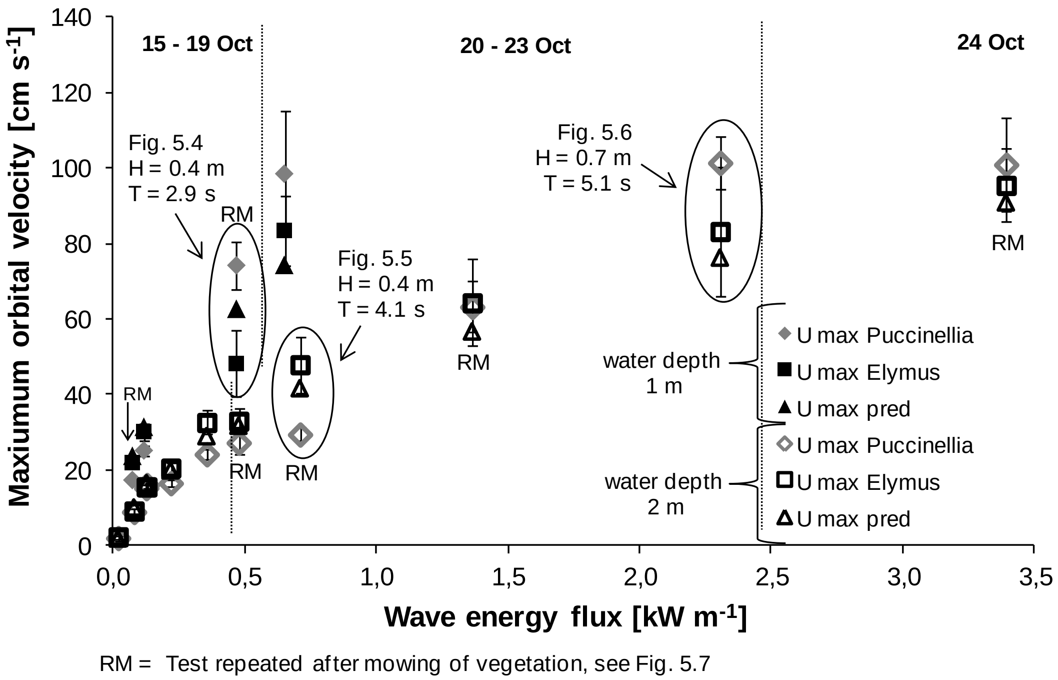


Fig. 5.3. Maximum orbital velocity in direction of wave travel (U_{max}) within canopies of *Puccinellia* and *Elymus* and predictions of U_{max} according to linear wave theory ($U_{max\ predicted}$) during wave tests with 1 m water level above the marsh surface. Error bars refer to the mean ± 1 SD of time series measurements over the complete wave test. Vertical lines mark times when physical damage of vegetation was assessed (Fig. 5.8).

Under 2 m water depth, the presence of the *Puccinellia* canopy led to a reduction of U_{max} and presence of the *Elymus* canopy to an increase of U_{max} (Fig. 5.7, Table 5.2). For P = 0.48 kW m^{-1}, U_{max} within P*uccinellia* was lower than U_{max} over the mowed *Puccinellia* canopy (-19%; 6 cm s^{-1}) and $U_{max\ pred}$ (-13%; 4 cm s^{-1}). U_{max} within *Elymus* by contrast exceeded U_{max} over the mowed *Elymus* canopy (+ 21%; 6 cm s^{-1}) and $U_{max\ pred}$ (+4%; 1 cm s^{-1}). The same pattern occurred in the wave test with P = 0.71 kW m^{-1}. Here, U_{max} in *Puccinellia* was lower than U_{max} over the mowed *Puccinellia* canopy (-40%; 16cm s^{-1}) and $U_{max\ pred}$ (-29%; 12 cm s^{-1}). In *Elymus, U_{max}* in the canopy exceeded U_{max} over the mowed canopy (+10%; 4 cm s^{-1}) and $U_{max\ pred}$ (15%; 6 cm s^{-1}).

In the two wave tests with high wave energy (P = 1.36 and 3.39 kW m^{-1}), U_{max} recorded in *Puccinellia* and U_{max} when the *Puccinellia* canopy was mowed exceeded $U_{max\ pred}$ (+6–14%; 5–10 cm s^{-1}) (Fig. 5.7a, Table 5.2). Presence of the Elymus canopy led to an increase of U_{max}: for P = 1.36 kW m^{-1} U_{max} exceeded U_{max} over the mowed *Elymus* canopy(+12%; 7 cm s^{-1}) and $U_{max\ pred}$ (+14%; 8 cm s^{-1}). The same pattern occurred under P = 3.39 kW m^{-1}. Here U_{max} recorded in *Elymus* exceeded U_{max} over the mowed *Elymus* canopy by 20% (16 cm s^{-1}) and $U_{max\ pred}$ 5% (4 cm s^{-1}) (Fig. 5.7b, Table 5.2).

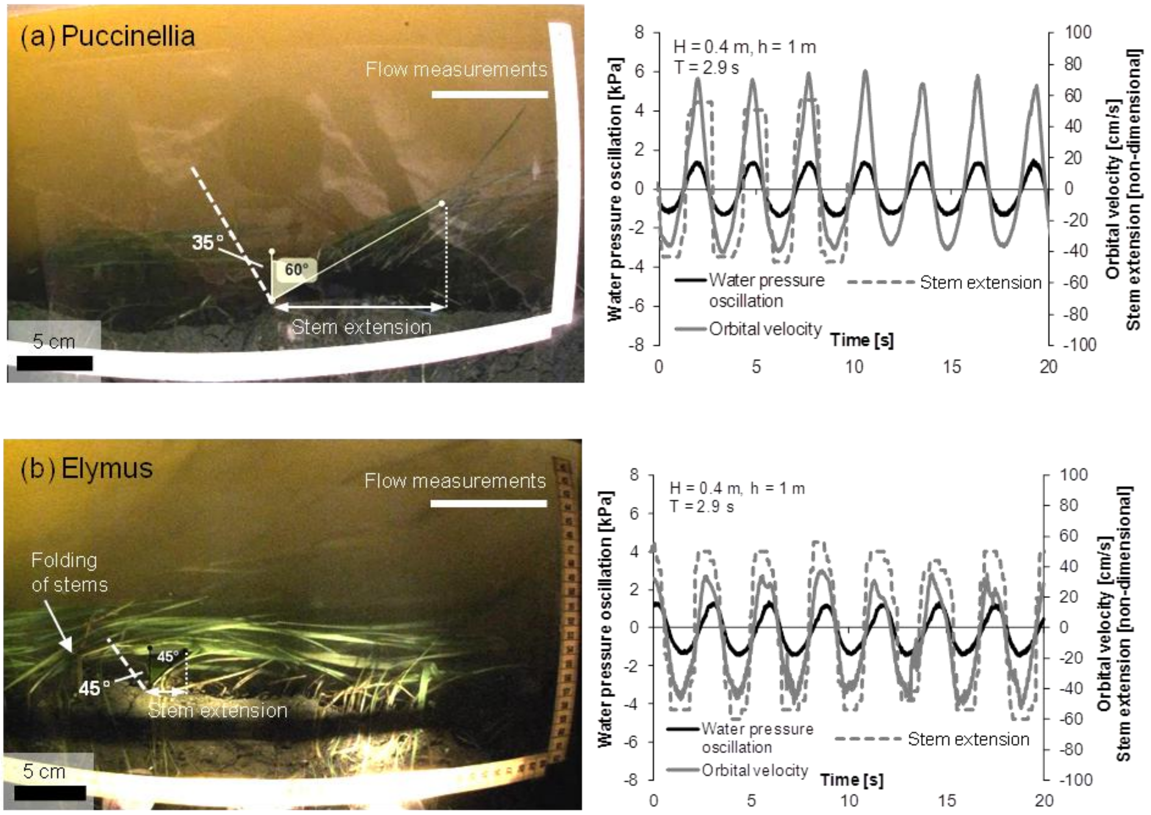


Figure 5.4. Orbital flow velocity 15 cm above the soil surface and canopy movement under a medium level of wave energy with water depth (h) = 1 m, wave height (H) = 0.4 m and wave period (T) = 2.9 s. Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in direction of wave motion). **(a)** Whip-like movement of the *Puccinellia* canopy, **(b)** swaying movement of the *Elymus* canopy. Maximum orbital velocity in the direction of wave travel in *Puccinellia* was approx. 50% higher than in *Elymus* (see Fig. 5.3).

Physical damage of the vegetation canopy

Cumulatively around 30% (approximately 30 kg) of the total 98 kg of above ground biomass were lost under the wave forces applied in the experiment (Fig. 5.8). Photo documentation of *Puccinellia* and records of stem density in *Elymus* during the course of the experiment revealed that the two canopies differed in their susceptibility to plant stem breakage under increasing wave forces: the *Puccinellia* canopy with its high stem flexibility withstood the hydrodynamic forces without substantial damage (Fig. 5.9). The *Elymus* canopy with its low flexibility experienced severe physical damage in the course of the experiment (Fig. 5.8). Folding and breakage of *Elymus* stems occurred from a medium level of wave energy onwards (P ≥0.47 kW m^{-1}), corresponding to wave heights ≥ 0.4 m, and in total caused a loss of approximately 75% of *Elymus* stems (Fig. 5.8).

Experimental runs with wave heights of 0.4–0.7 m and $U_{max\,pred}$ of 32–76 cm s^{-1} resulted in folding and breakage of 40% of *Elymus* stems (Fig. 5.5). This loss of *Elymus* stems occurred simultaneously with the largest share of biomass loss as averaged over the whole test section. Another 35% of *Elymus* stems were lost during tests with breaking waves, with a height of 0.9–1.1 m and $U_{max\,pred}$ of 61–126 cm s^{-1}.

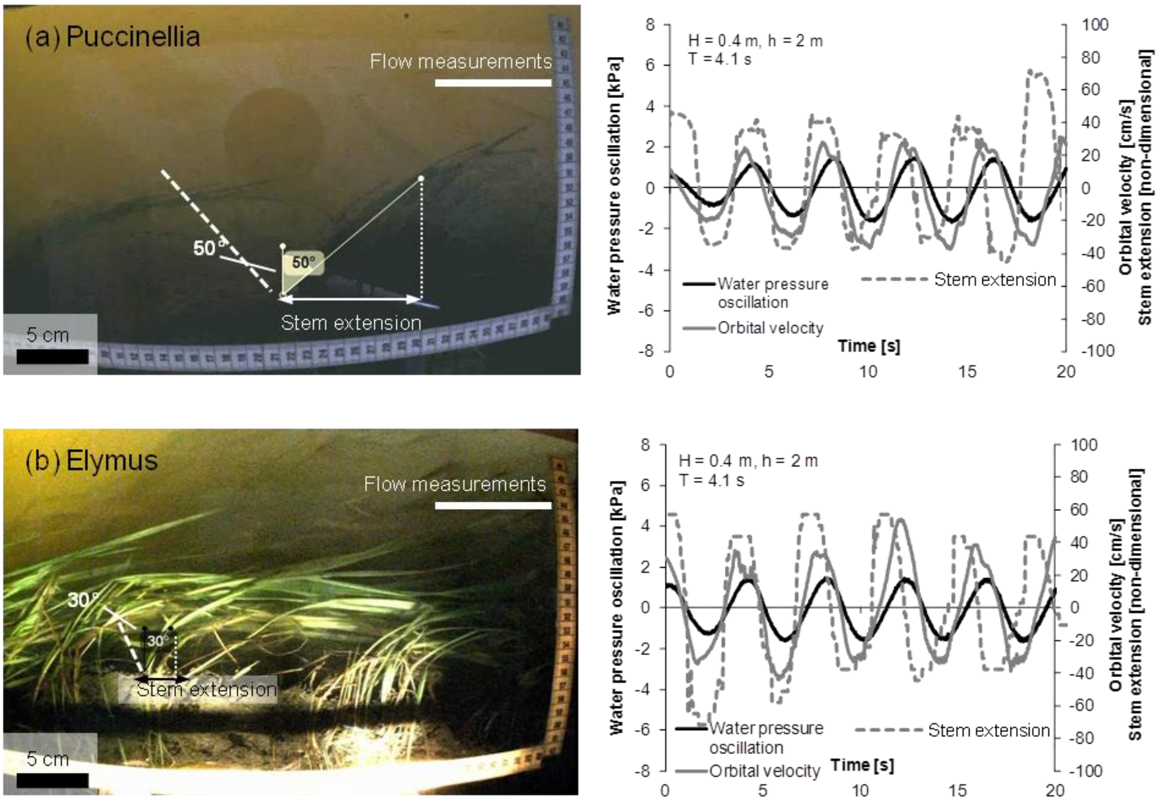


Figure 5.5. Orbital flow velocity 15 cm above the soil surface and canopy movement under wave motion under a medium level of wave energy for water depth (*h*) = 2 m, wave height (*H*) = 0.4 m and wave period (*T*) = 4.1 s. Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in the direction of wave motion). **(a)** Swaying movement of the *Puccinellia* canopy, **(b)** swaying movement of the *Elymu*s canopy. Despite the identical type of canopy movement, orbital velocity in the direction of wave travel in *Puccinellia* is 40% lower than in *Elymu*s (see Fig. 5.3).

Discussion

Vegetation-wave interactions are an important control of the tidal flow and wave energy dissipation potential of marshes, physical damage occurring to the vegetation canopy under wave forcing and of marsh recovery after storm events (Cahoon 2006; Möller 2006; Duarte et al. 2013; Möller et al. 2014). Numerous studies have investigated canopy movement and flow resistance provided by salt marsh canopies under average hydrodynamic conditions (Leonard and Luther 1995; Neumeier and Ciavola 2004; Neumeier and Amos 2006a; Mullarney and Henderson 2010; Riffe et al. 2011). However, data on the response of different plant species from salt marshes to higher levels of wave energy and energy thresholds, beyond which plant physical damage may affect the wave dissipation of capacity of marshes, are scarce (Möller et al. 2014).

In this study we analysed vegetation-wave interactions in canopies of two salt marsh grasses, the low growing and flexible *Puccinellia maritima* and the tall, less flexible *Elymus athericus*, under low, medium and high levels of wave energy.

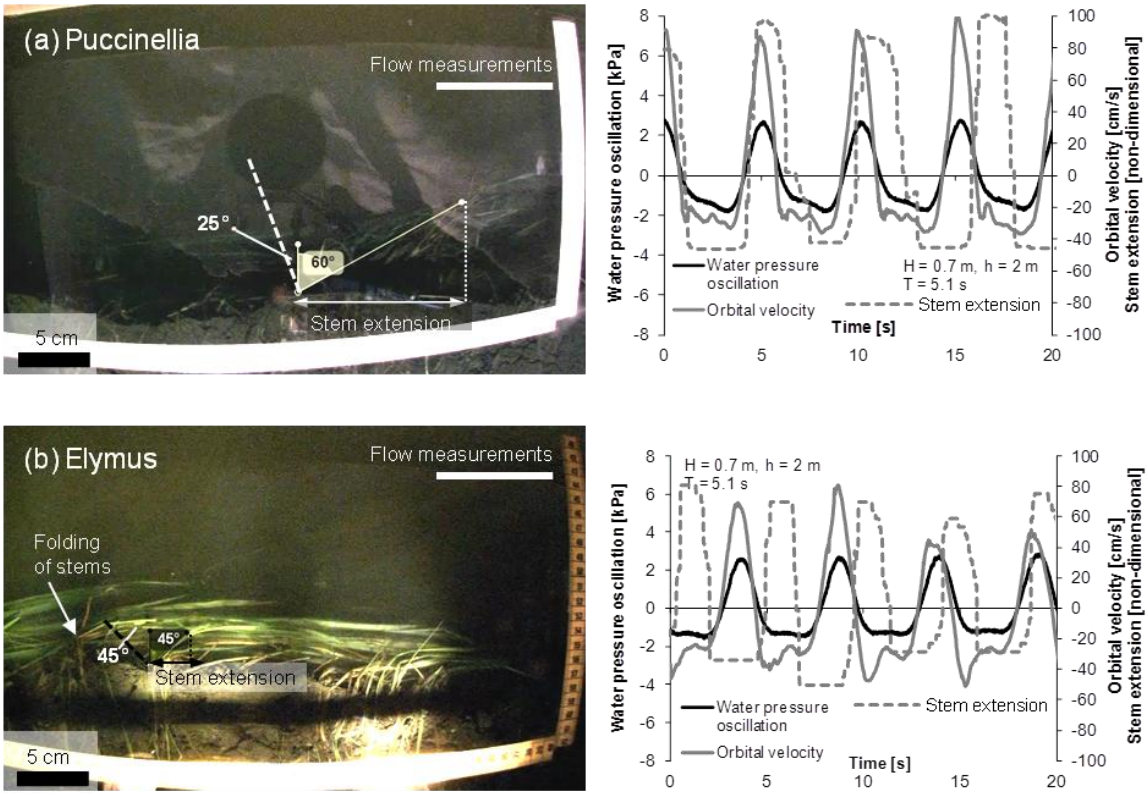


Figure 5.6. Orbital flow velocity 15 cm above the soil surface and canopy movement under wave motion under a high level of wave energy for water depth (*h*) = 2 m, wave height (*H*) = 0.7 m and wave period (*T*) = 5.1 s. Water pressure (left y-axis), orbital velocity and time trace of horizontal stem extension (right y-axis; positive values in the direction of wave motion). **(a)** Whip-like movement of the *Puccinellia* canopy, **(b)** Whip-like movement of the *Elymu*s canopy. Despite the identical type of canopy movement, orbital velocity in the direction of wave travel in *Puccinellia* is 20% higher than in *Elymu*s (see Fig. 5.3).

Our results provide insights into the ability of salt marsh vegetation to reduce near bed flow velocity and protect the bed from shear stress and erosion under a wide range of wave conditions and show how this ability varies with plant biophysical characteristics. Furthermore, we identified energy thresholds critical for physical damage occurring to vegetation under rising wave energy.

Effect of the *Puccinellia* and *Elymus* canopy on orbital flow

Low and medium wave energy

The swaying oscillatory movement and small differences between maximum orbital velocity under vegetated and mowed conditions both in *Puccinellia* and *Elymus* low wave energy (*P* ≤0.36 kW m^{-1}) suggest a minor effect of the vegetation canopy and its biophysical characteristics on orbital velocity near the bed and bed shear stress.

Similar findings were reported by Neumeier and Amos (2006b) who measured a reduction of orbital flow by 10–20% under low wave energy (h≤0.9 m, H≤0.09 m) in *Spartina anglica* salt marshes of Eastern England and assumed a minor importance of this flow reduction for the deposition and erosion of sediments.

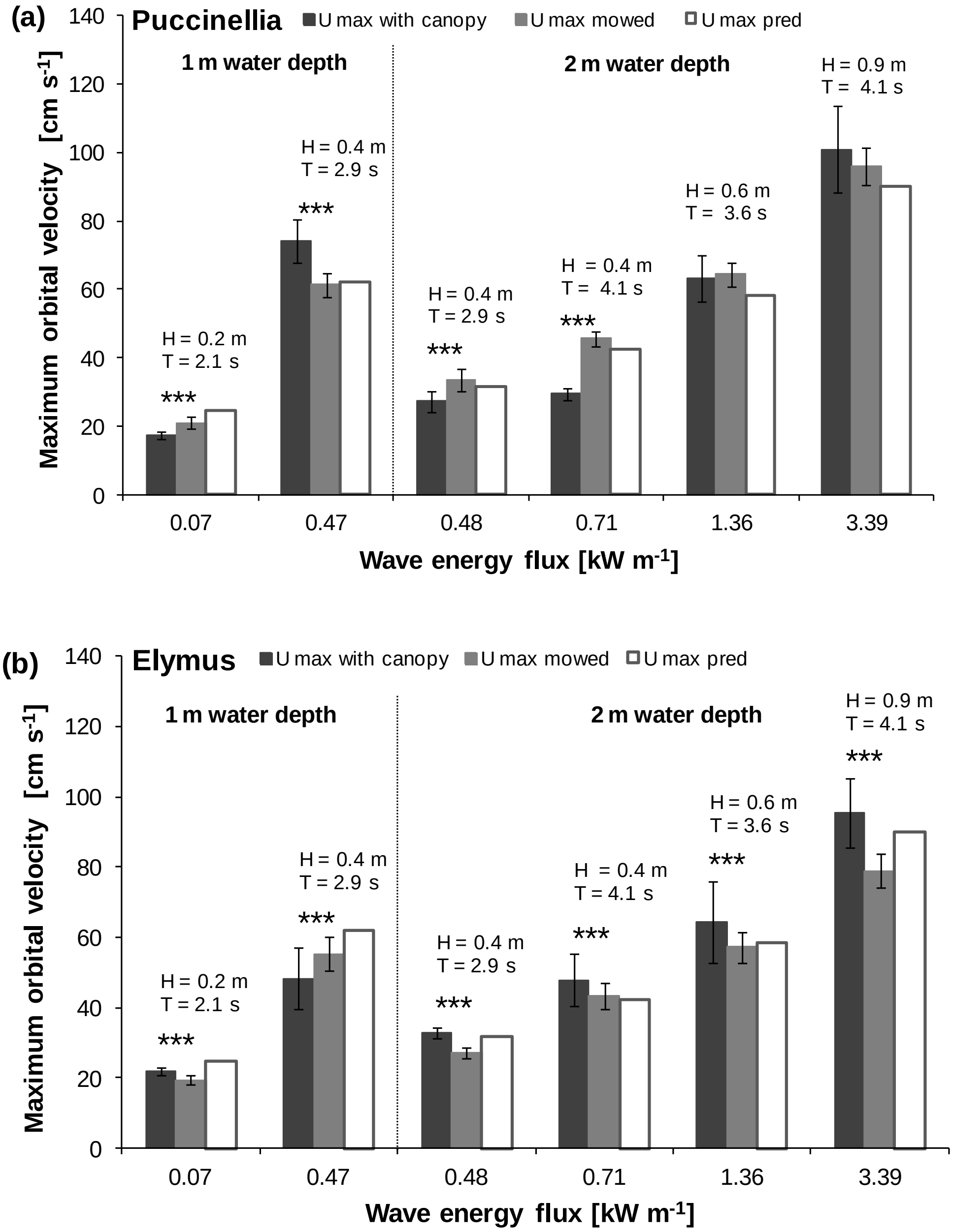


Figure 5.7. Maximum orbital velocity in the direction of wave travel (U_{max}) under presence of vegetation, when the marsh platform was mowed and as predicted from linear wave theory ($U_{max\ pred}$). **(a)** Measurements for the *Puccinellia* canopy, **(b)** measurements for the *Elymus* canopy. Error bars refer to the mean ± 1 SD of time series measurements over the complete wave test. Statistically significant differences at the 5% level (t-test) between U_{max} under vegetated and mowed conditions are marked with asterisks.

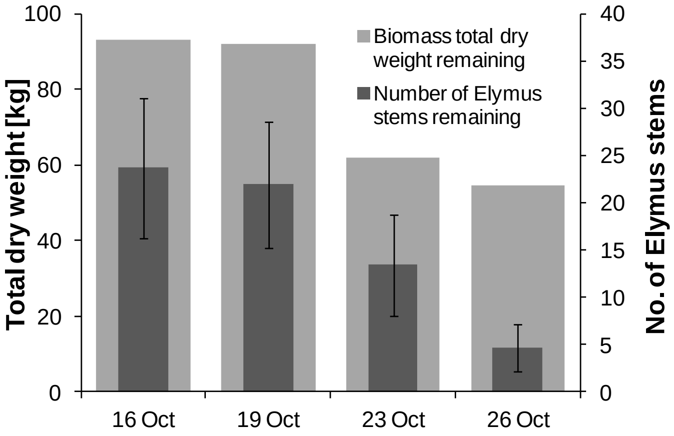


Figure 5.8. Plant biomass remaining on the test section (light thick bars) and number of *Elymus* stems (dark thin bars, mean ± 1 SD from 18 10x10 cm quadrats distributed over the test section) prior to the first wave test (16th of October) and at the three times when the flume was drained in the course of the experiment. The bar from the 26th October shows biomass and stem counts before the marsh platform was mowed i.e. at the end of wave tests with the vegetated marsh surface.

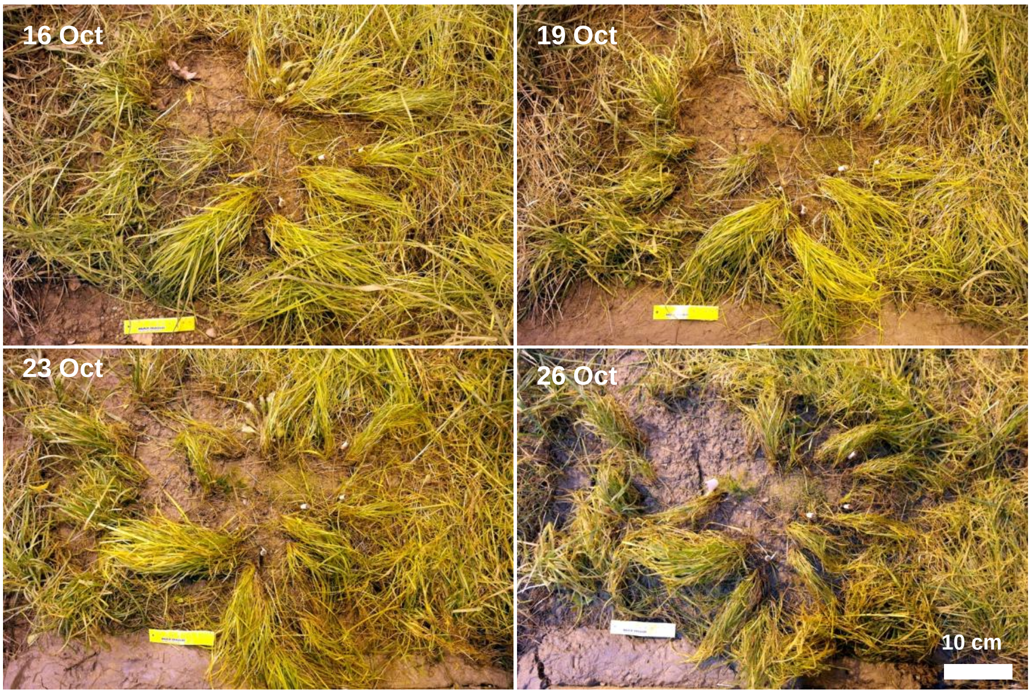


Figure 5.9. Photo documentation of the *Puccinellia* canopy prior to the first wave test (16th October) and at the three times when the flume was drained in the course of the experiment (16th, 19th, 23rd and 26th October). The photograph from the 26th October shows *Puccinellia* before the marsh platform was mowed i.e. at the end of wave tests with the vegetated marsh surface.

Under a water depth of 1 m and medium wave energy the *Elymus* canopy had a greater capacity to reduce orbital flow velocity than *Puccinellia*, presumably largely due to the fact that the tall *Elymus* canopy occupied three times the amount of space in the water column than the low-growing *Puccinellia*. This suggests a species-specific vegetation control on sediment transport and deposition under such hydrodynamic conditions, at least at spatial and temporal scales on which other controls, such as sediment supply and incident hydrodynamic conditions can be assumed to be relatively invariant (French and Spencer 1993).

Under 2 m water depth and medium wave energy (P = 0.48 kW m^{-1} and P = 0.71 kW m^{-1}) within the *Puccinellia* canopy, maximum orbital velocity was reduced by 20–40% (6–16 cm s^{-1}) compared to mowed conditions. This represents a considerable decline in flow velocity due to vegetation presence that may enhance sediment deposition and decrease bed shear stress. In the field, flow reduction by *Puccinellia* could even be higher given the lower flexibility and greater stem height in *Puccinellia* in the field compared to the flume (Table 5.1).

While in *Puccinellia* flow velocity was reduced under 2 m water depth and medium wave energy, in *Elymus* stem deflection and folding was observed under these conditions and maximum orbital velocity exceeded those found in *Puccinellia* by 63% and those under mowed conditions by 10%. The decline in flow resistance of *Elymus* from a medium level of wave energy onwards coincided with a leveling-off in the salt marsh wave-dissipation capacity (Möller et al. 2014; Wolters et al. (under review)). With *Elymus* being the dominant species in our flume experiment, our results suggest that changes in vegetation-wave interactions may exert an important control on wave dissipation by salt marshes under rising wave energy. Considering the great variability in biophysical properties between species (Feagin et al. 2011; Rupprecht et al. 2015b), this underlines the need of further experiments with different species such as e.g. *Spartina anglica* or *Spartina alterniflora* and calls for the consideration of species-specific energy thresholds marking changes in flow resistance in modelling studies.

High wave energy

High levels of wave energy and thus a high velocity and erosion potential of near-bed orbital flow occur during storm surges, when large amounts of sediment can be transported in suspension to low and high marsh zones (Stumpf 1983; Turner et al. 2006; Schuerch et al. 2013). In such conditions, the ability of salt marsh canopies to slow down flow velocity, protect the bed from erosion and enhance sediment deposition is of great importance (Leonard and Reed 2002; Neumeier and Ciavola 2004).

Our results show that under high wave energy (P ≥1.36 kW m^{-1}) both *Puccinellia* and *Elymus* reconfigured to a flattened 'shielding' posture close to the soil surface for a large part of the wave cycle. The increase of U_{max} compared to mowed conditions or $U_{max\ pred}$ in *Puccinellia* and *Elymus* suggests that the smooth 'canopy surface' formed by the flattened canopies caused less flow resistance and friction forces than stumps of mowed plant stems or bottom friction as assumed in linear wave theory. Similar to the wave tests in 1 m water depth, this canopy behaviour can be expected to protect the bed from erosive processes. However, while still acting to protect the bed, the relocation of a large share of the flow as higher velocity 'skimming' flow above the canopy may reduce the chance of sediment particles settling on the bed, thus leading to a passive protective role of the canopy rather than an active sediment-enhancing role (Neumeier and Ciavola 2004; Peralta et al. 2008).

Apart from high levels of wave energy and water depths of around 2 m above the marsh platform, long wave periods (4–8 s) are characteristic for storm surges. The dependence of wave-vegetation interactions on wave period has been observed in many flume, field and modelling studies (Lowe et al. 2007; Bradley and Houser 2009; Mullarney and Henderson 2010; Paul and Amos 2011; Jadhav et al. 2013). It has been suggested that depending on the biophysical properties of the plant species, canopies can act as a band-pass filter preferentially damping short or long-period waves while most easily passing intermediate frequencies (Mullarney and Henderson 2010). Moreover, it is to be expected that biophysical plant properties impact most on the vegetation-wave interactions under long-period waves as those tend to have larger velocities throughout the water column than short period waves (Anderson et al. 2011). Results of our study show that under 2 m water depth and medium to high wave energy, larger differences between orbital velocities within the *Puccinellia* and *Elymus* canopy occurred in the wave tests with wave periods exceeding 4 s. This suggests that biophysical properties of the vegetation canopy affect vegetation-wave interactions and the flow and wave dissipation capacity of salt marshes even under storm surge conditions.

Under a wave period of 4.1 s and medium wave energy, differences in the capacity of *Puccinellia* and *Elymus* to provide flow resistance and reduce orbital velocity resulted from the different degree of ‘canopy flattening’ i.e. the susceptibility of plant stems to folding under wave forward motion. Under a wave period of 5.1 s and high wave energy, both *Puccinellia* and *Elymus* were flattened by the high velocity flow. However, both canopies showed differences in their capacity to provide flow resistance due to relative motion between plants and water (i.e. the phase difference between canopy and water movement). The greater phase difference and lower values of U_{max} suggest a higher flow resistance and hence a higher potential for flow and wave dissipation of the *Elymus* canopy.

Susceptibility of salt marsh vegetation to physical damage under rising wave forces

Throughout the experiment the salt marsh vegetation canopy as a whole experienced moderate physical damage and the soil surface withstood larger wave forces without substantial erosion (Möller et al. 2014) suggesting a high resilience of vegetated salt marsh surfaces to storm surge conditions. With the root mat remaining intact, damage to the vegetation canopy reported in our paper can be considered to be of a temporary nature with recovery expected within the next growing season. This is especially valid for plant species that can reproduce by clonal growth like both grass species investigated in this study.

The canopies of *Puccinellia* and *Elymus* differed in their susceptibility to stem folding and breakage under rising wave energy. The very low amount of physical damage occurring to *Puccinellia* can be attributed to its very flexible stems allowing reconfiguration of the canopy to a flat shielding posture close to the bed under fast orbital flow. A similar strategy to survive under drag forces imparted by fast flow velocities is also known for flexible sea grasses and freshwater plants (O'Hare et al. 2007; Peralta et al. 2008). Following the low flow resistance under higher energy wave conditions provided by very flexible plants such as *Puccinellia*, their direct contribution to the dissipation of hydrodynamic energy is small. The flattened plant canopies under high velocity flows, however, reduce friction forces at the water-sediment interface and plant roots have also been shown to stabilise sediments (Neumeier and Ciavola 2004; Peralta et al. 2008). This may reduce erosive processes, facilitate the establishment of seedlings from other (pioneer and low) marsh species, and hence contribute to long-term marsh stability.

In contrast to *Puccinellia*, the less flexible and tall *Elymus* canopy, experienced a high percentage of stem breakage from a medium level of wave energy onwards (P ≥0.47 kW m^{-1}) and wave heights equal or higher than 0.4 m. Previous measurements of stem flexibility in salt marsh grasses have shown that variation of stem flexibility between the bottom, middle and top stem part of *Elymus* is much higher than in *Puccinellia* (Rupprecht et al. 2015b). The rather brittle bottom part of *Elymus* stems in comparison to the rest of the stem favours the formation of 'lines of weakness' during stem deflection and subsequent stem breakage around 5-10 cm above the soil surface. Turbulence around stumps remaining on the marsh surface after stem breakage may increase bed shear stress and bed erosion. The fact that *Elymus* stem's flexibility in the flume significantly exceeded that recorded in the field (see Methods, Table 5.1) suggests that the susceptibility of *Elymus* stems to breakage in the field may be even higher than observed in our experiment. Changes in the vitality of *Elymus* in the course of the experiment due to long periods of submergence and lack of oxygen, however, may have also facilitated the breakage of stems.

Conclusions

In this paper we investigated salt marsh vegetation-wave interactions over a wide range of wave conditions from low to high levels of wave energy in a large-scale flume experiment. The results of our study indicate that canopy height and flexibility, as well as incident wave and water depth conditions, play an important role in determining how salt marsh vegetation interacts with the orbital flows under waves. Our observations also highlight that the susceptibility of plants to physical damage under differing wave and water depth conditions varies between species.

The potential of the flexible, low-growing *Puccinellia* and the relatively stiff, tall *Elymus* to reduce wave orbital flow was small under low and high levels of wave energy. Under a medium level of wave energy (P ≥0.47 ≤0.71 kW m^{-1}) the effect of *Elymus* and *Puccinellia* on maximum orbital velocity varied with the degree of canopy submergence: while under 1 m water depth, *Elymus* had a higher ability to reduce flow velocity than *Puccinellia*; and under 2 m water depth, folding of *Elymus* stems led to a decline in flow resistance of the canopy and increase of flow velocity, while within *Puccinellia* flow velocity was still considerably reduced. The *Puccinellia* canopy experienced no visible physical damage even under extreme levels of wave energy that implies a continuous contribution to erosion protection and suggests a high resilience of salt marsh vegetation dominated by *P. maritima* to storm surge conditions. In the *Elymus* canopy by contrast, stem folding and breakage occurred under wave heights exceeding 0.4 m suggesting lower resilience to storm surge conditions in comparison to *Puccinellia* and a decline in the contribution of *Elymus* to wave dissipation and erosion protection under repeated storm and flooding events.

Based on our findings, we recommend further studies to focus on the behaviour of a wider range of mono-specific salt marsh canopies under the full range of water depth and wave conditions that can be expected to occur, particularly in macro-tidal settings. While *Elymus athericus* and *Puccinellia maritima* are common species in the NW European region, the occurrence of mono-specific stands of *Spartina anglica* and *Spartina alterniflora* along the coastline of the United States and China, as well as NW Europe, where the coastal protection function provided by salt marshes is being considered as part of coastal management approaches in the framework of pilot projects (Kabat et al. 2009; Borsje et al. 2010; Temmerman et al. 2013), calls for a separate investigation of vegetation-wave interactions in those types of marshes. Knowledge on wave energy and water depth thresholds relating to plant breakage in mono-specific stands as well as future studies providing such thresholds for mixed canopies can then inform predictions of marsh stability and resilience over longer time-scales, feeding into the growing body of knowledge that will ultimately allow salt marshes to be fully incorporated into coastal protection schemes.

Acknowledgements

We thank all of the staff at the Grosser Wellenkanal as well as B. Evans, J. Tempest, K. Milonidis and C. Edwards, Cambridge University, and D. Schulze, Hamburg University, for their invaluable logistical assistance, Fitzwilliam College for supporting the research time of I.M., and C. Rolfe, Cambridge University, for the soil analysis and Deltares for the support by the Strategic Research Programme on dikes, levees and dams. The work described in this publication was supported by the European Community's 7th Framework Programme through the grant to the budget of the Integrating Activity HYDRALAB IV, Contract no. 261529 and a grant from The Isaac Newton Trust, Trinity College, Cambridge.

6

Synthesis

Franziska Rupprecht

Key findings of this thesis

In the following the key findings of this thesis are summarised and related to the research objectives outlined in chapter 1. The **four main objectives of this study** were **(1)** to analyse large-scale and long-term patterns in vegetation succession after abandonment of grazing and drainage in mainland salt marshes of the Wadden Sea and to identify the major environmental drivers, **(2)** to quantify biophysical vegetation characteristics with application to wave dissipation in canopies of four plant species typically occurring in salt marshes of the Wadden Sea and North-West Europe, **(3)** to measure wave dissipation, erosion stability of the marsh surface and physical damage occurring to the vegetation canopy in these salt marshes under average up to storm surge wave conditions, and **(4)** to analyse the effect of vegetation on wave orbital flow and susceptibility of plants to breakage under rising wave forces in canopies of two salt marsh plant with different flexibility and height.

1.1) Considered from a large-scale and long-term perspective, abandonment of grazing and drainage caused the spread of grazing sensitive plant species from mid and late successional stages in the Wadden Sea mainland salt marshes. This change in vegetation composition may affect species diversity and ecosystem functions.
1.2) Grazing-regime and elevation were found to be the most important drivers of succession.
1.3) Retardation of succession in salt marshes at the northern Wadden Sea (Northern Frisia) in comparison to the central Wadden Sea area (near the estuary of the river Elbe) suggests a geographical variation in the pace of succession along large-scale gradients of salinity, inundation frequency and sediment deposition.

2.1) Stem flexibility of salt marsh plants differed significantly both between species and between the different parts of their stems. *Puccinellia maritima* was found to be the species with the most flexible stems, and, as a result of their relatively large stem diameter, *Spartina anglica* the species with the stiffest stems.
2.2) Above ground biomass and hence potential canopy obstruction to water flow could be estimated more accurately by side-on photography of vegetation than from measurement of light availability within the canopy.

3.1) Vegetated salt marsh surfaces caused considerable wave attenuation even under wave heights and water depths typically found during storms. The dissipation of non-breaking waves over salt marshes reached a maximum of 20% over a 40 m distance under wave heights of 0.3 m and water depths of 2 m.
3.2) The contribution of salt marshes to wave dissipation was generated not only by the marsh platform but also, and significantly, by the vegetation canopy that was responsible for up to 60% of the observed wave reduction.

3.3) Under higher energy conditions (wave height ≥0.4 m) the vegetation canopy experienced flattening and plant stem breakage resulting in a loss of about 30% of biomass which possibly reduced wave dissipation. The marsh soil surface by contrast remained stable and resistant to surface erosion under all conditions.

4.1) Under low wave energy the flexible, low-growing *Puccinellia maritima* and the relatively stiff, tall *Elymus athericus* had no substantial effect on wave orbital velocities near the bed, while under high wave energy both canopies caused an increase of flow velocity in direction of wave travel. Under a medium level of wave energy (wave height = 0.4 m) the effect of *Elymus atheriucs* and *Puccinellia maritima* on orbital velocity varied with the degree of canopy submergence: while under 1 m water level *Elymus athericus* had a higher ability to reduce flow velocity than *Puccinellia maritima*, under 2 m water level, folding of *Elymus athericus* stems resulting in a loss of flow resistance and an increase of flow velocity, while within *Puccinellia maritima* flow velocity was reduced considerably.

4.2) In relatively stiff, tall *Elymus athericus* canopy stem folding and breakage was observed from a medium level of wave energy onwards (corresponding to wave heights ≥0.4 m) both in 1 m and 2 m water depth and coincided with a leveling-off in the marsh wave dissipation capacity. The flexible and low-growing *Puccinellia maritima* canopy experienced even under extreme wave forces very little physical damage.

The effect of vegetation on the wave dissipation capacity of salt marshes

The process of wave dissipation over vegetated salt marsh surfaces can be considered as a large-scale process depending on small-scale interactions (Zeller et al. 2014). At the scale of the vegetated landform (e.g. a coastal salt marsh), the interactions between waves and vegetation are affected by the wave regime as well as by the spatial configuration of vegetation patches (vegetation cover) and the ratio of water depth to canopy height (Kirwan and Murray 2007; Vandenbruwaene et al. 2011). At the scale of plant stands and individual plants, the interactions between vegetation and wave orbital flow are governed by the biophysical properties of vegetation canopies such as plant flexibility, density and height as well as by the hydrodynamic conditions (water depth, wave height and wave period) (Anderson et al. 2011).

The course and speed of temporal vegetation change (vegetation succession) determines changes in vegetation cover, plant species composition and biophysical vegetation characteristics, as well as marsh recovery time after disturbance and consequently affects the process of wave dissipation both at larger and smaller scales. In many mainland salt marshes of the Wadden Sea, abandonment of grazing and artificial drainage favoured succession towards late successional stages and the large-scale spread of the dwarf shrub *Atriplex portulacoides* in the low marsh and the grass *Elymus athericus* in the high marsh (chapter 2). In comparison to plant species from early successional stages such as e.g. the grasses *Spartina anglica* and *Puccinellia maritima*, characterised by flexible stems and a canopy height of around 0.3–0.4 m, *Elymus atherius* is rather tall (canopy height around 0.7 m) and shows a high variability of flexibility within its stems, with brittle bottom stem parts and more flexible middle and top stem parts (chapter 3).

In the framework of this thesis, the wave dissipation capacity of a typical North-West European salt marsh with a mixed canopy of *Elymus athericus* (dominant species), *Puccinellia maritima* and the annual herbaceous plant *Atriplex prostrata*, was quantified for average up to storm surge wave conditions in a real-scale flume experiment (chapter 4). The results showed that the presence of salt marsh caused considerable wave dissipation even under high water levels (2 m) and extreme wave heights (0.9–1.1 m), with the vegetation accounting for up to 60% of the observed wave reduction. Around 30% of above ground biomass was lost due to plant breakage in the course of the experiment, however, physical damage to the vegetation can be considered of temporary nature, as the marsh surface was stable and resistant to surface erosion under all wave conditions and the plant root mat remained intact.

Vegetation-induced wave dissipation is achieved by the interaction of orbital water motion under waves with the vegetation canopy. The flow resistance provided by plants reduces orbital flow velocities, resulting in the reduction of wave height and wave energy (Mullarney and Henderson 2010). Moreover salt marsh vegetation has an important influence on sedimentary processes through flow reduction. It enhances sediment deposition and protects the bed against erosion (French and Reed 2001). A detailed study on vegetation-wave interactions in the canopies of *Puccinellia maritima* and *Elymus athericus* (chapter 5) was conducted in the framework of the large-scale flume experiment mentioned above. The results revealed that canopy flexibility and height, as well as incident wave and water depth conditions, play an important role in the ability of vegetation to reduce the velocity of wave orbital flow and in the susceptibility of plants to folding and subsequent breakage under wave forcing.

Under wave conditions frequently occurring on tidal marshes with low to medium wave energy and 1 m water level, the overall contribution of the tall, stiff *Elymus athericus* to the reduction of orbital flow and wave energy exceeded that of the low-growing, flexible *Puccinellia maritima. S*pecies-specific vegetation-wave interactions can hence be expected to exert an important control on sediment transport and deposition alongside sediment supply and wave conditions. Under high to extreme wave energy and 2 m water level, both *Puccinellia maritima* and *Elymus athericus* took a flattened, streamlined posture close to the bed under wave forward motion, resulting in a relocation of the flow above the canopy as a higher velocity 'skimming' flow. Consequently, during storm events vegetation may reduce the chance of sediment particles settling on the bed and thus likely play a passive protective role against bed erosion, rather than an active sediment-enhancing role (Peralta et al. 2008). *Puccinellia maritima* experienced no visible physical damage even under extreme levels of wave energy. In *Elymus athericus* by contrast, stem folding and breakage occurred under wave heights exceeding 0.4 m both under 1 m and 2 m water level and coincided with a leveling-off in the marsh wave dissipation capacity.

The differences between the canopies of *Puccinellia maritima* and *Elymus athericus* in their ability to reduce orbital flow and wave energy and to survive under higher wave forces confirm results of a previous study by Bouma et al. (2005), reporting that trade-offs between stem flexibility and stem stiffness are an important aspect of plant response in hydrodynamically stressful environments. Plants with flexible stems (such as *Puccinellia maritima*) avoid high forces imparted by the flow by reconfiguration to a streamlined posture in the direction of water motion. Thus they survive even under extreme flow velocities without experiencing physical damage and provide continuous ‘passive’erosion protection to the bed. Plants with rather stiff and brittle stems (such as *Elymus athericus*) have a higher capacity to dissipate hydrodynamic energy, but suffer from a greater risk of breakage. This suggests lower resilience of their canopies to storm surge conditions compared to canopies of flexible plants and implies a decline in their contribution to wave dissipation and erosion protection under repeated storm and flooding events.

Overall, the results reported in this thesis demonstrate that vegetated salt marsh surfaces contribute considerably to wave dissipation under average up to storm surge conditions and hence can be a valuable component of coastal protection schemes. Furthermore, the results provide insights into the species-specific control of flow and wave dissipation by salt marshes with a high relevance for the prediction of the marsh wave dissipation capacity by numerical modeling of wave dissipation over vegetation fields and future studies on marsh stability and resilience under sea level rise and increasing storminess.

Implications for salt marsh conservation and management

European salt marshes are protected under international legislation for nature conservation. The European Habitats Directive or the Ramsar Convention on Wetlands of International Importance, aim to maintain or restore designated habitats in a favourable conservation status and to achieve a sustainable use of wetlands and the ecosystem services they provide.

In addition to legislation at the global or European level, many salt marshes are protected at the national level as parts of National Parks and Nature Reserves. With respect to salt marshes of the Wadden Sea, the Wadden Sea Plan, a trilateral agreement between The Netherlands, Germany and Denmark was set up as a framework for the integrated management of the Wadden Sea Area as an ecological entity. In accordance with existing conservation aims in the three Wadden Sea countries, the Wadden Sea Plan seeks to increase the area, stability and ‘naturalness’ as part of the main aims for salt marsh conservation in the Wadden Sea region (CWSS 2010).

Naturally formed salt marshes show a large-scale heterogeneity in marsh topography, soil conditions and vegetation composition. In many of the man-made Wadden Sea mainland salt marshes the abandonment of grazing and artificial drainage (hereafter referred to as abandonment) as a management practice to enhance their natural character caused an increase of progressive succession and dominance of late-successional species (chapter 2). With respect to the coastal protection service of salt marshes this may have both positive and negative implications.

During salt marsh succession, vegetation cover, canopy density and canopy height increase from early- to late-successional stages (van Wijnen et al. 1997). This applies also to secondary succession, e.g. after abandonment of grazing, when the short turf of grazing tolerant grasses is gradually replaced by a structurally complex vegetation canopy. Given that salt marsh vegetation accounts for a large share of the marsh wave dissipation capacity (chapter 4) as well as the positive correlation between vegetation density, biomass and wave dissipation (Koch and Gust 1999; Bouma et al. 2005; Möller 2006), progressive succession and the associated increase of canopy height and density is likely to cause an increase of the marsh wave dissipation capacity. Moreover, enhanced vegetation growth may favour sediment trapping by vegetation and in the long run result in an increase of marsh surface elevation and thus reduced water depths and wave heights over the marsh surface (Gedan et al. 2011). Considering the erosion stability of abandoned salt marshes, results of the large-scale flume experiment conducted in the frame work of this thesis demonstrated that the marsh substrate, originating from the high marsh zone of abandoned salt marshes, was highly resistant to surface erosion even under extreme wave forcing (chapter 4). This result confirms a finding of a previous study by Erchinger et al. (1994) on the erosion stability of man-made mainland salt marshes, reporting that ungrazed salt marshes with good soil aeration (provided either by drainage or by location in the high marsh zone) show a higher erosion stability than grazed salt marshes due to a higher stability of soil structure and deeper rooting of plants.

Apart from an enhanced vegetation contribution to wave dissipation and erosion stability as possible positive consequences of salt marsh abandonment and associated vegetation change, there are also critical issues in abandonment as a management practice with respect to the coastal protection service provided by salt marshes. In the case where the increase of progressive succession fails to be compensated by the establishment of pioneer vegetation and the formation of young marshes at the seaward marsh edge, large parts of the marsh platform will be characterised by tall and dense canopies of late successional species. Mainland salt marshes are especially sensitive to this phenomenon – also known as 'marsh ageing' (Esselink et al. 2009) due to their fixed position between seawalls and sedimentation works which strongly reduces their dynamic character (Bakker 2005). While in the medium-term, positive feedbacks between plant growth and sediment deposition may enhance the marsh wave dissipation capacity as described above, in the long-term salt marshes may approach a critical state as the edge of the salt marsh and the adjacent intertidal flat might become increasingly steep and vulnerable to wave attack and lateral erosion. Disturbance caused, for instance, by a storm may then trigger cascade of vegetation collapse and severe erosion on the cliff edge, leading to destruction of the salt marsh (Van de Koppel et al. 2005). Once degraded, the restoration of salt marshes may be rather cumbersome, as the re-establishment of pioneer species and the initiation of stabilising feedbacks between plant growth and sediment deposition typically requires biomass and size thresholds to be surpassed and hence a ‘window of opportunity’ for plant establishment, i.e. a time period with a very low intensity and frequency disturbance (Van Wesenbeeck et al. 2008; Bouma et al. 2009a; Bouma et al. 2009b).

The study on vegetation-wave interactions reported in chapter 5 of this thesis shows that salt marsh canopies from different successional stages such as *Puccinellia* (early- to mid-successional) and *Elymus* (late-successional) can differ markedly in their capacity to contribute to the dissipation of wave energy as well as in their ability to reduce near-bed orbital flow velocity, enhance sediment deposition and protect the bed from erosive processes. To profit from the benefits that various plant species and successional stages of vegetation provide in terms of the salt marsh wave dissipation capacity and erosion stability, management schemes should aim for the maintenance of all successional stages. In man-made mainland salt marshes where the uniform marsh topography and the dense artificial drainage system cause a lack in natural dynamics, this may require – to a limited extent – human inference with salt marshes.

To identify salt marshes where (temporary) human intervention may be necessary to maintain all successional stages of vegetation, it can be helpful to consider marsh width as well as large-scale gradients of salinity, inundation frequency and sediment deposition, acting as drivers of vegetation succession at the landscape-scale.

Generally the long-term erosion stability, and thereby reliability, of salt marshes as an element of coastal defence schemes increases with marsh width. Wide salt marshes (>2 km) develop on large foreshores and are exposed to less strong gradients in wave energy than narrow marshes. Consequently, if sediment supply is sufficient, salt marshes can go through cycles of plant growth, accretion, erosion and re-establishment of vegetation while always maintaining the minimal area needed for coastal defence. Moreover, the low inundation frequency and sediment input in inner parts of large high marsh areas may also lead to the formation of depressions and waterlogged conditions after tidal inundations or rainfall, induce retrogressive succession and favour large-scale heterogeneity of vegetation (Esselink 2000; Veeneklaas et al. 2013).

On narrow or intermediate foreshores by contrast, re-establishment of pioneer species following marsh erosion and rejuvenation of the marsh are likely to be hampered by the stronger gradients in wave energy (Bouma et al. 2014). Consequently, measures to reinforce rewetting, e.g. the closure of drainage ditches, may be necessary here to induce retrogressive succession and prevent the risk of marsh aeging and subsequent erosion. In addition, temporary engineering measures may be used to facilitate the establishment of pioneer species in front of eroding marsh cliffs.

Perspectives for further research

The findings of the four studies presented in this thesis are an important step forward towards the recognition of salt marshes as a valuable element of coastal defence schemes, but also give rise to new research questions with respect to vegetation dynamics and the process of wave dissipation over vegetation fields.

The analysis of trends in vegetation succession in the Wadden Sea mainland salt marshes revealed that, considered from a large-scale and long-term perspective, abandonment of grazing and drainage caused an increase of progressive succession and a spread of grazing-sensitive plant species from mid- and late-successional stages such as *Elymus athericus* (high marsh) and *Atriplex portulacoides* (low marsh). The pace of succession appeared to vary along landscape-scale gradients of salinity, inundation frequency and sediment deposition. Does *Elymus athericus* represent a climax state of succession and how will spatial patterns in succession develop in the future? In order to answer these questions, continuation of the large-scale (TMAP) vegetation monitoring and further study of vegetation succession is of vital importance. Moreover a detailed quantitative assessment of regional differences in salinity, sediment deposition and accretion as well as inundation frequency and wave climate is needed in order to verify the effect of landscape-scale gradients in these factors on the course and speed of succession.

The successful incorporation of salt marshes in coastal defence schemes requires a full exploration and quantitative understanding of their wave dissipation capacity. Existing studies on wave dissipation by salt marshes have highlighted that this process is highly non-linear both in space and time (Barbier et al. 2008; Koch et al. 2009) and depends apart from biophysical vegetation characteristics (Bouma et al. 2005; Möller 2006) on hydrodynamic conditions (Möller et al. 1999; Möller et al. 2014) and marsh topography (Möller and Spencer 2002). Given the impracticality of conducting field studies in a high number of locations and time periods to capture the spatio-temporal variability in wave dissipation, the further development of numerical models predicting the marsh wave dissipation capacity under varying types of vegetation cover and hydrodynamic conditions is of vital importance to inform coastal defence schemes (Pinsky et al. 2013).

In numerical models of wave dissipation, flow resistance (drag) provided by vegetation is represented by a vegetation factor consisting of plant stem metrics (height, density, diameter) and an empirical drag coefficient C_D, accounting for the effect of canopy bulk properties such as flexibility and three-dimensional canopy structure. In order to generate accurate model predictions, C_D needs to be calibrated against observed dissipation in the considered type of salt marsh vegetation.

Existing modeling studies of wave dissipation have shown that an exponential decay relationship exists between the flow velocity within a canopy at a defined stem diameter (expressed as the ‘stem Reynolds number’ Re_v) and C_D (Kobayashi et al. 1993; Paul and Amos 2011;

Möller et al. 2014). One challenge to be met in future research projects is to combine data on plant flexibility as well as canopy biomass and structure (see chapter 3) with measurements of flow regime and wave dissipation, in order to investigate whether it is possible to derive the relationship between flow velocity under waves and C_D a priori, so that wave dissipation models could be applied without the requirement for empirical calibration of drag against observed dissipation. The provisioning of an enhanced data base on biophysical characteristics of salt marsh plants with application to wave dissipation and their seasonal and spatial variability, as well as standardised methods to assess these properties, is an integral part of this challenge (chapter 3).

Another issue in numerical modeling of wave dissipation is that C_D, in the way in which it is currently implemented in numerical models, does not accurately predict wave dissipation under high energy and water levels. One reason for this appears to be vegetation flexing, plant breakage and biomass loss beyond critical thresholds of wave conditions. Breaking and removal of vegetation is currently not incorporated into any wave dissipation model. This can be done through adjusting C_D, resulting in enhanced model reliability over a wide range of water level and wave conditions (Wolters et al. (under review)).

The detailed study of vegetation-wave interactions reported in chapter 5 of this thesis provided insights into wave energy and water depth thresholds relating to vegetation flexing and plant breakage for *Puccinellia maritima* and *Elymus athericus*, both species that are common in the North-West European region. Further studies on canopy movement and plant susceptibility to breakage under wave forcing of a wider range of mono-specific salt marsh canopies should be conducted under the full range of water depth and wave conditions that can be expected to occur, particularly in macro-tidal settings. A special focus should be laid on the species form the genus *Spartina* (e.g. *Spartina anglica* or *Spartina alterniflora*) due to the occurrence of large, mono-specific stands of *Spartina* spp. along the coastline of the United States and China, as well as North-West Europe, both caused by natural spread and by deliberate transplantation.

Finally, deeper insights are needed into mechanisms and time of marsh recovery after storm surges in relation to vegetation composition, soil substrate and marsh topography (Feagin et al. 2009; Howes et al. 2010). Given that the marsh platform is highly resistant to surface erosion, debates about marsh stability and resilience are shifted to those locations where the marsh profile is exposed. In such settings, lateral marsh erosion may be enhanced by vegetation when plant roots become exposed to wave impact (Feagin et al. 2009). The long-term balance between vertical and lateral marsh dynamics as a function of both physical factors such as sea level rise, sediment availability and landward marsh transgression as well as human impact on these factors thus represents a key research area in further studies on marsh stability (Kirwan and Megonigal 2013) and the coastal protection service provided by salt marshes in future times.

References

A

Adam, P. 1988. Geographical variation in British salt marsh vegetation. *Journal of Ecology* 66:339–366.

Adam, P. 1993. *Saltmarsh ecology*, Cambridge University Press, Cambridge, UK.

Adam, P. 2002. Saltmarshes in a time of change. *Environmental Conservation* 29:39–61.

Ahrendt, K. 2006. Ein Beitrag zur holozänen Entwicklung Nordfrieslands. *Die Küste* 71:1–32.

Ahrendt, K. 2007. Vergangenheit und Zukunft des nordfriesischen Wattenmeers. In: Gönnert G., Pflüger B. & Bremer J.-A. (eds.) *Von der Geoarchäologie über die Küstendynamik zum Küstenzonenmanagement* pp. 45–57, Coastline Reports, Rostock, DE.

Allen, J. R. L. 2000. Morphodynamics of Holocene salt marshes: A review sketch from the Atlantic and Southern North Sea coasts of Europe. *Quaternary Science Reviews* 19:1155–1231.

Andersen, T. J., Svinth, S. & Pejrup, M. 2010. Temporal variation of accumulation rates on a natural salt marsh in the 20th century - The impact of sea level rise and increased inundation frequency. *Marine Geology* 279:178–187.

Anderson, M. E. & Smith, J. M. 2014. Wave attenuation by flexible, idealized salt marsh vegetation. *Coastal Engineering* 83:82–92.

Anderson, M. E., Smith McKee, J. & Keyle McKay, S. 2011. Wave dissipation by vegetation. Coastal and Hydraulics Engineering Technical Note ERDC/CHL CHETN-I-82, Vicksburg MS, U.S. Army Engineer Research and Development Center.

Arkema, K. K., Guannel, G., Verutes, G., Wood, S. A., Guerry, A., Ruckelshaus, M., Kareiva, P., Lacayo, M. & Silver, J. M. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change* 3:913–918.

Augustin, L. N., Irish, J. L. & Lynett, P. 2009. Laboratory and numerical studies of wave damping by emergent and near-emergent wetland vegetation. *Coastal Engineering* 56:332–340.

B

Bakker, J. P. 1989. *Nature management by grazing and cutting*, Kluwer, Dordrecht, NL.

Bakker, J. P., Deleeuw, J., Dijkema, K. S., Leendertse, P. C., Prins, H. H. T. & Rozema, J. 1993. Salt marshes along the coast of the Netherlands. *Hydrobiologia* 265:73–95.

Bakker, J., Kellermann, A., Farke, H., Laursen, K., Knudsen, T. & Marencic, H. 1997. Implementation of the Trilateral Monitoring and Assessment Program (TMAP), Common Wadden Sea Secretariat (CWSS) Trilateral Monitoring and Assessment Group (TMAG), Wilhelmshaven, DE.

Bakker, J. P., Esselink, P., Dijkema, K. S., Van Duin, W. E. & De Jong, D. J. 2002. Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478:29–51.

Bakker, J. P., Bos, D. & De Vries, Y. 2003. To graze or not to graze: that is the question. In: Wolff W. J., Essink K., Kellerman A. & Van Leeuwe M. A. (eds.) *Proceedings of the 10th International Scientific Wadden Sea Symposium*, pp. 67–88. Ministry of Agriculture, Nature Management and Fisheries and Department of Marine Biology University of Groningen, Groningen, NL.

Bakker, J. P. 2005. Salt marshes. In: Essink K., Dettmann C., Farke H., Laursen K., Lüerßen G., Marencic H. & Wiersinga W. (eds.) *Wadden Sea Quality Status Report 2004 Wadden Sea Ecosystem No 19*, Trilateral Monitoring and Assessment Group, Common Wadden Sea Secretariat, Wilhelmshaven, DE.

Bantelmann, A. 1960. Forschungsergebnisse der Marschenarchäologie zur Frage der Niveau-veränderungen an der schleswig-holsteinischen Westküste. *Die Küste* 8:45–65.

Barbier, E. B., Koch, E. W., Silliman, B. R., Hacker, S. D., Wolanski, E., Primavera, J., Granek, E. F., Polasky, S., Aswani, S., Cramer, L. A., Stoms, D. M., Kennedy, C. J., Bael, D., Kappel, C. V., Perillo, G. M. E. & Reed, D. J. 2008. Coastal ecosystem-based management with nonlinear ecological functions and values. *Science* 319:321–323.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C. & Silliman, B. R. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81:169–193.

Bazelmans, J., Meier, D., Nieuwhof, A., Spek, T. & Vos, P. 2012. Understanding the cultural historical value of the Wadden Sea region. The co-evolution of environment and society in the Wadden Sea area in the Holocene up until early modern times (11,700 BC–1800 AD): An outline. *Ocean and Coastal Management* 68:114–126.

Behre, K. 2002. Landscape development and occupation history along the southern North Sea coast. In: Wefer G., Berger W., Behre K. & Jansen E. (eds.) *Climate development and history of the North Atlantic realm*, pp. 299–312. Springer.

Bockelmann, A. C. & Neuhaus, R. 1999. Competitive exclusion of Elymus athericus from a high-stress habitat in a European salt marsh. *Journal of Ecology* 87:503–513.

Bockelmann, A. C., Bakker, J. P., Neuhaus, R. & Lage, J. 2002. The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. *Aquatic Botany* 73:211–221.

Bockelmann, A.-C., Wels, T. & Bakker, J. P. 2011. Seed origin determines the range expansion of the clonal grass *Elymus athericus*. *Basic and Applied Ecology* 12:496–504.

Borsje, B. W., Van Wesenbeeck, B. K., Dekker, F., Paalvast, P., Bouma, T. J., Van Katwijk, M. M. & De Vries, M. B. 2010. How ecological engineering can serve in coastal protection. *Ecological Engineering* 37:113–122.

Bos, D., Bakker, J. P., De Vries, Y. & Van Lieshout, S. 2002. Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Applied Vegetation Science* 5: 45–54.

Bouma, T. J., De Vries, M. B., Low, E., Peralta, G., Tanczos, C., Van de Koppel, J. & Herman, P. M. J. 2005. Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. *Ecology* 86:2187–2199.

Bouma, T. J., Friedrichs, M., Klaassen, P., Van Wesenbeeck, B. K., Brun, F. G., Temmerman, S., Van Katwijk, M. M., Graf, G. & Herman, P. M. J. 2009a. Effects of shoot stiffness, shoot size and current velocity on scouring sediment from around seedlings and propagules. *Marine Ecology Progress Series* 388:293–297.

Bouma, T. J., Friedrichs, M., Van Wesenbeeck, B. K., Temmerman, S., Graf, G. & Herman, P. M. J. 2009b. Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte Spartina anglica. *Oikos* 118:260–268.

Bouma, T. J., De Vries, M. B. & Herman, P. M. J. 2010. Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. *Ecology* 91:2696–2704.

Bouma, T. J., Temmerman, S., Van Duren, L. A., Martini, E., Vandenbruwaene, W., Callaghan, D. P., Balke, T., Biermans, G., Klaassen, P. C., Van Steeg, R., Dekker, F., Van de Koppel, J., De Vries, M. B. & Herman, P. M. J. 2013. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: A flume study on three intertidal plant species. *Geomorphology* 180: 57–65.

Bouma, T. J., Van Belzen, J., Balke, T., Zhu, Z., Airoldi, L., Blight, A. J., Davies, A. J., Galvan, C., Hawkins, S. J., Hoggart, S. P. G., Lara, J. L., Losada, I. J., Maza, M., Ondiviela, B., Skov, M. W., Strain, E. M., Thompson, R. C., Yang, S., Zanuttigh, B., Zhang, L. & Herman, P. M. J. 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. *Coastal Engineering* 87:147–157.

Bradley, K. & Houser, C. 2009. Relative velocity of seagrass blades: Implications for wave attenuation in low-energy environments. *Journal of Geophysical Research-Earth Surface* 114: F01004, doi:10.1029/2007JF000951.

Breiman, L., Friedman, J. H., Olshen, R. A. & Stone, C. J. 1984. *Classification and regression trees*, Wadsworth & Brooks/Cole, Pacific Grove, US.

Burningham, H. & French, J. 2011. Seabed dynamics in a lage coastal embayment: 180 years of morphological change in the outer Thames estuary. *Hydrobiologia* 672:105–119.

C

Cahoon, D. R. 2006. A review of major storm impacts on coastal wetland elevations. *Estuaries and Coasts* 29:889–898.

Chang, E. R., Veeneklaas, R. M., Buitenwerf, R., Bakker, J. P. & Bouma, T. J. 2008. To move or not to move: determinants of seed retention in a tidal marsh. *Functional Ecology* 22:720–727.

Chen, S.-N., Sanford, L. P., Koch, E. W., Shi, F. & North, E. W. 2007. A nearshore model to investigate the effects of seagrass bed geometry on wave attenuation and suspended sediment transport. *Estuaries and Coasts* 30:296–310.

Cingolani, A. M., Noy-Meir, I. & Diaz, S. 2005. Grazing effects on rangeland diversity: A synthesis of contemporary models. *Ecological Applications* 15:757–773.

Clausen, K. K., Stjernholm, M. & Clausen, P. 2013. Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of Applied Ecology* 50:528–537.

Costanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. & Van Den Belt, M. 1998. The value of the world's ecosystem services and natural capital (Reprinted from Nature, vol 387, pg 253, 1997). *Ecological Economics* 25:3–15.

Cott, G. M., Reidy, D. T., Chapman, D. V. & Jansen, M. A. K. 2013. Waterlogging affects the distribution of the saltmarsh plant *Atriplex portulacoides* (L.) Aellen. *Flora* 208:336–342.

CPSL 2005. Coastal Protection and Sea Level Rise – Solutions for sustainable coastal protection in the Wadden Sea region. Wadden Sea Ecosystem No. 21. Common Wadden Sea Secretariat, Trilateral Working Group on Coastal Protection and Sea Level Rise (CPSL), Wilhelmshaven, DE.

Crain, C. M., Albertson, L. K. & Bertness, M. D. 2008. Secondary succession dynamics in estuarine marshes across landscape-scale salinity gradients. *Ecology* 89:2889–2899.

CWSS 2010. *Wadden Sea Plan 2010. Eleventh Trilateral Governmental Conference on the Protection of the Wadden Sea*, Common Wadden Sea Secretariat, Wilhelmshaven, DE.

D

Dalrymple, R. A., Kirby, J. T. & Hwang, P. A. 1984. Wave diffraction due to areas of energy-dissipation. *Journal of Waterway Port Coastal and Ocean Engineering* 110:67–79.

Davidson, D. W. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23–35.

De'ath, G. & Fabricius, K. E. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.

Dijkema, K. S. 1987. Geography of salt marshes in Europe. *Zeitschrift für Geomorphologie* 31:489–499.

Dijkema, K. S. & Heydemann, B. 1984. Description of salt marsh ecosystems in Europe. Western-European salt marshes: Wadden Sea and southwest Netherlands. In: Dijkema K. S. (ed.) *Salt marshes in Europe*, pp. 82–103. Council of Europe. European Committee for the Conservation of Nature and natural Resources, Straßbourg, FR.

Dittmann, S. & Wilhelmsen, U. 2004. In Umweltbundesamt (ed.) *Gesamtsynthes Ökosystemforschung Wattenmeer. Zusammenfassender Bericht zu Forschungsergebnissen und Systemschutz im deutschen Wattenmeer,* pp. 10–45. Forschungsbericht 296 85 905 UBA-FB 000190.

Donat, M. G., Renggli, D., Wild, S., Alexander, L. V., Leckebusch, G. C. & Ulbrich, U. 2011. Reanalysis suggests long-term upward trends in European storminess since 1871. *Geophysical Research Letters* 38:E1–E6.

Duarte, C. M., Dennison, W. C., Orth, R. J. W. & Carruthers, T. J. B. 2008. The charisma of coastal ecosystems: Addressing the imbalance. *Estuaries and Coasts* 31:233–238.

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I. & Marbà, N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change* 3:961–968.

E

Erchinger, H. F., Coldewey, H.-G., Frank, U., Manzenrieder, H., Meyer, C., Schulze, M. & Steinke, W. 1994. *Erosionsfestigkeit von Hellern*, Staatliches Amt für Insel- und Küstenschutz, Norden, DE.

Esselink, P. 2000. *Nature management of coastal salt marshes, interactions between anthropogenic influences and natural dynamics*. Unpubl. PhD thesis. University of Groningen, Groningen, NL.

Esselink, P., Fresco, L. F. M. & Dijkema, K. S. 2002. Vegetation change in a man-made salt marsh affected by a reduction in both grazing and drainage. *Applied Vegetation Science* 5:17–32.

Esselink, P., Petersen, J., Arens, S., Bakker, J. P., Bunke, J., Dijkema, K. S., Hecker, N., Hellwig, U., Jensen, A.-V., Kers, A. S., Körber, P., Lammerts, E. J., Stock, M., Veeneklaas, R. M., Vreeken, M. & Wolters, M. 2009. Salt Marshes. Thematic Report No. 8. In: Marencic H., de Vlas J. (eds.) *Quality Status Report 2009 Wadden Sea Ecosystem No 25*, Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, DE.

F

Fagherazzi, S., Carniello, L., D'alpaos, L. & Defina, A. 2006. Critical bifurcation of shallow microtidal landforms in tidal flats and salt marshes. *Proceedings of the National Academy of Sciences of the United States of America* 103:8337–8341.

Fagherazzi, S., Mariotti, G., Wiberg, P. L. & Mcglathery, K. J. 2013. Marsh collapse does not require sea level rise. *Oceanography* 26:70–77.

Feagin, R. A., Lozada-Bernard, S. M., Ravens, T. M., Moeller, I., Yeager, K. M. & Baird, A. H. 2009. Does vegetation prevent wave erosion of salt marsh edges? *Proceedings of the National Academy of Sciences of the United States of America* 106:10109–10113.

Feagin, R. A., Mukherjee, N., Shanker, K., Baird, A. H., Cinner, J., Kerr, A. M., Koedam, N., Sridhar, A., Arthur, R., Jayatissa, L. P., Lo Seen, D., Menon, M., Rodriguez, S., Shamsuddoha, M. & Dahdouh-Guebas, F. 2010. Shelter from the storm? Use and misuse of coastal vegetation bioshields for managing natural disasters. *Conservation Letters* 3:1–11.

Feagin, R. A., Irish, J. L., Möller, I., Williams, A. M., Colon-Rivera, R. J. & Mousavi, M. E. 2011. Short communication: Engineering properties of wetland plants with application to wave attenuation. *Coastal Engineering* 58:251–255.

Fingerut, J. T., Zimmer, C. A. & Zimmer, R. K. 2003. Larval swimming overpowers turbulent mixing and facilitates transmission of a marine parasite. *Ecology* 84:2502–2515.

Fonseca, M. S. & Cahalan, J. A. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine Coastal and Shelf Science* 35:565–576.

Fonseca, M. S. & Koehl, M. A. R. 2006. Flow in seagrass canopies: The influence of patch width. *Estuarine Coastal and Shelf Science* 67:1–9.

Ford, H., Garbutt, A., Jones, L. & Jones, D. L. 2013. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conservation and Diversity* 6:189–200.

French, J. R. & Spencer, T. 1993. Dynamics of sedimentation in a tide-dominated backbarrier salt-marsh, Norfolk, UK. *Marine Geology* 110:315–331.

G

Gedan, K. B., Kirwan, M. L., Wolanski, E., Barbier, E. B. & Silliman, B. R. 2011. The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Climatic Change* 106:7–29.

Gedan, K. B., Silliman, B. R. & Bertness, M. D. 2009. Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* 1:117–141.

Gönnert, G., Jensen, J., Thumm, S., Storch, H., Wahl, T. & Weisse, R. 2010. Der Meeresspiegelanstieg. Ursachen, Tendenzen und Risikobewertung. *Die Küste* 76:225–256.

H

Hacker, S. D. & Bertness, M. D. 1995. Morphological and physiological consequences of a positive plant interaction. *Ecology* 76:2165–2175.

Herman, W. M. 1999. *Wave dynamics in a macro-tidal estuary*. Unpubl. PhD thesis, University of Cambridge, Cambridge, UK.

Harmsworth, G. C. & Long, S. P. 1986. An assessment of salt-marsh erosion in Essex, England, with reference to the Dengie Peninsula. *Biological Conservation* 35:377–387.

Hobbs, R. J., Walker, L. R. & Walker, J. 2007. Integrating restoration and succession. In: Walker L. R., Walker J. & Hobbs J. R. (eds.) *Linking Restoration and Ecological Successio,* pp. 168–179. Springer, New York, NY, US.

Hofstede, J. L. A. 2003. Integrated management of artificially created salt marshes in the Wadden Sea of Schleswig-Holstein, Germany. *Wetlands Ecology and Management* 11:183–194.

Hothorn, T., Hornik, K. & Zeileis, A. 2006. Unbiased recursive partitioning: A conditional inference framework. *Journal of Computational and Graphical Statistics* 15:651–674.

Howes, N. C., Fitzgerald, D. M., Hughes, Z. J., Georgiou, I. Y., Kulp, M. A., Miner, M. D., Smith, J. M. & Barras, J. A. 2010. Hurricane-induced failure of low salinity wetlands. *Proceedings of the National Academy of Sciences of the United States of America* 107:14014–14019.

I

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., Van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. & Loreau, M. 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477:199–U196.

IPCC 2007. Climate change 2007: synthesis report. In: Pachauri R. K., Reisinger A. (eds.) *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, 104 pp.. IPCC, Geneva, CH.

J

Jadhav, R. S., Chen, Q. & Smith, J. M. 2013. Spectral distribution of wave energy dissipation by salt marsh vegetation. *Coastal Engineering* 77:99–107.

Jones, C. G., Lawton, J. H. & Shachak, M. 1994. Organisms as Ecosystem Engineers. *Oikos* 69:373–386.

K

Kabat, P., Fresco, L. O., Stive, M. J. F., Veerman, C. P., Van Alphen, J. S. L. J., Parmet, B. W. A. H., Hazeleger, W. & Katsman, C. A. 2009. Dutch coasts in transition. *Nature Geoscience* 2:450–452.

Kappenberg, J. & Fanger, H.-U. 2007. *Sedimenttransportgeschehen in der tidebeeinflussten Elbe, der Deutschen Bucht und in der Nordsee*, GKSS-Forschungszentrum Geesthacht GmbH, Geesthacht, DE.

Kiehl, K., Eischeid, I., Gettner, S. & Walter, J. 1996. Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. *Journal of Vegetation Science* 7:99–106.

Kiehl, K., Esselink, P. & Bakker, J. P. 1997. Nutrient limitation and plant species composition in temperate salt marshes. *Oecologia* 111:325–330.

King, S. E. & Lester, J. N. 1995. The value of salt-marsh as a sea defense. *Marine Pollution Bulletin* 30: 180–189.

Kirwan, M. L. & Murray, A. B. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences of the United States of America* 104:6118–6122.

Kirwan, M. L., Guntenspergen, G. R., D'alpaos, A., Morris, J. T., Mudd, S. M. & Temmerman, S. 2010. Limits on the adaptability of coastal marshes to rising sea level. *Geophysical Research Letters* 37:L23401, doi:10.1029/2010GL045489.

Kirwan, M. L. & Megonigal, J. P. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504:53–60.

Kleyer, M., Feddersen, H. & Bockholt, R. 2003. Secondary succession on a high salt marsh at different grazing intensities. *Journal of Coastal Conservation* 9:123–134.

Kobayashi, N., Raichle, A. W. & Asano, T. 1993. Wave attenuation by vegetation. *Journal of Waterway Port Coastal and Ocean Engineering* 119:30–48.

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M. E., Hacker, S. D., Granek, E. F., Primavera, J. H., Muthiga, N., Polasky, S., Halpern, B. S., Kennedy, C. J., Kappel, C. V. & Wolanski, E. 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment* 7:29–37.

Koch, E. W. & Gust, G. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 184:63–72.

L

Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer und Umweltbundesamt (1998) *Umweltatlas Wattenmeer. Band I: Nordfriesisches und Dithmarscher Wattenmeer.* Ulmer, Stuttgart, DE.

Lang, S. & Blaschke, T. 2007. *Landschaftsanalyse mit GIS*, Ulmer, Stuttgart, DE.

Lanta, V. & Leps, J. 2009. How does surrounding vegetation affect the course of succession: A five-year container experiment. *Journal of Vegetation Science* 20:686–694.

Leendertse, P. C., Roozen, A. J. M. & Rozema, J. 1997. Long-term changes (1953-1990) in the salt marsh vegetation at the Boschplaat on Terschelling in relation to sedimentation and flooding. *Plant Ecology* 132:49–58.

Leonard, L. A. & Luther, M. E. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnology and Oceanography* 40:1474–1484.

Leonard, L. A. & Reed, D. J. 2002. Hydrodynamics and sediment transport through tidal marsh canopies. *Journal of Coastal Research* SI36:459–469.

Levine, J. M., Brewer, J. S. & Bertness, M. D. 1998. Nutrients, competition and plant zonation in a New England salt marsh. *Journal of Ecology* 86:285–292.

Loder, N. M., Irish, J. L., Cialone, M. A. & Wamsley, T. V. 2009. Sensitivity of hurricane surge to morphological parameters of coastal wetlands. *Estuarine Coastal and Shelf Science* 84:625–636.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D. A. 2001. Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804–808.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H. & Jackson, J. B. C. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.

Lowe, R. J., Falter, J. L., Koseff, J. R., Monismith, S. G. & Atkinson, M. J. 2007. Spectral wave flow attenuation within submerged canopies: Implications for wave energy dissipation. *Journal of Geophysical Research-Oceans* 112: C05018, doi:10.1029/2006JC003605.

M

Ma, Z., Melville, D. S., Liu, J., Chen, Y., Yang, H., Ren, W., Zhang, Z., Piersma, T. & Li, B. 2014. ECOSYSTEMS MANAGEMENT Rethinking China's new great wall. *Science* 346:912–914.

Manca, E. 2010. *Effects of Posidonia oceanica seagrass on nearshore waves and wave-induced flows*. Unpubl. PhD thesis, University of Southampton, Southampton, UK.

Mandema, F. S., Tinbergen, J. M., Ens, B. J. & Bakker, J. P. 2013. Spatial diversity in canopy height at Redshank and Oystercatcher nest-sites in relation to livestock grazing. *Ardea* 101:105–112.

Mansard, E. P. D. & Funke, E. R. 1980. The measurement of incident and reflected spectra using a least squares method. In: American Society of Civil Engineers (eds.) *Proceedings of the 17th Coastal Engineering Conference* Vol. 1, pp. 154–172.

Mariotti, G. & Fagherazzi, S. 2013. Critical width of tidal flats triggers marsh collapse in the absence of sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America* 110:5353–5356.

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Bjork, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H. & Silliman, B. R. 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment* 9:552–560.

MEA (Millenium Ecosystem Assessment) 2005. *Ecosystems and Human Well-Being: Synthesis*, Island Press, Washington, DC, US.

Mendez, F. J., Losada, I. J. & Losada, M. A. 1999. Hydrodynamics induced by wind waves in a vegetation field. *Journal of Geophysical Research-Oceans* 104:18383–18396.

Mendez, F. J. & Losada, I. J. 2004. An empirical model to estimate the propagation of random breaking and nonbreaking waves over vegetation fields. *Coastal Engineering* 51:103–118.

Miler, O., Albayrak, I., Nikora, V. & O'Hare, M. 2012. Biomechanical properties of aquatic plants and their effects on plant-flow interactions in streams and rivers. *Aquatic Science* 74:31–44.

Mitsch, W. J. & Gosselink, J. G. 2008. *Wetlands*, Van Nostrand Reinhold, New York, NY, US.

Möller, I., Spencer, T., French, J. R., Leggett, D. J. & Dixon, M. 1999. Wave transformation over salt marshes: A field and numerical modelling study from north Norfolk, England. *Estuarine, Coastal and Shelf Science* 49:411–426.

Möller, I., Spencer, T., French, J. R., Leggett, D. J. & Dixon, M. 2001. The sea-defence value of salt marshes: Field evidence from north Norfolk. *Journal of the Chartered Institution of Water and Environmental Management* 15:109–116.

Möller, I. & Spencer, T. 2002. Wave dissipation over macro-tidal saltmarshes: Effects of marsh edge typology and vegetation change. *Journal of Coastal Research* SI36:506–521.

Möller, I. 2006. Quantifying saltmarsh vegetation and its effect on wave height dissipation: Results from a UK East coast saltmarsh. *Estuarine Coastal and Shelf Science* 69:337–351.

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. 2014. Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience* 7:727–731.

Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B. & Cahoon, D. R. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869–2877.

Mullarney, J. C. & Henderson, S. M. 2010. Wave-forced motion of submerged single-stem vegetation. *Journal Of Geophysical Research-Oceans* 115:C12061, doi:12010.11029/12010JC006448.

Müller, F., Struyf, E., Hartmann, J., Weiss, A. & Jensen, K. 2013. Impact of grazing management on silica export dynamics of Wadden Sea saltmarshes. *Estuarine Coastal and Shelf Science* 127:1–11.

N

Neumeier, U. & Ciavola, P. 2004. Flow resistance and associated sedimentary processes in a *Spartina maritima* salt-marsh. *Journal of Coastal Research* 20:435-447.

Neumeier, U. 2005. Quantification of vertical density variations of salt-marsh vegetation. *Estuarine Coastal and Shelf Science* 63:489–496.

Neumeier, U. & Amos, C. L. 2006a. The influence of vegetation on turbulence and flow velocities in European salt-marshes. *Sedimentology* 53:259–277.

Neumeier, U. & Amos, C. L. 2006b. Turbulence reduction by the canopy of coastal *Spartina* salt-marshes. *Journal of Coastal Research* SI39:433–439.

Niklas, K. J. 1992. *Plant biomechanics*, University of Chicago Press, Chicago, US.

Nolte, S., Mueller, F., Schuerch, M., Wanner, A., Esselink, P., Bakker, J. P. & Jensen, K. 2013. Does livestock grazing affect sediment deposition and accretion rates in salt marshes? *Estuarine Coastal and Shelf Science* 135:296–305.

O

O'Hare, M. T., Hutchinson, K. A. & Clarke, R. T. 2007. The drag and reconfiguration experienced by five macrophytes from a lowland river. *Aquatic Botany* 86:253–259.

Olff, H., De Leeuw, J., Bakker, J. P., Platerink, R. J., Van Wijnen, H. J. & De Munck, W. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* 85:799–814.

P

Paul, M. & Amos, C. L. 2011. Spatial and seasonal variation in wave attenuation over *Zostera noltii*. *Journal of Geophysical Research-Oceans* 116:C08019, doi:10.1029/2010JC006797.

Paul, M., Bouma, T. J. & Amos, C. L. 2012. Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. *Marine Ecology Progress Series* 444:31–41.

Paul, M., Thomas, R. E., Dijkstra, J. T., Penning, W. E. & Vousdoukas, M. I. 2014a. Plants, hydraulics and sediment dynamics. In: Frostick L. E., Thomas R. E., Johnson M. F., Rice S. P. & McLelland S. J. (eds.) *Users Guide to Ecohydaulic Modelling and Experimentation: Experience of the Ecohydraulic Research Team (PICES) of the HYDRALAB network*, CRC Press/Balkema, Leiden, NL.

Paul, M., Henry, P.-Y. T. & Thomas, R. E. 2014b. Geometrical and mechanical properties of four species of northern European brown macroalgae. *Coastal Engineering* 84:73–80.

Pennings, S. C. & Callaway, R. M. 1992. Salt-Marsh Plant Zonation – The Relative Importance of Competition and Physical Factors. *Ecology* 73:681–690.

Peralta, G., Van Duren, L. A., Morris, E. P. & Bouma, T. J. 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. *Marine Ecology Progress Series* 368:103–115.

Petersen, J., Kers, B. & Stock, M. 2013. *TMAP-typology of Coastal Vegetation in the Wadden Sea Area*, Common Wadden Sea Secretariat, Wilhelmshaven, DE.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. 1987. A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* 69:109–114.

Pickett, S. T. A., Cadenasso, M. L. & Meiners, S. J. 2009. Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science* 12:9–21.

Pinsky, M. L., Guannel, G. & Arkema, K. K. 2013. Quantifying wave attenuation to inform coastal habitat conservation. *Ecosphere*. http://dx.doi.org/10.1890/ES13-00080.1

Prach, K. & Walker, L. R. 2011. Four opportunities for studies of ecological succession. *Trends in Ecology & Evolution* 26:119–123.

Pringle, A. W. 1995. Erosion of a cyclic salt-marsh in Morecambe Bay, North-West England. *Earth Surface Processes and Landforms* 20:387–405.

Pye, K. 2000. Saltmarsh erosion in southeast England: mechanisms, causes and implications. In: Sherwood B. R., Gardiner, B.G. & Harris, T. (eds.) *British salt marshes* pp. 359–396. Forrest Text/Linnean Society of London, Cardigan/Cambridge, UK.

R

Rand, T. A. 2000. Seed dispersal, habitat suitability and the distribution of halophytes across a salt marsh tidal gradient. *Journal of Ecology* 88:608–621.

Redondo-Gomez, S., Mateos-Naranjo, E., Davy, A. J., Fernandez-Munoz, F., Castellanos, E. M., Luque, T. & Figueroa, M. E. 2007. Growth and photosynthetic responses to salinity of the salt-marsh shrub *Atriplex portulacoides*. *Annals of Botany* 100:555–563.

Reed, D. J. 1988. Sediment dynamics and deposition in a retreating coastal salt-sarsh. *Estuarine Coastal and Shelf Science* 26:67–79.

Reise, K. 2005. Coast of change: habitat loss and transformations in the Wadden Sea. *Helgoland Marine Research* 59:9–21.

Reise, K., Baptist, M., Burbridge, P., Dankers, N., Fischer, L., Flemming, B., Oost, A. P. & Smit, C. 2010. *The Wadden Sea – A Universally Outstanding Tidal Wetland. Wadden Sea Ecosystem No. 29*, Common Wadden Sea Secretariat, Wilhelmshaven, DE.

Riffe, K. C., Henderson, S. M. & Mullarney, J. C. 2011. Wave dissipation by flexible vegetation. *Geophysical Research Letters* 38: L18607, doi:10.1029/2011GL048773.

Rupprecht, F., Wanner, A., Stock, M. & Jensen, K. 2015a. Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage. *Applied Vegetation Science* 18:86–98.

Rupprecht, F., Möller, I., Evans, B., Spencer, T. & Jensen, K. 2015b. Biophysical properties of salt marsh canopies – Quantifying plant stem flexibility and above ground biomass. *Coastal Engineering* 100: 48–57.

Russell, G., Marshall, B. & Jarvis, P. G. 1990. *Plant canopies: their growth, form and function*, Cambridge University Press, Cambridge, UK.

S

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591–596.

Schrautzer, J. & Jensen, K. 2006. Relationship between fight availability and species richness during fen grassland succession. *Nordic Journal of Botany* 24:341–353.

Schröder, H. K., Kiehl, K. & Stock, M. 2002. Directional and non-directional vegetation changes in a temperate salt marsh in relation to biotic and abiotic factors. *Applied Vegetation Science* 5:33–44.

Schuerch, M., Vafeidis, A., Slawig, T. & Temmerman, S. 2013. Modeling the influence of changing storm patterns on the ability of a salt marsh to keep pace with sea level rise. *Journal of Geophysical Research-Earth Surface* 118:84–96.

Seto, K. C. 2011. Exploring the dynamics of migration to mega-delta cities in Asia and Africa: Contemporary drivers and future scenarios. *Global Environmental Change – Human and Policy Dimensions* 21:S94–S107.

Shepard, C. C., Crain, C. M. & Beck, M. W. 2011. The protective role of coastal marshes: a systematic review and meta-analysis. *Plos One* 6:e27374.

Silliman, B. R. & Bertness, M. D. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America* 99: 10500–10505.

Silliman, B. R., Van de Koppel, J., Bertness, M. D., Stanton, L. E. & Mendelssohn, I. A. 2005. Drought, snails, and large-scale die-off of southern US salt marshes. *Science* 310:1803-1806.

Spalding, M. D., Mcivor, A. L., Beck, M. W., Koch, E. W., Moeller, I., Reed, D. J., Rubinoff, P., Spencer, T., Tolhurst, T. J., Wamsley, T. V., Van Wesenbeeck, B. K., Wolanski, E. & Woodroffe, C. D. 2014. Coastal Ecosystems: A Critical Element of Risk Reduction. *Conservation Letters* 7:293–301.

Stock, M. & Kiehl, K. 2000. Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig-Holsteinisches Wattenmeer. In: Stock M. & Kiehl K. (eds.) *Die Salzwiesen der Hamburger Hallig Schriftenreihe Nationalparks Schleswig-Holsteinisches Wattenmeer* 1, pp.74–77. Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, DE.

Stock, M., Gettner, S., Hagge, H., Heinzel, K., Kohlhus, J. & Stumpe, H. 2005. Salzwiesen an der Westküste von Schleswig-Holstein 1988-2001. *Schriftenreihe Nationalpark Schleswig-Holsteinisches Wattenmeer* 15:1–239.

Stock, M. 2011. Patterns in surface elevation change across a temperate salt marsh platform in relation to sea-level rise. In: Karius, Hadler, Deicke, Eynatten v, Brückner, Vött (eds.) *Dynamische Küsten – Prozesse, Zusammenhänge und Auswirkungen*, pp. 33–48, Coastline Reports, Rostock, DE.

Suchrow, S., Pohlmann, N., Stock, M. & Jensen, K. 2012. Long-term surface elevation changes in German North Sea salt marshes. *Estuarine, Coastal and Shelf Science* 98:71–83.

Stumpf, R. P. 1983. The process of sedimentation on the surface of a salt-marsh. *Estuarine Coastal and Shelf Science* 17:495–508.

Summers, R. W., Stansfield, J., Perry, S., Atkins, C. & Bishop, J. 1993. Utilization, diet and diet selection by brent geese *Branta-Bernicla-Bernicla* on salt-marshes in Norfolk. *Journal of Zoology* 231:249–273.

T

Temmerman, S., Bouma, T. J., Govers, G., Wang, Z. B., De Vries, M. B. & Herman, P. M. J. 2005. Impact of vegetation on flow routing and sedimentation patterns: Three-dimensional modeling for a tidal marsh. *Journal of Geophysical Research-Earth Surface* 110: F04019, doi:10.1029/2005JF000301.

Temmerman, S., Meire, P., Bouma, T. J., Herman, P. M. J., Ysebaert, T. & De Vriend, H. J. 2013. Ecosystem-based coastal defence in the face of global change. *Nature* 504:79–83.

Törnqvist, T. E., Wallace, D. J., Storms, J. E. A., Wallinga, J., Van Dam, R. L., Blaauw, M., Derksen, M. S., Klerks, C. J. W., Meijneken, C. & Snijders, E. M. A. 2008. Mississippi Delta subsidence primarily caused by compaction of Holocene strata. *Nature Geoscience* 1:173–176.

Turner, R. E., Baustian, J. J., Swenson, E. M. & Spicer, J. S. 2006. Wetland sedimentation from Hurricanes Katrina and Rita. *Science* 314:449–452.

U

USACE (US Army Corps of Engineers, Coastal Risk Reduction and Resilience 2013. http://www.corpsclimate.us/docs/USACE_Coastal_Risk_Reduction_final_CWTS_2013-3.pdf.

Usherwood, J. R., Ennos, A. R. & Ball, D. J. 1997. Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments. *Journal of Experimental Botany* 48: 1469–1475.

V

Valéry, L., Bouchard, V. & Lefeuvre, J. C. 2004. Impact of the invasive native species *Elymus athericus* on carbon pools in a salt marsh. *Wetlands* 24:268–276.

Vandenbruwaene, W., Temmerman, S., Bouma, T. J., Klaassen, P. C., De Vries, M. B., Callaghan, D. P., Van Steeg, P., Dekker, F., Van Duren, L. A., Martini, E., Balke, T., Biermans, G., Schoelynck, J. & Meire, P. 2011. Flow interaction with dynamic vegetation patches: Implications for biogeomorphic evolution of a tidal landscape. *Journal of Geophysical Research-Earth Surface* 116:F01008, doi:10.1029/2010JF001788.

Van de Koppel, J., Van der Wal, D., Bakker, J. P. & Herman, P. M. J. 2005. Self-organization and vegetation collapse in salt marsh ecosystems. *American Naturalist* 165:E1–-E12.

Van Klink, R., Rickert, C., Vermeulen, R., Vorst, O., Wallisdevries, M. F. & Bakker, J. P. 2013. Grazed vegetation mosaics do not maximize arthropod diversity: Evidence from salt marshes. *Biological Conservation* 164:150–157.

Van Wesenbeeck, B. K., Van de Koppel, J., Herman, P. M. J., Bertness, M. D., Van der Wal, D., Bakker, J. P. & Bouma, T. J. 2008. Potential for sudden shifts in transient systems: distinguishing between local and landscape-scale processes. *Ecosystems* 11:1133–1141.

Van Wijnen, H. J., Bakker, J. P. & De Vries, Y. 1997. Twenty years of salt marsh succession on a dutch coastal barrier island. *Journal of Coastal Conservation* 1:9–18.

Veeneklaas, R. M., Dijkema, K. S., Hecker, N. & Bakker, J. P. 2013. Spatio-temporal dynamics of the invasive plant species *Elytrigia atherica* on natural salt marshes. *Applied Vegetation Science* 16:205–216.

Verhulst, J., Kleijn, D., Loonen, W., Berendse, F. & Smit, C. 2011. Seasonal distribution of meadow birds in relation to in-field heterogeneity and management. *Agriculture Ecosystems & Environment* 142:161–166.

W

Wanner, A., Suchrow, S., Kiehl, K., Meyer, W., Pohlmann, N., Stock, M. & Jensen, K. 2014. Scale matters: Impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. *Agriculture Ecosystems & Environment* 182:69–79.

Webb, N., Nichol, C., Wood, J. & Potter, E. 2008. *User Manual for the SunScan Canopy Analysis System type SS1*, Delta-T Devices Ltd, Cambridge, UK.

Wisskirchen, R. & Haeupler, H. 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*, Ulmer, Stuttgart (Hohenheim), DE.

Wolters, G., Van Wesenbeeck, B. K., Möller, I., Kudella, M., Rupprecht, F., Paul, M., Spencer, T., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. (under review). Wave attenuation over salt marshes under storm surge conditions: Comparison of large scale measurements with SWAN. *Coastal Engineering*.

Wong, P. 2014. Impacts, Adaption, and Vulnerability. In: Fields C. B. et al. (eds.) *IPCC Ch. 5, Climate change*, Cambridge University Press, Cambridge, UK.

Woodruff, J. D., Irish, J. L. & Camargo, S. J. 2013. Coastal flooding by tropical cyclones and sea-level rise. *Nature* 504:44–52.

Y

Yang, S. L., Shi, B. W., Bouma, T. J., Ysebaert, T. & Luo, X. X. 2012. Wave attenuation at a salt marsh margin: A case study of an exposed coast on the Yangtze Estuary. *Estuaries and Coasts* 35: 169–182.

Young, I. R., Zieger, S. & Babanin, A. V. 2011. Global trends in wind speed and wave height. *Science* 332:451–455.

Z

Zedler, J. B. & Kercher, S. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30:39–74.

Zehm, A., Nobis, M. & Schwabe, A. 2003. Multiparameter analysis of vertical vegetation structure based on digital image processing. *Flora* 198:142–160.

Zeller, R. B., Weitzman, J. S., Abbett, M. E., Zarama, F. J., Fringer, O. B. & Koseff, J. R. 2014. Improved parameterization of seagrass blade dynamics and wave attenuation based on numerical and laboratory experiments. *Limnology and Oceanography* 59:251–266.

Summary

Zusammenfassung

Summary

Salt marshes form at shallow tidal coasts under conditions of low water currents and continuous sedimentation and are characterised by a low species diversity and a high primary productivity. Salt marshes are highly dynamic ecosystems with periods of areal extension and contraction and plants in this environment are subjected to stress imposed by frequent flooding with saline water and mechanical forces like currents, wave action and ice scour. Many plant species in intertidal areas act as ecosystem engineers i.e. reduce physical stress levels by modifying their environment through the interaction of their shoots with hydrodynamics. The interaction of salt marsh plant canopies with orbital flow under waves causes dissipation of flow and wave energy thus initiating positive bio-geomorphic feedbacks between plant growth and sediment deposition that enables both lateral expansion (increase of salt marsh width) and vertical accretion (increase in soil surface elevation) of salt marshes. The effect of vegetation on wave orbital flow is a function of both biophysical characteristics of salt marsh canopies such as plant flexibility, canopy density and canopy height and hydrodynamic conditions. Consequently, changes in salt marsh canopies and their biophysical characteristics, as occurring during the process of vegetation succession, have important implications for the dynamics of salt marshes as well as for their wave dissipation capacity and erosion stability.

The ability of salt marshes to reduce hydrodynamic energy that would otherwise erode shorelines and cause damage on land implies that they can act as effective and sustainable elements of coastal protection schemes. Additionally, salt marshes possess the ability to keep up with sea level rise by increasing soil elevation (within boundary conditions of sediment supply, rate of sea level rise and tidal range) and hence may be adaptive to climate change processes. Despite the mounting scientific evidence of wave and surge dissipation by salt marshes and the growing political interest in coastal protection provided by salt marshes, their actual incorporation into quantitative flood or erosion risk assessments and coastal protection schemes remains challenging. One important caveat in building salt marshes into coastal protection schemes is the limited knowledge of their long-term persistence. Understanding the process of vegetation succession, an important control of salt marsh dynamics, is an important step towards an enhanced understanding of salt marsh persistence and hence the reliability of salt marshes in contributing to coastal protection. Another important knowledge gap hampering application of salt marshes in coastal protection is the lack of empirical evidence for their capacity to act as wave dissipaters under extreme water levels and wave conditions i.e. when most disturbances occur and coastal protection is most required. Moreover, a quantitative understanding of salt marsh erosion stability and wave energy thresholds beyond which plant canopies suffer from physical damage with the loss of above ground biomass due to plant breakage leading to a reduced wave dissipation, is needed.

The Wadden Sea represents Europes’s largest intertidal ecosystem complex and includes around 400 km^2 (20%) of the European salt marshes. Man-made mainland salt marshes

encompass around 60% of this area and can be considered as representative of many salt marshes in North-West Europe. Traditionally the Wadden Sea mainland salt marshes have been used as grazing ground for domestic livestock such as sheep or cattle and hence vegetation was characterised by a short turf of palatable grass species like *Puccinellia maritima* and *Festuca rubra.* In the early 1990s, grazing and artificial drainage were abandoned in many of the man-made mainland salt marshes to increase their natural character and the heterogeneity of vegetation.

The overall aim of this thesis was to assess trends in vegetation succession in mainland salt marshes of the Wadden Sea after the change in salt marsh management, and to quantify the capacity of marshes to contribute to coastal protection by the dissipation of wave energy. For this purpose four research objectives were addressed:

(1) to analyse large-scale and long-term patterns in vegetation succession and its major driving factors after abandonment of grazing and drainage in mainland salt marshes of the Wadden Sea, (2) to quantify biophysical vegetation characteristics with application to wave dissipation in canopies of four plant species typically occurring in salt marshes of the Wadden Sea and North-West Europe, (3) to measure wave dissipation, erosion stability of the marsh surface and physical damage occurring to the vegetation canopy in these salt marshes under average up to storm surge wave conditions, and (4) to analyse the effect of vegetation on wave orbital flow and susceptibility of plants to breakage under rising wave forces in two salt marsh canopies of different flexibility and height.

In the first study (chapter 2) main successional pathways of vegetation characterised by *P. maritima* and *F. rubra*, two grasses that dominated low and high marsh areas under intensive grazing, were analysed. Vegetation monitoring data covering around half of the Wadden Sea mainland salt marshes over an 18 year time period (1988–2006) was used. Drivers of succession were analysed with classification tree models, a non-parametric vegetation modelling technique. The results revealed that since the abandonment of grazing and drainage, progressive succession towards vegetation determined by the dwarf shrub *Atriplex portulacoides* (low marsh) and the tall grass *Elymus athericus* (high marsh) strongly increased. The grazing regime and abiotic conditions related to elevation, large-scale environmental gradients of salinity, inundation frequency and vertical accretion were the major drivers of successional pathways. Persistence of vegetation determined by the early successional species *P. maritima* in the salt marshes of the Northern Wadden Sea suggests that large-scale gradients of these abiotic factors led to geographical variation in the pace of succession. These findings imply that considered from a large-scale and long-term perspective, abandonment of grazing and drainage caused the spread of grazing-sensitive plant species from mid- and late-successional stages. To achieve and maintain a large-scale heterogeneity in vegetation, a mosaic of grazed and ungrazed areas is recommended as well as the consideration of landscape-scale gradients of abiotic drivers of succession in management schemes.

Apart from plant species composition, the course of vegetation succession affects primary productivity as well as biophysical characteristics of the vegetation canopy such as plant flexibility, canopy density and canopy height with a high relevance for many ecosystem processes and services provided by salt marshes like carbon storage, silica delivery, habitat provisioning and coastal protection by wave dissipation. Plant flexibility, canopy density and canopy height are key controls of canopy movement and susceptibility of plants to breakage under wave orbital flow and hence in the contribution of salt marsh vegetation to wave dissipation. Detailed quantitative information on biophysical characteristics of salt marsh canopies is still scarce and studies providing a systematic evaluation of methodologies to assess biophysical plant characteristics are missing.

In the second study of this thesis (chapter 3), stem flexibility, diameter and height was measured for three grasses (*Spartina anglica*, *P. maritima* and *E. athericus*) commonly occurring in North-West European salt marshes and above ground biomass and canopy height was quantified in stands of *E. athericus* and *A. portulacoides*. Furthermore, two non-destructive methodologies to assess above ground biomass as a proxy for more complex canopy bulk properties such as canopy structure and density were evaluated: Measurement of light availability within the canopy and side-on photography of vegetation (photo-method). Stem flexibility significantly differed between species: *P. maritima* had the most flexible stems, and as a result of their relatively large stem diameter, *S. anglica* the stiffest stems. The photo-method is a more appropriate technique than the measurement of light availability for the non-destructive assessment of above ground biomass. The data presented extend the existing knowledge base on plant properties with relevance to studies of ecosystem processes and services in salt marsh environments and can be used for the development of a more realistic representation of vegetation in physical and numerical models of wave dissipation over vegetation fields.

In the third study of this thesis (chapter 4), the wave dissipation capacity of a vegetated salt marsh with a mixed canopy of *E. athericus*, *P. maritima*, and the herbaceous forb *Atriplex prostrata*, under average up to storm surge wave conditions, was experimentally assessed in a real-scale flume experiment. The results revealed that the salt marsh caused considerable wave attenuation (around 20% over a 40 m distance), even when water levels and waves were highest. From a comparison with experiments without vegetation, it was estimated that up to 60% of observed wave reduction can be attributed to vegetation. Although waves progressively flattened vegetation and broke plant stems resulting in a loss of 30% of above ground biomass and reduced dissipation, the marsh substrate remained stable and resistant to surface erosion under all conditions. These results underline the effectiveness and reliability of salt marshes in acting as wave dissipaters and support their incorporation into coastal protection schemes. Moreover, empirical data on wave dissipation by salt marshes acquired in this experiment can serve as a validation data set in numerical models of wave dissipation by salt marshes under storm conditions.

The high interspecific variability of salt marsh plants with respect to their biophysical characteristics (chapter 3) suggests that their canopies may interact in different ways with wave orbital flow and hence may also differ in their ability to contribute to the flow and wave dissipation capacity of salt marshes. In the fourth study of this thesis (chapter 5), vegetation-wave interactions in the canopies of *P. maritima* and *E. athericus* were analysed in the framework of the large-scale flume experiment on wave dissipation by salt marshes mentioned above. The results revealed that canopy flexibility and height, as well as incident wave and water depth conditions, play an important role in the ability of vegetation to reduce the velocity of wave orbital flow and in physical damage occurring to vegetation under rising wave forces. Under wave conditions frequently occurring on tidal marshes with low to medium wave energy and 1 m water level, the overall contribution of the tall, stiff *E. athericus* to the reduction of orbital flow and wave energy exceeded that of the low-growing, flexible *P. maritima.* Under these conditions, species-specific vegetation-wave interactions can hence be expected to exert an important control on sediment transport and deposition. Under high to extreme wave energy and 2 m water level, both *P. maritima* and *E. athericus* took a streamlined posture close to the bed under wave forward motion, resulting in a decrease in roughness of the marsh surface and relocation of the flow on top of the smooth surface formed by the flattened vegetation canopies. Accordingly an increase of flow velocity due to vegetation presence was observed. Consequently, during storm events vegetation may reduce the chance of sediment particles to settle on the bed and thus likely plays a passive protective role against bed erosion, *P. maritima* experienced no visible physical damage even under extreme levels of wave energy, implying a continuous contribution to erosion protection and also suggesting a high resilience of salt marsh vegetation dominated by *P. maritima* to storm surge conditions. In *E. athericus* by contrast, stem folding and breakage occurred from a medium level of wave energy ondwards (wave heights ≥0.4 m) both under 1 m and 2 m water level and coincided with a leveling-off in the capacity of the marsh for wave dissipation. The physical damage which occurred to *E. athericus* would require about one growing season for recovery. These results suggest that *E. athericus* has a higher capacity to dissipate hydrodynamic energy than *P. maritima*, however its greater susceptibility to stem breakage is likely to cause a decline in the contribution of *E. athericus* to wave dissipation and erosion protection under repeated storm and flooding events and suggests a lower resilience of salt marsh vegetation dominated by *E. athericus* to storm surge conditions.

Overall, the results reported in this thesis demonstrate that vegetated salt marsh surfaces considerably contribute to wave dissipation under average up to storm surge conditions and hence can be a valuable component of coastal protection schemes. Furthermore, the results provide insights into the species-specific control of flow and wave dissipation by salt marshes and have a high relevance for the prediction of the marsh wave dissipation capacity by numerical modelling of wave dissipation over vegetation fields and for future studies on marsh stability and resilience under sea level rise and increasing storminess.

Management schemes with the objective to optimise coastal protection provided by salt marshes should aim for a large-scale heterogeneity of vegetation and the maintenance of all successional-stages to profit from the benefits that various plant species offer in terms of the marsh wave dissipation capacity and erosion stability. In man-made mainland salt marshes where the uniform marsh topography and the dense artificial drainage system cause a lack in natural dynamics, this may require – to a limited extent – human inference with salt marshes such as e.g. the closure of drainage ditches to induce rewetting of marshes. In the long run and at larger-scales however, sea level rise, sediment availability and the possibility for landward marsh migration as well as human impact on these factors will determine the fate of salt marshes and their contribution to coastal protection.

Zusammenfassung

Salzmarschen sind gezeitengeprägte Ökosysteme und entwickeln sich an flachen, strömungsarmen Küsten im Übergangsbereich zwischen Land und Meer durch die Ablagerung von Sedimenten. Sie zeichnen sich durch eine geringe Artenvielfalt und eine hohe Primärproduktion aus. Wie die Küstengebiete selbst unterliegen Salzmarschen einer starken räumlichen Dynamik mit Phasen von Flächenzuwachs und Flächenabnahme. Salzmarschen bieten einen einzigartigen und wertvollen Lebensraum für zahlreiche Pflanzen- und Tierarten, die an die extremen Standortbedingungen wie häufige Überflutung mit Salzwasser und mechanischen Stress durch Strömung, Wellen und Eisschur angepasst sind. Die meisten Pflanzenarten in Salzmarschen besitzen die Fähigkeit durch die Interaktion ihrer Sprosse mit der Strömung unter Wellen, die Strömungsgeschwindigkeit zu verlangsamen und so die Wellenhöhe und die Wellenenergie zu reduzieren (Wellendämpfung). Dies führt zu positiven Rückkopplungseffekten zwischen dem Wachstum von Pflanzen und der Ablagerung von Sedimenten und ermöglicht sowohl die Zunahme der Marschbreite (laterales Wachstum) als auch die Zunahme der Marschhöhe (vertikales Wachstum).

Die Auswirkung der Vegetation von Salzmarschen auf die Strömung unter Wellen hängt von ihren biophysikalischen Eigenschaften wie Flexibilität, Dichte und Höhe und den vorherrschenden hydrodynamischen Bedingungen (z. B. Wassertiefe und Wellenhöhe) ab. Veränderungen in der Vegetation der Salzmarschen und ihren biophysikalischen Eigenschaften, wie sie in der zeitlichen Entwicklung der Vegetation (Sukzession) geschehen, haben daher einen bedeutenden Einfluss auf die räumliche Dynamik, die Wellendämpfungskapazität und die Erosionsstabilität von Salzmarschen.

Die Fähigkeit von Salzmarschen, durch Wellendämpfung die auf die Küste treffende Wellenenergie zu reduzieren und das Hinterland gegen Überflutung zu schützen, legt nahe, dass Salzmarschen einen wichtigen Beitrag zum Küstenschutz leisten. Darüber hinaus können sich Salzmarschen an Auswirkungen des Klimawandels, wie den Meeressspiegelanstieg, anpassen: Mit der Überflutungshäufigkeit nimmt auch die Ablagerung von Sedimenten und damit die Geländehöhe von Salzmarschen zu. Dies bewirkt ein „Mitwachsen“ der Salzmarschen mit dem steigenden Meeresspiegel – solange kritische Werte der Meeresspiegelanstiegsrate und des Tidenhubs nicht überschritten und mit dem Überflutungswasser genügend Sedimente angeliefert werden.

Trotz zahlreicher wissenschaftlicher Untersuchungen, welche die Wellendämpfung durch Salzmarschen belegen und dem wachsenden politischen Interesse an der Küstenschutzfunktion von Salzmarschen, bleibt deren Einbeziehung in Abschätzungen des Erosions- und Überflutungsrisikos für Küstengebiete und den darauf basierenden Küstenschutzplänen eine Herausforderung.

Eine Schwierigkeit bei der Berücksichtigung von Salzmarschen in Küstenschutzplänen besteht in dem begrenzten Wissen über die Dynamik von Salzmarschen in Bezug auf ihre Flächengröße und die Pflanzenartenzusammensetzung ihrer Vegetation (Vegetationszusammensetzung). Die Sukzession in Salzmarschen spielt eine Schlüsselrolle für deren Bildung, Erosionsstabilität und Flächengröße und hat einen großen Einfluss auf die Vegetationszusammensetzung. Ein besseres Verständnis der Sukzession und der sie steuernden Faktoren ist daher ein wichtiger Schritt auf dem Weg zu einem besseren Verständnis der Dynamik von Salzmarschen und der Verlässlichkeit ihres Beitrags zum Küstenschutz. Während Sturmfluten, wenn Wasserstände und Wellenhöhen extreme Werte erreichen, wird die Küstenschutzfunktion von Salzmarschen am meisten benötigt. Bislang wurde die Wellendämpfungskapazität von Salzmarschen aber nur unter durchschnittlichen Wassertiefen und Wellenhöhen gemessen. Der Mangel an Messungen der Wellendämpfungskapazität und Erosionsstabilität von Salzmarschen unter extremen hydrodynamischen Bedingungen stellt eine weitere große Wissenslücke dar, welche die Einbeziehung von Salzmarschen in Küstenschutzpläne behindert. Mit steigender Wellenenergie wächst auch das Risiko der Beschädigung der Vegetation (durch Knicken und Brechen der Sprosse), was möglicherweise zur Abnahme der Wellendämpfungskapazität von Salzmarschen führt. Daher ist es wichtig, Schwellenwerte der Wellenenergie, ab denen eine Beschädigung der Vegetation auftritt und die Auswirkung dieser Beschädigung auf die Wellendämpfungskapazität von Salzmarschen, zu erfassen.

Das Wattenmeer ist Europas größter Komplex tidebeeinflusster Ökosysteme. Die Salzmarschen des Wattenmeers nehmen eine Fläche von ca. 400 km^2 ein, was etwa 20 % der Fläche aller Salzmarschen Europas entspricht. Etwa 60 % der Salzmarschen des Wattenmeers wurden entlang der Festlandsküste künstlich durch den Menschen angelegt und sind in ihrer Vegetation und Geomorphologie repräsentativ für viele Salzmarschen Nordwesteuropas. Die Nutzung der künstlich angelegten Festlandssalzmarschen des Wattenmeers als Weideland für Schafe und Rinder hat eine lange Tradition und wurde im Verlauf des 19. Jahrhunderts stark intensiviert. Dies führte zu einer kurzrasigen Vegetation dominiert von beweidungstoleranten Gräsern wie *Puccinellia maritima* (Andelgras) und *Festuca rubra* (Rotschwingel). Ab den frühen 90er Jahren wurden die Beweidung in vielen Festlandssalzmarschen des Wattenmeers reduziert und das künstliche Entwässerungssystem nicht weiter unterhalten, um einen naturnäheren Zustand der Salzmarschen und eine größere Heterogenität der Vegetation zu erreichen.

Ziel dieser Arbeit war die Erfassung von Haupttrends der Sukzession seit der Umstellung des Managements in den Festlandssalzmarschen des Wattenmeers und die Quantifizierung der Wellendämpfungskapazität von Salzmarschen. Zu diesem Zweck wurden vier Untersuchungen durchgeführt: (1) Analyse der großräumigen und langfristigen Trends der Sukzession in den Festlandssalzmarschen des Wattenmeers seit der Reduzierung der Beweidung und Aufgabe der künstlichen Entwässerung; (2) Quantifizierung der biophysikalischen Vegetationseigenschaften mit Wichtigkeit für die Wellendämpfung in Beständen von vier Pflanzenarten, die typischerweise in Salzmarschen des Wattenmeers und Nordwesteuropas vorkommen; (3) Messung der Wellendämpfungskapazität und der Erosionsstabilität der Marschoberfläche sowie der

Beschädigung der Vegetation unter durchschnittlichen bis extremen Wassertiefen und Wellenhöhen; (4) Analyse des Effekts der Vegetation auf die Strömungsgeschwindigkeit unter Wellen und der Empfindlichkeit der Vegetation gegen Abknicken und Brechen bei ansteigender Wellenenergie in Beständen zweier Salzmarschpflanzen von unterschiedlicher Flexibilität und Höhe.

In der ersten Studie (Kapitel 2) wurden die Sukzession von Salzmarschvegetation bestehend aus den Gräsern *P. maritima* und *F. rubra*, welche die untere und obere Marsch unter intensiver Beweidung dominierten, analysiert. Dafür wurden Monitoringdaten für rund die Hälfte aller Festlandssalzmarschen des Wattenmeers über einen Zeitraum von 18 Jahren (1988–2006) ausgewertet. Die steuernden Faktoren der Sukzession wurden mit Klassifikationsbaummodellen analysiert, ein nicht-parametrischer Ansatz der Vegetationsmodellierung. Die Ergebnisse der Studie zeigten, dass seit Reduzierung der Beweidung und Aufgabe der Entwässerung die Sukzession von frühen zu späten Stadien (vorwärtsgerichtete Sukzession), dominiert durch den Zwergstrauch *Atriplex portulacoides* (Portulak-Keilmelde) und das Gras *Elymus athericus* (Strandquecke), stark zugenommen hat. Das Beweidungsregime (intensive Beweidung, extensive Beweidung, unbeweidet), die Geländehöhe sowie Gradienten auf Landschaftsebene in der Salinität des Überflutungswassers, der Überflutungshäufigkeit und des Höhenzuwachses der Marschen durch Sedimentablagerung, wurden als die wichtigsten steuernden Faktoren der Sukzession identifiziert. Das Überdauern von *P. maritima*, einer Pflanzenart, die typisch für ein frühes Stadium der Sukzession in Salzmarschen ist, in den Salzmarschen des nördlichen Wattenmeers legt nahe, dass die großräumigen Gradienten der oben genannten Umweltfaktoren zu einer geographischen Variation in der Geschwindigkeit der Sukzession führen. Langfristig und großräumig gesehen hat die Reduzierung der Beweidung und die Aufgabe des künstlichen Entwässerungssystems zu der Ausbreitung beweidungsempfindlicher Pflanzenarten aus mittleren und späten Sukzessionsstadien, wie *A. portulacoides* und *E. athericus*, geführt. Um eine größere Heterogenität der Vegetation von künstlich angelegten Festlandssalzmarschen zu erreichen und zu erhalten, empfiehlt sich ein großräumiges „Mosaik“ von beweideten und unbeweideten Flächen sowie die Berücksichtigung von großräumigen Gradienten der Salinität, der Überflutungshäufigkeit und des vertikalen Wachstums von Salzmarschen durch die Ablagerung von Sedimenten in Managementplänen.

Neben der Vegetationszusammensetzung beeinflusst der Verlauf der Sukzession auch die Primärproduktion und die biophysikalischen Eigenschaften der Vegetation wie Flexibilität, Dichte und Höhe und wirkt sich damit bedeutend auf viele Ökosystemprozesse und -dienstleistungen von Salzmarschen aus, wie Kohlenstoffspeicherung, Siliziumspeicherung und -freisetzung, die Bereitstellung von Habitaten für Tier- und Pflanzenarten und Küstenschutz durch Wellendämpfung. Die Flexibilität von Pflanzen sowie die Dichte und Höhe von Pflanzenbeständen bestimmen die Bewegung und die Bruchempfindlichkeit der Pflanzen in der durch Wellen verursachten Strömung und somit den Beitrag, den die Vegetation von Salzmarschen zur Wellendämpfung leisten kann. Es existieren jedoch nur sehr wenige Studien, in denen die biophysikalischen Eigenschaften von Salzmarschpflanzen quantifiziert und die verwendeten Messmethoden geprüft und bewertet werden.

In der zweiten Studie dieser Arbeit (Kapitel 3) wurden Sprossflexibilität, Sprossdurchmesser und Sprosshöhe für drei Gräser bestimmt, die in den Salzmarschen Nordwesteuropas sehr häufig vorkommen: *Spartina anglica* (Schlickgras), *P. maritima* und *E. athericus*. Darüber hinaus wurde die Genauigkeit von zwei Methoden verglichen, mit deren Hilfe es möglich ist, die oberirdische Biomasse zu quantifizieren ohne die Vegetation zu beschädigen: Messung der Lichtverfügbarkeit im Pflanzenbestand und Fotografie der Vegetation an ihrem Standort (Foto-Methode). Die Ergebnisse zeigten signifikante Unterschiede in der Flexibilität der Sprosse von *S. anglica*, *P. maritima* und *E. athericus*: Die höchste Sprossflexibilität wurde für *P. maritima* gemessen und die geringste Sprossflexibilität für *S. anglica*. Die geringe Flexibilität der Sprosse von *S. anglica* war dabei auf den relativ großen Durchmesser der Sprosse zurückzuführen. Bei der Bestimmung der oberirdischen Biomasse lieferte die Foto-Methode genauere Ergebnisse als Messungen der Lichtverfügbarkeit im Pflanzenbestand. Die in Kapitel 3 präsentierten Ergebnisse erweitern das Wissen über die biophysikalischen Eigenschaften der Vegetation von Salzmarschen und sind von hoher Relevanz für Studien, die sich mit Ökosystemprozessen und -dienstleistungen von Salzmarschen befassen. Außerdem ermöglichen die Ergebnisse eine realitätsgetreuere Darstellung der Vegetation von Salzmarschen in physikalischen und numerischen Modellen der Wellendämpfung.

In der dritten Studie dieser Arbeit (Kapitel 4) wurde die Wellendämpfungskapazität einer mit den Gräsern *E. athericus* und *P. maritima* sowie der einjährigen Hochstaude *Atriplex prostrata* (Spieß-Melde) bewachsenen Salzmarsch, unter durchschnittlichen Wassertiefen und Wellenhöhen bis hin zu extremen Sturmflutbedingungen, in einem Wellenkanalexperiment mit Echtmaßstab quantitativ erfasst. Die Ergebnisse zeigten, dass Salzmarschen Wellen selbst unter extremen Bedingungen deutlich dämpfen (20 % Wellendämpfung auf einer Strecke von 40 m). Durch den Vergleich der Wellendämpfung über der bewachsenen und der gemähten Marschoberfläche konnte ermittelt werden, dass etwa 60 % der gemessenen Wellendämpfung durch die Vegetation der Salzmarsch verursacht wurde. Unter dem Einfluss steigender Wellenhöhe und -energie wurde die Vegetation zunehmend flachgedrückt. Dies führte zum Abknicken und Brechen von Pflanzensprossen und damit zu einem Verlust von etwa 30 % der oberirdischen Biomasse. Die Bodenoberfläche der Salzmarsch zeigte über das gesamte Experiment keine Anzeichen von Erosion. Insgesamt zeigen die Ergebnisse des Wellenkanalexperiments, dass Salzmarschen effektiv und verlässlich zur Wellendämpfung beitragen, und unterstützen die Einbeziehung von Salzmarschen in Küstenschutzpläne. Darüber hinaus ermöglichen die empirischen Daten, die in dem Experiment gewonnen wurden, eine Überprüfung und Weiterentwicklung numerischer Modelle der Wellendämpfung durch Salzmarschen unter Sturmflutbedingungen.

Die großen Unterschiede zwischen verschiedenen Pflanzenarten von Salzmarschen hinsichtlich ihrer biophysikalischen Eigenschaften (s. Kapitel 3) lassen vermuten, dass Bestände verschiedener Pflanzenarten auf unterschiedliche Weise mit der Strömung unter Wellen interagieren und dadurch einen unterschiedlicher Beitrag zur Wellendämpfungskapazität von Salzmarschen leisten. In der vierten Studie dieser Arbeit (Kapitel 5) wurde im Rahmen des oben beschriebenen Wellenkanalexperiments die Interaktion der Vegetation mit der Strömung unter Wellen in Beständen der Gräser *P. maritima* und *E. athericus* analysiert. Die Ergebnisse zeigten, dass die Flexibilität der Sprosse und die Höhe der Vegetation sowie die Wassertiefe und Wellenhöhe sowohl für die Fähigkeit der Vegetation, die Strömung zu verlangsamen, als auch für die Beschädigung, die sie dabei erlitt, eine wichtige Rolle spielten. Unter hydrodynamischen Bedingungen, denen Salzmarschen häufig unterliegen (niedrige bis mittlere Wellenenergie, 1 m Wassertiefe), leistete *E. athericus* mit seinen relativ steifen, hochwachsenden Sprossen einen größeren Beitrag zur Reduzierung der Strömungsgeschwindigkeit und zur Wellendämpfung als *P. maritima*, mit niedrigwachsenden, flexiblen Sprossen. Es ist daher wahrscheinlich, dass pflanzenartenspezifische Interaktionen zwischen Vegetation und Wellen den Sedimenttransport und die Menge der auf der Marschoberfläche abgelagert Sedimente beeinflussen. Unter hoher bis extremer Wellenenergie und 2 m Wassertiefe wurde sowohl für *P. maritima* als auch für *E. athericus* eine stromlinienförmige Ausrichtung der Vegetation in Wellenfortschrittsrichtung beobachtet. Dies führte zu einer Abnahme der Rauigkeit und damit des Strömungswiderstands der Marschoberfläche, da das Wasser (für einen Teil des Wellenzyklus) nun nicht mehr durch die Vegetation, sondern über die glatte, aus der flachgedrückten Vegetation gebildete Oberfläche hinweg floss. Dementsprechend wurde in *P. maritima* und *E. athericus* eine Zunahme der Strömungsgeschwindigkeit im Vergleich zu Kontrollmessungen bei gemähter Marschoberfläche festgestellt. Aus diesen Ergebnissen kann geschlossen werden, dass während Sturmfluten die am Boden liegende, flachgedrückte Vegetation einen passiven Schutz vor Erosion bietet, jedoch nicht aktiv zum Erosionsschutz beiträgt, da die schnelle, über die Vegetation verlagerte Strömung die Ablagerung von Sedimentpartikeln auf der Marschoberfläche behindert. Für *P. maritima* konnte keine wesentliche sichtbare Beschädigung selbst unter extremer Wellenenergie festgestellt werden. Vegetation, die von *P. maritima* dominiert ist, trägt daher kontinuierlich zum Schutz vor Erosion bei und besitzt vermutlich eine hohe Resilienz gegen Störung durch Sturmfluten, d. h. die Vegetation kehrt nach einer Sturmflut sehr schnell in ihren Ausgangszustand zurück. Für *E. athericus* dagegen wurde ein Abknicken und Brechen von Sprossen ab einem mittleren Niveau der Wellenenergie (Wellenhöhen ≥ 0,4 m) sowohl unter Wassertiefen von 1 m als auch 2 m beobachtet. Die Beschädigung von *E. athericus* geschah zeitgleich mit einer Abflachung der anfänglichen Zunahme der Wellendämpfungskapaziät der Salzmarsch mit zunehmender Wellenenergie. Insgesamt zeigte *E. athericus* also eine größere Kapazität, die Strömung zu verlangsamen und Wellen zu dämpfen als *P. maritima*, war aber empfindlicher gegen Beschädigung durch Abknicken und Brechen der Sprosse. Es ist zu erwarten, dass der Verlust an oberirdischer Biomasse zu einer Abnahme des Beitrags der Vegetation zur Wellendämpfungskapazität von Salzmarschen bei wiederholten Sturmflutereignissen führt und dass die Zeit einer Vegetationsperiode vergehen muss, bis die geknickten und abgebrochenen Sprosse wieder vollständig nachgewachsen sind. Dies weist darauf hin, dass Salzmarschvegetation, die durch hochwachsende Pflanzenarten mit relativ steifen, bruchempfindlichen Sprossen wie *E. athericus* dominiert wird, eine geringere Resilienz gegen Sturmfluten aufweist als Salzmarschvegetation, die von niedrigwachsenden Pflanzenarten mit flexiblen Sprossen wie *P. maritima* geprägt ist.

Insgesamt zeigen die vier Studien dieser Arbeit, dass Salzmarschen einen großen Beitrag zum Küstenschutz leisten können und dass die Vegetation eine Schlüsselrolle für die Wellendämpfungskapazität von Salzmarschen spielt. Wellen werden durch Salzmarschen deutlich gedämpft, sowohl unter durchschnittlichen Wassertiefen und Wellenhöhen als auch unter extremen, für Sturmfluten typischen Wassertiefen und Wellenhöhen. Die Erkenntnisse zu der pflanzenartenspezifischen Auswirkung der Vegetation auf die Strömung unter Wellen sind von großer Wichtigkeit für die Vorhersage der Wellendämpfungskapazität von Salzmarschen mittels numerischer Modellierung und für zukünftige Forschungsarbeiten zur Stabilität und Resilienz von Salzmarschen bei steigendem Meeresspiegel und zunehmender Häufigkeit von Stürmen.

Salzmarschmanagement mit dem Ziel, den Küstenschutz durch Salzmarschen zu optimieren, sollte eine großräumige Heterogenität der Vegetation und die Erhaltung aller Sukzessionsstadien fördern, um von den verschiedenen Qualitäten der Salzmarschpflanzen im Bezug auf Wellendämpfungskapazität und Erosionsstabilität der Salzmarsch zu profitieren. In künstlich angelegten Salzmarschen verursacht die einheitliche, flache Topographie und das Entwässerungssystem einen Mangel an natürlicher Dynamik. Dies kann – in begrenztem Maß – menschliches Eingreifen erforderlich machen, wie etwa das Schließen von Bewässerungsgräben zur Wiedervernässung von Salzmarschen. Langfristig und auf Landschaftsebene betrachtet werden jedoch der Meeresspiegelanstieg, die Verfügbarkeit von Sedimenten und die Möglichkeit von Marschen, sich in landwärtige Richtung auszudehnen sowie der menschliche Einfluss auf diese Faktoren, die Zukunft der Salzmarschen und ihres Beitrags zum Küstenschutz bestimmen.


DANKE
17

Danksagung

In der Zeit meiner Doktorarbeit bin ich von vielen Menschen unterstützt worden. Dafür möchte ich mich sehr bedanken.

Mein größter Dank gilt Kai Jensen für die sehr gute Betreuung meiner Doktorarbeit und die umfassende fachliche und moralische Unterstützung, auf die ich mich immer verlassen konnte. Lieber Kai, vielen Dank für die vielen unvergesslichen und sehr lehrreichen Erfahrungen der letzten 5 Jahre, zu denen auch eine Reise nach China und eine Salzmarschausgrabung mit schwerem Gerät zählen!

Ein ganz besonderer Dank geht weiterhin an Iris Möller für die Zweitbetreuung meiner Arbeit. Liebe Iris, vielen Dank für die sehr gute Betreuung während meines Aufenthalts an der Cambridge Coastal Research Unit und in der darauffolgenden Zeit, bis zum Ende meiner Doktorarbeit. Danke, dass Du Dein großes Fachwissen über Salzmarschen und Wellen in zahlreichen Gesprächen mit mir geteilt hast – und für die erlebnisreiche Zeit im Wellenkanal von Hannover!

Bei Antonia Wanner, Martin Stock, Frauke Müller und Cynthia Erb möchte ich mich bedanken für die sehr gute Zusammenarbeit im Forschungsprojekt BASSIA (gefördert durch die Bauer-Hollmann Stiftung und die Universität Hamburg). Besonders bedanken möchte ich mich bei Antonia für die vielen langen Gespräche über Salzmarschen und ihre Vegetationsentwicklung aus denen ich eine Menge gelernt habe.

Bei Iris Möller, Tom Spencer, Anna McIvor und Ben Evans bedanke ich mich für die schöne Zeit an der Cambridge Coastal Research Unit, die meine Doktorarbeit und auch mich selbst ein großes Stück voran gebracht hat. Dem Deutschen Akademischen Austauschdienst (DAAD) danke ich für das Stipendium (D/12/44810), das mir den Aufenthalt an der Universität Cambridge ermöglicht hat.

Der gesamten AG Angewandte Pflanzenökologie danke ich für das gute Arbeitsumfeld und ihre Unterstützung!! Insbesondere möchte ich mich bedanken bei bei Claudia Mählmann für die Unterstützung in sämtlichen organisatorischen und formalen Angelegenheiten und bei Kristin Ludewig und Christian Butzeck dafür, dass Ihr die Freuden und Leiden des Doktoranden-(Büro)Alltags beständig mit mir geteilt habt! Ein großes Dankeschön geht weiterhin an Dennis Schulze. Vielen Dank, dass Du die Salzmarsch am Wellenkanal in Hannover im Sommer 2013 so gut betreut hast, für Deine Hilfe im Gelände und Dein großes Engagement bei der Anfertigung der Masterarbeit zu den biophysikalischen Eigenschaften von Salzmarschpflanzen!

Bei Jürn Bunje (Nationalparkverwaltung Niedersächsisches Wattenmeer),
dem III. Oldenburgischen Deichverband und der AG Elisabethgroden bedanke ich mich ganz herzlich für die sehr gute Zusammenarbeit bei der Ausgrabung und dem Transport von 200 m^2 Salzmarsch von Ostfriesland zum Wellenkanal nach Hannover.

Das Experiment zur Wellendämpfung durch Salzmarschen wurde durch die Europäischen Forschungsinitiative HYDRALAB IV (Vertrag Nr. 261529) und den Isaac Newton Trust des Trinity College, Cambridge, gefördert. Bei allen Projektbeteiligten möchte ich mich bedanken für die sehr gute Zusammenarbeit, die Unterstützung bei der Datenauswertung und bei der Interpretation der Ergebnisse und die spannende, lustige, anstrengende Zeit im/am Wellenkanal des Forschungszentrums Küste in Hannover!

Hans Stökl danke ich für das Korrekturlesen der deutschen Zusammenfassung sowie für das großes Interesse an meiner Doktorarbeit und das Verständnis wenn es einmal schwierig war, diese mit der freiberuflichen Arbeit im Naturschutzamt in Einklang zu bringen.

Tom Maxfield danke ich für das Korrekturlesen aller unveröffentlichten Teile dieser Arbeit. Thank you!

Ganz besonders möchte ich mich bei meiner Familie und bei allen meinen Freunden bedanken.

Meinen Eltern Johanna und Walter und meinen Schwestern Katrin und Miriam danke ich sehr für den verlässlichen Rückhalt, die Ermutigung an meinen Zielen festzuhalten und das lange Zuhören was manchmal nötig war.

Sehr bedanken möchte ich mich auch bei Diego, bei Lu, bei Marike, bei Markus – und vorallem bei Dir Zdenka! Danke, dass Ihr mich durch viele Höhen und Tiefen der letzten Jahre begleitet habt!

Outline of the author´s contributions

This thesis consists of three manuscripts published in peer-reviewed international scientific journals (chapter 2, 3 and 4) and one unpublished manuscript (chapter 5).

The author of this thesis contributed to the chapters as follows:

Chapter 1: Introduction
Writing of the manuscript

Chapter 2: Succession in salt marshes – large-scale and long-term patterns after abandonment of grazing and drainage
Conception of the study, data analysis, writing of the initial manuscript

Chapter 3: Biophysical properties of salt marsh canopies – Quantifying plant stem flexibility and above ground biomass
Conception of the study in cooperation with Dr. Iris Möller, data collection, data analysis, writing of the initial manuscript

Chapter 4: Wave attenuation over coastal salt marshes under storm surge conditions
Construction and running of the experiment in cooperation with the whole project group, data analysis in cooperation with Dr. Iris Möller (project lead) and Matthias Kudella, contribution to the manuscript

Chapter 5: Vegetation-wave interactions in salt marshes under storm surge conditions
Conception of the study, data analysis, writing of the initial manuscript

Chapter 6: Synthesis
Writing of the manuscript

Affilitation of co-authors:

Tjeerd J. Bouma: Yerseke Spatial Ecology, Netherlands Institute for Sea Research (NIOZ), Korringaweg 7, 4401 NT, Yerseke, The Netherlands. E-mail: Tjeerd.Bouma@nioz.nl

Ben Evans: Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, United Kingdom. E-mail: ben.evans@geog.cam.ac.uk

Kai Jensen: Applied Plant Ecology, Biocenter Klein Flottbek, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany. E-mail: kai.jensen@uni-hamburg.de

Matthias Kudella: Forschungszentrum Küste (FZK), Merkurstr. 11, 30419 Hannover, Germany.
E-mail: kudella@fzk-nth.de

Martin Miranda-Lange: Forschungszentrum Küste (FZK), Merkurstr. 11, 30419 Hannover, Germany.
E-mail: ml@fzk-nth.de

Iris Möller: Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, United Kingdom. E-mail: iris.moeller@geog.cam.ac.uk

Maike Paul: Forschungszentrum Küste (FZK), Merkurstr. 11, 30419 Hannover, Germany.
E-mail: paul@fzk-nth.de

Stefan Schimmels: Forschungszentrum Küste (FZK), Merkurstr. 11, 30419 Hannover, Germany.
E-mail: schimmels@fzk-nth.de

Tom Spencer: Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, United Kingdom. E-mail: tom.spencer@geog.cam.ac.uk

Martin Stock: Administration of the Wadden Sea National Park of Schleswig-Holstein, Schlossgarten 1, 25832 Tönning, Germany. E-mail: martin.stock@lkn.landsh.de

Antonia Wanner: Applied Plant Ecology, Biocenter Klein Flottbek, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany. E-mail: antonia.wanner@uni-hamburg.de

Bregje K. van Wesenbeeck: Boussinesqweg 1, 2629 HV Delft, The Netherlands.
Email: Bregje.vanWesenbeeck@deltares.nl

Guido Wolters: Deltares, Boussinesqweg 1, 2629 HV Delft, The Netherlands.
E-mail: Guido.Wolters@deltares.nl

List of photographs:

Tom Maxfield
Crew Building
University of Edinburgh
West Mains Road
Edinburgh
UK
EH9 3JN

Tel: +44 (0)131 650 5103
Email: t.maxfield@ed.ac.uk

15th June 2015

Re: PhD thesis by Franziska Rupprecht

To whom it may concern,

as a native English speaker and experienced proof-reader, I do hereby declare that the PhD thesis “***Vegetation succession and coastal protection by wave dissipation in salt marshes of North-West Europe***” has been written in concise and correct English (UK).

Yours sincerely,

Tom Maxfield
English Proof-reader, University of Edinburgh

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und ausschließlich die angegebenen Quellen und Hilfsmittel verwendet habe.

Hamburg, den 22.06.2015 Franziska Rupprecht