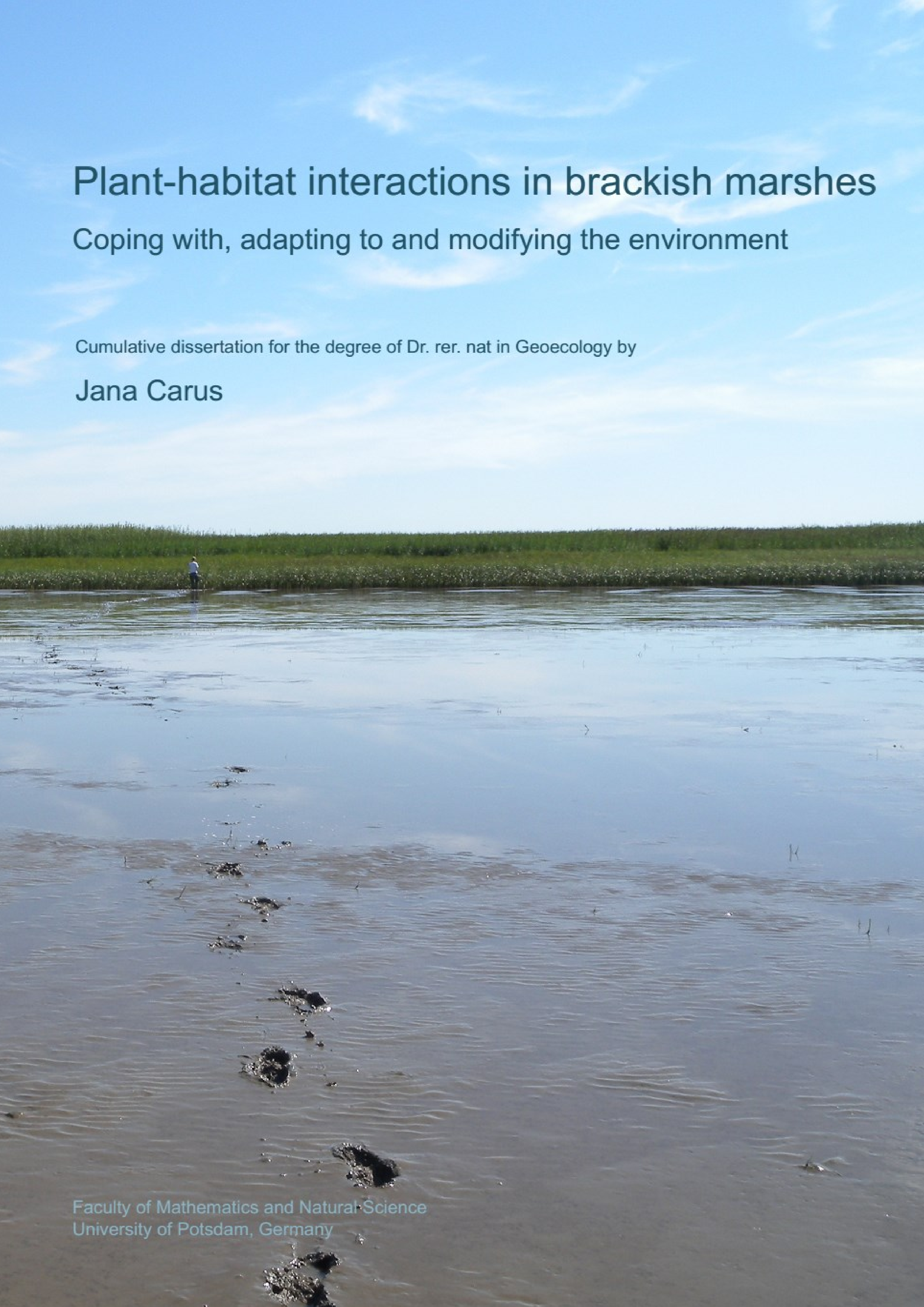
Plant-habitat interactions in brackish marshes

Coping with, adapting to and modifying the environment

Cumulative dissertation for the degree of Dr. rer. nat in Geoecology by

Jana Carus



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Jana Carus

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Summary

Estuarine marshes are ecosystems that are situated at the transition zone between land and water and are thus controlled by physical and biological interactions. Marsh vegetation offers important ecosystem services by filtrating solid and dissolved substances from the water and providing habitat. By buffering a large part of the arriving flow velocity, attenuating wave energy and serving as erosion control for riverbanks, tidal marshes furthermore reduce the destructive effects of storm surges and storm waves and thus contribute to ecosystem-based shore protection. However, in many estuaries, extensive embankments, artificial bank protection, river dredging and agriculture threaten tidal marshes. Global warming might entail additional risks, such as changes in water levels, an increase of the tidal amplitude and a resulting shift of the salinity zones. This can affect the dynamics of the shore and foreland vegetation, and vegetation belts can be narrowed or fragmented. Against this background, it is crucial to gain a better understanding of the processes underlying the spatio-temporal vegetation dynamics in brackish marshes. Furthermore, a better understanding of how plant-habitat relationships generate patterns in tidal marsh vegetation is vital to maintain ecosystem functions and assess the response of marshes to environmental change as well as the success of engineering and restoration projects.

For this purpose, three research objectives were addressed within this thesis: (1) to explore the possibility of vegetation serving as self-adaptive shore protection by quantifying the reduction of current velocity in the vegetation belt and the morphologic plasticity of a brackish marsh pioneer, (2) to disentangle the roles of abiotic factors and interspecific competition on species distribution and stand characteristics in brackish marshes, and (3) to develop a mechanistic vegetation model that helps analysing the influence of habitat conditions on the spatio-temporal dynamic of tidal marsh vegetation. These aspects were investigated using a combination of field studies and statistical as well as process-based modelling.

To explore the possibility of vegetation serving as self-adaptive coastal protection, in the first study, we measured current velocity with and without living vegetation, recorded ramet density and plant thickness during two growing periods at two locations in the Elbe estuary and assessed the adaptive value of a larger stem diameter of plants at locations with higher mechanical stress by biomechanical measurements. The results of this study show that under non-storm conditions, the vegetation belt of the marsh pioneer *Bolboschoenus maritimus* is able to buffer a large proportion of the flow velocity. We were furthermore able to show that morphological traits of plant species are adapted to hydrodynamic forces by demonstrating a positive correlation between ramet thickness and cross-shore current. In addition, our measurements revealed that thicker ramets growing at the front of the vegetation belt have a significantly higher stability than ramets inside the vegetation belt. This self-adaptive effect improves the ability of *B. maritimus* to grow and persist in the pioneer zone and could provide an adaptive value in habitats with high mechanical stress.

In the second study, we assessed the distribution of the two marsh species and a set of stand characteristics, namely aboveground and belowground biomass, ramet density, ramet height and the percentage of flowering ramets. Furthermore, we collected information on several abiotic habitat factors to test their effect on plant growth and zonation with generalised linear models (GLMs). Our results demonstrate that flow velocity is the main factor controlling the distribution of *Bolboschoenus maritimus* and *Phragmites australis*. Additionally, inundation height and duration, as well as intraspecific competition affect distribution patterns. This study furthermore shows that cross-shore flow velocity does not only directly influence the distribution of the two marsh species, but also alters the plants' occurrence relative to inundation height and duration. This suggests an effect of cross-shore flow velocity on their tolerance to inundation. The analysis of the measured stand characteristics revealed a negative effect of total flow velocity on all measured parameters of *B. maritimus* and thus confirmed our expectation that flow velocity is a decisive stressor which influences the growth of this species.

To gain a better understanding of the processes and habitat factors influencing the spatio-temporal vegetation dynamics in brackish marshes, I built a spatially explicit, mechanistic model applying a pattern-oriented modelling approach. A sensitivity analysis of the parameters of this dynamic habitat-macrophyte model HaMac suggests that rhizome growth is the key process for the lateral dynamics of brackish marshes. From the analysed habitat factors, *P. australis* patterns were mainly influenced by flow velocity. The competition with *P. australis* was of key importance for the belowground biomass of *B. maritimus*. Concerning vegetation dynamics, the model results emphasise that without the effect of flow velocity the *B. maritimus* vegetation belt would expand into the tidal flat at locations with present vegetation recession, suggesting that flow velocity is the main reason for vegetation recession at exposed locations.

Overall, the results of this thesis demonstrate that brackish marsh vegetation considerably contributes to flow reduction under average flow conditions and can hence be a valuable component of shore-protection schemes. At the same time, the distribution, growth and expansion of tidal marsh vegetation is substantially influenced by flow. Altogether, this thesis provides a clear step forward in understanding plant-habitat interactions in tidal marshes. Future research should integrate studies of vertical marsh accretion with research on the factors that control the lateral position of marshes.

Zusammenfassung

Tidemarschen sind Ökosysteme, die sich am Übergang zwischen Land und Wasser befinden und deshalb von Wechselwirkungen zwischen physikalischen und biologischen Prozessen beherrscht werden. Marschvegetation bietet wichtige Ökosystemleistungen, wie das Filtern von festen und gelösten Stoffen aus dem Wasser und die Bereitstellung von Lebensraum für Tiere. Außerdem verringern Marschen die zerstörerische Wirkung von Sturmfluten und Sturmwellen und tragen so zu einem ökosystembasierten Uferschutz bei. Doch in vielen Flussmündungen bedrohen umfangreiche Eindeichungen, künstlicher Uferschutz, Flussvertiefungen und die Landwirtschaft die Tidemarschen. Die globale Erwärmung könnte zusätzliche Risiken, wie etwa Änderungen der Wasserstände, eine weitere Erhöhung der Gezeitenamplitude und eine daraus resultierende Verschiebung der Salinitätszonen mit sich bringen. Dies kann die Dynamik der Ufer- und Vorlandvegetation beeinflussen und die Vegetationsgürtel verschmälern oder fragmentieren. Vor diesem Hintergrund ist es entscheidend, ein besseres Verständnis der Prozesse zu erlangen, die der raum-zeitlichen Vegetationsdynamik in Tidemarschen zugrunde liegen. Darüber hinaus ist sind zusätzliche Erkenntnisse darüber, wie Pflanzen-Umwelt-Beziehungen die Muster in Marschen beeinflussen, von entscheidender Bedeutung um Ökosystemfunktionen aufrechtzuerhalten und die Reaktion von Marschen auf Umweltveränderungen sowie den Erfolg von Ingenieur- und Restaurierungsprojekten zu bewerten.

Zu diesem Zweck wurden in dieser Arbeit drei Forschungsziele gesetzt: (1) das Erforschen der Möglichkeit der Vegetation als selbstanpassender Uferschutz zu dienen, (2) das Ermittlen der Rolle verschiedener Faktoren auf die Artenverbreitung und verschiedene Pflanzenmerkmale in Tidemarschen und (3) die Entwicklung eines prozess-basierten Vegetationsmodells, das die Analyse des Einflusses von Lebensraumbedingungen auf die raum-zeitliche Dynamik der Marschvegetation unterstützt. Diese Aspekte wurden anhand einer Kombination von Feldstudien und statistischer sowie prozessbasierter Modellierung untersucht.

Um die Möglichkeit der Vegetation zu erforschen, als selbstanpassender Uferschutz zu dienen, habe wurden für die erste Studie Strömungsgeschwindigkeiten mit und ohne lebende Vegetation gemessen. Außerdem wurde die Pflanzendichte und der Pflanzendurchmesser der Marschpflanzenart *Bolboschoenus maritimus* festgehalten. Des Weiteren wurde der adaptive Wert des größeren Stieldurchmessers von Pflanzen an Standorten mit höherer mechanischer Belastung durch biomechanische Messungen ermittelt. Die Ergebnisse dieser Studie zeigen, dass der Vegetationsgürtel unter ungestörten Bedingungen in der Lage ist, einen großen Teil der Strömungsgeschwindigkeit abzupuffern. Außerdem zeigen unsere Messungen, dass die dickeren, am wasserseitigen Rand des Vegetationsgürtels wachsenden Pflanzen eine deutlich höhere Stabilität aufweisen, als die Pflanzen innerhalb des Vegetationsgürtels. Diese Anpassung verbessert die Fähigkeit von *B. maritimus*, in der Pionierzone zu wachsen und könnte einen adaptiven Wert in Lebensräumen mit hohem mechanischem Stress darstellen.

In meiner zweiten Studie untersuchte ich die Verbreitung der beiden Marschpflanzenarten *Bolboschoenus maritimus* und *Phragmites australis* und nahm eine Reihe von Bestandscharakteristiken auf. Darüber hinaus sammelte ich Informationen über mehrere abiotische Habitatfaktoren, um ihre Wirkung auf die Marschzonierung mit generalisierten linearen Modellen (GLMs) zu testen. Ich fand heraus, dass die Strömungsgeschwindigkeit der Hauptfaktor ist, der die Verbreitung von *B. maritimus* und *P. australis* kontrolliert. Darüber hinaus beeinflussen die Überschwemmungshöhe und -dauer sowie die intraspezifische Konkurrenz die Verteilungsmuster. Unsere Ergebnisse zeigen, dass die Strömungsgeschwindigkeit nicht nur direkt die Verteilung der beiden Marscharten beeinflusst, sondern auch die Verbreitung der Pflanzen im Verhältnis zur Überflutungshöhe und -dauer ändert. Dies deutet auf eine Auswirkung der Strömungsgeschwindigkeit auf die Toleranz der Pflanzen gegenüber Überflutungen hin. Die Analyse der gemessenen Bestandscharakteristiken zeigt eine negative Auswirkung der Strömungsgeschwindigkeit auf alle gemessenen Parameter von *B. maritimus* und bestätigt damit unsere Erwartung, dass die Strömungsgeschwindigkeit ein entscheidender Stressfaktor ist, der besonders das Wachstum dieser Art beeinflusst.

Um ein besseres Verständnis der Prozesse und Habitatfaktoren zu erlangen, die die raumzeitliche Vegetationsdynamik in Marschen beeinflussen, habe ich ein räumlich explizites, mechanistisches Modell entwickelt. Eine Sensitivitätsanalyse der Modellparameter deutet darauf hin, dass das Rhizomwachstum der wichtigste Prozess für die laterale Dynamik der Tidemarschen ist. Die Muster von *P. australis* wurden hauptsächlich durch die Strömungsgeschwindigkeit beeinflusst. In Bezug auf die Vegetationsdynamik unterstreichen die Modellergebnisse, dass sich *B. maritimus* ohne die Wirkung der Strömungsgeschwindigkeit an den Orten mit der gegenwärtigem Vegetationsrückgang in die Wattfläche ausdehnen würde, was darauf hindeutet, dass die Strömungsgeschwindigkeit der Hauptgrund für den Vegetationsrückgang an exponierten Standorten ist.

Insgesamt zeigen die Ergebnisse dieser Arbeit, dass die Marschvegetation erheblich zur Strömungsreduktion unter durchschnittlichen Strömungsverhältnissen beiträgt und somit ein wertvoller Bestandteil von Uferschutzsystemen sein kann. Darüber hinaus konnte Strömung als Hauptfaktor für die Verbreitung, das Wachstum und die Expansion von Marschvegetation identifiziert werden. Diese Arbeit trägt maßgeblich zur Verbesserung des Verständnisses von Pflanzen-Habitat Interaktionen in Tidemarschen bei. Zukünftige Forschung sollte Studien des vertikalen Marschwachstums mit der Analyse der Faktoren, die die laterale Position der Marschen kontrollieren verknüpfen.

Contents

1 General introduction

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Brackish marsh vegetation

Tidal estuaries form the transition zone between sea and river and are thus characterised by both marine influences such as tidal dynamics, waves and saline water as well as riverine influences such as currents and fresh water (McLusky and Elliott, 2004). By entering the estuary twice a day, the tide is the driving force of all physical processes in tidal marshes. The degree of tidal influence is determined by estuarine morphology, tidal range, water and sediment discharge, winds, and shelf processes (Wells, 1995). Tides, currents and waves produce complex water movements. Flow velocity in estuaries depends on the one hand on river discharge and is on the other hand linked to the tide. Flow almost stands still at high and low water, whereas maximum flow velocities are reached in the interval between high and low tide. The water level rises while the current flows inland (flood tide) and drops as long as the current flows seawards (ebb tide). Additional to currents, waves play an important role in tidal estuaries and can be subdivided into those generated by wind and those generated by ships (Silinski et al., 2016). While in most estuaries the main source of sediments is the sea, they are as well carried in from the rivers and from the surrounding land (McLusky and Elliott, 2004). The deposition of these sediments in the estuary, as well as erosion processes are controlled by current velocity and particle size. Estuarine water-salinity lies between 0.5 and 35 psu varying during the tidal cycle as well as along the estuary. Marine saltwater entering the estuary during flood tide, is diluted by freshwater discharge from the river and thus the salinity decreases in upstream direction and during ebb tide.

Estuarine marshes are ecosystems that are situated between land and water and are thus substantially influenced by hydrodynamic conditions. Since there is an almost constant interaction between water and estuarine marshes, these ecosystems consist of a type of vegetation that is adapted to flooding. In the temperate and arctic regions, tidal marshes are dominated by emergent herbaceous plants that often form conspicuous monospecific plant zones. They feature a high primary productivity and low species diversity (Adam, 1990). Plant species that occur in the different salinity zones are restricted in their distribution by their physiological niche (Adams, 1963; Cooper, 1982). This leads to a decrease in species diversity (Engels and Jensen, 2009; Wolf, 1988) with increasing water-salinity. Depending on soil-water salinity and the thereon adapted vegetation one distinguishes salt, brackish and freshwater marshes. Brackish marshes occur in the intertidal zone of coastal estuaries at the boundary of salt- and freshwater and often comprise *Bolboschoenus maritimus*, *Phragmites australis* and tall forbs like *Angelica archangelica* and *Urtica dioica* (Engels and Jensen, 2009). The zonation of brackish marshes is often attributed to elevation which determines the exposure to tidal flooding and thus the duration, frequency and height of inundation (e.g. Bertness and Ellison, 1987; Coops et al., 1999; Heuner et al., submitted). The vegetation belts of emergent macrophytes mostly begin at 1.50 m to 2 m below the mean high water and often consist of *B. maritimus* in the pioneer zone and *P. australis* in the low and mid marshes (Figure 1.1). In most areas, however, the ranges of inundation height and duration that are tolerated by the marsh species overlap (Pielou and Routledge, 1976). This might be caused by the existence of other important abiotic factors (Coops and Van der Velde, 1996) such as hydrodynamic forces, sedimentation and erosion processes, soil water salinity and biotic interactions (Meire et al., 2005; Odum, 1988). A sound knowledge about the interaction of the factors that generate vegetation patterns is vital for assessing the response of tidal marshes to changes in environmental conditions (Elliott et al., 2016; Heuner et al., 2016).

Figure 1.1 Typical zonation of brackish marsh vegetation: *B. maritimus* in the pioneer zone and *P. australis* in the low and mid marshes in winter (left) and summer (right).

Although the term zonation suggests a static system, estuarine marshes are highly dynamic environments and are thus constantly subject to change, giving rise to recession and expansion of the tidal vegetation belts. These lateral dynamics are as important as vertical marsh evolution because they determine the future extent of marshes (Fagherazzi et al., 2012; Van De Koppel et al., 2005). In many estuaries, extensive embankments, artificial bank protection, river dredging and agriculture threaten tidal marshes (Temmerman et al., 2013). Global warming might entail additional risks, such as sea level rise-related changes in water levels, an increase of the tidal amplitude and a resulting shift of the salinity zones (Chua and Xu, 2014; Seiffert and Hesser, 2014). These factors can affect the dynamics of the shore and foreland vegetation, and vegetation belts can be narrowed or fragmented. Tidal marsh areas have already been reduced by anthropogenic influences since the middle of the past century (Fickert and Strotmann, 2007). Against this background, it is crucial to gain a better understanding of the processes underlying the spatio-temporal vegetation dynamics in brackish marshes.

The estuarine ecosystem is controlled by feedbacks between physical and biological processes. For plants, the costs of living in such a stressful environment are high. The consequence is a high degree of adaptation in the occurring plant species. Most emergent macrophytes propagate mainly vegetatively by the growth of rhizomes (Figure 1.2). This means that although many species still produce seeds, changes in the abundance and distribution are mainly determined by the pattern of clonal growth (de Kroon and Visser, 2003). Clonal reproduction allows plants to react with more frequent branching on good, and with longer rhizomes on bad habitat conditions and thus increases the density of ramets in more favourable habitat patches of a heterogeneous environment (de Kroon and Hutchings, 1995). Furthermore, ramets that colonise physiologically harsh habitats can be supported with nutrients and water by ramets in more favourable habitats (Amsberry et al., 2000). This allows that even locations with unfavourable habitat conditions to be populated by clonal plant species. Clonal plants can even adapt to environmental conditions by the formation of specialised units (Clausen et al., 1948; Richards et al., 2005). This phenotypic or morphologic plasticity can lead to selective advantages in heterogeneous habitats (Alpert and Stuefer, 1997; Eriksson and Jerling, 1990). A brackish marsh consists mostly of several genes, which differ in their tolerance to environmental factors. High genetic variability in marshes thus allows a high adaptability to a changing environment (Reusch et al., 2005). Although some studies approached phenotypic adaptation to environmental conditions (e.g. Clausen et al. 1948; Richards et al., 2005), to my knowledge, current velocity has so far not been addressed as influencing factor for growth characteristics of the tidal marsh pioneer *B. maritimus*.

Figure 1.2 Rhizome und roots of *B. maritimus* (left) and *P. australis* (right).

Ecosystem-based shore protection

Apart from adaptation to stressful environments, altering their habitat is another possibility for marsh plants to improve living conditions (van Wesenbeeck et al., 2008). Especially in stressful environments where organisms are substantially influenced by habitat conditions, they often tend to modify their environment (Jones et al., 1997). In doing so, tidal marsh vegetation also improves living conditions for other species and provides important ecosystem services for humans by filtering solid and dissolved substances from the water (Mitsch and Gosselink, 2015). By reducing shoreline erosion and increasing sedimentation (Coops and Van der Velde, 1996; Neumeier and Ciavola, 2004), an intact marsh vegetation belt furthermore promotes natural accretion of sediments and has the ability to adapt to projected sea level changes (Kirwan et al., 2010). Brackish marsh vegetation protects the shoreline by acting as a buffer between land and sea (Kirwan and Megonigal, 2013; Möller et al., 1999). The presence of plants strongly reduces current velocity inside the vegetation (Neumeier and Ciavola, 2004) by exerting drag on the flow. The degree of reduction depends on the amount of dampening plant mass, thus on vegetation type, vegetation height and density, and width of the vegetation belt (Christiansen et al., 2000; Leonard and Luther, 1995; Paul et al., 2016). By reducing current velocity and attenuating waves (Christiansen et al., 2000; Temmerman et al., 2005), marsh vegetation can diminish the destructive effects of storm surges and storm waves (Möller et al., 2014; Wamsley et al., 2010). The shoreline protection service of tidal marshes is of particular importance as the banks of many estuaries are amongst the most heavily populated areas of the world (Wolanski, 2007). Climate change induced sea level rise and increased probabilities of storm events make these areas more vulnerable to flooding. As the effect of conventional defence structures on natural processes is large and can result in undesirable side effects, the potential of ecosystem-based flood defence gains more and more attention (Temmerman et al., 2013; van Wesenbeeck et al., 2014). Although shore protection is a pressing issue, there are still large knowledge gaps in the quantification of the flow reduction performance of marsh vegetation. For instance, field studies published so far have not explicitly considered the flow reduction effect of vegetation by comparing measurements with and without living above-ground biomass. While the attenuation of hydrodynamic forces of several marsh species has been investigated, to my knowledge no study investigates the effect of *Bolboschoenus maritimus*, although it is one of the most common primary colonisers on brackish tidal flats (Boaden and Seed, 1988).

Methods for analysing habitat-plant interactions

Field and flume experiments, field measurements and subsequent data analyses as well as modelling approaches can contribute to gaining a better understanding of habitat-plant interactions in tidal marshes.

Flume studies provide valuable insights into drag and turbulence caused by vegetation and its effect on vertical flow and turbulence profiles (e.g. Nepf and Vivoni, 2000; Nepf, 1999; Temmerman et al., 2005). Furthermore, flume experiments help quantify the effect of waves and currents on vegetation (Puijalon et al., 2005; Silinski et al., 2015). However, the canopy used in flumes is much less complex than a naturally grown vegetation belt. Field studies account for this complexity. By conducting measurements in spring and summer, it is even possible to compare current velocity with and without living vegetation at the same site. Laboratory experiments can furthermore help to evaluate the effect of abiotic factors on the growth of marsh plant species. However, as it is difficult to imitate the complex composition of natural habitat factors in the laboratory, the relevance of laboratory studies for explaining field patterns is limited (Davy and Costa, 1992). With their conspicuous vegetation zonation, wetlands can serve as a ‘natural experiment’ (Diamond, 1983) with a set of environmental gradients to investigate. Especially salt marshes have for long been used as such a model system (e.g. Pennings et al., 2005; Snow and Vince, 1984) whereas tidal freshwater and brackish marshes have received much less attention (Meire et al., 2005).

The driving factors of marsh zonation can be evaluated with transplant experiments (e.g. Amsberry et al., 2000; Coops et al., 1994; Engels and Jensen, 2010). By this means, abiotic factors can be separated from each other or from biotic influences (Snow and Vince, 1984).

A valuable tool for analysing species-habitat relationships is provided by statistical modelling (Schröder, 2008). By disentangeling the effects of different factors on species distribution and growth parameters, statistical modelling helps to analyse field data of species-habitat relationships. Generalised linear models (GLM, McCullough and Nelder 1989) offer the possibility to include a wide range of environmental data using link functions between response and predictor variables (Bio et al., 2002) and can help improving the understanding of species' responses to environmental variables, because of the good interpretability of the relationships between responses and predictors. GLMs use link functions to establish a relationship between the mean of the response variable and the linear combination of the explanatory variables (Guisan et al., 2002). Compared to other statistical methods, GLMs provide some advantages for the purpose of this study: as presence-absence data is easily obtained for tidal marsh vegetation, presence-absence methods like GLMs are more suitable than so called presence-only methods like the maximum entropy method (MAXENT, Phillips et al., 2005). Furthermore, MAXENT does not estimate occurrence probabilities but only relative suitability (Guillera-Arroita et al., 2014). Although semi-parametric generalised additive models (GAMs, Hastie and Tibshirani, 1990) produce more complex and therewith often better fitting functions, the parametric functions of GLMs may capture most of the same variation and have a more reasonable ecological explanation (Austin, 2002). Non-parametric, machine learning methods like classification and regression trees (CART, Efron and Tibshirani, 1991) and sophisticated ensemble prediction methods such as random forests (RF, Breiman, 2001) and boosted regression trees (BRT, Elith et al., 2008; Friedman, 2002) proved to perform better in predicting species distribution (e.g. Zurell et al., 2009, Valle et al., 2013). However, the continuous functions of GLMs are more suitable for explaining species responses to environmental gradients (Vayssières et al., 2000).

The drawbacks of species distribution models are that they do not explicitly consider processes and that they assume vegetation and environment to be in equilibrium and hence do not account for dynamics (Araújo and Guisan, 2006; Zurell et al., 2009). Process-based models proved to be beneficial for the evaluation of the ecological processes underlying distributional patterns of animal and plant species (Grimm et al., 2005), because they account for transient dynamics and explicitly consider mechanisms such as dispersal limitation (e.g. Schurr et al., 2012).

Study area

With a length of 142 km, the estuary of the river Elbe is the longest estuary on the German coast. From the weir in Geesthacht (km 586) to the mouth at Cuxhaven (km 727) the Elbe is influenced by the tide (Figure 1.3).

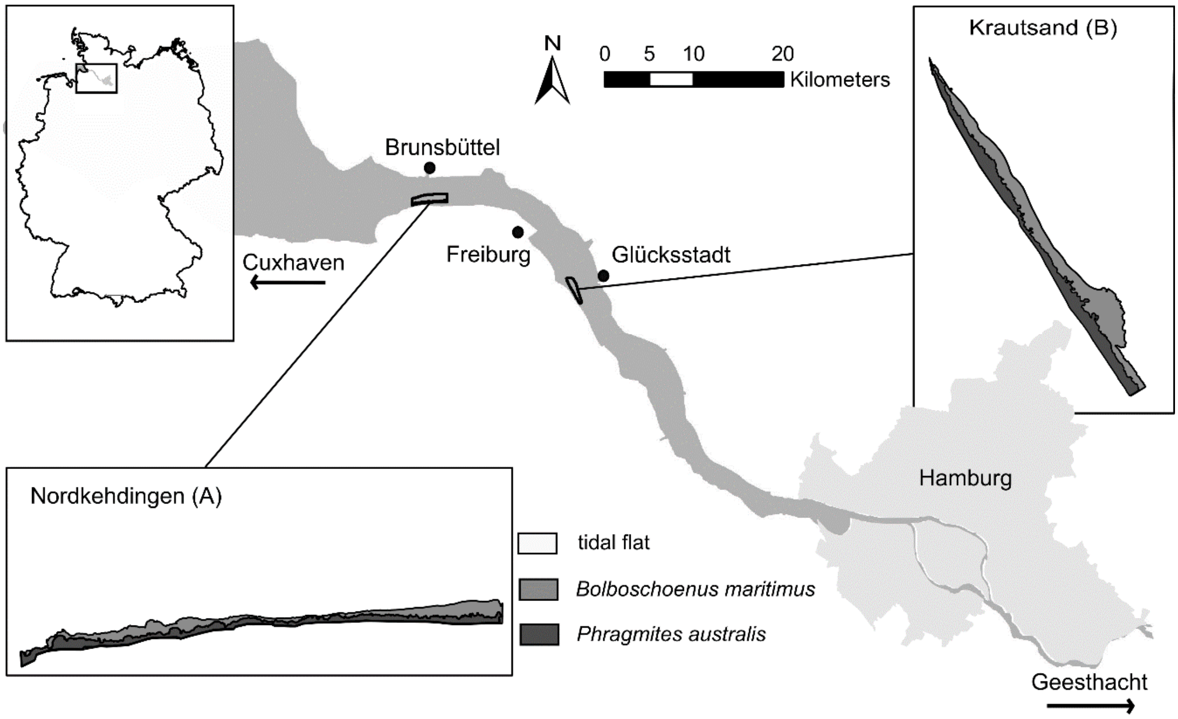


Figure 1.3 Location of the two study sites in the Elbe estuary.

Additional to the tidal wave entering from the North Sea, the Elbe estuary is influenced by freshwater inflow from the catchment area (Boehlich and Strotmann, 2008). Because of strong tides and high sediment transport, the shape of the Elbe estuary is highly diverse and continuously changing. While the channel system at the mouth is steadily moving, further upstream, only side arms have such a natural dynamic. The tidal flat and the adjacent marsh are regularly flooded by water entering from the mouth of the Elbe at high tides. Since the settlement of men, the natural development of the estuary was affected by the construction of dikes and barriers hindering a natural marsh accretion by sediments. Furthermore, the Elbe has since long been a waterway for freight transports and is thus of high water-economic significance. Due to an ever-increasing size of transport vessels, water-engineering measures such as channel straightening and deepening and the expansion of harbour basins have been and are still frequently conducted. These anthropogenic influences have altered the tidal dynamics (Fickert and Strotmann, 2007). Changes in the flow conditions and sediment dislocations have for long been observed on the banks (Wolf, 1988). Since the Elbe estuary lost the characteristics of a near-natural estuary with its diverse, wide and constantly changing riverbed, its ability to dampen the tidal wave decreased (Dücker et al., 2006). The water-engineering measures have led to an increase in tidal range and to a shift in salinity zones upstream (Fickert and Strotmann, 2007). Today, the tidal range of the Elbe has its maximum with 3.6 m in Hamburg. The tidal period is asymmetric with a shorter flood period (5hrs 5min) than ebb period (7hrs 20min). The speed of the flood current is thus higher than that of the ebb current, leading to a heavy upstream transport of sediments (Fickert and Strotmann, 2007). The mean discharge of the Elbe is 700 m^3s^{-1}, ranging from 200 - 3600 m^3s^{-1}. Along many parts of the Elbe estuary, the marsh is dominated by the above mentioned zonation of *B. maritimus* and *P. australis*.

The studies for this thesis were conducted at two sites in the tidally influenced brackish part of the Elbe estuary (Figure 1.3). One study site lies in the nature reserve Nordkehdingen (A) (53°51'46.419"N, 9°5'50.027"E) and the other about 30 km further upstream on the peninsula of Krautsand (B) (53°45'50.626"N, 9°22'46.052"E). These sites were selected because of the presence of the two study species and an unobstructed shoreline. The sites are described in more detail in the Chapters 2, 3 and 4.

Objectives and chapter outline

As can be summarised from the above paragraphs, tidal marshes provide important ecosystem services by reducing wave and current energy and serving as erosion control for the riverbanks. At the same time, marsh vegetation is substantially influenced by hydrodynamic conditions. The estuarine ecosystem is thus controlled by feedbacks between physical and biological processes. As the hydrodynamic conditions in estuaries are continually changing, their effect on the vegetation leads to recession and expansion of the tidal marsh. However, the present understanding of the interaction of tidal marsh vegetation and its habitat is not sufficient to allow predictions of marsh development. It is thus of vital importance to gain a deeper understanding of the drivers of species distribution, stand structure and vegetation dynamics and at the same time further investigate the shore protection potential of marsh vegetation.

The overall aims of this theses were (1) to explore the possibility of vegetation serving as self-adaptive shore protection by quantifying the reduction of current velocity and the morphologic plasticity of a brackish marsh pioneer, (2) to disentangle the roles of abiotic factors and interspecific competition on plant traits and species distribution in brackish marshes, and (3) to develop a mechanistic vegetation model that helps analysing the influence of habitat conditions on the spatio-temporal dynamic of tidal marsh vegetation (Figure 1.4).

To achieve these aims, in this thesis I quantify the effect of standing pioneer vegetation on flow velocity at the marsh edge. Furthermore, I examine the influence of habitat conditions on the marsh vegetation across scales: from considering the effect of flow velocity on morphology and stability of single plants, over the effect of a range of habitat factors on species occurrence and stand structure in 1 m^2 plots to the process-based modelling of the patterns of spatio-temporal vegetation dynamic at the landscape scale.

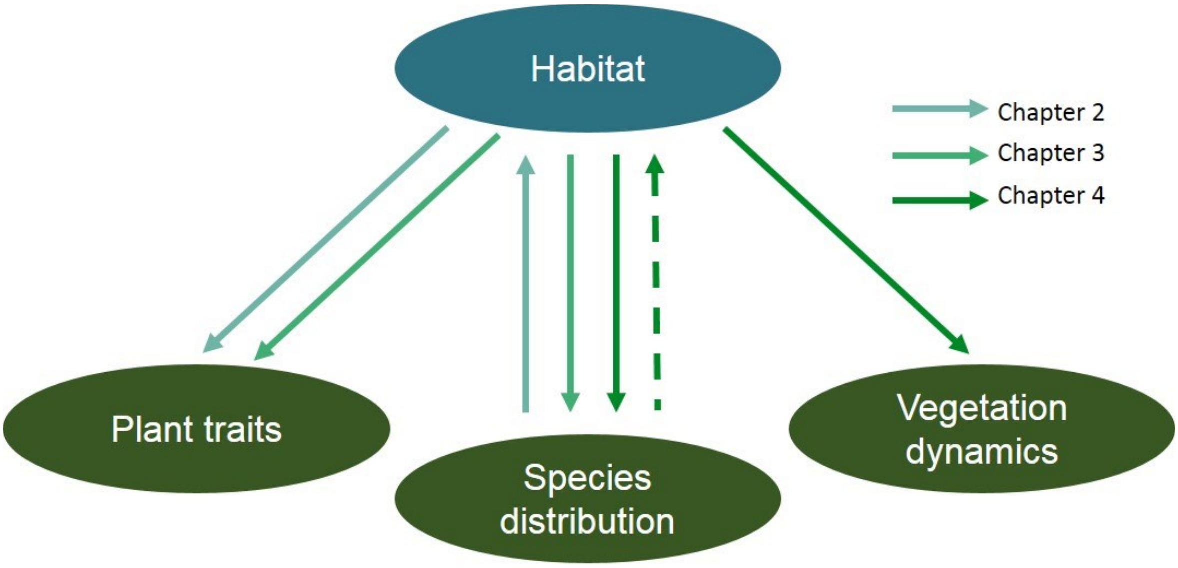


Figure 1.4 Schematic overview of issues addressed in this thesis.

Chapter 2: Vegetation as self-adaptive coastal protection: Reduction of current velocity and morphologic plasticity of a brackish marsh pioneer

To explore the possibility of vegetation serving as self-adaptive coastal protection, I measured current velocity with and without living vegetation, recorded ramet density and plant thickness during two growing periods at two locations in the Elbe estuary and assessed the adaptive value of a larger stem diameter at locations with higher mechanical stress by biomechanical measurements.

Aims of this study:

(i) Quantifying the reduction of current velocity of *B. maritimus* by comparing field measurements with and without living vegetation as well as by estimating effect functions from the data.

(ii) Identifying the morphological traits of *B. maritimus'* ramets, which adapt to environmental conditions and assess their adaptive value.

Chapter 3: Plant distribution and stand structure in brackish marshes: unravelling the roles of abiotic factors and interspecific competition

To evaluate the effect of abiotic factors and interspecific competition on plant distribution and stand characteristics, I assessed the distribution of two selected marsh plant species and measured a set of stand characteristics, namely aboveground and belowground biomass, ramet density, ramet height and the percentage of flowering ramets. Furthermore, I collected information on several abiotic habitat factors to test their effect on plant zonation and stand characteristics with generalised linear models (GLMs).

Aims of this study:
(i) Evaluating the effect of abiotic habitat conditions and competition on the distribution of the two brackish marsh species *B. maritimus* and *P. australis*.
(ii) Quantifying the influence of habitat conditions on the stand characteristics of these two species.

Chapter 4: Which factors and processes drive the spatio-temporal dynamics of brackish marshes? - Insights from development and parameterisation of a mechanistic vegetation model

As it is crucial for the analysis of marsh dynamics to detect and consider the processes that drive the spatio-temporal dynamics and hence generate patterns in tidal marsh vegetation, I build a spatially explicit, mechanistic model applying a pattern-oriented modelling approach.
Aims of this study:
(i) Gaining a better understanding of the processes underlying the spatio-temporal vegetation dynamics in brackish marshes.
(ii) Identifying the habitat factors that mostly influence the patterns of tidal marsh vegetation.
(iii) Developing a tool for testing scenarios.

Chapters 2 to 4 are based on the following publications:

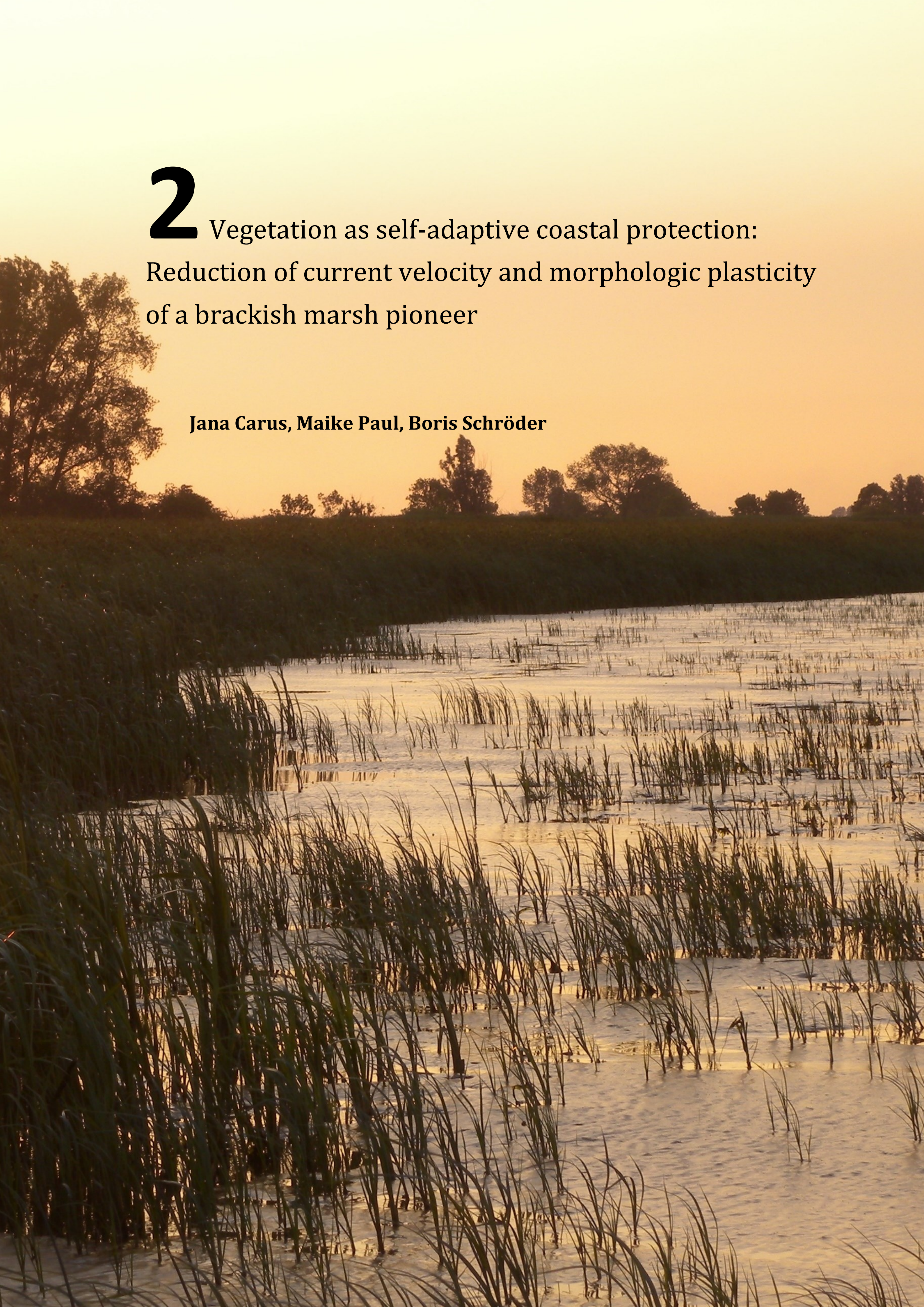
Chapter 2:	Carus, J., Paul, M., Schröder, B., 2016. Vegetation as self-adaptive coastal protection: Reduction of current velocity and morphologic plasticity of a brackish marsh pioneer. Ecol. Evol. 6, 1579–1589. doi:10.1002/ece3.1904
Chapter 3:	Carus, J., Heuner, M., Paul, M., Schröder, B., 2017. Plant distribution and stand characteristics in brackish marshes: Unravelling the roles of abiotic factors and interspecific competition. Estuar. Coast. Shelf Sci. 196, 237–247. doi:10.1016/j.ecss.2017.06.038
Chapter 4:	Carus, J., Heuner, M., Paul, M., Schröder, B., 2017. Which factors and processes drive the spatio-temporal dynamics of brackish marshes? -Insights from development and parameterisation of a mechanistic vegetation model. Ecol. Modell. 363, 122–136. doi:10.1016/j.ecolmodel.2017.08.023

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

2

Vegetation as self-adaptive coastal protection: Reduction of current velocity and morphologic plasticity of a brackish marsh pioneer

Jana Carus, Maike Paul, Boris Schröder



Abstract

By reducing current velocity, tidal marsh vegetation can diminish storm surges and storm waves. Conversely, currents often exert high mechanical stresses onto the plants and hence affect vegetation structure and plant characteristics. In our study, we aim at analysing this interaction from both angles. On the one hand, we quantify the reduction of current velocity by *Bolboschoenus maritimus,* and on the other hand, we identify functional traits of *B. maritimus'* ramets along environmental gradients. Our results show that tidal marsh vegetation is able to buffer a large proportion of the flow velocity at currents under normal conditions. Cross-shore current velocity decreased with distance from the marsh edge and was reduced by more than 50% after 15 m of vegetation. We were furthermore able to show that plants growing at the marsh edge had a significantly larger diameter than plants from inside the vegetation. We found a positive correlation between plant thickness and cross-shore current which could provide an adaptive value in habitats with high mechanical stress. With the adapted morphology of plants growing at the highly exposed marsh edge, the entire vegetation belt is able to better resist the mechanical stress of high current velocities. This self-adaptive effect thus increases the ability of *B. maritimus* to grow and persist in the pioneer zone and may hence better contribute to ecosystem-based coastal protection by reducing current velocity.[1]

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[1] Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.np6b8.

Introduction

Tidal marshes play an important role for coastal flood defence (Kirwan and Megonigal, 2013; Temmerman et al., 2013). By reducing current velocity and attenuating waves (Christiansen et al., 2000; Temmerman et al., 2005b), marsh vegetation reduces the destructive effects of storm surges and storm waves (Gedan et al., 2010; Shepard et al., 2011). Moreover, it reduces shoreline erosion and increases sedimentation (Neumeier and Ciavola, 2004). An intact marsh vegetation belt hereby promotes natural accretion of sediments and has the ability to adapt to projected sea level changes (Kirwan et al., 2010). Temmerman *et al.* (2013) argued that the maintenance of conventional coastal engineering solutions may become unsustainable with increasing flood risk propelled by rising sea levels and therefore, the creation or restoration of coastal ecosystems could replace or improve and support conventional levee structures. For the plants, however, the costs of living in such a stressful environment are high. In tidal marshes, vegetation is flooded up to twice a day, often for several hours and waves and currents often exert high mechanical stress on the plants (Bal et al., 2011; Coops et al., 1994). As vegetation buffers current and wave energy to some extent, the hydrodynamic forces together with related mechanical stresses are not evenly distributed in the vegetation belt. Thus, vegetation structure and zonation are influenced by hydrodynamic forcing. Because current often has an adaptive effect on growth traits (Puijalon et al., 2005; Puijalon and Bornette, 2004; Szmeja and Galka, 2008), even ramets of one species can vary within the vegetation belt (Barrett et al., 1993) and thereby enhance the ability of vegetation to serve as self-adaptive flood defence. Hence, hydrodynamic forcing influences vegetation structure and zonation, as well as variability of individuals in populations (Barrett et al., 1993).

Effect of vegetation on current velocity

In tidally influenced estuaries, currents are strongly affected by the rise and fall of the water level (Le Hir et al., 2000). In general, these currents can be split into two components: a long-shore component, which is shore-parallel, and a cross-shore component, which runs vertically to the shore (Le Hir et al., 2000). In these systems, long-shore current velocity is mainly generated by water draining into the sea and by the inflow of the rising tide. The highest velocities are reached during storms coinciding with spring tides. In contrast, cross-shore currents result from filling and emptying of the intertidal flats. Cross-shore current velocity depends mainly on the tidal range (McAnally and Mehta, 2001) and the width of the mudflat (Le Hir et al., 2000). It can exceed long-shore current velocity when the intertidal flat is particularly wide, and/or when long-shore currents are reduced by the presence of natural or man-made obstructions.

Previous studies found that the presence of plants strongly reduces current velocity inside the vegetation (Neumeier and Ciavola, 2004). The degree of reduction depends on the amount of dampening plant mass, thus on vegetation type, vegetation density, canopy height, and width of the vegetation belt (Christiansen et al., 2000; Leonard and Luther, 1995; Neumeier and

Ciavola, 2004). The reduction of current energy by vegetation has mostly been studied in laboratory flumes. These studies have enlarged knowledge on drag and turbulence caused by vegetation and its different effects on vertical flow and turbulence profiles (e.g. Nepf 1999; Nepf and Vivoni 2000; Temmerman et al. 2005). However, important differences exist between natural marshes and their laboratory models (Neumeier and Ciavola, 2004). For example, the canopy used in flumes is much less complex than a naturally grown vegetation belt. Field studies published so far accounted for this complexity but flow velocity measurements did not explicitly consider the effect of vegetation by comparing measurements with and without living aboveground biomass. Several marsh species have been investigated, but to our knowledge no study explicitly considers *Bolboschoenus maritimus (L.) Palla* and its role in the attenuation of hydrodynamic forces, although it is one of the most common primary colonisers on brackish tidal flats (Boaden and Seed, 1988).

Morphological plant response

For many plant species it has been found that individuals differ in phenotype (Richards et al., 2005). These differences can, for example, occur through the creation of different phenotypes from one genotype as an adaptation to differing environmental conditions (Clausen et al., 1948; Richards et al., 2005). This phenotypic plasticity can be very advantageous in spatially or temporally heterogeneous environments (Alpert and Simms, 2002; Givnish, 2002). For clonal plants, it has been hypothesised that phenotypic plasticity can result in the formation of specialised units and thus selective advantages in heterogeneous habitats (Alpert and Stuefer, 1997; Eriksson and Jerling, 1990).

The clonal plant *B. maritimus* forms populations consisting of many independent units, called ramets. These units are connected by rhizomes which (i) serve as storage organs (Suzuki and Stuefer, 1999), and (ii) facilitate vegetative dispersal (Karagatzides and Hutchinson, 1991). For *B. maritimus* it has been shown that the proportion of aboveground dry matter increased at the expense of roots and rhizomes with increasing water depth (Clevering and Hundscheid, 1998). Furthermore, the species is able to develop different groups of ramets specialised in sexual reproduction, resource storage, carbon assimilation and vegetative growth depending on their position along the rhizome system (Lieffers and Shay, 1981; Zákravský and Hroudová, 1994). Charpentier and Stuefer (1999) showed that this specialisation is affected by environmental conditions.

Species distribution and community dynamics of tidal marsh vegetation are highly affected by mechanical stress produced by hydrodynamic forces (Denny, 1988; Vogel, 1994). Especially in the pioneer zone, mechanical stress plays a dominant role in the establishment, survival and expansion of vegetation (Bruno, 2000; Houwing, 2000; van Katwijk and Hermus, 2000) because it can lead to breakage and uprooting of ramets. For submerged plants, it has been shown that current often has an adaptive effect on growth traits (Puijalon et al., 2005; Puijalon and Bornette, 2004; Szmeja and Galka, 2008) which can in some circumstances lead to greater hydrodynamic performance (Puijalon et al., 2005), i.e. the ability to withstand hydrodynamic forces induced by water movement. Hydrodynamic performance can be enhanced through alternative morphologies which either minimize mechanical forces (avoidance strategy, e.g. by adopting a streamlined form or by size reduction) or increase resistance to mechanical failure (tolerance strategy, e.g. by enhancing the proportion of strengthening tissue or by higher radial growth resulting in higher stem diameter) (Puijalon et al., 2011, 2008). The adaptive value of plant traits for withstanding mechanical forces can be assessed by stability measurements which determine bending stiffness and breaking force. Bending stiffness describes the resistance of a stem to bending. Breaking force is the maximal flexural force applied to the plant probe before it breaks. Although some studies approached phenotypic adaptation to environmental conditions (e.g. Clausen et al. 1948; Richards et al. 2005), to our knowledge, current velocity has so far not been addressed as influencing factor for growth characteristics of the tidal marsh pioneer *B. maritimus*.

As the effect of marsh vegetation on flow velocity is closely linked to its response to current energy (Butcher, 1933), a holistic view is crucial for understanding the ability of vegetation to serve as self-adaptive flood defence. Therefore, this study aims at analysing this interaction from both angles. On the one hand, we quantified the reduction of current velocity by *B. maritimus* by comparing field measurements with and without living vegetation as well as by estimating effect functions from the data. As the *B. maritimus* belt consists of very dense vegetation, we expected both long- and cross-shore current velocity to be reduced directly behind the boundary between vegetation and open water. On the other hand, we identified the functional traits of *B. maritimus'* ramets which adapt to environmental conditions and assessed their adaptive value. As current velocity exerts high mechanical stress especially on ramets growing at the marsh edge, we anticipated some degree of morphological adaptation of these ramets.

To explore the possibility of the vegetation serving as self-adaptive coastal protection, we measured current velocity with and without living vegetation, recorded ramet density and plant thickness during two growing periods at two locations in the Elbe estuary and assessed the plants adaptive value.

Methods

Study system and species description

With a length of 170 km and a maximum width of 10 km, the estuary of the river Elbe is the largest estuary along the German coast. It is influenced by tides from the mouth in Cuxhaven to the weir in Geesthacht. The tidal range is highest in Hamburg (3.6 m) and decreases by 0.6 m in Cuxhaven (120 km downstream) and by 1.6 m in Geesthacht (40 km upstream). For the investigation of a tidally influenced marsh, it was crucial to select sites without dampening of the tidal influence (e.g. by embankments or wave breakers). For this reason, we selected one site in the nature reserve Nordkehdingen (A) (53°51'46.419"N, 9°5'50.027"E) and one site about 30 km upstream on the peninsula of Krautsand (B) (53°45'50.626"N, 9°22'46.052"E) (Figure 2.1). The sites are both situated in the brackish part of the River Elbe and exhibit a mean soil water salinity of 4.5 ppt (A) and 1.5 ppt (B). The dominating species at both sites are *B. maritimus* at the waterfront and *Phragmites australis* further landwards. *B. maritimus* usually occurs in the pioneer zone of brackish marshes up to 1.2 m below mean high water and forms dense monospecific stands (Lieffers and Shay, 1982a, 1982b). It is a perennial clonal plant with a strongly branched system of rhizomes, interconnecting single ramets (Hroudová et al., 2007). In one growth period, *B. maritimus* can form many rhizomes and roots which contribute to a fast vegetative dispersal (Dykyjová, 1986). In the study region, the above ground ramets sprout between March and April, grow up to 2 m high and consist of a triangular stem with up to 10 lineal leafs. Brown flowers rise above the leaves from June to August with oval spikelets clustered just below their tips. At the end of the growth period, all aboveground plant parts die back (Lillebø et al., 2003), and only belowground organs persist (Charpentier and Stuefer, 1999). Due to the strong tidal influence, the littoral zone of the Elbe estuary is regularly flooded at high tide and drained at low tide. Maximum inundation height at the marsh edge ranges from 0.58 to 1.4 m in study site A and from 1.23 to 2.19 m in study site B. Maximum daily inundation time lies between 3.5 and 5.5 h in study site A and between 6.3 and 9.3 h in study site B. In most parts of the two study sites, *B. maritimus* is spreading with a dispersal rate of up to 9 m per year, but is retreating in other areas.

Data collection and processing

To evaluate how currents progress through the vegetation belt of *B. maritimus,* we took detailed measurements of long-shore and cross-shore velocities at one transect in study site A (Figure 2.1) in April and August 2012, respectively. Measurements were conducted with four self-recording Acoustic Doppler Velocimeters (ADV, Nortek Vector) at plots oriented on vegetation patterns: Plot 0 was placed at previous years' marsh edge (Figure 2.2 a). All other plots were located at predefined distances from Plot 0 inside and in front of the *B. maritimus* belt (the latter is indicated by negative distance specifications).

Distances from the marsh edge were -5, 0, 5 and 15 m, corresponding to 1.19, 1.22, 1.26 and 1.31 m above sea level (Figure 2.2 a) and plot size was 0.5 × 0.5 m (Figure 2.2 b), the waterfront side of the plot being situated at the given distances. The ADVs were fixed horizontally on wooden crosses, positioned behind the plot in order to limit the effects of the support system on the measurements and to locate the measuring volume in the middle of the plot (Figure 2.2 a and b).

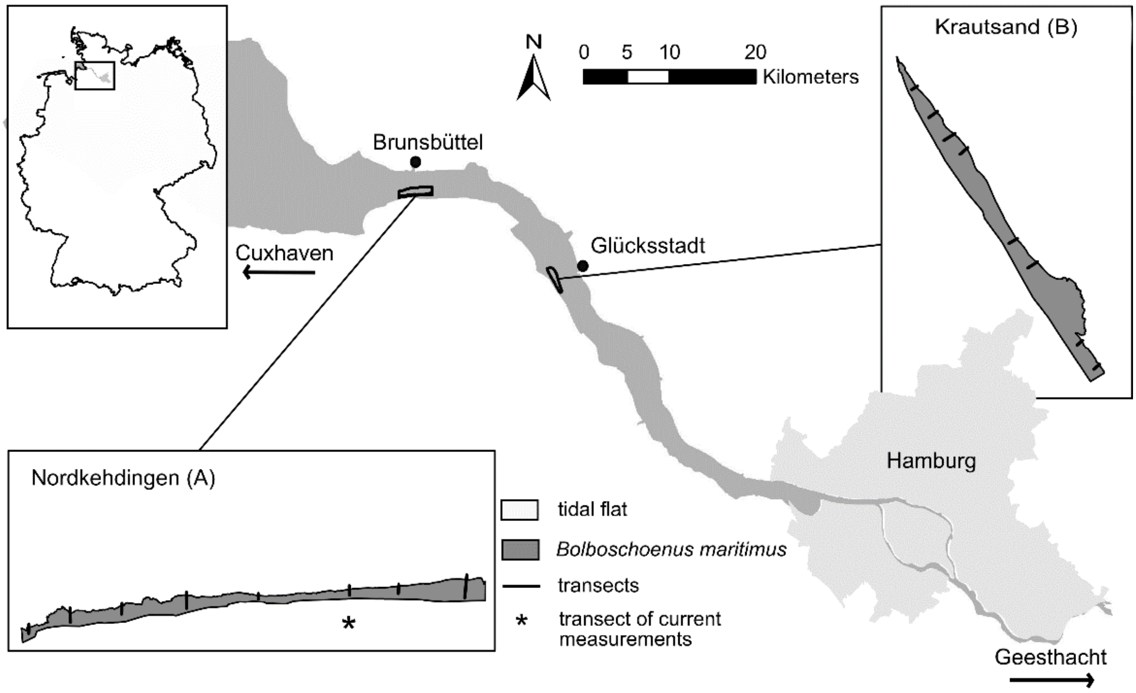

Figure 2.1 Location of the two study sites in the Elbe estuary and position of the 16 transects.

Since the ADV is sensitive to objects between the probe and the sampling volume, the canopy was cut back within a 0.15 m radius around the sampling volume. The ADVs were positioned 0.1 m above the sediment in order to conduct simultaneous measurements for at least one hour per flood at all plots (Leonard, 1997). Particular caution was taken to minimize damage to vegetation during all operations. The instruments were programmed to measure up- and downstream (long-shore) and on- and off-shore (cross-shore) velocity with a frequency of 4 Hz for up to four hours, corresponding to the inundation time during one flood. In the course of pre-processing we excluded all measurements with missing data due to the dry falling of one of the ADVs, which resulted in time series of 60 min around high tide. Running means were calculated with a bin width of one minute, corresponding to 240 measurements. To calculate flow velocity means for each location we averaged across the respective time series. Error bars on mean velocities represent mean ±1 standard error of measured flow velocities from 60 min around high tide ($\sqrt{\frac{\boldsymbol{var(flow\ velocity)}}{\boldsymbol{n(flow\ velocity)}}}$). Changes during the growing season were quantified by comparing measurements without living vegetation (April) with measurements with maximal *B. maritimus* cover (August). To compare measurements in April with measurements in August, we used the plot in front of the vegetation (Plot -5) as reference. For this purpose, we calculated a normalised flow velocity by dividing the mean flow velocity in the vegetation plots (Plots 0, 5, 15) by the mean velocity in the vegetation-free first plot (Plot -5). To quantify the effect of the living vegetation along the transect, we divided the results of the measurements in August by the results from April and fitted functions to the data. This was accomplished by least squares regression of the mean of the original or the logarithmised data.

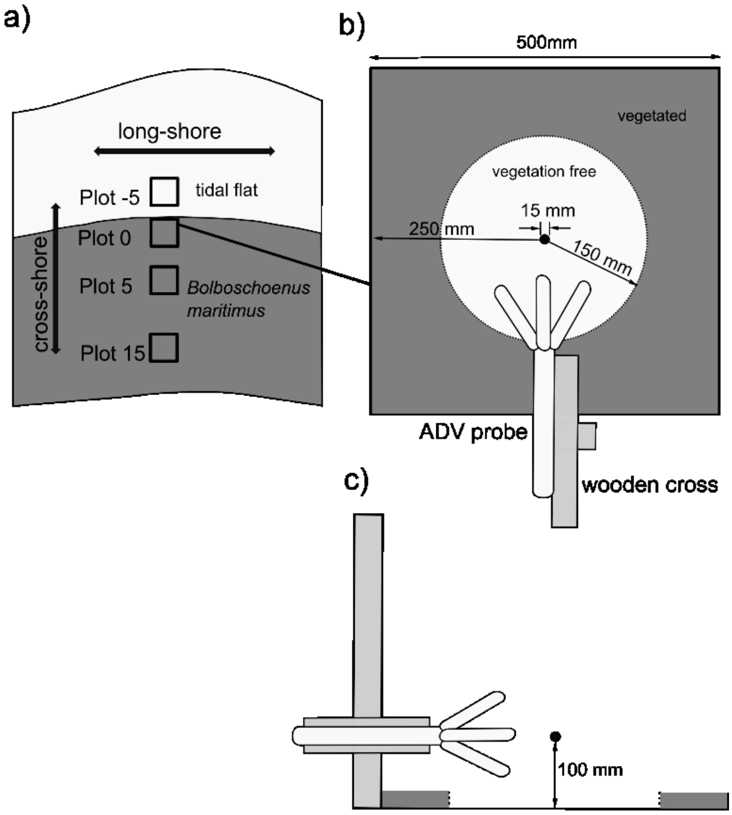

Figure 2.2 Scheme of the measurement locations. a) Positioning of current measurements along the transect. b) Top view of the installation design of ADV devices (measuring volume ●). c) Side view of the installation design of ADV devices. Grey colouring indicates vegetated areas.

To evaluate the effect of current velocity on plant morphology, we conducted further current measurements in front of 16 transects (Plot -5) in August 2013 (Figure 2.1). The plots were again oriented on vegetation patterns and thus located at different elevations. For this purpose, we simultaneously measured at four transects during one flood, covering all 16 transects over the course of four floods. To gain a reference for comparing the different floods, we additionally measured during one more flood with one ADV at one of the transects of the four preceding measurements. In August 2013, we sampled three ramets of *B. maritimus* from the water front (Plot 0) and from 15 m inside the vegetation belt (Plot 15) at each transect (n = 96) for biomechanical measurements. Mechanical resistance of these stems was assessed in a three point measuring setup with a universal testing machine (Zwick/Roell Modell BZ2.5/TN1S) (Kempe et al., 2013; Vincent, 1992). The samples were loosely placed on the measuring device with two supporting points at 100 and 450 mm measured from the basal end of the stem. Flexural force was applied at 275 mm and the ramets then bent until breakage. Before measurement, all ramets were prepared as follows: the undermost leaves were removed from the stems and samples cut at 550 mm. Height and width of the plant cross section was measured at 100 mm and the mean used as a measure for stem diameter during further analyses. On the basis of the recorded flexural force, which was applied per bending distance, bending stiffness (*EI*) was calculated. For this purpose, the distance between the two supporting points (l = 350 mm) and the slope of the linear elastic range of the force deflection graph (b) was used: $EI = \mathrm{l}^3 * \frac{\mathrm{b}}{48}$. As the minimum length-diameter-relation of a sample depends mainly on material properties of the sample (Lilholt, 1886), l was determined experimentally (minimum length-diameter-ratio = 0.012 mm). Recorded data permitted the identification of the force, applied just before the buckling of the probe ($Fmax$).

In addition to these measurements, we recorded ramet density to characterise vegetation structure and evaluate the density effect on plant morphology. These measurements were conducted at all 16 transects at the marsh edge (Plot 0) and inside the vegetation belt (Plot 15). At each location, three plots of 0.25 m^2 were placed 5 m apart, parallel to the shoreline. The coordinates and elevation of all plots were recorded with a differential GPS. The plant density was measured at the peak of the growing season in 2012 (28 July - 02 August) and 2013 (30 July - 05 August).

The significance of differences in characteristics of plants from inside the vegetation and plants from the marsh edge was tested by the non-parametric Wilcoxon rank-sum statistic because data was not normally distributed. The Wilcoxon rank-sum statistic tests for differrences between two groups on a single, ordinal variable without specific distribution (Wilcoxon, 1945). Functions describing the correlation of stem diameter and flow velocity or plant stability were fitted to the data via linear regression using ordinary least squares for parameter estimation. To deal with heterogeneity of variance in the pant stability data, variables were log-transformed before analysis. All data analysis was carried out within the free software environment R 3.0.2 (R Development Core Team, 2014).

Results

Effect of *Bolboschoenus maritimus* vegetation on current velocity

Measured absolute long-shore flow velocity at the current transect ranged from 0 to 0.18 $m\ s^{-1}$ with a mean of 0.03 $m\ s^{-1}$ and cross-shore velocity ranged from 0 to 0.12 $m\ s^{-1}$ with a mean of 0.01 $m\ s^{-1}$. During the growing season flow velocity data revealed differences in the development of long-shore and cross-shore flow. Already in April, i.e. without living aboveground biomass, normalised long-shore flow velocity ($\frac{\text{flow velocity in plot } [m\ s^{-1}]}{\text{flow velocity in the vegetation free first plot } [m\ s^{-1}]}$) decreased with distance from the marsh edge (d) (Figure 2.3 a). However, this decrease was much stronger in August at the peak of the growing season, when mean flow velocities decreased by more than half immediately after entering the vegetation belt and then continued to gradually decrease with distance from the marsh edge. Normalised cross-shore flow in April was very similar in all plots (Figure 2.3 b). In August, however, flow velocity decreased with distance from the mudflat into the vegetation. The net reduction of normalised flow velocity ($\frac{\text{normalised flow velocity in August}}{\text{normalised flow velocity in April}}$), which we interpret as the buffering effect of living vegetation, was higher for long-shore than for cross-shore velocity (Figure 2.3 c and d). Owing to patterns in the data points, we fitted an exponential function to the data of normalised long-shore velocity (Figure 2.3 c, normalised long-shore velocity $= 3.76 \times (d + 10)^{-0.8}$, $p < 0.001$, $R^2 = 0.63$) and a linear function for normalised cross-shore velocity (Figure 2.3 d, normalised cross-shore velocity $= -0.027 \times d + 0.89$, $p < 0.001$, $R^2 = 0.41$).

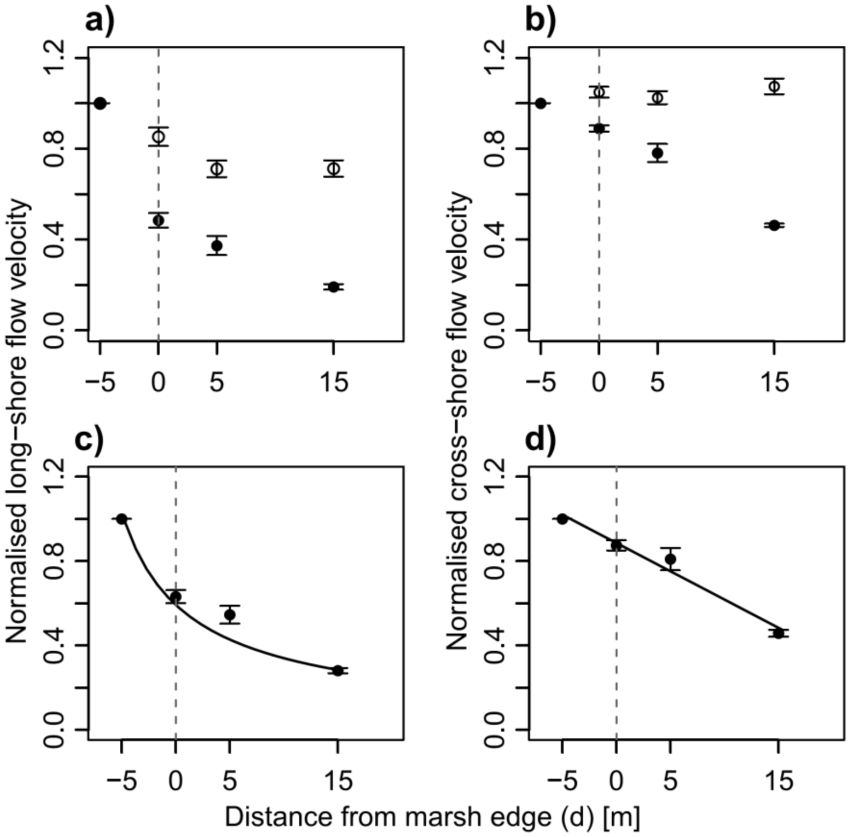

Figure 2.3 Normalised mean flow velocity at four distances from the marsh edge (*d*). The dashed line symbolises the marsh edge. a) and b) Mean of measurements in April (white) and August (black) at the respective location. c) and d) Quantification of the effect of the vegetation on flow velocity ($\frac{norm.flow\ velocity\ in\ August}{norm.flow\ velocity\ in\ April}$). Continuous lines are the functions fitted to the data.

Running means of velocities around high tide show that the long-shore velocity changed from upstream to downstream after high tide (Figure 2.4 a). The comparison of long-shore velocities in April and August (Figure 2.4 a and c) shows a reduced long-shore velocity at the plots inside the vegetation belt in August. Although not as pronounced, cross-shore velocity was as well damped by vegetation in August and showed lower amplitudes inside than in front of the vegetation belt, while no reduction could be observed in April (Figure 2.4 b and d).

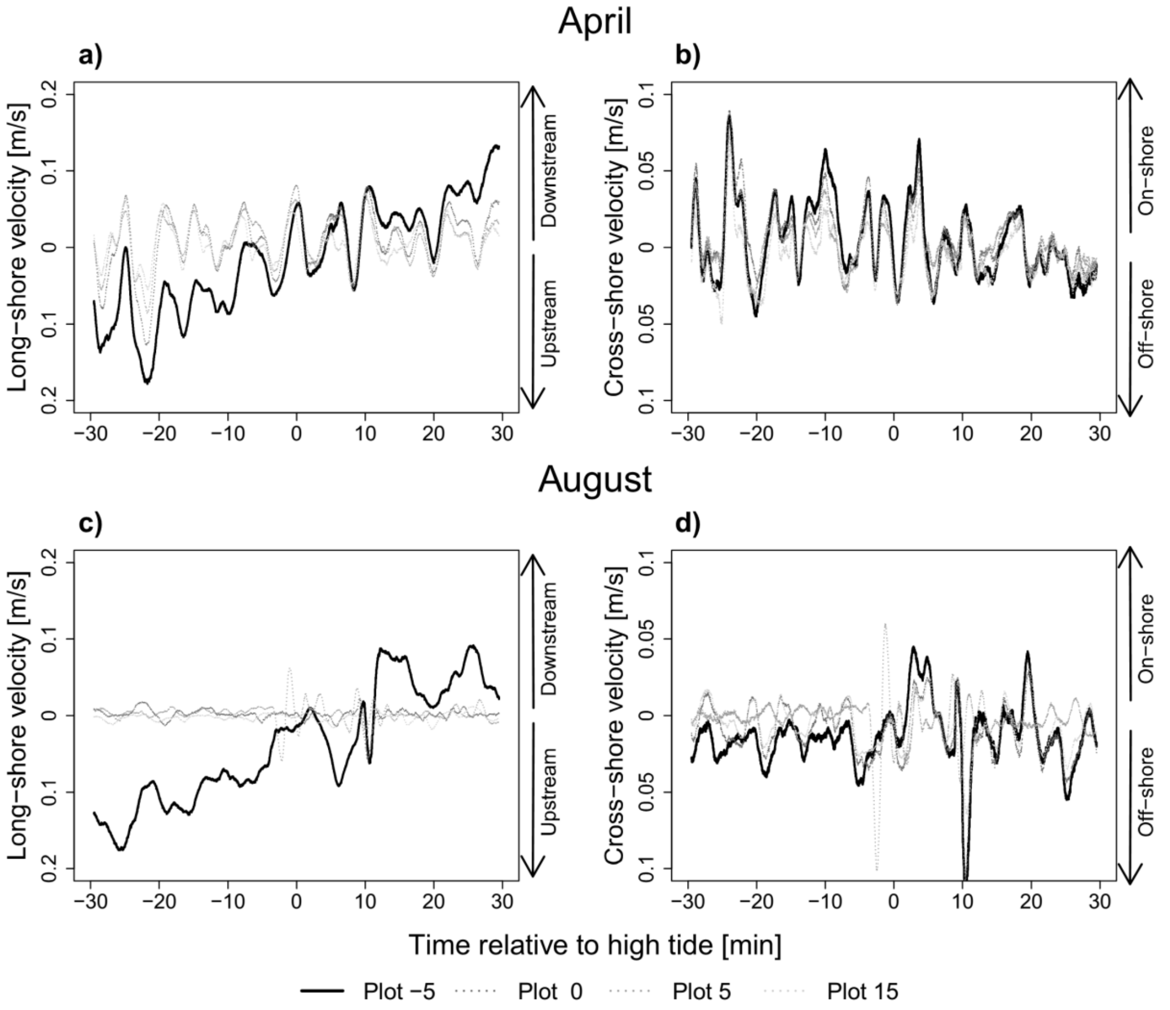

Figure 2.4 Running means of flow velocities during one flood (30 minutes before until 30 minutes after high tide) in April (a and b) and August (c and d). a) and c) Long-shore flow velocity. b) and d) Cross-shore flow velocity. Bin width for running mean: 1 min. Flow velocities above 0 represent downstream/ on-shore flow; velocities below 0 represent upstream/ off-shore flow, respectively. Flow velocity in front of the vegetation is illustrated with a continuous black line. Vegetated plots are displayed in different shades of grey.

Morphological response of *Bolboschoenus maritimus* ramets

From the results of the current velocity measurements, we learned that plants inside the vegetation belt are less affected by currents than plants at the front. In analogy, the ramets of *B. maritimus* showed different growth types at the marsh edge and within the vegetation belt along all transects. Plants from the two study sites did not show any differences and were therefore regarded jointly in all further analyses.

The comparison of plants from the marsh edge (Plot 0) with plants from inside the vegetation (Plot 15) revealed a distinct difference in stem diameter: plants from Plot 15 were significantly thinner than plants from Plot 0 (Wilcoxon rank-sum statistic: $p < 0.001$, $n = 96$) (Figure 2.5). Moreover, plants grew denser inside the vegetation belt (mean ramet density: 308

Stems per m^2) than at the marsh edge (mean ramet density: 142 Stems per m^2, Wilcoxon rank-sum statistic: $p < 0.001$, $n = 96$). However, considering plants from the marsh edge and from inside the vegetation belt separately, there was no effect of ramet density on stem diameter (Plot 0: $p = 0.98$, $n = 48$, Plot 15: $p = 0.34$, $n = 48$).

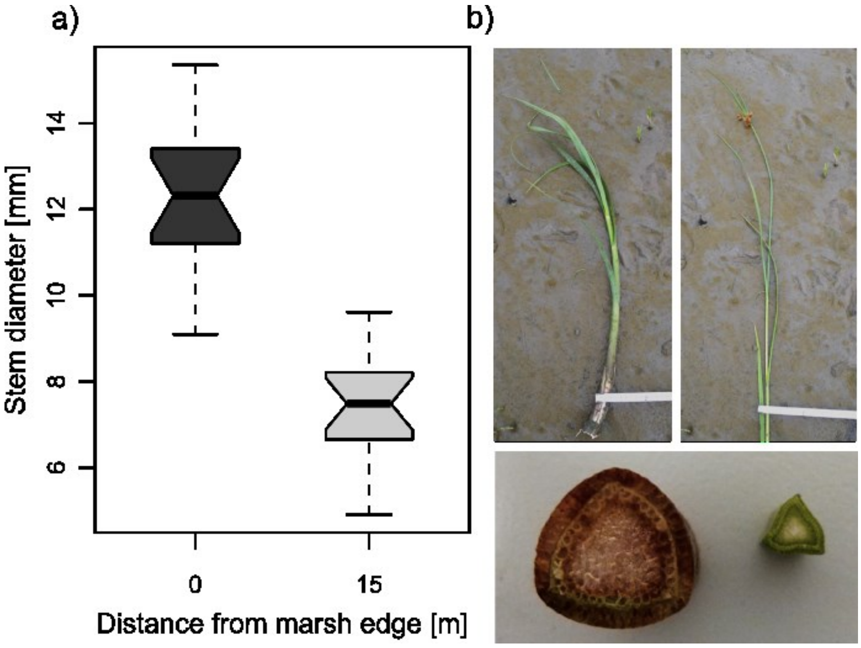

Figure 2.5 a) Comparison of ramet diameters at two different distances from the marsh edge b) prominent examples of ramets (above) and cross sections (below) from the marsh edge (left) and from inside the vegetation belt (right).

The current velocity measurements in front of all transects permitted the comparison of only plots from the marsh edge at the different sites. Mean long-shore flow velocity at the sites ranged from 0.026 to 0.087 $m\ s^{-1}$ with a mean of 0.054 $m\ s^{-1}$ and mean cross shore velocity from 0.01 to 0.041 $m\ s^{-1}$ with a mean of 0.028 $m\ s^{-1}$. Current data from the two study sites did not show significant differences. We found that stem diameter was positively correlated with mean cross-shore current velocity (stem diameter = $7.8 + 0.4 \times$ mean cross-shore current, $p = 0.001$, $R^2_{adj} = 0.52$, $n = 16$) (Figure 2.6) whereas stem diameter showed no correlation with mean long-shore velocity or elevation.

The biomechanical measurements - conducted to evaluate the adaptive value of higher stem diameter at locations with higher mechanical stress - showed a positive correlation of plant thickness and plant stability (bending stiffness $= 0.03 \times$ stem diameter $^{1.7}$, $p < 0.001$, $R^2_{adj} = 0.67$, $n = 32$, breaking force $= 0.07 \times$ stem diameter $^{1.7}$, $p < 0.001$, $R^2_{adj} = 0.7$, $n = 32$) (Figure 2.7).

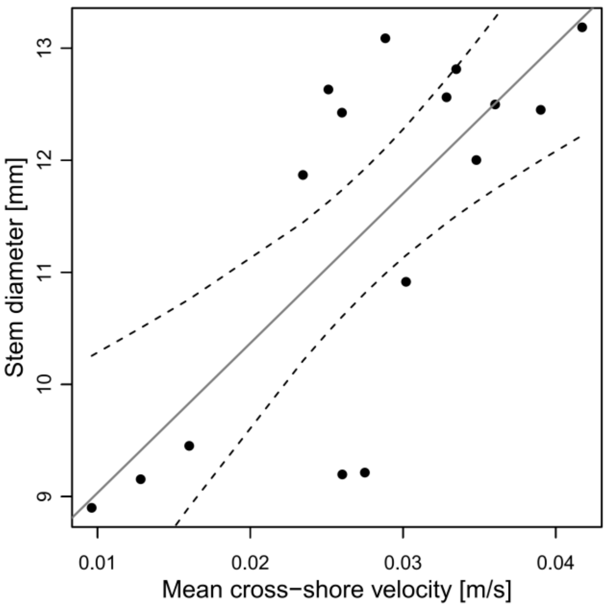

Figure 2.6 Correlation of mean cross-shore flow velocity and stem diameter. Black dots represent the mean of measured values of stem diameter and flow velocity time series at each transect and the continuous line is the result of a linear regression. Dashed lines define the 95% confidence interval.

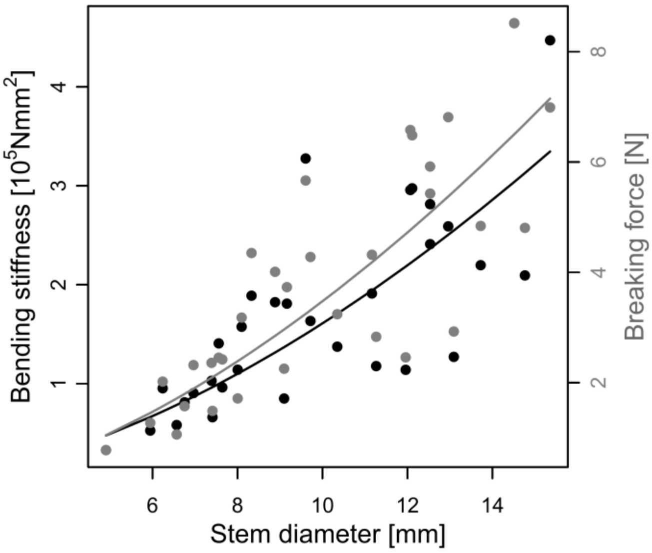

Figure 2.7 Correlation of stem diameter and breaking force and bending stiffness. Black and grey dots represent measured values and the respective lines are derived from linear regressions of the log-transformed data.

Consequently, plants from the front of the vegetation belt had a greater bending stiffness than plants from inside the vegetation (Wilcoxon rank-sum statistic: p = 0.0019, *n* = 16) and a significantly higher force had to be applied on them before breakage (Wilcoxon rank-sum statistic: p = 0.0002, *n* = 16) (Figure 2.8).

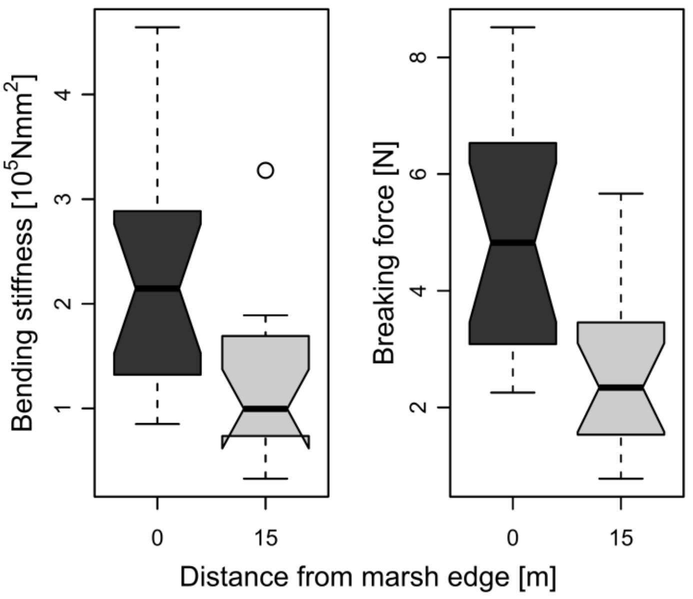

Figure 2.8 Bending stiffness and breaking force of ramets in relation to distance from marsh edge. Ramets from the marsh edge and from inside the vegetation differ significantly in bending stiffness and breaking force.

Discussion

Previous work documented that flood risk is a growing concern for most coastal societies in the coming centuries (Hirabayashi and Kanae, 2009). Temmerman *et al.* (2013) argued that the utilisation of coastal ecosystems in coastal protection could improve and support conventional coastal engineering solutions as it is more sustainable and cost effective with increasing flood risk. The ability of plants to adapt to environmental conditions, could further enhance the resistance of the whole vegetation belt against the mechanical stress of high current velocities.

In our study, we focused on the flow dampening potential of aboveground vegetation and its adaptation to the mechanic stress due to currents. On the one hand, we quantified the reduction of current velocity by *B. maritimus,* and on the other hand, we identified functional traits of *B. maritimus'* ramets which adapt to environmental differences and quantified their adaptive value.

Effect of *Bolboschoenus maritimus* vegetation on current velocity

Although the April measurements represent a situation without living above ground vegetation, they already identified a decrease in long-shore current with distance from the marsh edge which could be the effect of decreasing water depth originating in the different elevation of the plots (see Methods - Data collection and processing). Cross-shore velocity however, was stable along the entire transect (small variations lie within the range of natural variability).

Leonard and Luther (1995) discovered that mean flow velocity and flow energy inside vegetation are reduced by the plants' dampening of large scale eddies. Our study confirmed a distinct difference between velocities in front of and inside the vegetation belt and a decrease of cross-shore flow velocity with distance from the marsh edge into the marsh (Figure 2.3).

Considering only the measurements in August (Figure 2.3 b), our results for cross-shore currents are in accordance with Leonard and Croft (2006), who also found decreasing velocities with distance from the marsh edge, although with slightly higher dampening rates for *Spartina alterniflora*. In contrary to the study of Leonard and Croft (2006) and others (e.g. Christiansen et al., 2000; Leonard and Luther, 1995), our measurement design permitted the comparison of current velocity at the same site with and without living vegetation (Figure 2.3 a and b) and we considered cross-shore currents additionally to long-shore currents and were thus able to directly compare both (Figure 2.3 and 2.4). Christiansen et al. (2000) found that flow velocity in vegetation is inversely related to distance from open water. Our results show that cross-shore velocity decreases with distance from the marsh edge and that a 15 m wide belt of living *B. maritimus* vegetation is able to reduce an average cross-shore current by more than 50% (Figure 2.3 d). As long-shore flow runs parallel to the shore, it is not influenced by the vegetation growing normal to the marsh edge but by the vegetation stretch left and right along the shore (Bruno and Kennedy, 2000). Thus the buffering vegetation stretch can be much larger than the distance to marsh edge, explaining the higher difference of long-shore current between measurements in April and August (Figure 2.3 a and c). The reason for the lower vegetation effect on cross-shore current (Figure 2.3 d), especially just behind the marsh edge, could consequently be that cross shore current is only buffered by the vegetation growing in direction of the tidal flat.

The results of this study confirm our hypothesis that for currents under normal, i.e. non-stormy, conditions, the vegetation is able to buffer a large part of the current velocity. We quantified the reduction of long- and cross-shore current velocity by *B. maritimus*. Under moderate conditions, this reduction can lead to higher sedimentation and lower erosion rates inside the vegetated marsh (Neumeier and Ciavola, 2004) and thus promote natural surface accretion (Kirwan et al., 2010). However, we cannot extrapolate our results to storm surge conditions with much higher current velocities and water levels.

Morphological response of *Bolboschoenus maritimus* ramets

The differences in ramet density at different locations within the vegetation belt could, as Charpentier and Stuefer (1999) already suggested, partly be an effect of the positioning of the ramets in the rhizome system: Ramets seem to grow less dense at the front of the belt, because here the belowground biomass is not as developed as in the older parts of the rhizome system lying further inside the vegetation belt.

Although different growth types of *B. maritimus* have been found in other studies (Lieffers and Shay, 1981; Zákravský and Hroudová, 1994) no study reported differences in stem diameter or attributed different growth forms to current velocity. With our results, we revealed that *B. maritimus* ramets exhibit different stem morphologies not only at different positions in the vegetation belt, but as well in the same position at sites with different current velocity (Figure 2.6). In other studies, nutrient supply (Valiela et al., 1978) and elevation (Seliskar, 1985) were found to effect stem diameter of marsh plants. We were able to exclude an effect of elevation, but have no information on nutrient supply, which could hence possibly contribute to the differences in plant morphology. The simultaneous occurrence of thicker stems and lower ramet density at the marsh edge could give the impression that higher plant thickness was due to lower ramet density. By comparing *B. maritimus* diameters at different plots along the marsh edge, however, we found no correlation between ramet density and diameter, which could have been another plausible explanation for the two growth types.

For plants growing under such stressful conditions, maximum stability is an important functional trait to avoid breaking. In an experimental study on wave effects on *P. australis*, Coops and Van der Velde (1996) did not find an effect on the morphology of this species. Other studies however, showed that plants can adapt to flow stress by morphological adjustments which either minimize mechanical forces or increase resistance to mechanical failure (Puijalon et al., 2008, 2005). Our measurements revealed that plants growing at the front of the vegetation belt have significantly higher bending stiffness and a higher force has to be applied for breaking the ramets than inside the vegetation belt. The different growth forms could therewith provide an adaptive value in habitats with high mechanical stress (Figure 2.7 and 2.8). With our study, we were able to show a positive correlation between plant thickness and cross-shore current (Figure 2.6) and we propose that the higher diameter of plants growing in the exposed front position could be a morphological adaptation to enhanced stress due to higher current velocity.

With the adjusted morphology of plants growing at the highly exposed marsh edge, the whole vegetation belt could be able to better resist the mechanical stress of high current velocities. As thicker plants are more stable and do not break as easily, this self-adaptive effect thus increases the ability of *B. maritimus* to grow and persist in the pioneer zone and may hence contribute to ecosystem-based coastal protection by reducing current velocity.

Acknowledgements

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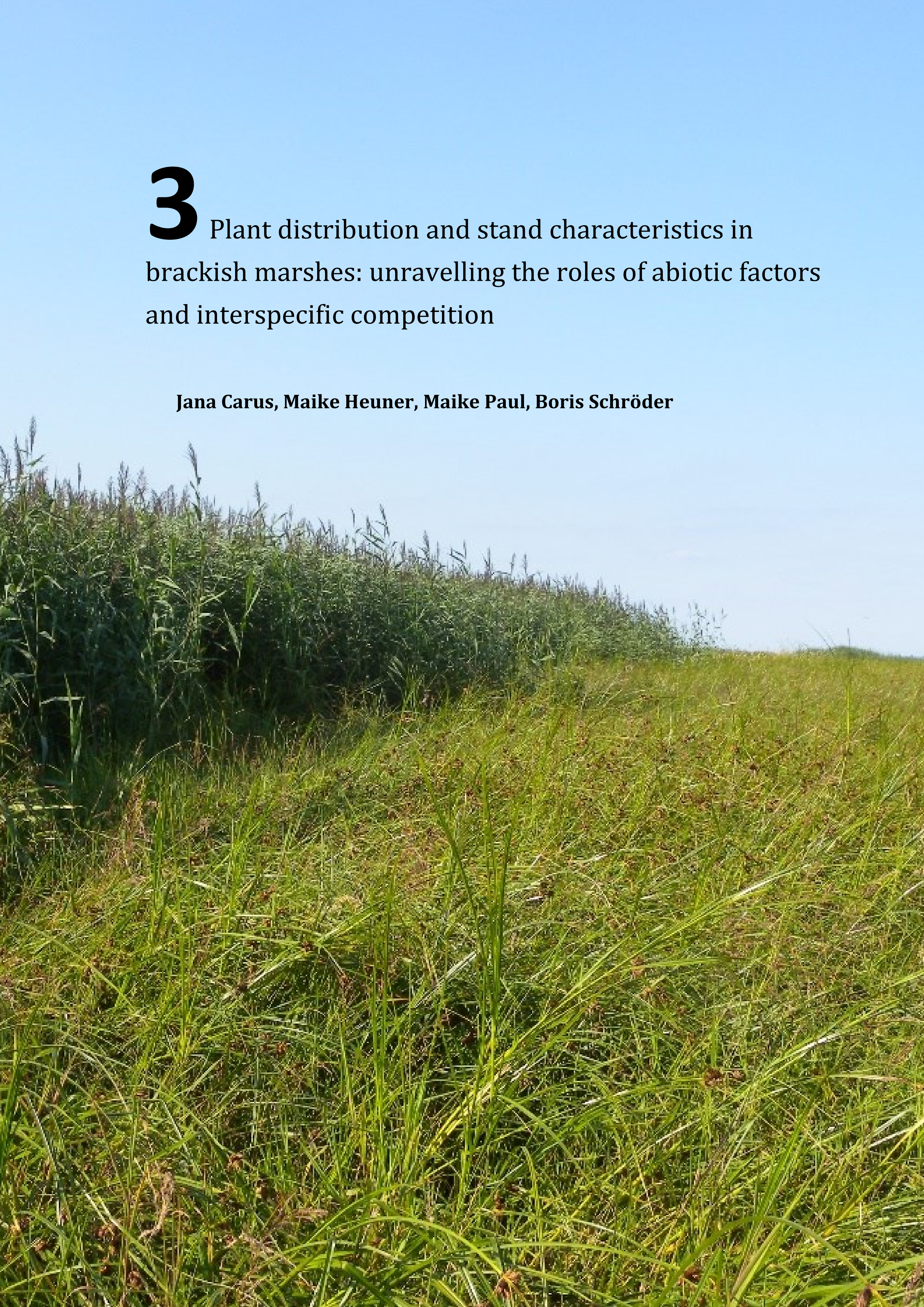

3 Plant distribution and stand characteristics in brackish marshes: unravelling the roles of abiotic factors and interspecific competition

Jana Carus, Maike Heuner, Maike Paul, Boris Schröder

Abstract

Due to increasing pressure on estuarine marshes from sea level rise and river training, there is a growing need to understand how species-environment relationships influence the zonation and growth of tidal marsh vegetation. In the present study, we investigated the distribution and stand characteristics of the two key brackish marsh species *Bolboschoenus maritimus* and *Phragmites australis* in the Elbe estuary together with several abiotic habitat factors. We then tested the effect of these habitat factors on plant growth and zonation with generalised linear models (GLMs). Our study provides detailed information on the importance of single habitat factors and their interactions for controlling the distribution patterns and stand characteristics of two key marsh species. Our results suggest that flow velocity is the main factor influencing species distribution and stand characteristics and together with soil-water salinity even affects the inundation tolerance of the two specie investigated here. Additionally, inundation height and duration as well as interspecific competition helped explain the distribution patterns and stand characteristics. By identifying the drivers of marsh zonation and stand characteristics and quantifying their effects, evidence from this study provides useful information for evaluating a future contribution of tidal marsh vegetation to ecosystem-based shore protection.[2]

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[2] Data can be found in Appendix A and B on the attached CD.

Introduction

Understanding the patterns of plant species distribution and stand characteristics along environmental gradients is a key goal in community ecology (Crain, 2007; Engels et al., 2011) providing substantial information for conservation and management (Bullock et al., 2011; Guisan and Thuiller, 2005) in the face of climate change and other increasing anthropogenic stressors. In tidal estuaries, two abiotic gradients prevail (Engels et al., 2011): (i) Water salinity decreases from coast to inland (Odum, 1988) and thus defines a horizontal gradient (Jensen et al., 2007; Wolf, 1988), whereas (ii) inundation duration, height and frequency as well as hydrodynamic forces form a vertical gradient at each shore location decreasing with distance from the shore (Jensen et al., 2007). Because plant species differ in terms of stress tolerance and competitive ability, local habitat conditions and biotic interactions control distribution patterns in tidal marshes so that the environmental gradients produce a pronounced vegetation zonation. Along the brackish part of many European estuaries occurs a typical zonation of *Bolboschoenus maritimus* in the low marshes and *Phragmites australis* in the high marshes. This zonation is often associated with inundation frequencies: according to this, the low marsh is flooded twice a day, the mid marsh at spring tides and the high marsh only at storm tides (Bockelmann and Neuhaus, 1999). Elevation relative to mean high water is often used as an indicator in studies on marsh zonation (e.g. Bertness and Ellison, 1987; Coops et al., 1999), although this variable merges the effect of more directly acting factors such as inundation height and duration as well as hydrodynamic forces from currents and waves (Silinski et al., 2015).

High inundation heights can inhibit plant growth by reducing photosynthetic performance. Hellings and Gallagher (1992), for instance, found that height and biomass of *P. australis* decreased with increased flooding level, whereas Clevering and Hundscheid (1998) discovered no difference in ramet dry weight of *B. maritimus* with varying water depth, but found higher ramets in deeper water. Long inundation durations limit the available oxygen in the soil (Silvestri et al., 2005). Kirwan and Guntenspergen (2015) describe a unimodal effect of inundation duration on the biomass of the marsh species *Schoenoplectus americanus*, as well as a negative effect on *Spartina patens*. High inundation heights and long inundation durations can thus indeed inhibit growth of flood-sensitive species (Yamasaki, 1984) and the plant distribution patterns in wetlands substatially depend on differences in tolerance to flooding stress among different species (Engels et al., 2011).

In most areas, however, the ranges of tolerated inundation height and duration of marsh species overlap (Pielou and Routledge, 1976), which might due to the existence of other important abiotic factors (Coops and van der Velde, 1996): hydrodynamic forces, for instance, also strongly affect marsh vegetation by causing mechanical stress on the plant (Heuner et al., 2015). By breaking and uprooting ramets, hydrodynamics influence the establishment, survival, and expansion of vegetation (Houwing, 2000; van Katwijk and Hermus, 2000) and can therewith affect species distribution (Hrivnák et al., 2012; Silinski et al., 2016). Furthermore, waves and current velocity have a significant impact on plant growth and morphology (Carus et al., 2016; Silinski et al., 2015).

Water salinity in the brackish part of an estuary spans from the oligohaline to the mesohaline zone and thus comprises salinities from 0.5 to 18. Although this range lies below the critical value for the occurrence of *B. maritimus* and *P. australis* (Hellings and Gallagher, 1992; Lillebø et al., 2003), higher soil-water salinities are stressful to the species (Burdick et al., 2001; Lillebø et al., 2003) and exhibit the potential to alter the effect of other habitat factors on competitive interactions or affect plant morphology. For *B. maritimus*, Lillebø et al. (2003) found that in brackish water, biomass increases with decreasing salinity. Lissner and Schierup (1997), however, detected no direct effect on *P. australis* productivity, and Hellings and Gallagher (1992) found no significant interaction of salinity and inundation height for *P. australis* density, height and biomass.

In addition to these abiotic factors, biotic factors - mainly interspecific competition and facilitation - play an important role in tidal marsh zonation (Bertness, 1991; Pennings et al., 2005; Pennings and Callaway, 1992). Species occurrence at the physically harsh end of a gradient is controlled by abiotic factors, whereas the occurrence towards the benign end is limited by competition (Pielou and Routledge, 1976; Scholten et al., 1987; Snow and Vince, 1984). In brackish mid and high marshes, *P. australis* can out-compete *B. maritimus* (Esselink et al., 2000), probably due to its high growth and a consequent advantage in competition for light (Bakker et al., 1985).

By buffering a large part of the arriving flow velocity (Carus et al., 2016) and attenuating wave energy (Coops et al., 1996), *B. maritimus* and *P. australis* contribute to ecosystem-based shore protection. However, global warming as well as further river training will entail changes in water levels, a further increase in tidal amplitude and a resulting shift of the salinity zones (Chua and Xu, 2014; Seiffert and Hesser, 2014) thus altering environmental conditions. At the same time, marshes can rise vertically by building up organic and inorganic matter on the marsh surface (French, 2006; Kirwan and Megonigal, 2013) and can thus potentially keep up with the sea level rise (Butzeck et al., 2015; Kirwan et al., 2016a). A better understanding of how species-environment relationships generate patterns in tidal marsh vegetation is vital to maintain ecosystem functions and assess the response of marshes to environmental change as well as the success of engineering and restoration projects (Elliott et al., 2016; Heuner et al., 2016).

Many laboratory experiments have been conducted to evaluate the effect of abiotic factors on the growth of marsh plant species. However, as it is difficult to mimic the complex composition of natural habitat factors in the laboratory, the relevance of laboratory studies for explaining field patterns is limited (Davy and Costa 1992). With their conspicuous vegetation zonation, wetlands can serve as a ‘natural experiment’ (Diamond, 1983) with a set of environmental gradients to investigate. Especially salt marshes have for a long time been used as such a model system (e.g. Snow and Vince 1984; Pennings, Grant and Bertness 2005) whereas tidal freshwater and brackish marshes have received much less attention (Meire et al., 2005).

A valuable tool for analysing species-habitat relationships is provided by statistical modelling (Schröder, 2008). However, many modelling studies focus on the prediction of species distribution (Austin, 2002), and not on the understanding of species-environment relationships (Guisan and Zimmermann, 2000). Moreover, modelling still focuses very often only on abiotic the factors of species distributions (Anderson, 2016). As it is known that biotic interactions play an important role for species distribution patterns (Lortie et al., 2004; Pulliam, 2000), it is, however, essential to incorporate them into the modelling process (Guisan and Thuiller, 2005; Pellissier et al., 2010). Despite the benefits of species distribution modelling, the occurance of a plant species cannot provide full insight into habitat quality, since it does not inform about that species' performance. The ability of plants to tolerate stress is often related to adaptation of plant morphology (Shi et al., 2015), such as biomass allocation (Fraser and Karnezis, 2005) and root traits (Xie et al., 2008). A set of stand charateristics can thus serve as indicator for plant adaptation. By providing detailed information on the importance of single habitat factors for the growth of the two plant species, the investigation of stand characteristics can help to better understand and predict the vegetation zonation patterns in marshes (Shi et al., 2015).

In the present study we address the following questions:

1) How is the distribution of the two brackish marsh species *B. maritimus* and *P. australis* affected by abiotic habitat conditions and competition?

We hypothesise that the occurrence of the two marsh species and thus the zonation of the two vegetation belts is influenced by inundation and current velocity. The range of soil-water salinity might not directly affect the distribution of the two species in the brackish part of an estuary. However, soil-water salinity and other habitat factors could indirectly affect species distributions by influencing the position of the waterward fringe of the *B. maritimus* and *P. australis* vegetation belts relative to inundation height and duration.

2) How do habitat conditions influence stand characteristics of these two species?

We hypothesise that the aboveground biomass of both species is negatively affected by inundation and that plant height increases with increasing inundation height to improve photosynthesis opportunity. Current velocity is a high stressor and probably negatively influences plant growth. We also expect lower productivity of especially *B. maritimus* with higher soil-water salinity. Due to the species' strong competitive effect, we furthermore expect a negative effect of *P. australis* biomass on the occurrence and stand characteristics of *B. maritimus*.

To test these hypotheses we assessed the distribution of the two marsh species and measured stand characteristics, i.e. the aboveground and belowground biomass, ramet density, ramet height and the percentage of flowering ramets. Furthermore, we collected information on several abiotic habitat factors to test their effect on plant growth and zonation with generalised linear models (GLMs).

Methods

The study was conducted in the tidally influenced, brackish part of the Elbe estuary, the largest estuary in Germany. Here, we selected two sites, one in the nature reserve Nordkehdingen (A) (53°51'46.419"N, 9°5'50.027"E) and one about 30 km upstream on the peninsula of Krautsand (B) (53°45'50.626"N, 9°22'46.052"E). The sites were selected because they contain the two target species *B. maritimus* and *P. australis*, as well as gradients in relevant habitat parameters and non-dampened hydrodynamic influence (e.g. from embankments or wave breakers). The two species grow in vegetation belts from 5 to 160 m in width, *B. maritimus* as pioneer on the marsh edge and *P. australis* further landwards. Parts of the vegetation are flooded by brackish water up to twice a day as high as 2 m and for a total time of up to 9 h a day.

Data collection

To evaluate the effect of potentially important habitat factors on the occurrence and morphology of *B. maritimus* and *P. australis*, we measured several parameters on eight transects in each study site perpendicular to the river line in 2012 and 2013 (Table A.1 and B.1). Each transect consisted of several measuring plots positioned relative to vegetation zonation (Figure 3.1). The first plot in each species belt was positioned along last year's waterward vegetation fringe of the respective species. All other plots were located further landwards at certain distances (5 m, 15 m, 35 m) from the first plot and waterwards into the tidal flat (5 m, 15 m, 35 m, 75 m, 135 m).

With the purpose of defining stand characteristics, a range of aboveground plant parameters was measured at the peak of the growing season in 2012 and 2013. We assessed the number of ramets, ramet height and the percentage of flowering ramets on three plots of 0.25 m^2 at each location, placed 5 m apart, parallel to the river line. To calculate the above-ground biomass per m^2, we applied allometric biomass estimates. For this purpose, we measured, harvested, dried and weighed more than 200 plants of different height in close vicinity to all plots to relate dry biomass to shoot height (Morris and Haskin, 1990; Thursby et al., 2002) each month (between 14 April and 02 August 2012). We analysed the difference between the ramets among the study sites and the position in the vegetation belt and fitted functions to the data via polynomial and power regression. The biomass of each shoot in the plots was thus calculated on based on its height. The mean of three replicate plots was used to extrapolate onto one square metre. Belowground biomass was measured once in April 2013 (before the start of aboveground growth) on all plots of two transects at each study site. For this purpose, an Eijkelkamp root corer (diameter: 80 mm) was applied in the *P. australis* zone. As it was not possible to keep water-saturated material in the root corer, we used PVC tubes (diameter: 68 mm) with rubber plugs in the *B. maritimus* zone. Test cores had confirmed that rhizomes did not penetrate deeper than 0.6 m and that the spatial variability of the belowground biomass was very high. To obtain a representative square meter estimate, we took four samples per 0.25 m^2 with the root corer and six samples with the PVC tubes (to obtain a similar volume despite the smaller diameter of this device) up to 0.6 m depth in a predefined grid. Before coring, all aboveground biomass was removed from the plots. By washing and sieving the samples (mesh size: 1 mm), we removed all sediment. Afterwards, samples were sorted into roots and rhizomes of the respective species and dried in an oven at 105 °C for 48 hours. All samples were then weighed; finally, we extrapolated the dry biomass onto 1 m^2.

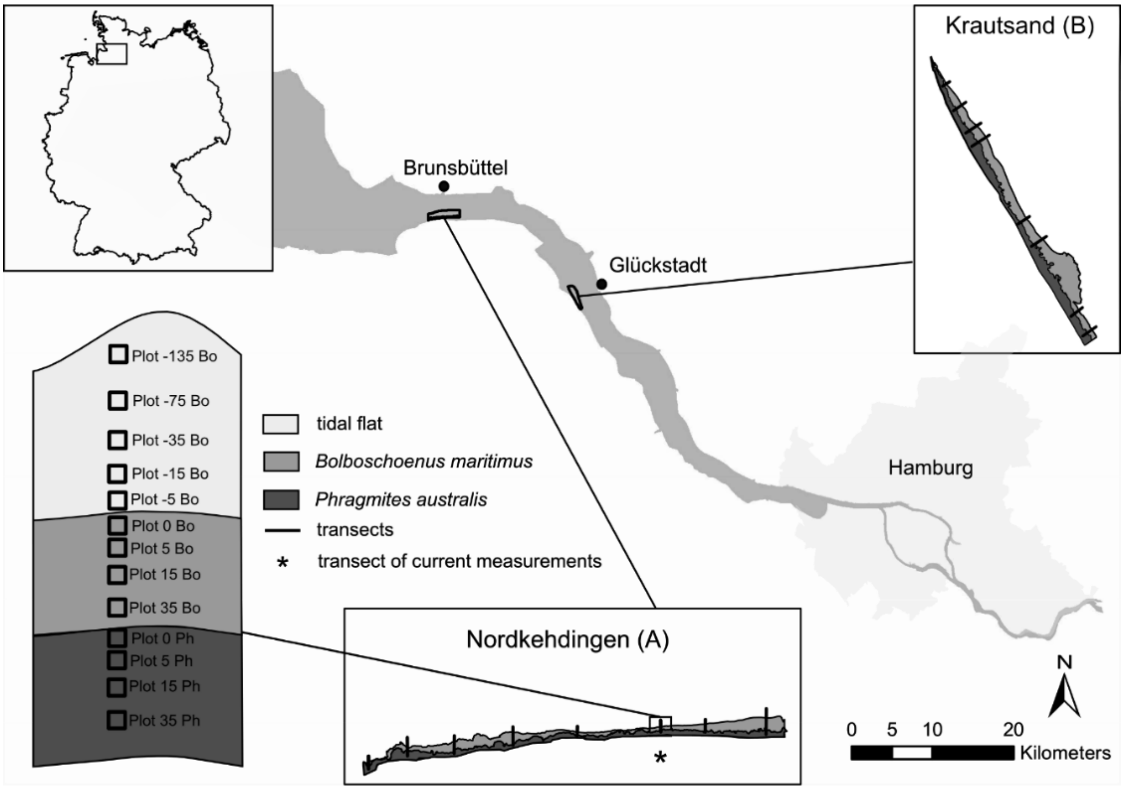

Figure 3.1 Location of the two study sites and scheme of the measuring plots along an exemplary transect. The 16 measuring transects are marked with black lines. The plots 0 Bo and 0 Ph were located at the waterward fringes of the *B. maritimus* and *P. australis* vegetation belts.

Inundation heights and durations were calculated for both study sites with the integrated floodplain model INFORM 3 (Fuchs et al., 2012; Giebel et al., 2011). Inundation height is expressed in terms of water height, in meters, above the sediment, whereas inundation duration denotes the time during which the inundation height is above zero. Water level data from five gauges (Waterways and Shipping Office Hamburg (WSA), http://www.portal-tideelbe.de) and a digital elevation model with a resolution of 1×1 m^2 from 2010 were used to determine maximal inundation height in the growing seasons 2012 and 2013 for all plots in the two study sites. Water level time-series from the day with the highest inundation were used to calculate the maximal inundation duration for this day.

Flow velocity was measured in April and August 2012 with four acoustic doppler velocity meters (ADV, Nortek Vector) at four plots (-5 Bo, 0 Bo, 5 Bo, 15 Bo) from one transect in study site A (Figure 3.1) and once in front of all transects in August 2013 (for details on measurement and data processing, see Carus et al., 2016). The first velocity measurements were conducted to quantify the effect of vegetation on flow velocity. For this purpose, we compared measurements without living vegetation (April) with measurements with maximal *B. maritimus* cover (August) and estimated effect functions from the data. The second measurement served to compare the flow velocities approaching the vegetation at the different transects. The functions parameterised with the first measurements (see Carus et al., 2016 for details) were then applied to the data from the second measurements to calculate an estimate of the flow velocity inside the vegetation. Flow velocity measurements were split into a shore-parallel long-shore component and a cross-shore component, which runs perpendicular to the shore (Le Hir et al. 2000).

Soil-water salinity was measured at 5-25 cm depth at each plot in August 2012 and 2013 with a handheld conductivity-meter (Cond 340i) inside perforated HTEM tubes using the Practical Salinity Scale. As the plot values the of salinity measurements showed no gradient along the transects, the mean of all soil-water salinity measurements per study site was used (study site A: mean = 4.5, sd = 1.7, study site B: mean = 1.47, sd = 0.4). Soil samples were taken with a soil auger in August 2012 at 5-25 cm depth to analyse organic carbon content, grain size distribution and pH-value. The exact elevation and positioning of the plots was determined with a differential global positioning system (DGPS).

Data analysis

A visual pre-analysis of data from 2012 showed no effect of the soil parameters of organic content, grain size distribution or pH on species distribution and stand characteristics. Only soil-water salinity had an effect and was therefore measured in further field campaigns and considered in the analyses. We thus used inundation height, inundation duration, flow velocity and soil-water salinity as predictor variables for both species. Through visual data inspection, we found a unimodal effect of inundation on *B. maritimus:* both high and long inundation as well as very low and short inundation had a negative effect on this species. We accounted for this by including the quadratic term of this predictor. In order to incorporate the strong competitive effect of *P. australis* (Dijkema, 1990; Raabe, 1981), we used the present aboveground biomass of *P. australis* as a predictor for *B. maritimus*.

The combined effect of abiotic and biotic site conditions on the distribution and morphology of the two marsh plant species was tested using a set of generalised linear models (GLM, McCullough and Nelder 1989) and generalised linear mixed models (GLMM, Wolfinger and O'connell 1993; Bates et al. 2014). GLM(M)s offer the possibility to include a wide range of environmental data using link functions between response and predictor variables (Bio et al., 2002) and can help improve the understanding of species' responses to environmental variables due to the good interpretability of the relationships between responses and predictors. We used GLMMs to consider the two years of the study as a random effect and tested the influence of this with a likelihood ratio (LR) test (Bolker et al., 2009). Since the random effect of the year of the measurement was not significant, we continued the analysis with GLMs.

The study design was set up to allow us to incorporate the gradients of possibly important habitat factors, hence we considered the different nesting levels of the data set by including the respective factors, i.e. the plot within the transects (maximum inundation height), transects within the study site (flow velocity in front of the transects), and study sites (soil-water salinity). Some of the measured predictor variables proved to be correlated (Spearman's rank correlation coefficient rho >0.7, cf. Dormann *et al.* 2013). Due to the high correlation between inundation height and duration (rho = 0.96), as well as cross-shore and long-shore flow velocity (rho = 0.81), these factors could not be used jointly in the models. To analyse the effect of flow velocity on the two marsh species, we calculated the resultant velocity of cross- and long-shore velocities as the vector sum of the two individual velocities. Since the two vectors to be added are at right angles to each other, the Pythagorean theorem was used to determine the resultant velocity ($total\ velocity = \sqrt{cross\text{-}shore\ velocity^2 + long\text{-}shore\ velocity^2}$) (McKnight and Zahopoulos, 2015). We applied the same approach for inundation to describe the intertwined effect of normalised inundation height and duration ($normalised\ inundation = \sqrt{(\frac{inundation\ height}{max.\ inundation\ height})^2 + (\frac{inundation\ duration}{max.\ inundation\ duration})^2}$). These two factors were included in the models. To test whether collinearity still influenced the models, we calculated the variance inflation factor for each model ($VIF_i = \frac{1}{1-r_i^2}$, where r_i^2 is the coefficient of determination obtained from the regression of each explanatory variable against all other explanatory variables, R Package car, Fox and Weisberg 2010). We used a value of three, which is defined as a negligible influence (Zuur et al., 2010), as the threshold. To detect possible spatial autocorrelation in model residuals, we plotted Moran's I correlograms (Legendre and Legendre 1998; Dormann *et al.* 2007). We assessed the models' goodness-of-fit by calculating the proportion of deviance explained (%dev$_{expl}$) by the models (Menard 2000).

In order to analyse the factors controlling the zonation and stand characteristics of *B. maritimus* and *P. australis,* we examined the relative importance and response curves of the predictor variables. The relative variable importance is quantified by calculating the reduction in model performance when this variable is removed. It was assessed by applying an F-Test for comparing the full model with the model without the respective predictor variable (Crawley, 2007). To get comparable values the obtained F-values were scaled to percentages.

Response curves show how model predictions respond to a specific predictor by keeping all other predictors at their mean value. Analysing their shape not only gives information on the relationship between predictor and response variable, but can furthermore serve as a plausibility test by displaying whether the species' ecological demands are correctly modelled (Schibalski et al., 2014).

Species distribution

We used binomial distribution and the logit-link function (i.e. logistic regression) for analysing the effect of the habitat factors on the occurrence probability of the two marsh species. To assess goodness-of-fit of the occurrence models, we calculated the area-under-the-curve AUC statistic in addition to the deviance explained. The AUC ranges between 0.5 for the null model and 1.0 for a perfect model (Swets, 1988). We applied wireframe (R Package lattice, Sarkar 2008) for visualising the three-dimensional response surfaces of the occurrence probability of the two species.

We took a more precise look at the waterward fringe of the vegetation belts of the two species to determine the factors possibly responsible for the variance in inundation tolerance. To quantify the effect of soil-water salinity and flow velocity on the positioning in the species' zones relative to inundation height and duration, we estimated linear regressions considering only the plots at the waterward vegetation fringe of each species (0 Bo and 0 Ph). We used inundation in these first plots as the response variable and soil-water salinity and flow velocity at the vegetation fringe as predictor variables.

Stand characteristics

For the examination of the stand characteristics, we only incorporated the plots in which the respective species occurred. As all stand characteristics are continuous and positive, we used a tweedie distribution with a power between 1 and 2 (R Package statmod, Dunn 2014; tweedie, Giner and Smyth 2016) for biomasses, ramet density, ramet height and the percentage of flowering ramets (Arcuti et al., 2013; Foster and Bravington, 2012).

Results

Inundation and flow velocity at the waterward vegetation fringes differed between the two species as well as between study sites. (Table 3.1). Mean inundation height was 0.83 m higher at the fringe of *B. maritimus* than that of *P. australis*, and inundation duration was 3.19 h longer. Mean long-shore flow velocity was 0.027 m s^{-1} and mean cross-shore velocity 0.023 m s^{-1} higher at the *B. maritimus* fringe. Comparing the sites, inundation height and duration as well as flow velocity during the considered flood were higher at study site A than at site B. Mean soil-water salinity was higher in study site A (mean = 4.5, sd = 1.7) than at site B (mean = 1.47, sd = 0.4).

Species distribution

After variable selection, the strongest models explaining the occurrence of the two species contained the predictor variables of total flow velocity inside the vegetation belt, normalised inundation and for *B. maritimus* additionally the biomass of *P. australis* (relative variable importance for *B. maritimus*: total flow velocity = 61%, *P. australis* biomass = 28%, normalised inundation = 11%; relative variable importance for *P. australis*: total flow velocity = 93%, normalised inundation = 7%,). We did not detect any residual spatial autocorrelation for any model. Soil-water salinity had no significant effect on the occurrence of the two marsh species. For both species, the GLMs achieved excellent performance (*B. maritimus*: AUC = 0.89, $\%dev_{expl} = 38$, *P. australis*: AUC = 0.98, $\%dev_{expl} = 76$). The two species differ especially with respect to their response to total flow velocity (Figure 3.2): The drop in *B. maritimus'* occurrence probability with increasing total flow velocity was much slower than that of *P. australis*. Furthermore, *B. maritimus* had its maximal occurrence probability at moderate, whereas *P. australis* had its optimum at plots with the lowest normalised inundation. For both species, occurrence probabilities above 0 start at lower normalised inundation with higher total flow velocity.

Table 3.1 Inundation and flow velocity at the water front fringes of the vegetation belts of *B. maritimus* and *P. australis in study site A and B*. The flow velocity values are based on one flood in August 2013. * indicates values that were calculated and not measured directly.

		B. maritimus		*P. australis*	
		Site A	Site B	Site A	Site B
Maximum inundation height (m)	mean	1.15	1.60	0.43	0.67
	min	0.85	1.23	0.13	0.33
	max	1.40	2.19	0.83	1.53
	sd	0.22	0.37	0.25	0.40
Inundation duration (h day^{-1})	mean	4.57	7.54	1.66	4.07
	min	3.48	6.32	0.50	2.60
	max	5.45	9.29	3.30	7.28
	sd	0.77	1.14	0.98	1.56
Long-shore flow velocity (m s^{-1})	mean	0.028	0.040	0.007*	0.007*
	min	0.016	0.024	0.003*	0.005*
	max	0.050	0.052	0.012*	0.010*
	sd	0.010	0.011	0.003*	0.002*
Cross-shore flow velocity (m s^{-1})	mean	0.027	0.020	0.002*	0.000*
	min	0.020	0.009	0.000*	0.000*
	max	0.037	0.035	0.005*	0.000*
	sd	0.006	0.010	0.003*	0.000*

The strongest model results for explaining the positioning of the waterward vegetation fringes were obtained with inundation duration as response and cross-shore flow velocity and soil-water salinity as predictors (*B. maritimus*: $R^2 = 0.86$, $p < 0.001$, *P. australis*: $R^2 = 0.74$, $p < 0.001$) (Figure 3.3 A and B). The models show that cross-shore velocity and soil-water salinity negatively influence the position of the waterward vegetation fringes of both species relative to maximum inundation duration. The position of the fringes of the vegetation belts relative to inundation height was only affected by cross-shore velocity (*B. maritimus*: $R^2 = 0.6$, $p < 0.001$, *P. australis*: $R^2 = 0.54$, $p < 0.001$) (Figure 3.3 C).

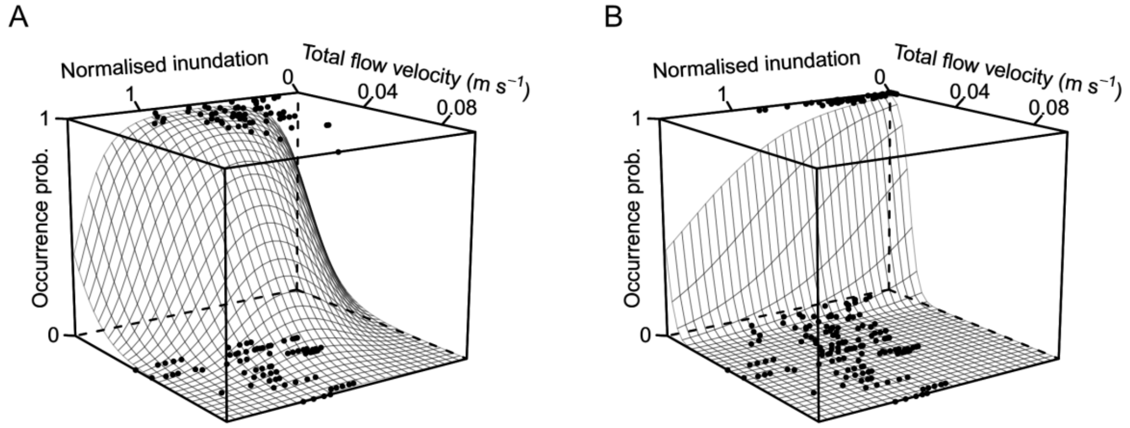

Figure 3.2 Occurrence probability (prob.) of *B. maritimus* (A) and *P. australis* (B) in dependence of normalised inundation (vector of normalised inundation height and time) and total flow velocity (vector of long- and cross-shore flow velocity). Black dots show the measured presences and absences and surfaces represent the model response. The plot for *B. maritimus* was produced under the assumption that *P. australis* is absent by setting the value of *P. australis* biomass to 0.

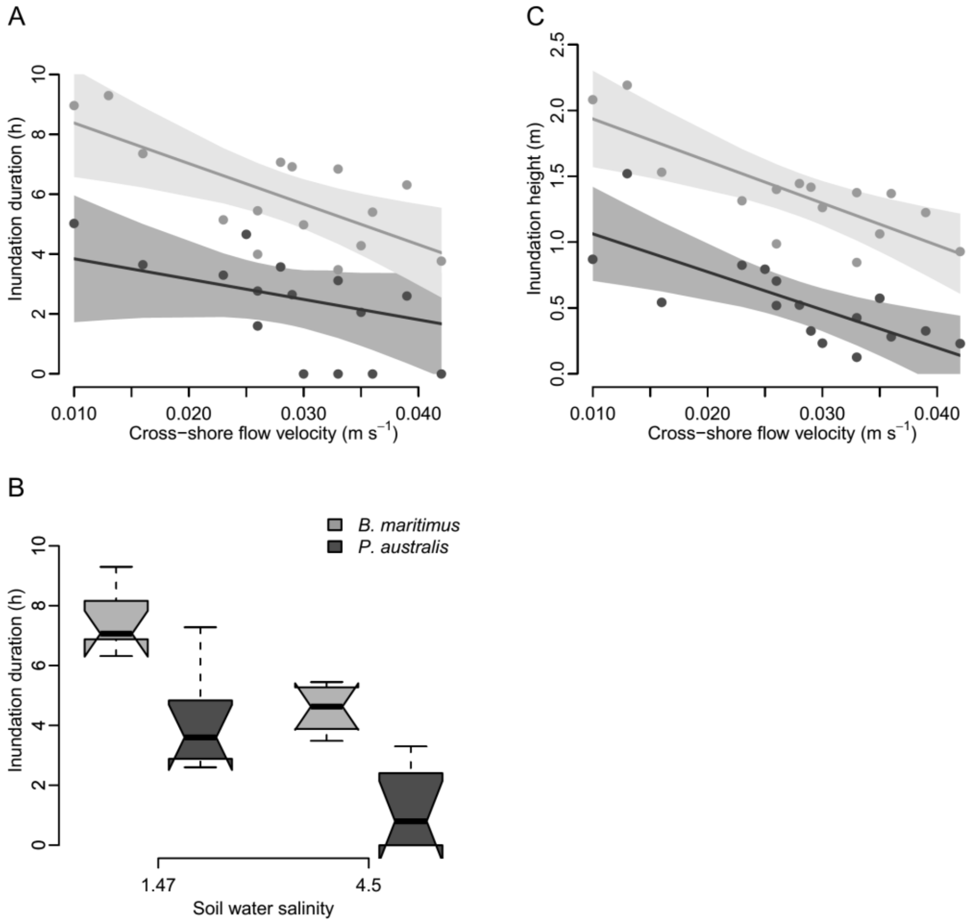

Figure 3.3 Effect of cross-shore flow velocity (m s-1) (A, C) and soil-water salinity (B) on the maximum daily inundation duration (A, B) and inundation height (C) at the waterward fringe of the *B. maritimus* and *P. australis* vegetation belts. Data points include 16 plots in each species belt (0 Bo and 0 Ph) and thus represent combinations of habitat factors at the waterward vegetation fringe. Shaded areas in plot (A, C) define the 95% confidence interval.

Stand characteristics

For both species, there were no significant differences in the height-weight relationship of the ramets from the two study sites. The analysis of plant height and weight resulted in the following equation for *P. australis*: $\mathit{dry\ weight} = 1.42 \times 10^{-3}\ \mathit{height} - 1.91 \times 10^{-8}\ \mathit{height}^2 + 7.5 \times 10^{-10}\ \mathit{height}^3$ (R^2: 0.98, $n = 241$) (Figure 3.4). For *B. maritimus*, we found a significantly different height-weight relationship for plants from the marsh edge (the waterward fringe of the vegetation belt) and plants from inside the vegetation belt (Wilcoxon rank-sum statistic of $\frac{ramet\ height}{ramet\ weight}$: $p < 0.001$, $n = 111$) (Figure 3.4). Due to this dimorphism, we calculated two formulas for the dry weight of *B. maritimus* ramets and hence the biomass per m^2 (marsh edge: $dry\ weight = e^{-11.8} \times height^{1.9}$, $R^2_{adj} = 0.9$, $n = 115$, vs. inside the vegetation belt: $dry\ weight = 9.7 \times 10^{-4}\ height + 6.1 \times 10^{-7} height^2 + 8.2 \times 10^{-10} height^3$, $R^2_{adj} = 0.98$, $n = 111$).

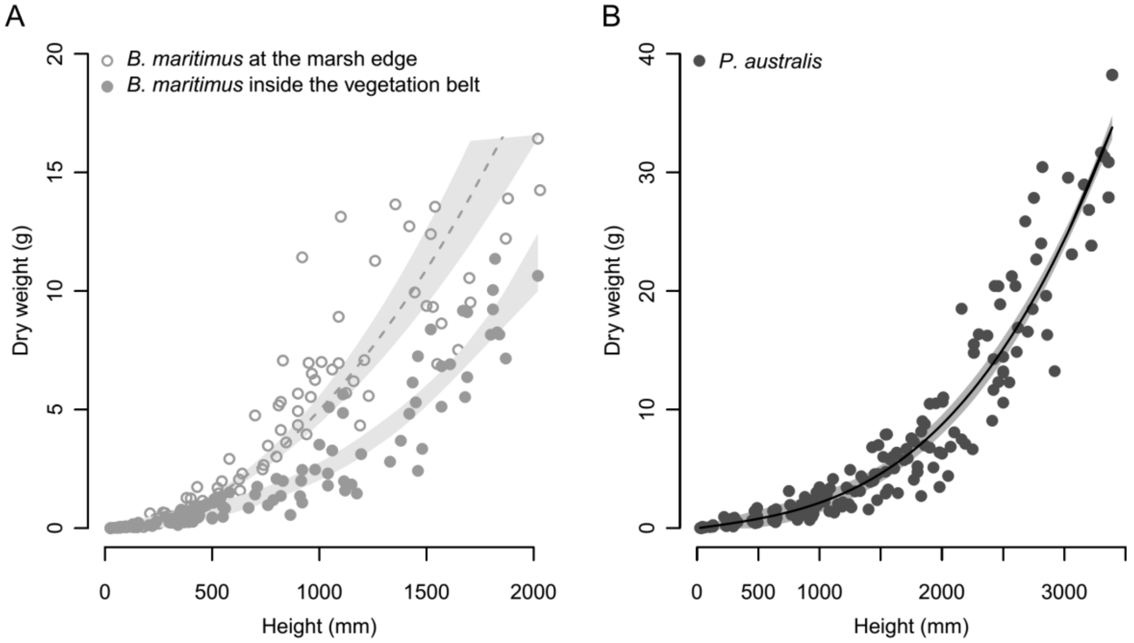

Figure 3.4 Allometric functions using height of ramets to predict ramet dry weight of *B. maritimus* (A) and *P. australis* (B). The lines represent the functions fitted to the data and shaded areas define the 95% confidence interval.

Most stand characteristics of *B. maritimus* first increased with distance from the waterward vegetation fringe and then decreased with the start of the *P. australis* vegetation belt (Figure 3.5 A); only ramet height further increased. Most *P. australis* characteristics increased over large parts of the transect, and only slightly decreased towards the upper end of the vegetation belt (Figure 3.5 B); here, only rhizome biomass strongly decreased.

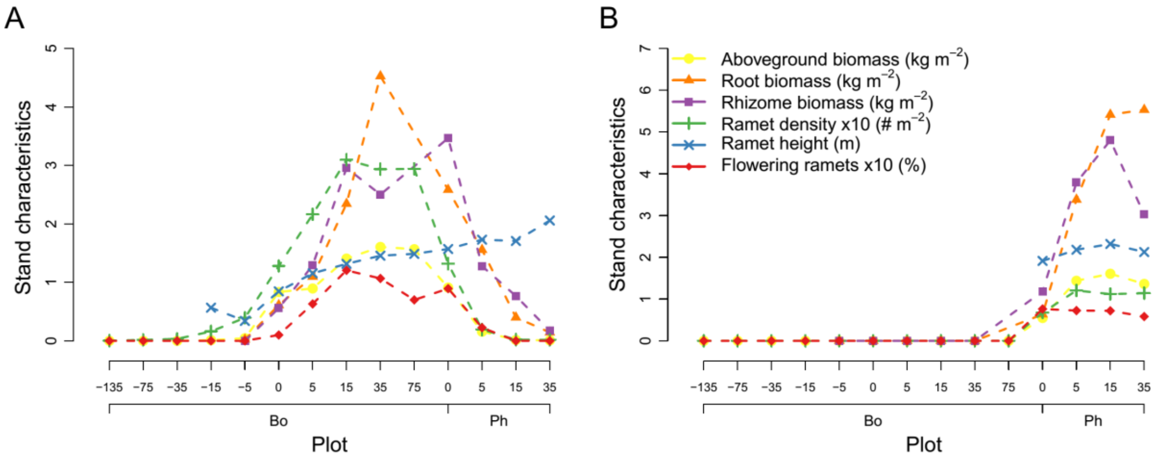

Figure 3.5 Profile of the mean values of the six characteristics of *B. maritimus* (A) and *P. australis* (B) along the transects (*n* = 16). The values on the x-axis represent the plot names (see Fig. 3.1).

The six characteristics of *B. maritimus* were affected by combinations of the measured habitat factors (Table 3.2): Total flow velocity negatively affected all characteristics of *B. maritimus*. It was most important for explaining root and rhizome biomass, ramet height and the percentage of flowering ramets (Figure 3.6). Normalised inundation slightly affected all parameters except for root and rhizome biomass. The response of *B. maritimus* parameters to this factor was unimodal, with a slightly different shape of the response of ramet height, which did not decrease much at low inundations. Soil-water salinity negatively affected aboveground biomass and ramet height and was the least important factor for aboveground biomass. The most important factor for aboveground biomass and ramet density of *B. maritimus* was the biomass of *P. australis,* which negatively affected the two parameters. However, it had no effect on ramet height and the percentage of flowering ramets. Low explained deviance levels indicated that the predictor variables used did not allow for modelling of any of the characteristics of *P. australis* (all %dev$_{expl}$ < 10).

Table 3.2 Proportion of deviance explained (%dev$_{expl}$) by the models and relative importance of the predictor variables (%) (rescaled results of F-Test comparing the full model with the model without the respective predictor variable) for explaining the stand characteristics of *B. maritimus*. Bold print of variable importance marks the most important parameter and a variable importance of zero indicates that the variable was not included in the model.

		Relative importance of predictor variables (%)			
	%dev$_{expl}$	Total flow velocity	Normalised inundation	*P. australis* biomass	Soil-water salinity
Above-ground biomass	34	25	9	**60**	5
Root biomass	35	**56**	0	44	0
Rhizome biomass	28	**51**	0	49	0
Ramet density	52	20	4	**76**	0
Ramet height	50	**79**	7	0	14
Flowering ramets	32	**55**	45	0	0

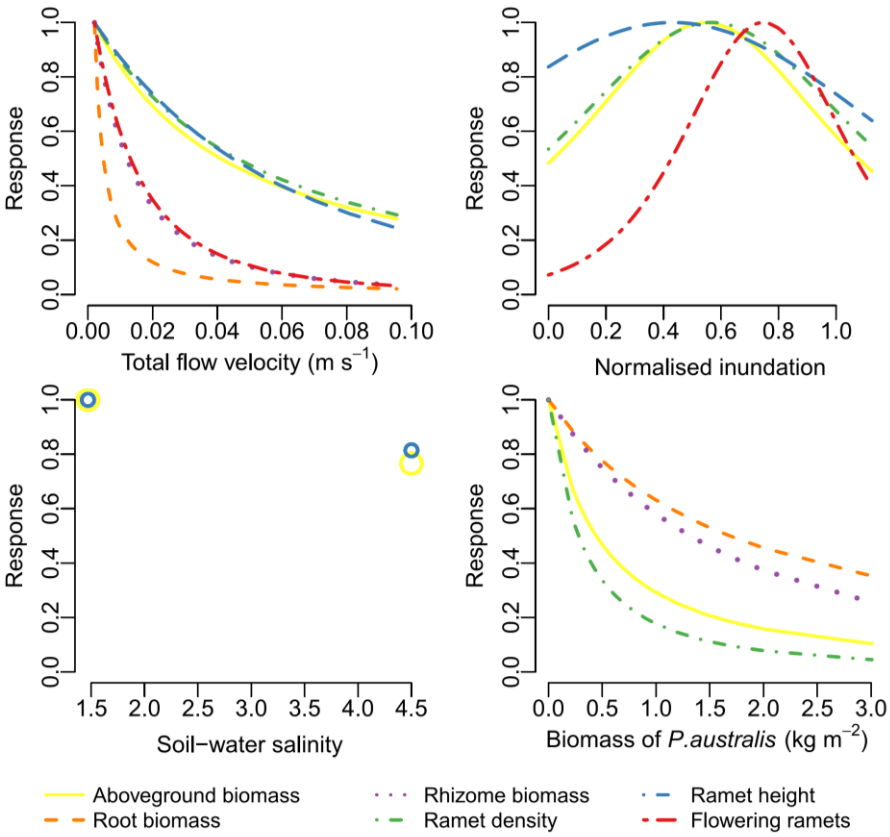

Figure 3.6 Response of the stand characteristics of *B. maritimus* to the four predictor variables. The response curves visualise the effect of a single predictor while all other predictors are kept at their mean value.

Discussion

Elevation relative to mean high water is often used as an indicator in order to gain a better understanding of plant species distribution patterns along environmental gradients (e.g. Bertness and Ellison, 1987; Coops et al., 1999). In this study, we used a set of observable predictor variables that directly influence plant growth instead of using elevation relative to mean high water as a proxy for the effect of more functionally relevant variables. These variables are based on point measurements from two vegetation periods and should be seen relative to each other and not regarded as absolute values. Especially the long- and cross-shore flow velocities illustrate the situation of individual flood events. We believe, however, that our data can reflect the relationship between the plots and thus provide a sound basis for our analyses.

Species distribution

In accordance with others (e.g. Raabe 1981; Dijkema 1990), our models suggest that *P. australis* out-competes *B. maritimus* at the benign end of the vertical stress gradient. Our results furthermore suggest that the occurrence of the two marsh species *B. maritimus* and *P. australis* and, thus, the zonation of the two vegetation belts, was mainly influenced by normalised inundation and total flow velocity (Figure 3.2). In contrast to what we anticipated, total flow velocity was by far the most important factor: Our results show that *B. maritimus* occurs at sites with much higher total flow velocity than does *P. australis*, whereas the inundation levels at which they occur do overlap. The reason for this may be the fact that its triangular stem morphology and its ability to develop different growth forms in response to mechanical stress from currents (Carus et al., 2016) might enable *B. maritimus* to better withstand higher flow velocities than *P. australis*.

In accordance with other studies (Coops et al., 1994; Coops and van der Velde, 1996; Heuner et al., 2016), we found that cross-shore flow velocity does not only directly influence the distribution of the two marsh species, but also alters the plants' occurrence relative to inundation height and duration (Figure 3.4 A, C). This suggests an effect of cross-shore flow velocity on their tolerance to inundation duration and therefore explains why, in calm waterbodies like lakes and rivers with lower hydrodynamic forcing, *P. australis* is often found directly at the marsh edge, whereas in the Elbe it mostly occurs protected by a belt of *B. maritimus*. Although Chambers, Meyerson and Saltonstall (1999) have suggested that *P. australis* distribution in tidal marshes might be limited by soil-water salinity, our hypothesis that the small salinity differences of our study sites would have no direct effect on species distribution was confirmed by our models. However, in contrast to the findings of Hellings and Gallagher (1992), in our case salinity influenced the plants' occurrence relative to inundation duration, which thus indicates an effect of salinity on their tolerance to inundation duration (Figure 3.4 B). It is possible that the effect of cross-shore velocity and soil-water salinity on inundation duration and height at the waterward vegetation fringe adds to the direct effects of inundation by determining (i) the time and height at which hydrodynamic forces can act on the plants and (ii) the time in which saline water can penetrate the soil. To evaluate the effect of sea level rise it is, however, also important to consider marsh accretion and a subsequent elevation change (Kirwan et al., 2016).

Stand characteristics

Many studies suggest that characteristics of *P. australis* vary strongly with abiotic conditions (for a review, see Engloner 2009). However, the pattern of *P. australis* stand characteristics could not be explained by the measuring setup presented in our study. One reason for this could be that the dynamics in the vegetation belt lead to different age structures. Thus, vegetation in the same plot position can be of very different ages depending on whether the stand is expanding or retreating at that specific location.

For *B. maritimus,* however, the analysis of the measured stand characteristics provided information on the importance of single habitat factors (Table 3.2 and Figure 3.6). A previous study (Carus et al. 2016) revealed that current velocity affects the stem morphology of *B. maritimus*: Ramets at more exposed sites had significantly higher diameters than ramets at sites with lower total flow velocity. Consequently, we hypothesised total flow velocity to be a decisive stressor which influences the growth of *B. maritimus.* This was confirmed, as we found a negative effect of total flow velocity on all measured parameters. Our results did not confirm the findings of Clevering and Hundscheid (1998), who discovered a positive effect of permanent inundation on ramet height possibly due to light limitation leading to higher plant growth: in our case, ramets were shortest at the highly inundated vegetation fringe. This could be due to the fact that, in tidal marshes*, B. maritimus* is not inundated the whole day and thus light might not be the limiting factor at the highly inundated plots.

Our results confirmed the findings of Lillebø *et al.* (2003) that *B. maritimus* biomass increases with decreasing salinity in brackish water (Figure 3.6). The effect of soil-water salinity was, however, very small and was possibly due to lower ramet heights at the site with higher soil-water salinity. As suggested by Esselink et al. (2000), competition with *P. australis* did indeed negatively affect the aboveground and belowground biomass of *B. maritimus* which developed fewer ramets at plots with a high biomass of *P. australis*.

Although our measurements were conducted over two consecutive years, the year in which the measurement took place had no significant effect on our results. This agrees with the study by Kirwan and Guntenspergen (2015), who found that although interanual variation of aboveground biomass of the two salt marsh species *Scirpus americanus* and *Spartina patens* was high, the optimum flooding durations stayed the same.

Conclusion

The GLMs estimated in this study achieved excellent performance levels and produced highly interpretable response curves for explaining the occurrence probabilities of the two key marsh species as well as the characteristics of *B. maritimus*. The present study can thus provide detailed information on the importance of individual habitat factors and their interplay for the distribution and stand characteristics of two common brackish marsh plant species.

Our results suggest that total flow velocity is the main factor, influencing species distribution and stand characteristics in regularly flooded estuarine marshes and together with soil-water salinity even affects the inundation tolerance of the two investigated species. The positioning of the water-front vegetation fringe in relation to elevation therefore depends not only on the species' direct inundation tolerance, but also on the pattern of hydrodynamic forces and soil-water salinity. Additionally, inundation height and duration as well as interspecific competition explained distribution patterns and stand characteristics. This leads us to the conclusion that the zonation of tidal marsh vegetation will not only be affected by potential water level changes, but that an increase in hydrodynamic forces as well as an upstream shift of the salinity zones could add indirect effects. Higher and longer inundation combined with a lower inundation tolerance would thus negatively affect distribution and stand characteristics of tidal marsh vegetation and reduce their potential as ecosystem-based shore protection.

Sound knowledge regarding the factors that generate vegetation patterns is vital for assessing the response of tidal marshes to sea level rise and river training and the success of engineering and restoration projects (Elliott et al., 2016; Heuner et al., 2016). By identifying the drivers of marsh zonation and stand characteristics and quantifying their effects, the evidence from this study provides valuable information for evaluating future contributions of tidal marsh vegetation to ecosystem-based shore protection.

Acknowledgements

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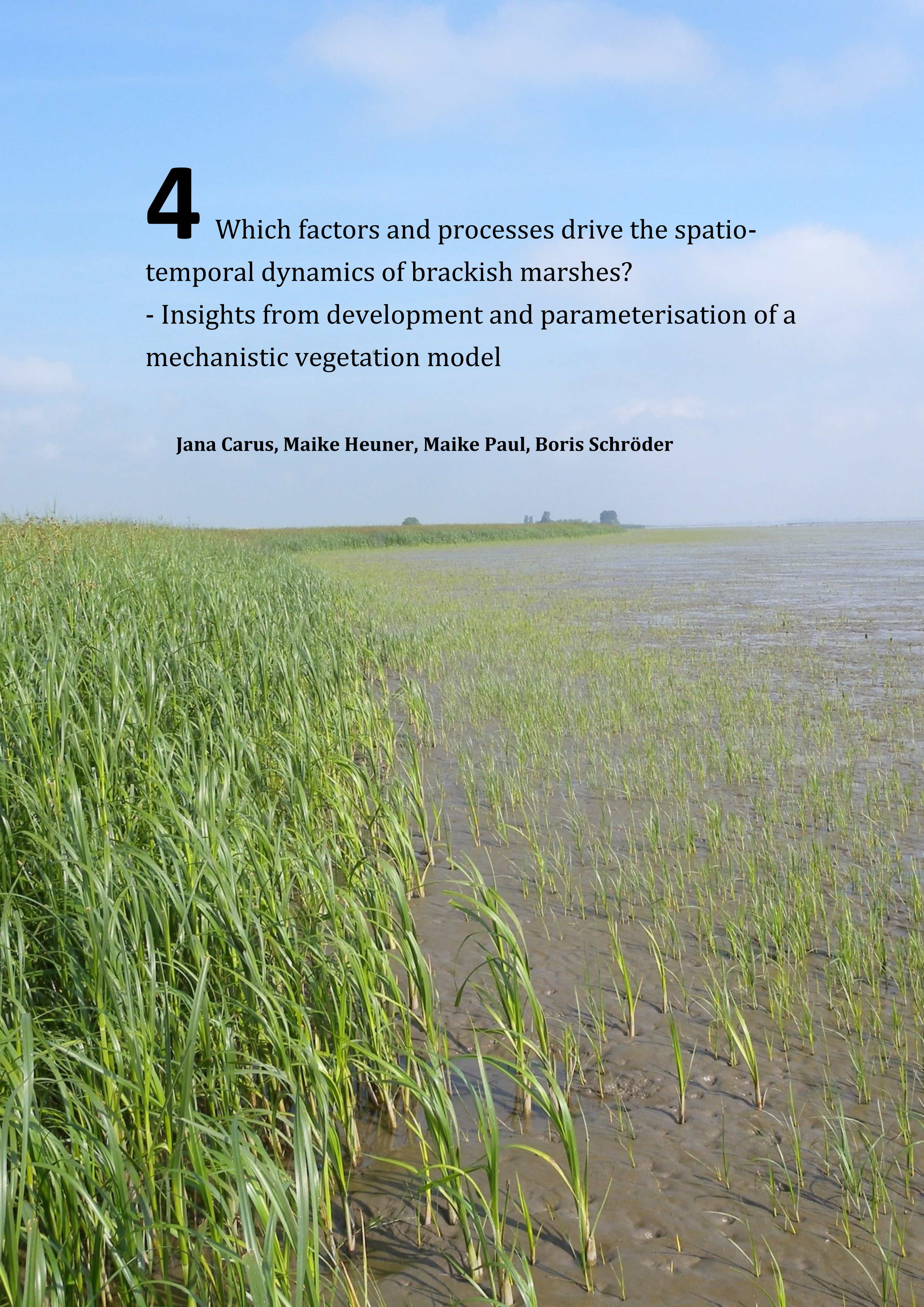
4

Which factors and processes drive the spatio-temporal dynamics of brackish marshes? - Insights from development and parameterisation of a mechanistic vegetation model

Jana Carus, Maike Heuner, Maike Paul, Boris Schröder



Abstract

Tidal marsh vegetation offers important ecosystem services. However, in many estuaries, extensive embankments, artificial bank protection, river dredging and agriculture threaten tidal marshes and the system is thus permanently subject to changes. In this study we analysed the processes underlying the spatio-temporal patterns of tidal marsh vegetation in the Elbe estuary and quantified the influence of specific habitat factors by developing the process-based dynamic habitat-macrophyte model HaMac in a pattern-oriented way. In order to develop and parameterise the model, we measured a wide range of biotic and abiotic parameters in two study sites in the Elbe estuary and compared observed and simulated patterns. The final model is able to reproduce the general patterns of vegetation zonation, development and growth and thus helps to understand the underlying processes. By considering the vegetative reproduction of marsh plants as well as abiotic influence factors and intraspecific competition, HaMac allowed to systematically analyse the significance of factors and processes for the dynamic of tidal marsh vegetation. Our results show that rhizome growth is the most important process and that flow velocity, inundation height and duration as well as intraspecific competition are the most important habitat factors for explaining spatio-temporal dynamics of brackish marshes. Future applications of HaMac could support the sustainable development and stabilisation of shore zones and thus contribute to the promotion and planning of ecosystem-based shoreline protection measures.[3]

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[3] The model code of the dynamic habitat-macrophyte model HaMac is available on the attached CD.

Introduction

Tidal marsh vegetation offers important ecosystem services (Barbier et al., 2011; Mitsch and Gosselink, 2000) by filtrating solid and dissolved substances from the water (Mitsch and Gosselink, 2015), providing habitat, reducing flow velocity (Christiansen et al., 2000; Leonard and Luther, 1995), attenuating waves (Barbier et al., 2008; Gedan et al., 2010) and serving as erosion control for riverbanks (Coops and Van der Velde, 1996). The intertidal zone of coastal estuaries is often populated by brackish marsh vegetation consisting of a distinct zonation of *Bolboschoenus maritimus* in the pioneer zone and *Phragmites australis* in the low and mid marshes. This zonation is often attributed to elevation, which determines the exposure to tidal flooding and thus the duration, frequency and height of inundation (e.g. Bertness and Ellison, 1987; Coops et al., 1999; Heuner et al., submitted). The vegetation belts of emergent macrophytes mostly begin at 1.50 m to 2 m below the mean high water. Other important habitat factors for brackish marsh vegetation are hydrodynamic forces, sedimentation and erosion processes, soil water salinity and biotic interactions like competition and facilitation (Meire et al., 2005; Odum, 1988).

Estuarine marshes are highly dynamic environments and constantly subject to change. Variations in the above mentioned abiotic and biotic habitat factors give thus rise to recession and expansion of the tidal vegetation belts. These lateral dynamics are as important as vertical marsh evolution because they determine the future extent the marsh (Fagherazzi et al., 2012; Kirwan et al., 2016a; Van De Koppel et al., 2005). In many estuaries, extensive embankments, artificial bank protection, river dredging and agriculture threaten tidal marshes (Temmerman et al., 2013). Global warming might entail additional risks, such as changes in water levels, further increase of the tidal amplitude and a resulting shift of the salinity zones (Chua and Xu, 2014; Seiffert and Hesser, 2014). Against this background, it is pivotal to gain a better understanding of the processes underlying the spatio-temporal vegetation dynamics in brackish marshes, to quantify the influence of specific habitat factors on marsh vegetation and to develop a tool for testing different scenarios.

Statistical models provide a valuable instrument for identifying the drivers of marsh zonation and for quantifying their effects on vegetation vitality (e.g. Heuner et al., 2016, Carus et al., 2017). However, the drawback of these models is that they do not explicitly consider processes and that they assume vegetation and environment to be in equilibrium and hence do not explicitly consider dynamics (Araújo and Guisan, 2006; Zurell et al., 2009). Furthermore the history of a region (e.g. variations in influential habitat factors, like an increase in tidal amplitude or particularly severe storm events) is of high importance for the future species distribution (Guisan and Zimmermann, 2000). Mechanistic models proved to be a helpful tool to evaluate the ecological processes underlying distributional patterns of animal and plant species (Grimm *et al.*, 2005), because they allow for transient dynamics and explicitly consider mechanisms such as dispersal limitation (e.g. Schurr et al., 2012). Existing mechanistic models provide, for instance, numerical simulations of the biomass of *Phragmites australis,* but are not spatially explicit (Asaeda and Karunaratne, 2000; Soetaert et al., 2004). Spatially explicit clonal growth models. (Oborny et al., 2017) on the other hand are too detailed to enable predictions on the landscape scale. Wortmann, Hearne and Adams (1997) developed a discrete simulation model for the dynamics of a submerged macrophyte (*Zostera capensis Setchell*). It describes the vegetative spread of *Z. capensis* and was also used to analyse the role of freshwater inflow on spatial patterns and biomass of estuarine macrophytes (Wortmann et al., 1998). This model considers vegetative reproduction and a dynamic environment without being too fine-grained to study whole shore segments, but does not consider seasonal aspects of vegetation growth.

For the analysis of marsh evolution, it is vital to detect and consider the factors and processes that drive spatio-temporal dynamics in tidal marsh vegetation. Hence, our approach was building a spatially explicit, mechanistic model considering vegetative reproduction, seasonal aspects of vegetation growth and its interaction with a dynamic environment. As model building should be guided not only by the aim of the model and the available knowledge, but also by the patterns that can be identified in the system in question (Wiegand et al., 2003), we chose to build our model in a pattern-oriented way (Grimm et al., 2005, 1996; Wiegand et al., 2003). The pattern-oriented modelling approach aims to use multiple patterns (i.e. characteristic, clearly identifiable structures in the landscape) at different scales that can be observed in real systems to guide model structure, design and parametrisation (Grimm et al., 2005) and serve as indicators for the underlying processes.

Our paper describes the modelling procedure for the case of marsh dynamics by the subsequent steps: (1) we defined observable patterns in brackish marshes and formulated hypotheses on the factors and processes necessary to reproduce the observed patterns, (2) we collected information on these patterns as well as on single parameter values by field observations and (3) we developed and implemented a process-based model allowing for reproducing of the observed patterns. In order to determine parameter values, test model performance and transferability and optimise the model structure, we (4) systematically compared observed and simulated patterns. Steps three and four were repeated in a cyclic manner (Thulke et al., 1999), to optimise model structure and understand the mechanisms behind the observed patters (Wiegand et al., 2003). Lastly, exploring the model further enabled us to (5) analyse the influence of growth parameters and abiotic habitat conditions on the spatio-temporal dynamics of tidal marsh vegetation.

Methods

Studied species

Along many estuaries, *Bolboschoenus maritimus and Phragmites australis* form the characteristic vegetation of brackish marshes. The main reproduction path of these two emergent macrophytes is vegetative propagation by an extensive rhizome system. Thus, changes in their abundance and distribution are mainly determined by the pattern of clonal reproduction (de Kroon and Visser, 2003). One feature of vegetative propagation is the ability to "react" plastically to spatially heterogeneous environmental factors (morphologic plasticity; de Kroon and Hutchings, 1995). By building out more branches in suitable habitats and longer rhizomes in unsuitable habitats, clonal plants can increase ramet density in favourable locations. Aboveground plant parts of the two species start growing between March and April and continue until August (Windham, 2001).

Study sites

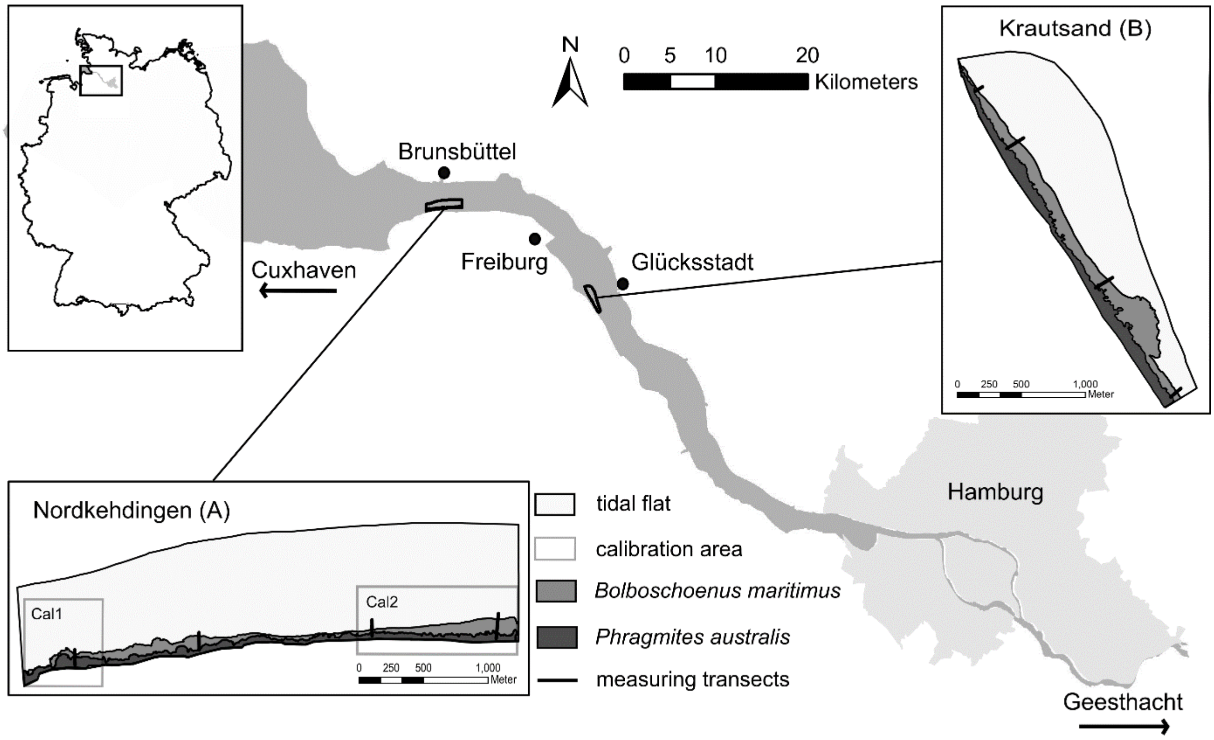


Figure 4.1 Location of the two study sites and position of the eight transects in the Elbe estuary.

Our study focusses on the Elbe estuary (Germany), which is the roughly 120 km long tidally influenced part of the river Elbe between the outlet in Cuxhaven and the weir at Geesthacht (Figure). Due to the Port of Hamburg, the Elbe estuary is heavily frequented by ships and has for many years been subject to channel straightening and deepening which affected tidal amplitude, flow conditions, water salinity and sediment shift (Dücker et al., 2006; Fickert and Strotmann, 2007). Our study was conducted at two sites in the tidally influenced brackish part of the river Elbe. These sites lay about 30 km apart and were selected because of the presence of the two study species and an unobstructed shoreline. One study site lies in the nature reserve Nordkehdingen (A) (53°51'46.419"N, 9°5'50.027"E) and the other on the peninsula of Krautsand (B) (53°45'50.626"N, 9°22'46.052"E). Mean tidal ranges are 2.9 m at site A and 2.8 m at site B. Tidal period is asymmetrical, with a shorter flood period. The speed of the flood current is thus higher than that of the ebb current, leading to a heavy upstream transport of sediments (Fickert and Strotmann, 2007). Both sites are characterised by vegetation belts of *Bolboschoenus maritimus* at the water front and *Phragmites australis* further landwards which are permanently subject to changes, with areas where vegetation retreats next to areas where it further expands into the tidal flat.

Patterns and hypotheses

The choice of observable patterns in the brackish marsh was based on the interest to cover a wide spectrum of scales, as well as accounting for spatial and temporal changes simultaneously. We identified six patterns characterising the system at different scales (Table).

Table 4.1 Observed patterns and their spatial scale.

No.	Pattern	Spatial scale
1	species distribution, i.e. presence or absence	landscape scale
2	waterward dispersal, i.e. expansion and recession	landscape scale
3	spatial distribution of rhizome biomass	plot scale
4	spatial distribution of root biomass	plot scale
5	spatial distribution of aboveground biomass	plot scale
6	seasonality of aboveground biomass	plot scale

As first pattern (P1) we used the spatial distribution of *B. maritimus* and *P. australis,* whereas the second pattern (P2) quantifies the waterward dispersal i.e. expansion and recession of the two species. These first two patterns are of key importance for the future development of the vegetation belts. They were used to identify and parameterise processes on the scale of the entire study sites (landscape scale) and can thus give insight into large-scale lateral vegetation dynamics. For the other four patterns (P3-P6), we focussed on the plot scale (0.25 m^2): As target values, we used below- and aboveground biomasses at the time and place of the measurement. To additionally consider a short temporal scale and test the implementation of the plants' phenology, we used the seasonal development of aboveground biomass (P6).

By formulating hypotheses on the factors and processes necessary to reproduce the observed patterns, it is possible to assure that the model contains the key structural elements of the real system (Wiegand et al., 2003). Our main hypothesis was that considering vegetative reproduction in combination with the effects of abiotic and biotic habitat factors is the key to simulating tidal marsh dynamics. Due to the importance of vegetative propagation for reproduction of the two species (de Kroon and Visser, 2003) and the consequent ability of the species to “react” plastically to their environment, we expected that rhizome growth is an important process for explaining lateral dispersal of the two emergent macrophytes. As hydrodynamic conditions have a significant impact on plant growth and morphology (Carus et al., 2017, 2016) we hypothesise that flow velocity is the main reason for recession of *B. maritimus* in the exposed pioneer zone, whereas inundation height and duration limit expansion of *P. australis*.

Data collection

We used vegetation maps (scale 1:4300) with focus on emergent macrophytes from 2006 and 2010 (Petersen et al., 2011, 2010, 2007) to gain information on the landscape scale patterns (P1 & P2). The maps where derived from digital aerial photographs with a ground resolution of 0.25 m which were verified in the field (Petersen et al., 2011, 2010, 2007). These vegetation maps have a high accuracy regarding geometrical locations (less than 2 m boundary uncertainties) and vegetation classification (correct classification rate: approximately 99%). Species distribution (P1) was extracted directly from the 2010 vegetation map by defining presence (1) and absence (0) of the respective species. The waterward dispersal of the two species (P2) was calculated by subtracting species distribution in 2006 from distribution in 2010. This way, we received new maps containing information on the expansion (1) and recession (-1) of the two species.

Field measurements were conducted at four transects in each study site (Figure) perpendicular to the river line. The positioning of measurement plots along the transect was oriented on vegetation patterns, i.e. for each of the two species, the first plot was positioned at last years' waterward fringe of the species' vegetation belt. All other plots were positioned further landwards at predefined distances (5, 15, 35 m) from these two reference plots. Exact height and position of the plots was determined with a differential global positioning system (DGPS).

To gain information on plot-scale patterns (P3-P6), we quantified below- and aboveground plant characteristics of the two species in 0.25 m^2 squares. Belowground biomass was measured in April 2013 at all plots of two transects in each study site. Aboveground biomass was estimated via allometric relationships on the basis of plant heights and densities recorded monthly from April to August 2012 in one plot for each species (15 m from the waterward border of the respective vegetation belt) and once in August 2012 in all plots. A detailed description of the sampling procedures, visualisations of the data and the allometric relationships can be found in Carus et al. (2016, 2017).

Information on the abiotic habitat factors was gained by field measurements as well as by the analysis of existing data. To compare situations with and without living aboveground biomass, flow velocity was measured before the start of the growing season in April and at the peak of the growing season in August 2012 with four acoustic doppler velocity meters (ADV, Nortek Vector) at four plots of one transect and once in front of all transects in August 2013. The mean of the flow velocity measurements at the waterfront plots was adjusted for the effect of the vegetation ($effect_{Veg}$) with distance from the marsh edge (d) by a function determined by Carus et al. (2016):

$$effect_{Veg} = 3.76 \times (d + 10)^{-0.8} \tag{1}$$

Soil-water salinity was measured in 5-25 cm depth at each plot monthly during the vegetation period of 2012 and in August 2013 with a handheld conductivity-meter (Cond 340i) inside perforated HTEM tubes using the Practical Salinity Scale. As plot values of salinity measurements showed no gradient along the transects, we used the mean (± sd) of all measurements per study site (study site A: 4.5 PSU ± 1.7 PSU, study site B: 1.5 PSU ± 0.4 PSU). We determined the maximum water level of the vegetation period 2012 (Apr.-Aug.) from gauge data (Waterways and Shipping Office Hamburg (WSA), http://www.portal-tideelbe.de) and calculated inundation height and duration for this water level with the GIS tool INFORM (Fuchs et al., 2012; Giebel et al., 2011). An estimation of the rate of elevation change was calculated by subtracting high resolution digital elevation models (DEMs) from 2006 ($5m \times 5m$) and 2010 ($1m \times 1m$).

Mean daily air temperature was obtained from a weather station in Freiburg (53°49'30.4"N 9°17'18.4"E), less than 15 km from both study sites (Deutscher Wetterdienst (DWD)).

Model structure

We sought a model structure allowing for reproducing the observed patterns. As vegetation dynamics of the two species highly depend on vegetative reproduction, competition with other species as well as habitat conditions, we coupled dynamic habitat conditions via transfer functions with a spatially explicit grid-based simulation of vegetation dynamics of both plant species (Figure 4.).

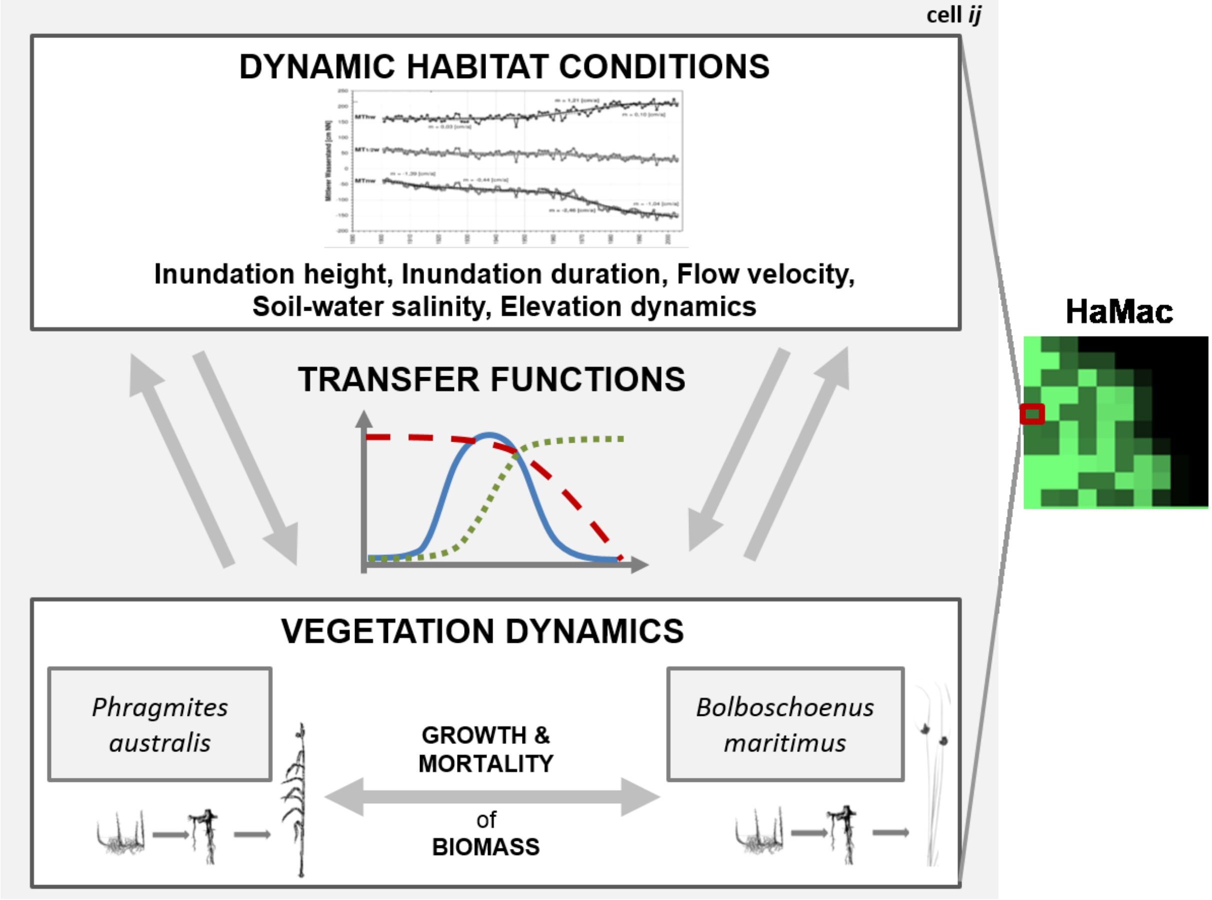


Figure 4.2 Schematic description of the dynamic habitat-macrophyte model (HaMac). In each cell, a simulation of the vegetation dynamics of both plant species is coupled with dynamic habitat conditions via transfer (effect- and response-) functions. Five abiotic factors are considered to dynamically simulate habitat conditions (see Habitat conditions). Effects and responses of

vegetation and habitat are considered by transfer functions that were derived via statistical modelling (see Transfer functions). On a daily basis, the model calculates responses of the two species for each habitat factor, from which the model then derives a habitat quality value for each cell. This habitat quality serves as input for the vegetation model, which simulates vegetation dynamics by calculating aboveground and belowground biomass in each grid cell (see Vegetation dynamics). Vegetation in neighbouring cells interacts via lateral rhizome expansion.

The structure of the dynamic habitat-macrophyte model (HaMac) was inspired by Wortmann et al. (1998, 1997) and also comprises elements of the models presented by Soetaert et al. (2004) as well as Asaeda and Karunaratne (2000). The simulation is conducted on a grid of square cells and all calculations are preformed per cell. The spatial resolution of the simulation is 1 m², and the extent of the two reference regions about 3 km² (study site A) and 14 km² (study site B); the temporal resolution of the simulation is 1 day and the simulation time is from 2006 to 2013.

Habitat conditions

After preceding analyses and based on previous work (Carus et al., 2017), we considered five abiotic habitat factors as possibly important for growth and distribution of the two emergent macrophytes: maximum daily inundation height, daily inundation duration, median of the daily flow velocity, elevation change and soil-water salinity. Water level and depth-averaged flow velocity were simulated externally with the three-dimensional hydrodynamic HAMburg Shelf Ocean Model (HAMSOM) developed by (Backhaus, 1985, 1983). Simulation results were extracted at discrete points along three lines perpendicular to the vegetation border (Hein et al., 2014) and a lowpass filter was used before calculating maximum daily values of water level and depth-averaged mean flow velocity. Daily values of maximum high water level and mean flow velocity were spatially interpolated by inverse distance weighting (Lam, 1983). To calculate the inundation height, maximum high water level was combined with a DEM of 1 m² resolution. To obtain the daily inundation duration, a water level time series with a resolution of 20 minutes was linearly interpolated to gain a five minute resolution. After a subsequent spatial inverse distance interpolation of each five minutes time series, the DEM was subtracted from this water levels and five minutes inundation time was added at locations with positive inundation heights.

Elevation change was calculated using semi-terrestrial elevation measurements which were conducted in 2006 and 2010 along transects located 200 m apart perpendicular to the river line. The data points were triangulated for each study site and the obtained elevations subtracted to gain comprehensive estimations for accretion and erosion rates. As there were no significant differences of soil-water salinities within each study site, we used the mean of all measurements per site.

Transfer functions

Effect and response of vegetation and habitat is considered by transfer functions coupling the vegetation model with the dynamic habitat. As the hydrodynamic model HAMSOM does not account for vegetation, we added Eq. (1) for calculating flow reduction by aboveground plant parts.

Because of the collinearity of some of the considered habitat factors (Spearman's rank correlation coefficient rho > 0.7, cf. Dormann et al., 2013) and no significant interactions among these, we used univariate generalised linear models (GLM, McCullough and Nelder, 1989) with binomial distribution and the logit-link function (i.e. logistic regression) for quantifying the response of the two target species to their habitat. In these GLMs, the occurrence of the two species served as response variable, whereas maximum daily water level, daily inundation time, mean daily current velocity, elevation change and soil-water salinity were used as predictor variables. To consider species competition, biomass of *P. australis* was included as a biotic predictor for *B. maritimus,* because *P. australis* outcompetes *B. maritimus* at places were abiotic habitat conditions allow its growth (Esselink et al., 2000).

Once the GLMs linking species performance with habitat conditions are estimated, HaMac calculates model responses for each habitat factor on a daily basis. Resulting values are combined to habitat quality values for each cell ($\varphi[i,j]$, with i and j being the coordinates on the model grid) by calculating their weighted sum using the explained deviances of the respective univariate GLMs as weights. This habitat quality is used in the vegetation model as a factor controlling the growth of above- and belowground biomass and vegetation expansion.

Vegetation dynamics

To simulate vegetation dynamics, we developed a grid based model, consisting of a structure of linked growth processes calculating above- and belowground biomass (B) in each grid cell. Assuming a maximum amount of biomass a cell can support i.e. a carrying capacity (K), B is calculated with logistic equations (Eqs. (4), (5), (6)).

Belowground biomass is subdivided into vertical (roots) and horizontal (rhizomes) structures. Change of belowground biomass is specified by growth (r) and mortality (m); both depend on habitat quality, but growth is additionally density dependent.

One of the main functions of rhizomes, as horizontal growth structures, is dispersal (Chapin et al., 1990) which we model as directional expansion. Whether vegetation expands into a neighbouring cell is decided with the help of a random factor *f*. The value of f (0 or 1) depends on habitat quality which makes dispersal into good habitat more likely (morphologic plasticity):

$$f = 0 \; if \; z > \; \varphi[i,j] \; \text{ and } \; f = 1 \; if \; z < \; \varphi[i,j]; \quad (2)$$

$$\text{with } z = random\ number\ drawn\ from\ uniform\ disitribution\ between\ 0\ and\ 1$$

Rhizome biomass at time [t+1] in a cell [i,j] is thus calculated by adding growth inside the cell and expansion from the eight neighbouring cells to existing biomass at time [t] and subtracting dead and expanded biomass:

$$
\begin{aligned}
B_{\text{Rhizomes }[[i,j][t+1]]} = {} & B_{\text{Ramets }[[i,j][t]]} + \Big(r_{\text{Rhizomes}} \times B_{\text{Rhizomes }[[i,j][t]]} \\
& \times \frac{K_{\text{Rhizomes}} - N_{\text{Rhizomes }[[i,j][t]]}}{K_{\text{Rhizomes}}} \\
& + f \times \sum_{(k,l \in N)} \frac{e_{\text{Rhizomes}} \times B_{\text{Rhizomes }[[k,l][t]]}}{8} \times \frac{K_{\text{Rhizomes}} - B_{\text{Rhizomes }[[i,j][t]]}}{K_{\text{Rhizomes}}}\Big) \\
& \times \varphi[i,j] \; - e_{\text{Rhizomes}} \times B_{\text{Rhizomes }[[i,j][t]]} - m_{\text{Rhizomes}} \times B_{\text{Rhizomes }[[i,j][t]]} \times (1 \\
& - \varphi[i,j])
\end{aligned}
\tag{3}
$$

Where B is the set of the eight neighbours of the cell [i,j], given by{(i−1, j−1), (i-1, j), (i−1, j+1), (i, j+1), (i+1, j+1), (i+1, j), (i+1, j-1), (i, j−1)}.

Table 4.1 Model parameters and values

Discription	Parameter	*B. maritimus*	*P. australis*	Source
Threshold for summing up temperatures	t_{min}	4	4	Soetaert et al. (2004)
Critical threshold of the temperature sum	t_{crit}	90	90	extra calibration
Start of the growing period	t_1	variable	variable	calculated in the model
End of rhizome remobilization phase	t_2	11.06.	11.06.	Soetaert et al. (2004)
End of growth of above-ground biomass	t_3	01.08.	01.08.	Soetaert et al. (2004)
End of relocalisation phase	t_4	25.10.	25.10.	Soetaert et al. (2004)
Above-ground biomass (g/m^2)	B_{Ramets}	state variable	state variable	calculated in the model
Rhizome biomass (g/m^2)	B_{Rhizomes}	state variable	state variable	calculated in the model
Root biomass (g/m^2)	B_{Roots}	state variable	state variable	calculated in the model
Response factor (g/m^2)	Φ	variable	variable	calculated in the model
Random factor	f	variable	variable	calculated in the model
Multiplier for the calculation of the initiation parameter	ini_{mul}	0.06	0.06	Asaeda & Karunaratne (2000)
Power for the calculation of the initiation parameter	ini_{power}	0.19	0.19	Asaeda & Karunaratne (2000)
Capacity of rhizome biomass (g/m^2)	K_{Rhizomes}	4500	6400	own field data
Capacity of root biomass (g/m^2)	K_{Roots}	5900	8800	own field data
Capacity of above ground biomass (g/m^2)	K_{Ramets}	4150	3400	own field data
Growth rate of rhizome biomass (g/g/day)	r_{Rhizomes}	0.051	0.064	calibrated
Growth rate of root biomass (g/g/day)	r_{Root}	0.034	0.046	calibrated
Growth rate of above ground biomass (g/g/day)	r_{Ramet}	0.11	0.09	calibrated
Rate of expansion	e_{Rhizome}	0.018	0.01	calibrated
Proportion of translocated above-ground biomass	trans	0.01	0.01	calibrated
Mortality rate of rhizomes	m_{rhizomes}	0.0007	0.00025	calibrated
Mortality rate of roots	m_{roots}	0.003	0.00033	calibrated
Mortality rate of above-ground biomass during senescence	m_{sene}	0.1	0.1	Soetaert et al. (2004)

As new root biomass can either grow from old roots or from rhizomes, both contribute to the growth of roots:

$$B_{\text{Roots [[i,j] [t+1]]}} = B_{\text{Ramets [[i,j][t]]}} + r_{\text{Roots}} \times (B_{\text{Roots [[i,j][t]]}} + B_{\text{Rhizomes [[i,j][t]]}}) \times \frac{K_{\text{Roots}} - B_{\text{Roots [[i,j][t]]}}}{K_{\text{Roots}}} - m_{\text{Roots}} \times B_{\text{Roots [[i,j][t]]}} \times (1-\varphi[i,j]) \tag{4}$$

An extensive root system can support large amounts of aboveground biomass whereas growth of ramets is impossible without root biomass (Wortmann et al. 1998). Hence root biomass determines the growth of aboveground biomass:

$$\mathrm{B}_{\text{Ramets [[i,j] [t+1]}} = \mathrm{B}_{\text{Ramets [[i,j][t]]}} + \mathrm{r}_{\text{Ramets}} \times \mathrm{B}_{\text{Ramets [[i,j][t]]}} \times \frac{\mathrm{B}_{\text{Ramets [[i,j][t]]}} \times \mathrm{K}_{\text{above}}}{\mathrm{K}_{\text{above}}} \tag{5}$$

with: $\mathrm{K}_{\text{above}} = \mathrm{B}_{\text{Roots [[i,j][t]]}} * \frac{\mathrm{K}_{\text{Ramets}}}{\mathrm{K}_{\text{Roots}}}$

Phenology was implemented temperature dependent as well as coupled to predefined dates.

Similar to Soetaert et al. (2004), we distinguished four phenological events (t_1 to t_4). The start of the growth period (t_1) is determined by summing up mean daily air temperatures above the minimum temperature t_{min}. Like Soetaert et al. (2004), we set the starting date of temperature accumulation at January 1. Growth of aboveground biomass starts, when the accumulated degree days (i.e. the temperature sum) exceeds the critical value (t_{crit}) which was calibrated for the research region based on the start of the growth in 2012. All other dates (t_2, t_3, t_4) are fixed (Table 4.1), because linked processes are assumed to be determined by day length, not temperature (Hay, 1990). At the start of the growth period of aboveground biomass, a remobilisation of rhizome stored nutrients for shoot growth takes place (Karunaratne et al., 2003). Rhizome biomass in winter is positively correlated with mean diameter of shoots (Mook et al. 1982), initial aboveground biomass and shoot density (Asaeda and Karunaratne 2000). In spring or after disturbance, translocation of nutrients from rhizomes into aboveground plant parts takes place and serves as growth impulse. Based on Asaeda and Karunaratne (2000), initial aboveground biomass (Ini) is calculated in the vegetation model as follows:

$$Ini = ini_{\text{mult}} \times N_{\text{Rhizomes [[i,j][t]]}}{}^{ini_{\text{power}}} \times N_{\text{Rhizomes [[i,j][t]]}} \tag{6}$$

With ini_{mult} and ini_{power} being regression coefficients obtained by Asaeda and Karunaratne (2000). In the remobilisation phase (between t_1 and t_2), the growth of aboveground biomass is supplied by present aboveground biomass as well as by rhizome biomass. In this phase, rhizome biomass decreases (Chapin et al., 1990; Dykyjová and Hradecká, 1976; Granéli et al., 1992) because all energy is directed into the growth of aboveground biomass. For this reason, growth of belowground biomass only starts at t_2 in the model. At t_3 the shoot growth period ends. This marks the start of senescence of aboveground biomass and translocation of reserves from shoot to rhizomes, which ends at t4. As air temperature greatly effects metabolic reactions, all growth processes were implemented temperature dependent according to the Q10 concept (e.g. Čížková and Bauer, 1998; Arrhenius constant θ of 1.07).

To obtain initial conditions for the simulation it was necessary to estimate biomass distribution of *B. maritimus* and *P. australis* in 2006. Our field data showed a distinct relationship between the position in the vegetation belt and aboveground biomass (see Eqs A1 in the appendix). We thus used this relationship in combination with vegetation maps from 2006 (Petersen et al., 2011, 2010) to estimate aboveground biomass with a linear model. Belowground biomass was calculated by using field derived relationships between above- and belowground biomass (see Eqs. A2 in the appendix). Model simulation time (2006- 2013) was preceded by a spin-up period of 10 years, where the model was driven with a repeated cycle consisting of the conditions of 2006.

Comparison of observed and simulated patterns

Before applying the full model, we tested the influence of the random factor *f* by conducting ten simulations with the same parameter combination and the effect of the spin-up time by simulations with one to 20 years spin-up. We furthermore conducted several tests (e.g. different implementations of clonal growth) to optimise the model structure.

To reduce computation time, we used only two segments of the study site A for model calibration. One of these segments was located in the east of the study site (Cal1) and is characterised by strong expansion of *B. maritimus,* whereas the western segment (Cal2) comprises areas of recession of this species (Figure). By randomly varying all parameter values that were not fixed before calibration, 100 parameter sets were obtained and used for simulations from 2006 to 2013. Model results were evaluated by visually comparing the patterns extracted from the field data with the patterns simulated by the model. This way, we identified necessary changes to the model and defined new (smaller or shifted) parameter ranges for each parameter. This procedure was repeated until no enhancement was reached. To accept a model parametrisation, all criterions had to be satisfied simultaneously (Wiegand et al., 2003). The final vegetation model includes a total of 23 parameters (Table 2) for each species of which seven were calibrated via Monte Carlo simulations (Doubilet et al., 1985). We used different measures to quantify model performance considering the patterns (Table). P1 and P2, i.e. distribution and dispersal of the two species, are spatial comparisons of pairs of maps. For these patterns model performance was quantified with Cohen's kappa (κ) (Cohen, 1960), a discrimination measure for the proportion of correctly predicted presences and absences that accounts for the possibility of the agreement occurring by chance. For P3 to P6, i.e. below- and aboveground biomasses and seasonality, we used Spearman's rank correlation coefficient (ρ) as performance criteria which calculates the correlation of the ranks of simulated and observed values. Both performance criteria range from 0 to 1, with 1 indicating a perfect model fit. We calculated the model performance for model runs with the final parameter set, compared observed and simulated patterns and furthermore prepared confusion matrices for P1 and P2. To test for model generality and transferability, we conducted a validation by transferring the model with the parametrisation for the calibration areas to the rest of study site A and to study site B.

Factors affecting spatio-temporal dynamic of tidal marsh vegetation

Once calibrated and validated, we used the model in a hypotheses-driven framework to study the influence of a number of factors which might control the dynamic of the two marsh species. For this purpose, local parameter sensitivity was assessed by varying each parameter value by $\pm$ 90%. We then used the minimum and maximum of each parameter value (p_i) in combination with the mean value of all other parameters as model input and calculated the effect on the model performance for all patterns ($mod.perf_j$) ($local\ sensitivity_{ij} = \frac{\Delta mod.perf_j}{\Delta p_i}$). In order to compare the influence of each parameter on changes in the regarded patterns, we calculated the relative proportional parameter sensitivities ($rel.sensitivity_{ij} = \frac{local\ sensitivity_{ij}}{\sum_{j=1}^{n} local\ sensitivity}$).

Furthermore, model runs were conducted excluding all habitat factors in turn to evaluate the effect of the respective factor. By comparing the relative change of the goodness-of-fit, we quantified the effect on the observed patterns ($rel.change\ of\ mod.perf = \frac{mod.perf_{\ without\ factor} - mod.perf_{\ full\ model}}{mod.perf_{\ without\ factor}}$).

The model was written within the free software environment R 3.2.5 (R Core Team, 2016) using the package simecol (Petzoldt and Rinke, 2007). Geographical analyses and visualisation were performed with ArcGIS 10.2.2 (ESRI) and within the R environment with SAGA GIS using the package rsaga (Brenning, 2008)

Results

Habitat conditions and transfer functions

Inundation height, inundation duration as well as flow velocity inside the vegetation belt were higher in the western than in the eastern part of study site A (Figure 4.3a). At study site B, highest values of the three factors occurred in the southern part. Between 2006 and 2010, changes in elevation range between -0.6 and 1.1 m at study site A and between -1.06 and 1.67 m at study site B (Figure 4.3a). Inside the vegetation belt, an increase in elevation was recorded in most parts of both study sites; only in the western part of study site A and in the southern part of site B erosion took place inside the *B. maritimus* belt (see Table A1 in the appendix for a summary of the characteristics of the habitat factors in the two study sites). The response functions (Figure 4.3b and Table A2 & A3 in the appendix) show a hump-shaped response of *B. maritimus* to inundation height and duration, a negative response to flow velocity and a positive response to elevation change. The response of *P. australis* to inundation height and duration, and flow velocity was negative but positive to elevation change. The spatial distribution of the considered habitat factors combined with the response functions resulted for both species in a high habitat quality in front of the actual vegetation belts in the eastern part of study site A and in the northern part of study site B (Figure 4.3c). In the western part of study site A and in the southern part of site B, however, habitat quality was low, even inside the vegetation belt of the two species.

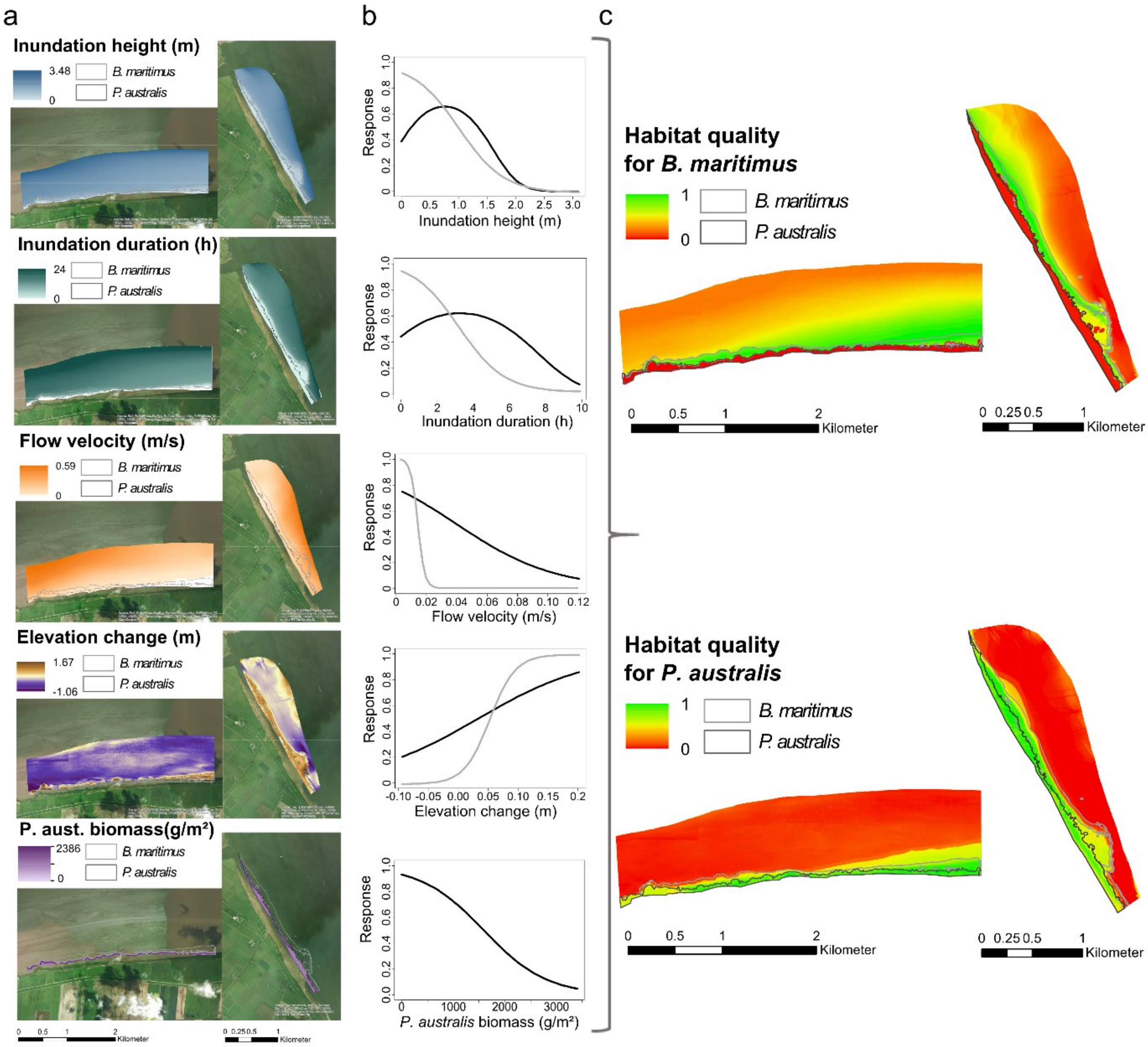


Figure 4.3 Determination of habitat quality for the two species. (a) Spatial distribution of habitat factors exemplary for the 01.01.2006 in the study sites A (left) and B (right). Soil-water salinity was not included in the figure as the mean of all measurements was used per study site. (b) Response functions for *B. maritimus* (black) and *P. australis* (grey). c) Resulting habitat quality for *B. maritimus* and *P. australis* at the study sites A (left) and B (right).Values range from 0 = no habitat, unsuitable conditions to 1 = very high habitat quality.

Model performance

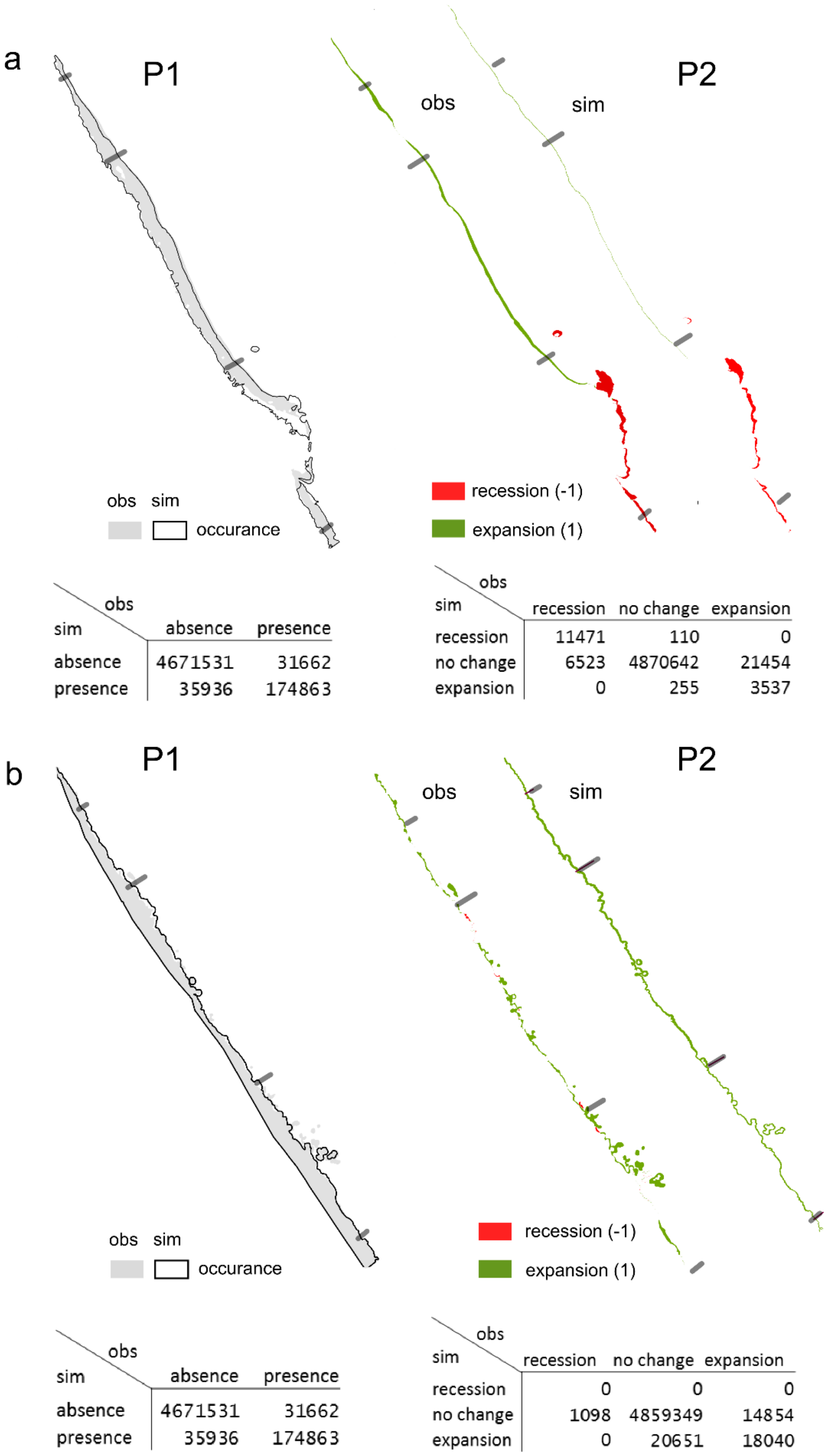
Both, inside the calibration areas and the validation area, the model was able to reproduce most patterns for both species very well (Table). Solely for P2 and P6 the model exhibited performances below 0.5. From Figure 4.4 and Figure , however, can be deduced that the model is none the less able to reproduce these patterns.

Table 4.3 Model performance for both species in the calibration and validation areas.

		B. maritimus		***P. australis***	
Pattern	**Criterion**	**Cal**	**Val**	**Cal**	**Val**
P1	κ	0.92	0.83	0.91	0.9
P2	κ	0.41	0.51	0.61	0.49
P3	ρ	0.79	0.71	0.89	0.74
P4	ρ	0.87	0.66	0.93	0.8
P5	ρ	0.68	0.67	0.93	0.82
P6	ρ	0.49	0.92	0.7	0.3

At the validation area, the model simulated the distribution (P1) of both species in 2010 very well (Table , Figure 4.4). Figure 4.4a shows that the general pattern of expansion and recession (P2) of *B. maritimus* is very well reproduced by the model. The confusion matrix confirms this visual impression, showing no dispersal in the wrong direction (simulated expansion in an area of observed recession or vice versa). Only the species expansion into the tidal flat was underestimated (mean of the transects with expansion: obs = 22 m, sim = 8 m). The *P. australis* vegetation belt expanded in most parts of the study site B (Figure 4.4b), which was reproduced well by the model. Only very small areas of recession were not detected and expansion was slightly underestimated (mean of the transects with expansion: obs = 34 m, sim = 30 m).

The model was in general able to reproduce the amount of belowground and aboveground biomass (P3, P4, P5) of both *B. maritimus* and *P. australis* (Table , Figure). Although the spatial distribution of biomass along the transects (T) was shifted in some cases (e.g. T2-P4, T3-P5), the shapes of the curves were met. However, some disparities between model and data exist. The seasonal development of *P. australis* aboveground biomass (P6) was, for instance, underestimated (mean of all transects: obs = 1744, g/m^2, sim = 959 g/m^2). In T6, there was even no biomass predicted by the model, whereas in T3, the model predicted aboveground biomass where none was observed.



sim \ obs	absence	presence
absence	4671531	31662
presence	35936	174863

sim \ obs	recession	no change	expansion
recession	11471	110	0
no change	6523	4870642	21454
expansion	0	255	3537

sim \ obs	absence	presence
absence	4671531	31662
presence	35936	174863

sim \ obs	recession	no change	expansion
recession	0	0	0
no change	1098	4859349	14854
expansion	0	20651	18040

Figure 4.4 Comparison of observed and simulated species distribution (P1) and dispersal (P2) of *B. maritimus* (a) and *P. australis* (b) in the validation area B and confusion matrices showing the sum of accordances and differences of observed (obs) and simulated (sim) results in each cell.

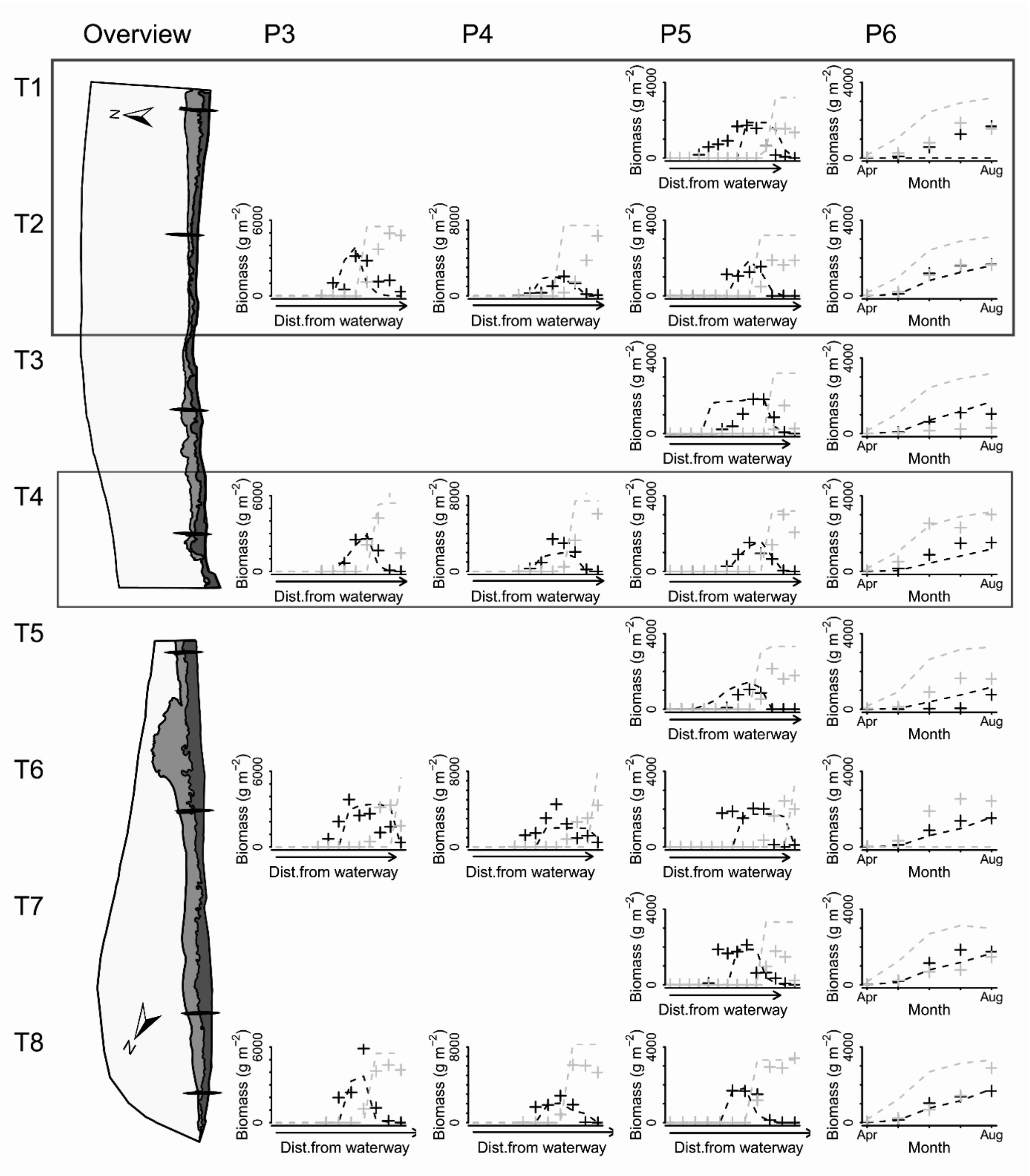


Figure 4.5 Comparison of observed (crosses) and simulated (dashed lines) rhizome (P3), root (P4) and aboveground (P5) biomass along the eight transects (T1-T8) and seasonal development of aboveground biomass (P6) in one plot per species (15 m from the waterward border of the respective vegetation belt) of *B. maritimus* (black) and *P. australis* (grey).

Factors affecting spatio-temporal dynamics of tidal marsh vegetation

Influence of growth parameters

Our sensitivity analysis gave evidence of the influence of each parameter on changes in the regarded patterns. Mortality of the rhizomes ($m_{Rhizome}$) was the most influential parameter for the reproduction of all patterns of *B. maritimus* dynamics (Table a). Growth and expansion rates of the rhizomes ($r_{Rhizomes}$, $e_{Rhizomes}$) were as well very sensitive and thus influential parameters. They had their highest effect on the distribution and expansion of the two species (P1 and P2), whereas ramet and root growth rates (r_{Roots}, r_{Ramets}) mainly influenced the corresponding biomasses (P4, P5). The rhizome biomass (P3) was almost only influenced by rhizome mortality ($m_{Rhizomes}$).

For *P. australis*, parameter sensitivities were distributed very similarly (Table b). The main difference between parameter sensitivities of the two species was that for *P. australis* the rhizome expansion rate ($e_{Rhizomes}$) was very important for explaining rhizome biomass (P3).

Table 4.4 Influence of each parameter on changes in the regarded patterns of *B. maritimus* (a) and *P. australis* (b). Values are the relative proportional parameter sensitivities.

a

Pattern	$r_{Rhizomes}$	r_{Roots}	r_{Ramets}	$e_{Rhizomes}$	trans	$m_{Rhizomes}$
P1	0.30	0.01	<0.01	0.25	0.001	0.44
P2	0.30	0.01	<0.01	0.28	0.001	0.42
P3	0.02	<0.01	<0.01	0.02	0.001	0.96
P4	0.04	0.07	<0.01	0.03	<0.001	0.86
P5	0.10	0.04	0.05	0.12	0.001	0.68
P6	0.24	0.13	0.06	0.09	<0.001	0.49

b

Pattern	$r_{Rhizomes}$	r_{Roots}	r_{Ramets}	$e_{Rhizomes}$	trans	$m_{Rhizomes}$
P1	0.38	0.01	<0.01	0.22	0.002	0.38
P2	0.29	0.01	<0.01	0.27	0.002	0.42
P3	0.19	0.07	0.01	0.43	0.004	0.30
P4	0.22	0.10	<0.01	0.10	<0.001	0.59
P5	0.15	0.09	0.13	0.03	0.001	0.59
P6	0.20	0.01	0.07	0.03	0.001	0.69

Influence of habitat factors

Omitting single habitat factors during model runs showed that all patterns of tidal marsh vegetation were influenced by the regarded factors (Table 4.5a & b). The competition with *P. australis* was of highest importance for the belowground biomass (P3 & P4) of *B. maritimus*. Soil-water salinity had only a very small effect on the rhizome biomass (P3) of this species. Aboveground biomass of *B. maritimus* (P5) and its seasonal development (P6) was only slightly influenced by the considered habitat factors (Table 4.5a). The pattern that was mainly influenced by omitting habitat factors was the dispersal (P2) of *B. maritimus* (Table 4.5a); mainly by flow velocity and inundation height and duration. *P. australis* patterns were mainly influenced by flow velocity (Table 4.5b), however, the measured habitat factors had altogether only a small effect on the spatio-temporal dynamics of *P. australis*.

Table 4.5 Influence of habitat factors on the patterns of spatio-temporal vegetation dynamics for *B. maritimus* (a) and *P. australis* (b) in the validation area (study site B). Values are the relative change of the model performance ($rel.change\ of\ mod.perf$) by omitting the respective factor.

a

Pattern	**Flow velocity**	**Inundation height**	**Inundation duration**	**Elevation change**	**Soil water salinity**	**Biomass of *P. australis***
P1	-0.02	-0.02	-0.02	-0.01	0	-0.01
P2	-1.04	-1.32	-0.89	-0.42	0	0
P3	0.14	0	0.13	0.13	-0.03	-1.15
P4	0.07	-0.1	0.11	0.1	0	-0.65
P5	0.01	0	0.03	0.03	0	-0.05
P6	-0.11	-0.05	-0.05	-0.03	0	0

b

Pattern	**Flow velocity**	**Inundation height**	**Inundation duration**	**Elevation change**	**Soil water salinity**
P1	-0.01	0	0	0	0
P2	0.02	0	0	0	0
P3	0.08	0	0.03	0.03	0
P4	0.08	0	0	0	0
P5	0.06	0	0	-0.01	0
P6	0.17	0	0	0	0

The waterward dispersal of *B. maritimus* (P2) was best reproduced by the full model (Table 4.5a, Figure a). The omission of the effects of elevation change, inundation duration and height as well as flow velocity led to a reduction in the recession of the vegetation belt (Figure b-e). Whereas the full model predicted a maximum of 50 m recession of the vegetation belt, without the effect of elevation change, recession at the same position was only 12 m and without the effect of inundation duration only 6 m. Without the effect of inundation height, no recession occurred at that position (Figure d) and without the effect of flow velocity the vegetation even expanded 2 m into the tidal flat (Figure e).

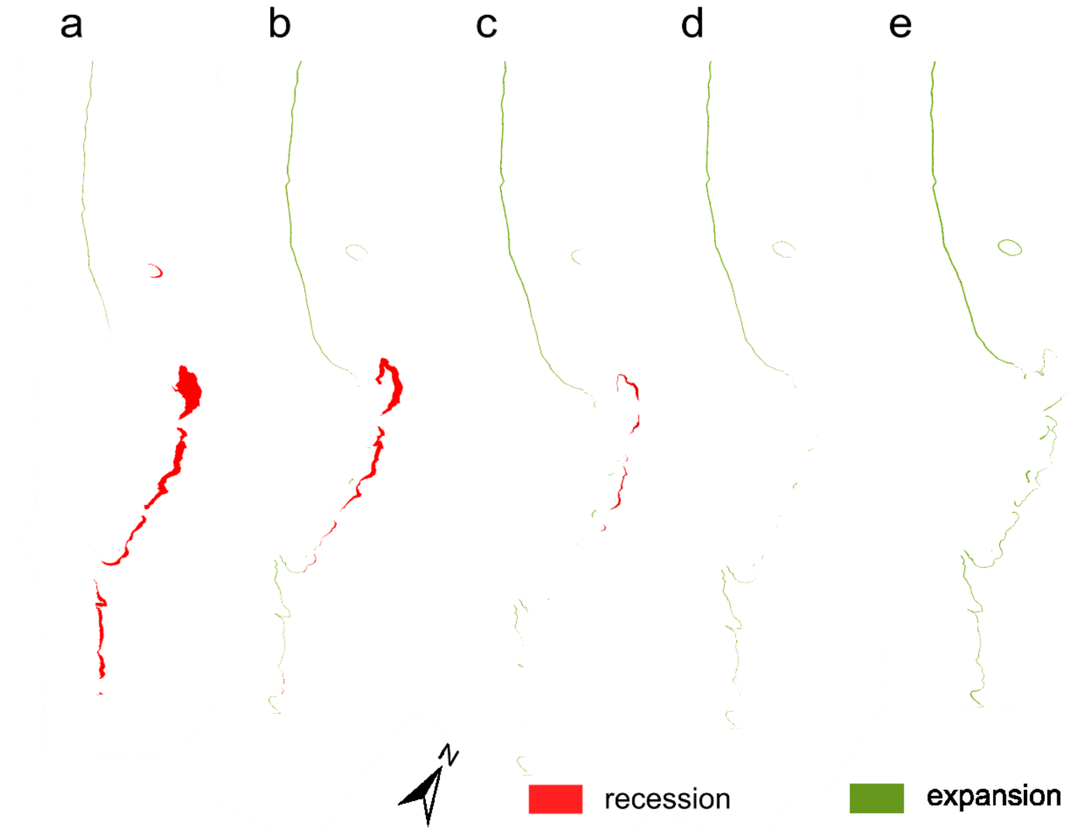


Figure 4.6 Effect of the habitat factors on waterward dispersal (P2) of *B. maritimus.* a) full model i.e. all habitat factors included, b) without elevation change c) without inundation duration, d) without inundation height, and e) without flow velocity. All illustrations comprise the southern part of study site B.

Discussion

The dynamic habitat-macrophyte model HaMac shares features with a previously developed, relatively simple, grid-based model (Wortmann et al., 1997), but also comprises elements of more complex and detailed growth models (Asaeda and Karunaratne, 2000; Soetaert et al., 2004) by e.g. incorporating temperature effects and seasonality. Compared to other modelling approaches (e.g. Sanderson et al., 2001; Visser et al., 2013), HaMac explicitly simulates the dynamic of marshes by considering the vegetative reproduction of macrophytes as well as abiotic influence factors and intraspecific competition. Our model thus allows analysing the effect of these factors on the growth and dispersal patterns of tidal marsh vegetation.

Model performance

The comparison of simulated and observed patterns of vegetation zonation, development and growth in brackish marshes of the Elbe estuary showed that the model is able to reproduce these patterns. This demonstrates an appropriate model structure, the consideration of the most important processes and a valid parameter combination (Grimm et al., 2005). Another reason for the good model performance is the comprehensive parameter calibration which was enabled by the collection of an extensive set of field data.

Above- and belowground biomass have been measured on a plot scale (0.25 m^2). It is important to take into account that these data have been collected locally and thus spatial representativity is limited while spatial variability is high. Consequently, an exact reproduction of these patterns is neither feasible nor required. The seasonal development of aboveground biomass, a temporal pattern, was as well based on local measurements and proved to be very important to verify and optimise the implementation of phenology. The mismatches of observed and simulated seasonal development of aboveground biomass of *P. australis* in transect 6 and transect 3 cannot be attributed to mistakes in the implementation of phenology, but are due to underestimation or overestimation of the dispersal of *P. australis* in these areas. This misestimate of *P. australis* dispersal could be due to the low influence of the implemented habitat factors on the spatio-temporal dynamics of *P. australis* which suggests that other factors than the ones considered here drive the dispersal of this species.

Factors affecting spatio-temporal dynamics of tidal marsh vegetation

A sensitivity analysis provides detailed insights into parameter importance, allows the verification of model structure for the research question (Aronica et al., 1998) and the identification of driving parameters (Cariboni et al., 2007). Vegetative reproduction is known to be the main dispersal path of clonal plants (de Kroon and Visser, 2003). However, many existing marsh vegetation models do not explicitly consider vegetation dispersal (e.g. Sanderson et al., 2001; Visser et al., 2013). Our results show that incorporating processes like vegetative growth helps gaining a clearer picture of the reasons for the recession and expansion of the tidal marsh vegetation. For the parametrisation of HaMac, all patterns were regarded at the same spatial position as the field measurements. Hence, their reproduction depends on the correct simulation of the location of the vegetation belt, and the central importance of the rhizome parameters seems very plausible. Recession of the vegetation belt is achieved by rhizome mortality ($m_{Rhizomes}$), whereas rhizome growth rate ($r_{Rhizomes}$) and expansion rate ($e_{Rhizomes}$) are together responsible for vegetation expansion. It is thus reasonable that rhizome mortality is more influential, than the other two parameters on their own. Added up, however, rhizome growth and expansion rate are more important for the distribution and dispersal of the two species (P1 & P2) than rhizome mortality.

The omission of single habitat factors allowed estimating their effect on the spatio-temporal patterns of tidal marsh vegetation. The relative change in model performance (Table 4.5) was used to rank the effect of the different habitat factors, but should not be understood as a quantitative measure. This is especially important, as the collinearity of some of the habitat factors implies that the omission of one does not only reflect the influence of this specific factor. The high importance of flow velocity, as well as inundation height and inundation duration for

B. maritimus (Table 4.5a) agrees with previous findings (Asaeda et al., 2005; Heuner et al., submitted.; Roberts and Ludwig, 1991). An increase in tidal inundation often leads to landwards retreat of the vegetation belt (Geselbracht et al., 2011; Raabe and Stumpf, 2016) and in riparian systems, flow regulation allows for vegetation expansion (Poff et al., 1997).

Due to the collinearity of some of the habitat factors, a very similar effect could have been expected when omitting theses. However, omitting elevation change and inundation duration led to a reduction in the recession of the *B. maritimus* belt (P2) (Figure 4.6), whereas, with the omission of inundation height as influencing factor, the vegetation belt did not withdraw at all. Without the effect of flow velocity, *B. maritimus* even expanded in the same areas, suggesting that flow velocity is the main reason for vegetation recession at exposed locations. Nevertheless, the omission of flow velocity does not have the highest negative effect on model performance for the waterward dispersal of the vegetation belt (Table 4.5a, P2). This is due to the fact that the underestimation of the expansion of the *B. maritimus* belt was lower without this factor.

Further research needs and possible future model applications

Despite the above mentioned good model performance, some aspects could be improved for subsequent model applications. (1) The simulation of habitat conditions took place in different levels of detail. Because we had a detailed digital elevation model, we were able to calculate inundation height and duration in high spatial resolution from the coarse point grid of the HAMSOM data. More problematic was the calculation of flow velocity, because input data from HAMSOM do not consider vegetation. By applying a function parametrised by own measurements (Carus et al., 2016), we were able to estimate vegetation effects on flow velocity. This estimation, however, contains a high level of uncertainty and could not be validated within this study. (2) Furthermore, although erosion of the shore is of high relevance for the development of marsh vegetation (Kirwan et al., 2016b; Mariotti and Fagherazzi, 2010), elevation change was so far included in the model in a rather simplified way by calculating the difference between two successive elevation measurements. Additionally, we only considered elevation change as predictor variable and did not directly implement marsh accretion. As it is widely known that marshes can rise vertically by building up organic and inorganic matter on the marsh surface (French, 2006; Kirwan and Megonigal, 2013), the model should not be used for the simulation of sea level rise scenarios without an explicit implementation of this accretion process. (3) As soil-water salinity only slightly influences vegetation growth in brackish marshes (Lissner and Schierup, 1997) and no local gradients were discovered within the study sites, we considered the assumption of a mean value per study site as sufficient. However, when using data from a wider salinity gradient, soil-water salinity should be considered in a higher spatial resolution. (4) Even though wave action influences biomass production and dispersal of the two emergent macrophytes (Coops et al., 1994; Heuner et al., 2015; Silinski et al., 2015), could so far not consider their effect due to a lack of relevant input data. (5) Because of the collinearity of some of the considered habitat factors, the response functions were constructed via univariate GLMs and combined via a model averaging approach (Bates and Granger, 1969). This has the advantage of avoiding to lose the complementary information, the additional parameters might provide and allowing the evaluation of the individual effect of each habitat factor. (6) Other approaches of modelling tidal marshes that also integrate ecological with physical modelling already exhibit a more detailed representation of hydrodynamics and morphology (e.g. Temmerman et al., 2005). However, most of these models do not explicitly consider spatial vegetation dynamics, but for example use species distribution models to predict vegetation distribution (Cozzoli et al., 2017) or simply calculate biomass as a function of the elevation relative to the tide (Mariotti and Fagherazzi, 2010; Wang and Temmerman, 2013). A combination of these more detailed representations of the abiotic surroundings with the explicit consideration of vegetation dynamics as proposed here could help improve model results. (7) The transfer of correlative species distribution models to new environments only yields reliable predictions, if the new environmental range was already covered by the training data so that predictions are not extrapolated (Elith and Graham, 2009; Zurell et al., 2012). Process-based models by contrast provide the possibility to explicitly represent environmental range shifts in the model (Kearney et al., 2009; Morin and Thuiller, 2009). However, the choice of parameters is usually tailored to certain species and environments and thus, there are not many comparative studies transferring process-based models (Dormann et al., 2012). Because the application of HaMac in the validation area yielded very good model performances for most patterns, we deduce that the model is also transferable to other study sites. By using a modular model structure with univariate transfer functions coupling habitat conditions and vegetation growth, the parametrisation of the vegetation part of the model is valid under a wide range of environmental conditions. The fitting of new response curves would thus allow transferring HaMac to new environmental ranges and even to areas with different relevant processes as long as the species composition remains constant. For the simulation of different species, the model would have to be newly parameterised. (8) The dynamic habitat-macrophyte model HaMac already proved to be a valuable tool for gaining insight in and testing hypotheses on the influence of habitat factors on the spatio-temporal distribution of two tidal marsh species. However, the very good validation results also allow applying the model for the simulation of habitat change scenarios. Hereby, general statements on the dynamics and structure of the foreland vegetation could be made, as well as areas identified that respond particularly sensitive to changes. Global warming will lead to changes in air temperature, water levels, further increase of the tidal amplitude and a resulting shift of the salinity zones (Chua and Xu, 2014; Seiffert and Hesser, 2014). HaMac can help estimating how changes in air temperature could affect biomass production and assess the impact of changes in water salinity of the Elbe estuary. After integrating the process of marsh accretion, e.g. by coupling the existing model with a model of tidal marsh accretion (e.g Kirwan and Murray, 2007; Temmerman et al., 2003), even sea level rise scenarios could be simulated with HaMac. (9) By reducing flow velocity (Christiansen et al., 2000; Leonard and Luther, 1995), attenuating waves (Barbier et al., 2008; Gedan et al., 2010) and serving as erosion control for riverbanks (Coops and Van der Velde, 1996), tidal marshes can play an important role in ecosystem-based shoreline protection systems (Temmerman et al., 2013). However, extensive embankments and artificial bank protection threaten the structure, species composition and functionality of tidal marshes (Temmerman et al., 2013). By simulations with HaMac, the effect of such conventional engineering projects, as well as the implementation of restoration measures on the dynamic of tidal marsh vegetation could be quantified and evaluated as well as the suitability of sites for management plans could be tested beforehand. Hence, the application of HaMac could support the sustainable development of shore zones and thus contribute to the promotion and planning of ecosystem-based shoreline protection systems.

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5

Synthesis

Jana Carus

Key findings of this thesis

Feedbacks between vegetation and habitat have an important influence on landscape evolution. Tidal marshes represent a clear example of the interplay between hydrodynamical, morphological and ecological dynamics (D'Alpaos et al., 2007). There are, however, few studies that take into account both sides of the interaction of vegetation and habitat in brackish marshes.

The main objectives of this study were (1) to explore the possibility of the vegetation serving as self-adaptive shore protection by quantifying the reduction of current velocity and the morphologic plasticity of a brackish marsh pioneer, (2) to disentangle the roles of abiotic factors and interspecific competition on species distribution and plant traits in brackish marshes, and (3) to develop a mechanistic vegetation model that helps analysing the influence of abiotic habitat conditions on the spatio-temporal dynamic of tidal marsh vegetation.

The present work provides many insights into habitat-plant interactions from field research and modelling:

1.1 The vegetation belt of the marsh pioneer *Bolboschoenus maritimus* is able to buffer a large proportion of the flow velocity under non-storm conditions. The net reduction of normalised flow velocity was higher for long-shore than for cross-shore velocity. Flow velocity decreased with distance from the marsh edge and 15 m into the vegetation, cross-shore flow velocity was reduced by more than 50%, and long-shore flow velocity was reduced by about 70%.

1.2 Plants growing at the more exposed marsh edge had a significantly larger stem diameter than plants from inside the vegetation belt. Plant diameter was positively correlated with cross-shore current when comparing only plots from the marsh edge.

1.3 Biomechanical measurements proved a positive correlation between plant thickness and plant stability: Plants from the front of the vegetation belt had a greater bending stiffness than plants from inside the vegetation, and a significantly higher force had to be applied on them before breakage.

2.1 Flow velocity was the main factor controlling the distribution of *B. maritimus* and *P. australis*. Additionally, inundation height and duration as well as intraspecific competition affect distribution patterns. Soil-water salinity had no direct effect on the distribution of the two marsh species.

2.2 Cross-shore velocity and soil-water salinity negatively influenced the position of the waterward vegetation fringes of both species relative to inundation duration, whereas the position of the fringe of the vegetation belts relative to inundation height was only affected by cross-shore flow velocity.

2.3 *B. maritimus* exhibited a different height-weight relationship of plants from the waterfront fringe of the vegetation belt and plants from inside the vegetation belt.

2.4 Analysing six stand characteristics revealed that most properties of *B. maritimus* increased with distance from the marsh edge and decreased with the start of the *P. australis* vegetation belt; only ramet height further increased. Most *P. australis* characteristics increased over large parts of the gradient, and only slightly decreased towards the end of the vegetation belt; here, only rhizome biomass strongly decreased.

2.5 Flow velocity negatively affected all stand characteristics of *B. maritimus*. Furthermore, normalised inundation influenced all parameters except for root and rhizome biomass. The response to this factor was unimodal. Soil-water salinity negatively affected the parameters aboveground biomass and ramet height. The most important factor for aboveground biomass and ramet density of *B. maritimus* was the biomass of *P. australis* with a negative effect; it was also important for belowground biomass.

3.1 The dynamic habitat-macrophyte model HaMac developed within the framework of this thesis was very well able to simulate the spatio-temporal dynamics of the tidal marsh vegetation.

3.2 A sensitivity analysis of the model parameters suggests that rhizome growth is the key process for the lateral dynamics of brackish marshes. For both species, mortality of the rhizomes was the most influential parameter followed by rhizome growth and expansion rates.

3.3 The competition with *P. australis* was of key importance for the belowground biomass of *B. maritimus*. Soil-water salinity had only a very small effect on the rhizome biomass of this species. Aboveground biomass of *B. maritimus* and its seasonal development was only slightly influenced by the considered habitat factors.

3.4 *P. australis* patterns were mainly influenced by flow velocity. However, the measured habitat factors had altogether only a small effect on the spatio-temporal dynamics of *P. australis*.

3.5 Omitting the effects of elevation dynamics, inundation duration and height as well as flow velocity from the full model entailed a reduction in the recession of the vegetation belt. Whereas the full model predicted a maximum of 50 m recession of the vegetation belt, without the effect of elevation dynamics, recession at the same position was only 12 m and without the effect of inundation duration only 6 m. Without the effect of inundation height, no recession occurred at that position and without the effect of flow velocity the vegetation even expanded 2 m into the tidal flat. The waterward dispersal of *B. maritimus* was best reproduced by simulations with the full model.

Overall, the presented work contributes to a better understanding of the effect of habitat on species distribution, stand structure and dynamics and improves our knowledge of how marsh vegetation reduces flow velocity.

Studying habitat-plant interactions

Plant-habitat feedbacks are changes to abiotic properties that are caused by vegetation and in turn influence the performance of plants. For instance, plant growth and the consequent water absorption changes soil moisture, but at the same time depends on soil moisture (Müller et al., 2014). These plant-habitat interactions do not only influence growth and distribution of the plant species in question, but also affect individuals of other species and influence whole ecosystems and landscapes.

Brackish marsh vegetation is strongly related to its abiotic habitat. Belowground biomass interacts with soil stability (Bouma et al., 2014; Silliman et al., 2012), aboveground biomass interacts with current and wave energy. By exerting drag on the water, aboveground vegetation parts reduce hydrodynamic forces (Bouma et al., 2005a, b; Widdows and Brinsley, 2002) and by this means affect sedimentation and erosion processes. At the same time, the reduced flow facilitates plant growth (Bruno, 2000; van Wesenbeeck et al., 2008), resulting in a positive feedback between plant growth, flow reduction and sedimentation. Studying tidal environments requires characterising the strong interaction among dynamical processes of physical and biological nature. The interaction of plants and their hydrological habitat is one of the key topics of ecohydrology (Müller et al., 2014). However, methods to analyse ecohydrological feedbacks are only beginning to develop (Asbjornsen et al., 2011; Turnbull et al., 2012) and only few models incorporate implicit numerical links of ecohydrological feedbacks (Müller et al., 2014).

In this thesis, I studied plant-habitat interactions by analysing the effect of brackish marsh vegetation on flow velocity and the response of brackish marsh vegetation to habitat conditions. In Chapter 2, I focused on the flow dampening potential of aboveground vegetation and its adaptation to the mechanic stress of currents. Flow velocity was reduced significantly by living above ground vegetation (Chapter 2) and in turn affected morphological plant traits and vegetation distribution (Chapter 2, 3). To consider effects and responses in a cyclic manner, I developed a dynamically coupled model system (Chapter 4).

Effect of brackish marsh vegetation on flow velocity

Plant-habitat interactions are of substantial importance for river hydrodynamics. By exerting drag on the flow, the presence of plants strongly reduces current velocity inside the vegetation (Neumeier and Ciavola, 2004). The degree of flow reduction depends on the amount of dampening plant mass, thus on vegetation type, vegetation height and density and width of the vegetation belt (Christiansen et al., 2000; Leonard and Luther, 1995; Neumeier and Ciavola, 2004). In Chapter 2 the flow reduction effect of *B. maritimus* vegetation was directly analysed. In contrary to other studies (e.g. Christiansen et al., 2000; Leonard and Croft, 2006; Leonard and Luther, 1995), the measurement design presented in Chapter 2 permitted the comparison of current velocity at the same site with and without living vegetation. Furthermore, cross-shore currents were considered additionally to long-shore currents which allowed a direct comparison between the two. Flow velocity in vegetation is inversely related to distance from open water (Christiansen et al., 2000). The study presented in Chapter 2 demonstrates a distinct difference between velocities in front of and inside the vegetation belt and a decrease of cross-shore flow velocity with distance from the marsh edge into the marsh. This is in line with Leonard and Luther (1995), who discovered that mean flow velocity and flow energy inside vegetation are reduced by the plants' dampening of large scale eddies. The results of Chapter 2 thus confirm that the vegetation is able to buffer a large part of the approaching current velocity.

Response of brackish marsh vegetation to flow velocity

The results from this thesis suggest that flow velocity strongly affects tidal marsh vegetation. In the presented studies, flow velocity not only affected the morphology of *B. maritimus* ramets, but also proved to be very important for marsh zonation and vegetation dynamics, as well as stand characteristics of *B. maritimus*.

Plants can adapt to stress by morphological adjustments (Clausen et al. 1948; Richards et al. 2005). For submerged plants, it has been shown that current often has an adaptive effect on growth traits (Puijalon et al., 2005; Puijalon and Bornette, 2004; Szmeja and Galka, 2008) by either minimising mechanical forces or increasing resistance to mechanical failure (Puijalon et al., 2008, 2005). This can in some cases lead to a greater ability to withstand hydrodynamic forces induced by water movement (Puijalon et al., 2005). Maximum stability can for instance be an important functional trait to avoid breaking of plants growing under hydrodynamically stressful conditions. The study described in Chapter 2 confirms that morphological traits of plant species can be adapted to hydrodynamic forces by showing a positive correlation between ramet thickness and cross-shore current. The performed measurements furthermore revealed that the thicker ramets growing at the front of the vegetation belt have a significantly higher bending stiffness, and a higher force has to be applied for breaking the ramets than inside the vegetation belt. This self-adaptive effect increases the ability of *B. maritimus* to grow and persist in the pioneer zone and could provide an adaptive value in habitats with high mechanical stress.

Previous work shows that a variety of abiotic factors also affect the occurrence and vitality of the vegetation of a tidally influenced marsh (e.g. Baldwin et al., 1996; Coops et al., 1999, 1996). Many studies propose that elevation is the most important factor for marsh zonation (Adams, 1963; Keddy, 2010; Smith, 2015), suggesting that the higher inundation tolerance of *B. maritimus* is the main reason for the distinct zonation of *B. maritimus* and *P. australis*. However, Heuner et al. (2016) found differences in the elevational response of *P. australis* and

B. maritimus with exposure. In accordance with other studies (Coops et al., 1994; Coops and van der Velde, 1996; Heuner et al., 2016), the study presented in Chapter 3 shows that cross-shore flow velocity does not only directly influence the distribution of the two marsh species, but also alters the plants' occurrence relative to inundation height and duration. This suggests a possible effect of cross-shore flow velocity on their tolerance to inundation.

By providing detailed information on the importance of single habitat factors for the growth of the two plant species, the investigation of stand characteristics helps to better understand and predict the vegetation zonation patterns in marshes (Shi et al., 2015). The analysis of the measured stand characteristics revealed a negative effect of total flow velocity on all measured parameters and thus confirmed the results from Chapter 2 and the subsequent expectation that flow velocity is a decisive stressor which influences the growth of *B. maritimus.*

An increase in tidal inundation often leads to a landwards retreat of the vegetation belt (Geselbracht et al., 2011; Raabe and Stumpf, 2016); whereas flow reduction in riparian systems leads to expansion of vegetation (Poff et al., 1997). Concerning vegetation dynamics, the results from the dynamic model HaMac (Chapter 4) emphasise that without the effect of flow velocity the vegetation would expand into the tidal flat at locations with present vegetation recession, suggesting that flow velocity is the main reason for vegetation recession at exposed locations.

Potential of brackish marshes for ecosystem-based shore protection – Implications and perspectives

Plant-habitat interactions shape the overall performance of river ecosystems (Albayrak et al., 2014) and thus the potential for tidal marshes to serve as ecosystem-based shore protection. The findings of the three studies presented in this thesis are an important step forward towards understanding the interaction of tidal marsh vegetation and its habitat, but also give rise to new research questions.

In the framework of this thesis, I developed and tested a dynamic process-based model which proved to be a valuable tool for gaining insights in and testing hypotheses on the influence of habitat factors on the spatio-temporal distribution of two tidal marsh species (Chapter 4). This model is now available for testing new hypotheses and simulating habitat change scenarios. In Chapter 4 I already discussed potential model applications for climate change and management scenarios; here I want to point out, how the dynamic habitat-macrophyte model HaMac can in combination with designed experiments contribute to solve further research questions.

Marsh communities were long believed to be regulated by abiotic processes, such as elevation, hydrodynamic conditions and water salinity (Mitsch and Gosselink 2008). However, experiments have shown that biotic interactions such as competition (Bertness 1991) and facilitation (Hacker and Bertness, 1995) among marsh plants are also important factors in controlling marsh zonation (Barbier et al., 2011). At exposed shores, *P. australis* grows behind a protective belt of pioneer vegetation, whereas in calm water bodies, it also occurs at the marsh edge (Coops and van der Velde, 1996; Heuner et al., 2016). This leads to the assumption, that the reduction of flow velocity by *B. maritimus* facilitates the growth of *P. australis*. Despite a high interest in positive and negative species' interactions, the facilitation effect of pioneer vegetation in brackish marshes under differing environmental stresses is still not sufficiently quantified. This effect was considered in Chapter 4 by calculating flow reduction by above-ground plant parts of *B. maritimus* resulting in high habitat quality for *P. australis* inside most of the *B. maritimus* vegetation belt. A future model application could thus be, to quantify the facilitation effect of *B. maritimus,* by omitting the influence of the *B. maritimus* vegetation belt on flow velocity. Engels and Jensen (2010) conducted reciprocal transplant experiments of *B. maritimus* and *P. australis* at two tidal elevations at salt and freshwater marshes. To test for facilitation and competition, the transplants were conducted with and without neighbouring vegetation. A similar experiment along different exposition gradients could support the model results.

In Chapter 3 I showed that statistical models provide a valuable instrument for identifying the drivers of marsh zonation and for quantifying their effects on stand characteristics. However, although the predictor variables in these correlative models are supposed to represent causal mechanisms (Austin, 2002), an often cited drawback of these models is that they do not explicitly consider processes (Araújo and Guisan, 2006; Zurell et al., 2009). As indicated in Chapter 4, mechanistic models are a helpful tool to evaluate the ecological processes underlying patterns in animal and plant distribution (Grimm et al., 2005). However, the extent to which mechanistic models represent processes explicitly can vary considerably (Dormann et al., 2012). More knowledge on the importance to consider single processes and the required detail of their integration would be valuable information, because process-based models often require a large amount of data for parameterising the implemented processes. In a more theoretical framework, this could be evaluated by another model experiment.

Tidal marshes play an important role for shore protection (Kirwan and Megonigal, 2013; Temmerman et al., 2013). By taking up and holding more water than unvegetated mudflats, marshes are likely to reduce storm surge duration and height (Barbier et al., 2011). Furthermore, marsh vegetation dampens hydrodynamic energy and thus reduces shoreline erosion and increases sedimentation (Neumeier and Ciavola, 2004). With the reduction of current velocity and the attenuation of waves (Christiansen et al., 2000; Temmerman et al., 2005), marsh vegetation can also diminish the destructive effects of storm surges and storm waves (Möller et al., 2014; Wamsley et al., 2010).

The incorporation of marshes into shore protection schemes is challenging also because it requires a thorough understanding and quantification of current reduction under different flow conditions. The results from Chapter 2 demonstrate that the marsh pioneer *B. maritimus* strongly reduces current velocity under normal, i.e. non-stormy, conditions. From the performed measurements it is, however, not reasonable to draw conclusions for storm surge conditions with much higher current velocities and water levels, as the decrease of the flow reduction potential is non-linear. That is, among other facts, because under storm surge conditions, the pioneer vegetation is completely submerged which enormously reduces the flow reduction potential (Leonard et al., 2002). Permanent wave and flow measurements could help to quantify the shore protection potential under storm surge conditions.

Apart from hydrodynamic conditions, feedback mechanisms between mechanical stress and plant traits affect the shore protection potential of marsh vegetation (Bouma et al., 2005; Möller, 2006). The study presented in Chapter 2, shows that ramets growing at the marsh edge were significantly thicker and thus more stable than ramets inside the vegetation belt. I propose that this could be a morphological adaptation to the stress of current velocity, which provides an adaptive value in habitats with high mechanical stress. The ability of plants to adapt to environmental conditions (Clausen et al., 1948; Richards et al., 2005) could thus enhance the resistance of the whole vegetation belt against the mechanical stress of current velocities. Reciprocal transplant experiments of ramets from the marsh edge and from inside the vegetation belt could undermine the proposed causalities.

Another important aspect for evaluating the shore protection potential of *B. maritimus* is how the adapted plant growth affects flow reduction. Heuner et al. (2015) found that although biomass had a higher effect on wave attenuation than plant morphology, stiffer stems have a greater ecosystem-engineering effect than flexible stems. Furthermore, the experienced drag forces depend on the frontal area of obstacles (Henry and Myrhaug, 2013; Nepf and Vivoni, 2000; Vogel, 1994). Thus, with a higher diameter of single plants, drag force rises and hydrodynamic forces are dissipated to a larger extent (Heuner et al., 2015; Möller et al., 2011). Whether this self-adaptive effect of pioneer plants contributes to ecosystem-based shore protection could be verified in flume experiments by comparing the flow reduction of ramets with different diameters.

By (i) identifying the drivers of marsh zonation, stand characteristics and marsh dynamics, (ii) quantifying their effects and thus (iii) helping to evaluate future marsh development, Chapters 3 and 4 provide further valuable information for evaluating future contributions of tidal marsh vegetation to ecosystem-based shore protection. The results of Chapter 3 and 4 lead to the conclusion that the future zonation of tidal marsh vegetation will not only be affected by potential water level changes, but that an increase in hydrodynamic forces as well as an upstream shift of salinity zones could add direct and indirect effects. Although the systematic observations presented in Chapter 3 suggest an effect of cross-shore flow velocity and soil-water salinity on the species tolerance to inundation, transplant experiments along elevation, salinity and exposure gradients could inform on causalities. This would be of high importance, as higher and longer inundation combined with a lower inundation tolerance would then negatively affect distribution and stand characteristics of tidal marsh vegetation and reduce their potential as ecosystem-based shore protection.

Although conventional engineering provides effective flood and erosion protection on short to intermediate time scales, it at the same time disturbs natural delta processes and thus accelerates local water level rise and increase long-term flood risks (Temmerman and Kirwan, 2015). An intact marsh vegetation, however, promotes natural accretion of sediments and has the ability to adapt to projected sea level changes (Kirwan et al., 2010). Temmerman et al.

(2013) argued that the maintenance of conventional coastal engineering solutions may become unsustainable with increasing flood risk propelled by rising sea levels and therefore, the creation or restoration of coastal ecosystems could improve and support conventional levee structures. In Chapter 4 of this thesis I focussed on lateral marsh dynamics and did not directly implement marsh accretion.

This this thesis substantially contributes to a better understanding of plant-habitat interactions and lateral dynamics of tidal marshes and thus their potential to serve as ecosystem-based shore protection, and highlights the need for additional process-level research. Integrating studies of vertical marsh accretion with research on the factors that control the lateral position of marshes thus represents a key research focus in further studies on tidal marsh stability and value (Kirwan and Megonigal, 2013).

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Author's declaration

I prepared this dissertation myself and without any illegal assistance. The work is original except where indicated by references in the text and no part of the dissertation has been submitted for any other degree.

This dissertation has not been presented to any other university for examination, neither in Germany nor in any other country.

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