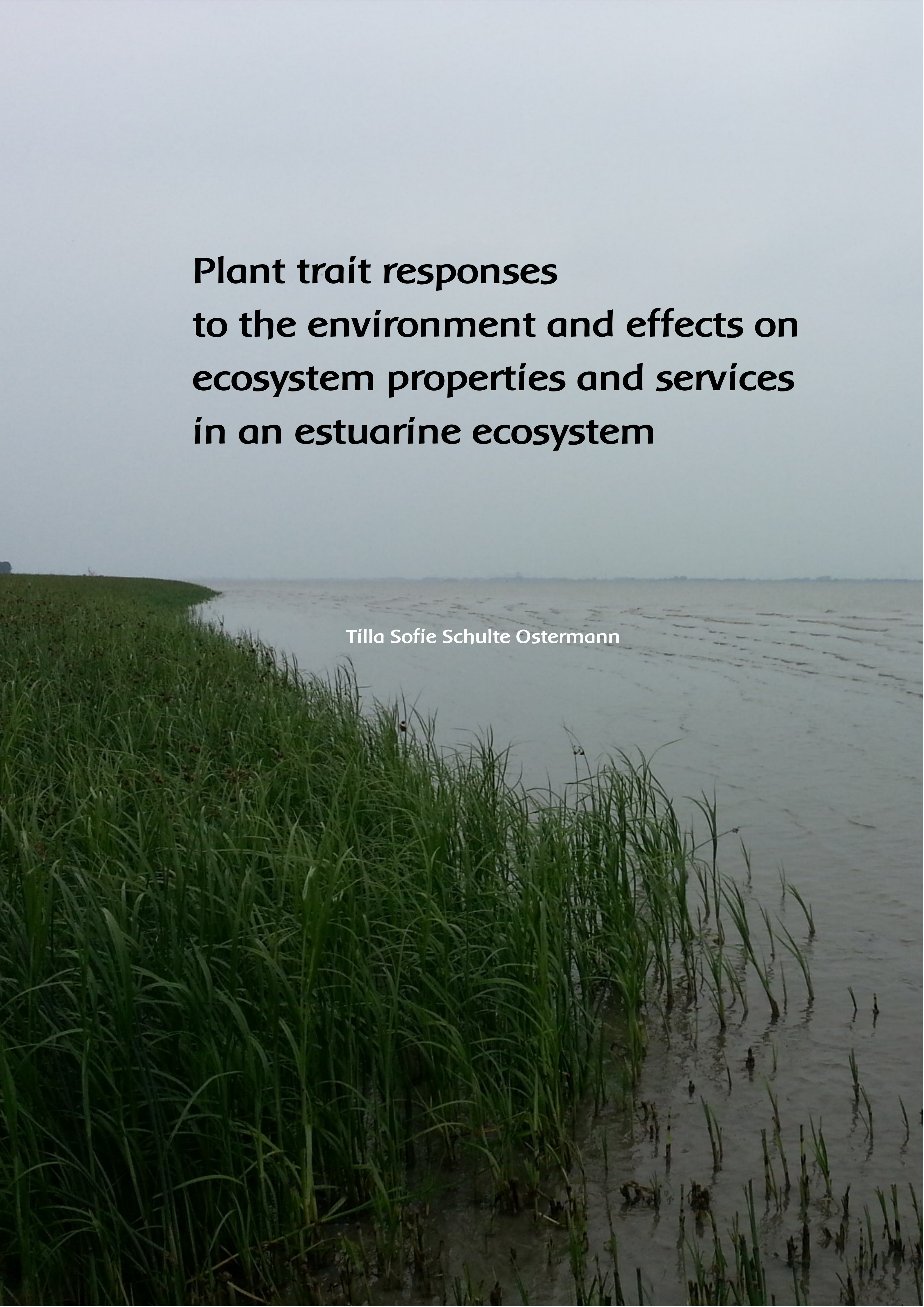


Plant trait responses to the environment and effects on ecosystem properties and services in an estuarine ecosystem

Tilla Sofie Schulte Ostermann

This research was funded by the German Federal Institute of Hydrology (BfG) in line with its R&D-Project TIBASS (Tidal Bank Science and Services) and carried out in cooperation with the University of Antwerp (Belgium).

Plant trait responses to the environment and effects on ecosystem properties and services in an estuarine ecosystem

Von der Fakultät für Mathematik und Naturwissenschaften
der Carl von Ossietzky Universität Oldenburg zur Erlangung des Grades und
Titels einer Doktorin der Naturwissenschaften (Dr. rer. nat.)
angenommene Dissertation von Frau

Tilla Sofie Schulte Ostermann

geboren am 04. August 1982 in Schönbek

Oldenburg 2020

Gutachter: Prof. Dr. Michael Kleyer

Zweitgutachter: Prof. Dr. Boris Schröder-Esselbach

Tag der Disputation: 23.03.2021

Content

Summary

Tidal wetlands are under threat worldwide, due land use practices, aquaculture, infrastructure, industry and activities around harbours. The need to elaborate the relationship between environmental drivers, the vegetation and its traits, the ecosystem properties and services is urgent in order to be able to protect and re-establish tidal marshes and communicate their value regarding delivered ecosystem services. To this cause, the present study is focusing on environmental drivers, species distribution and species trait expression in response to the environment and in their effect on ecosystem properties. As a model for temperate tidal wetlands, the research sites were placed in the Elbe estuary. The Elbe is mesotidal and salinities in the study sites changed with the rhythm of the tide, depending on the proximity to the sea and the distance to the marsh edge. The environmental gradients create a very dynamic system for the vegetation, with sometimes high waves (generated by wind and ships) and changing availability of light and oxygen due to the inundation regime. On 84 plots, soil samples were analysed, and hydrological data recorded based on different elevations. Trait information of the most abundant 17 species was gathered by collecting the whole plant and analysing all organs regarding mass, volume per mass, density, dry matter content, leaf area, specific leaf area, specific length and nutrient content.

The results showed that as a response to incoming waves, stem bending stiffness close to the water was low and plants showed high proportional investment into belowground organs. The low density of the belowground organs was probably connected to low oxygen availability due to long hydro periods. Neither the soil nutrients nor the salinity (other than affecting species composition) played a major role for the distribution of traits in the study area. The hydrodynamics caused a strict selection of species and traits – nutrient related responses were probably of minor importance.

Above the mean tidal high-water level, the vegetation was characterized by tall and stiff plants, with a substantial investment into stems and leaves. Here, with inundation and waves having less of an impact, traits regarding competition for light became essential. The leaf area was larger, due to less drag forces experienced. The species invested heavily into stems, in order to capture the available light, resulting in high overall biomass. There were strong correlations between traits detectable across all elevations. Mass investment was scaled proportionally, biomass density below- and aboveground correlated, with stem stiffness as well as dry matter content and stoichiometry. This highlighted the effect that trait responses and trait-trait interactions have on ecosystem properties.

Regarding the ecosystem property of biomass production, there was less aboveground community biomass (AGB) close to the tidal flat, where the incoming waves were high. This was

a consequence of the hydrodynamic gradients impacting on plant size and material density and leaf area. On higher elevations, the wave impact was lower and species stems were less bendy, with plants producing a high amount of biomass. The AGB, stem and leaf traits played an essential role in the delivery of the vegetation driven ecosystem service of wave attenuation. The reduction of wave height protects tidal banks and embankments from hydrodynamic forces and resulting erosion or flooding. Because of lower stem biomass density on low elevations (correlated with less stiff stems), the wave attenuation was smaller on the low bank. Stems moved with the currents rather than withstanding them. The first species after the open tidal flat, *Schoenoplectus tabernaemontani*, had bendy stems with low biomass aboveground and a proportionally high investment belowground. With stiffer stems withstanding waves and higher biomass on higher elevations, where *Bolboschoenus maritimus* grew in dense stands, wave attenuation was larger. The leaf area and the leaf dry matter content (which was lower on low elevations) also affected the attenuation of waves with a larger area causing more attenuation. Another important ecosystem service delivered by the vegetation is carbon sequestration in soils, reducing atmospheric CO_2 levels, mitigating climate change. Tidal marshes, because of the high biomass productivity, have a great potential to sequester carbon. In the study sites, this service was influenced by stem and leaf traits and the ecosystem property of decomposition. Decomposition was negatively influenced by stem traits on one hand and controlled by the environmental conditions on the other hand. Inundation duration and salinity were shown to have a strong negative effect on the decomposition rates of standard biomass (hay). This highlighted the influence of the environment, hampering decomposition on low elevations. The decomposition of native material in contrast was highest on the most low-lying plots. This was due to the low density of the native biomass as a result of adaptations to wave impact. For the soil organic carbon (SOC), a positive relationship with stem and leaf traits could be shown: low leaf dry matter content and small total leaf area were connected to low percentages of SOC present. Because of less AGB, there was also less carbon sequestration potential present on low elevations. These relationships led to the soil organic carbon stock being significantly lower on plots below MHW. Above MHW, SOC stocks were positively correlated with decomposition rates and intermediate stem stiffness and dry matter content. Decomposition rates above MHW were negatively correlated to inundation duration. A key aspect regarding the carbon cycle in this dynamic environment was the fact that the vegetation was often flushed away by the tides and washed up during high flood events, providing more biomass to be decomposed and potentially stored on the highest parts of the tidal bank.

The ecosystem service of wave attenuation in the Elbe estuary by the vegetation is valuable, despite the relatively small extent of the tidal marshes at the lower Elbe, and the carbon storage an important part in the national budget (Hansen et al., 2017). In context of the above mentioned threats to tidal marshes, management options include like for instance the abandonment of agricultural land to provide additional flooding space or the opening of dikes at suitable places, to allow the migration of the marsh.

Zusammenfassung

Tidebeeinflusste Marschen sind weltweit in Gefahr, aufgrund von Landnutzung, Aquakultur, Infrastrukturprojekten, Industrie und Hafenausbau und den Klimawandel. Die Analyse der Beziehungen zwischen Umweltfaktoren, der Vegetation und den Eigenschaften (Traits) der Pflanzenarten, sowie den Eigenschaften des Ökosystems drängt, um die Marschen zu schützen und wiederherzustellen und ihren Wert bezüglich ihrer Ökosystemleistungen zu kommunizieren. Vor diesem Hintergrund befasst sich die vorliegende Arbeit mit den Umweltfaktoren, der räumlichen Verteilung der Pflanzenarten, ihren Traits als Antwort auf die Einwirkung der Umwelt und den Wirkungen auf die Ökosystemeigenschaften. Als Modell-Untersuchungsgebiet für typische temperate Marschen und ein stark reguliertes Ästuar wurden Flächen im Elbe-Ästuar ausgewählt. Die Elbe ist mesotidal und die Salzgehalte im Untersuchungsgebiet wechselten im Rhythmus mit der Tide, abhängig von der Nähe zum Meer und der Entfernung zur Gewässerkante. Die Vegetation muss sich an sehr wechselhafte Umweltbedingungen anpassen, mit manchmal hohen Wellen (erzeugt von Wind und dem Schiffsverkehr) und aufgrund der Tide einer schwankenden Verfügbarkeit von Licht und Sauerstoff. Auf 84 Untersuchungsflächen, festgelegt basierend auf der Geländehöhe und der Vegetation, wurden Bodenproben analysiert und hydrologische Daten erhoben. Trait-Informationen der häufigsten 17 Pflanzenarten wurden erfasst, indem die ganzen Pflanzen ausgegraben und alle Organe analysiert wurden bezüglich ihres Gewichtes, des Volumens, der Dichte, des Trockengewichtanteils, der gesamten und spezifischen Blattfläche, der spezifischen Länge, Nährstoffgehalte der einzelnen Organe und mechanische Traits des Stängels.

Die Ergebnisse der Studie zeigten, dass als eine Reaktion auf Wellenhöhe, die Biegefestigkeit der Pflanzenstängel nahe der Gewässerkante am geringsten war und die Pflanzen investierten proportional mehr in unterirdische Organe. Die geringe Dichte der unterirdischen Biomasse war vermutlich auf die geringe Sauerstoffverfügbarkeit aufgrund der langen Überflutungszeiten zurückzuführen. Weder die Bodennährstoffe noch der Salzgehalt (abgesehen von einem Einfluss auf das Vorkommen der Pflanzenarten) spielte eine größere Rolle für die Verteilung der Traits im Untersuchungsgebiet. Die hydrologischen Faktoren sorgten für eine strenge Selektion der Arten und Traits – Nährstoffbedingte Trait-Reaktionen waren in diesem Zusammenhang vermutlich weniger wichtig.

Oberhalb des mittleren Tidehochwassers war die Vegetation von hochwüchsigen Arten mit festen Stängeln geprägt, mit einer starken Investition in Stängel und Blattbiomasse. Hier waren die Überflutungszeiten gering, Wellen hatten kaum einen Einfluss und Traits im Zusammenhang mit Konkurrenz waren wichtig. Die Blattfläche war größer, weil die Zugkraft des Was-

sers eine geringere Rolle spielte. Die Arten investierten viel in Stängelbiomasse, um das verfügbare Licht einzufangen, was zu einer hohen Gesamtbiomasse führte. Es gab starke Korrelationen zwischen Traits auf allen Geländehöhen. Die Biomasseinvestition in verschiedene Organe war proportional, die Festigkeit der unterirdischen und überirdischen Biomasse war korreliert, die Biegefestigkeit der Stängel, Trockengewichtsanteile und Nährstoffgehalte der Pflanzenorgane ebenfalls. Dies verdeutlichte den Einfluss, den Trait-Antworten und Trait-Interaktionen auf die Ökosystemeigenschaften haben.

Bezüglich der Ökosystemeigenschaft Biomasseproduktion, war weniger überirdische Biomasse der Pflanzengesellschaft nahe den offenen Wattflächen festzustellen, wo die Wellen am höchsten waren. Dies war eine Konsequenz der Wellenkraft, die auf Pflanzengröße, Gewebefestigkeit und Blattgröße einwirkte. Auf höheren Geländehöhen, bei geringerer Welleneinwirkung, waren die Pflanzenstängel weniger biegsam und die Biomasseproduktion war hoch. Diese Produktion und die Traits von Stängeln und Blättern spielten eine wichtige Rolle für die Ökosystemleistung der Wellendämpfung. Die Reduktion der Wellenhöhe schützt das Ufer und Uferschutzwälle vor den Wasserströmungen und möglicher Erosion oder Überschwemmung. Aufgrund der geringeren Dichte des Stängelgewebes (korreliert mit geringerer Biegefestigkeit) auf den niedrigen Geländehöhen, war auch die Wellenreduktion geringer. Die Stängel bewegten sich mit der Strömung, statt ihr zu widerstehen. Die erste Pflanzenart, die nach den freien Wattflächen vorkam, *Schoenoplectus tabernaemontani*, hatte biegsame Stängel mit einer geringen Biomasse und proportional hoher unterirdischer Biomasse. Mit festeren Stängeln, den Wellen widerstehend und einer höheren Biomasse, wuchs *Bolboschoenus maritimus* in dichten Beständen auf etwas höher gelegenen Flächen; die Wellendämpfung war hier stärker. Die Blattfläche und der Trockengewichtsanteil der Blattbiomasse (der bei niedrigen Geländehöhen geringer war), sorgte für eine größere Wellenreduktion durch stärkere Reibung.

Eine andere wichtige Ökosystemleistung, die durch die Vegetation geleistet wird, ist die Kohlenstoffspeicherung im Boden, die zu einer Reduktion des atmosphärischen CO_2-Gehaltes führt und bei der Reduzierung des Klimawandels helfen kann. Tidebeeinflusste Marschen haben aufgrund der hohen Biomasseproduktion ein großes Potential bei der Kohlenstoffspeicherung. Im Untersuchungsgebiet wurde diese Ökosystemleistung von Stängel- und Blatt-Traits und der Dekompositionsrate beeinflusst. Auf der einen Seite war die Dekomposition dort geringer, wo die Pflanzenstängel fester waren, auf der anderen Seite war sie durch die Umweltfaktoren beeinflusst. Die Überflutungsdauer und der Salzgehalt hatten einen starken negativen Effekt auf die Dekomposition von Standard-Biomasse (Heu). Dies hob die Wirkung der Umwelt hervor, die Dekomposition auf niedrigen Geländehöhen verzögerte. Die Dekomposition der vor Ort geernteten Biomasse war im Gegenteil am schnellsten auf den tiefliegenden Flächen. Dies war auf die geringe Dichte der Biomasse, welche eine Reaktion auf die Welleneinwirkung war, zurückzuführen. Bei dem Gehalt an organischem Kohlenstoff im Boden zeigte sich eine positive Beziehung mit Stängel- und Blatt-Traits: ein geringer Trockenmasseanteil der Blattbiomasse und eine geringe Blattfläche waren dort zu finden, wo auch geringe Prozente an Kohlenstoff im Boden zu finden waren. Aufgrund einer geringeren oberirdischen Biomasse war weniger Potential zu Kohlenstoffspeicherung auf niedrigen Geländehöhen vorhanden. Diese Beziehungen führten zu einem signifikant geringeren Kohlenstoffvorrat auf Untersuchungsflächen unterhalb des mittleren Tidehochwassers (MTHw). Oberhalb des MTHw, waren die Kohlenstoffvorräte positiv mit der Dekompositionsrate verbunden und mittleren Werten der Stängelfestigkeit und des Trockengewichtanteils der Stängelbiomasse. Die Dekomposition über dem MTHw war negativ beeinflusst von den Überflutungszeiten. Ein Kernaspekt betreffend den Kohlenstoffkreislauf in diesem dynamischen Ökosystem war, dass die Pflanzenbiomasse oft mit der Tide fortgespült wurde, was zu einer größeren Menge an Biomasse auf den höchstgelegenen Flächen führte, d. h. dort das Potential zur Speicherung erhöhte.

Trotz der relativ geringen Fläche der Marschen entlang der Unterelbe, ist die Ökosystemleistung der Wellendämpfung wertvoll und die Kohlenstoffspeicherung ein wichtiger Anteil im nationalen Budget (Hansen et al., 2017). Im Zusammenhang mit der oben benannten Gefährdung der tidebeeinflussten Marschen wurden Managementoptionen diskutiert, wie z. B. die Flächenfreigabe landwirtschaftlicher genutzter Gebiete als zusätzlicher Überflutungsraum oder die Öffnung von geeigneten Deichabschnitten, um die Migration der Marschen zu ermöglichen.

List of abbreviations

Environmental parameter

MHW	Mean high water
MLW	Mean low water

Plant traits

Leaf MF	Leaf mass fraction
Stem MF	Stem mass fraction
Root MF	Root mass fraction
Rhizome MF	Rhizome mass fraction
SLA	Specific leaf area
LDMC	Leaf dry matter content
SSD	Specific stem density
SSD	Stem specific density
RSD	Root specific density
RHSD	Rhizome specific density
SSL	Stem specific length
RSL	Root specific length
RHSL	Rhizome specific length

Ecosystem parameters

AGB	Aboveground community biomass
ANPP	Aboveground net primary productivity

Statistical

PCA	Principal component analysis
CCA	Canonical correlation analysis
RLQ	Three table analysis
Pls-SEM	Partial-least-squares structural equation model
LMR	Linear mixed models
SMA	Standard major axis regression

Miscellaneous

SLR	Sea level rise

Chapter 1. Thesis outline and major questions

Estuaries are highly dynamic ecosystems and were favored places for settlements, due to the many opportunities that arose from the proximity of the sea and the river for fishing and as transport routes (Valiela et al., 2009). The regular flooding of land adjacent to the estuary created fertile soils (Hopkinson et al., 2019). The dynamics of the system and the risk of storm surges were a dangerous element for the settlements of course and in medieval times, the first embankments of the Elbe river, which can be used as a model example for the history of large temperate estuaries, were built (Kappenberg & Fanger, 2007). Since then, the cities on the estuaries, Bremen on the Weser, Antwerp on the Scheldt, London on the Themes, Rotterdam at the Rhine estuary and Hamburg on the Elbe estuary for instance grew essentially which made flooding protection a primary task and simultaneously reduced the space that the river had. With improved technologies, the banks of the Elbe were stabilized, and dikes constructed to secure settlements, industrial and the agricultural use of the land closest to the river. The demands from rising numbers of cargo ship passages and the growing size of those container ships made adjustments to the bed of the river necessary too. The deepening of the Elbe is still taking place, with repercussions on the hydrological regime (WSA, 2007). The in-flow of the tide is faster, driving the saline zone further upstream. The tidal amplitude is larger, with a reduced mean low water and an increased tidal high water (Boehlich, 2003)). Additionally, the embankment of former floodplains meant, that they were cut off from sediment supply which would have risen the land surface previously and allowed for adaptations to sea level rises of past times (example for the Dutch Lowlands, van der Meulen et al., 2007). The reduction in vegetation cover also meant a reduction of its function for the ecosystem services of wave reductions, carbon sequestration and as a recreational space.

Future challenges will be posed by climate change and its consequences: rising sea levels and rising temperatures which will put pressure on artificial embankments (Temmerman & Kirwan, 2015) and may cause changes in species composition and zonation because of changed hydrodynamics (Carus et al., 2017b). These challenges make it urgent to further analyze the role of the vegetation in the protection of the tidal bank to possibly reduce the energy and cost invested in reinforcing artificial structures (Temmerman & Kirwan, 2015). The other essential role the tidal marshes could play relates to the potential of carbon sequestration and climate change mitigation (Chmura et al., 2003).

The present thesis aims to add pieces to this puzzle with the analysis of the abiotic factors and the role of plant species traits in mediating ecosystem properties and services. The major questions that this thesis addresses are concerning the relationship of environmental drivers, plant species distribution on the tidal bank, plant traits, ecosystem properties and their role for ecosystem services. When entering tidal marshes, one striking feature is the strict zonation in which the dominant species occur. Some species appear in a patchier cover, dotted in the dense cover of the dominant species, possibly due to sediment characteristics, nutrient supply or freshwater inflow. Which abiotic factors drive the species zonation in the Elbe estuary? How do the species respond to the stressful environmental drivers? Are there strategies detectable? What traits do the species express? How are traits interacting? How do plant traits affect ecosystem properties? What is the relationship of abiotic parameters and ecosystem properties? How are ecosystem services affected by the drivers, traits and ecosystem properties?

There are three parts that constitute this thesis, they are an introduction (Chapter 2 - Chapter 5), followed by three different analysis approaches (Chapter 6 -Chapter 8) and a synthesis (Chapter 9), discussing the overall implications of the findings.

Chapter 2 gives definitions and general information on concepts of plant traits and the analysis of plant functional traits as well as the concept of the response-and effect framework. Chapter 3 is focussed on ecosystem properties and associated ecosystem services, specifically wave attenuation and organic carbon sequestration as two essential ecosystem services of tidal marshes. Chapter 4 introduces to tidal wetlands in general and their specifics and then describes the Elbe estuary in more detail. Chapter 5 gives an overview of the study design with information on the site, sampling design, methods used and a synopsis of results of soil nutrient conditions, community weighted trait means and ecosystem properties. In Chapter 6, a descriptive analysis of the environmental factors driving species distribution and species respective trait expressions is elaborated through a RLQ, a three table analysis, combining abiotic, trait and data on species frequencies. This first step to answering the questions asked on the outset, is based on the species scale, using the mean trait value for each species. The following two chapters are scaled to the community level, using the community weighted means for the trait values. Chapter 7 is testing the effect- and response framework and its relevance for a brackish temperate tidal marsh with partial least-squares structural equation modelling, which allows the calculation and visualisation of an entire network of causes and responses. The focus of this chapter is on environmental drivers affecting ecosystem properties such as biomass production, decomposition and soil organic carbon directly and indirectly through species traits and therefore on the mediating role of plant traits. Chapter 8 encompasses analyses of the entire tidal bank, split into a zone below mean high water and a zone above mean high water, because of the surmount influence of the flooding regime and as a result very different habitat conditions. Here, the ecosystem service of wave attenuation on the low bank and the potential of carbon storage of the high bank is elaborated with mixed models and standard major axis regressions. Chapter 9 creates the overarching connection between the different chapters. The picture that emerges from the trait perspective for the brackish tidal marshes is discussed and the important findings derived from the analysis. The essential patterns are elaborated and their indication regarding future management options.

Chapter 2. Plant traits

2.1 The trait concept and functional types

The classification of species started with the systematic categorization into different families, genus and species and this system was invented by Carolus Linneaus in 1758 and described in his *Systema Naturae*. Raunkiaer classified species according to their life forms (Raunkiær, 1905) in order to be able to compare species across different floras. Another classification concept was based on the species ecological niche (Giller, 1984). The principle being, that two species adapted to the same ecological niche cannot exist at the same place because of competitive exclusion. Therefore, species that grow together in one habitat would have to limit their similarity in order to survive (Bazzaz et al., 1987; Díaz & Cabido, 2001). Species differ in characteristics in relation to their morphology, life cycle, the mass and distribution pattern of their diaspores, the size and thickness of their leaves for instance as a response to environmental drivers and competition (Simberloff & Dayan). Those characteristics are measurable and this was described as the principle aspect of a ˈtraitˈ (Shipley et al., 2006). The traits or the attributes of those traits (Lavorel et al., 2007) can be measured either in the field or the laboratory at plant individuals and encompass morphological features as well as physiological and phenological (Pérez-Harguindeguy et al., 2013; Garnier et al., 2016). The functional traits include all traits that are potentially affecting the plants fitness, for instance stoichiometric make-up, canopy height or strength of leaf fibers or its life-form (Pérez-Harguindeguy et al., 2013).

The functional approach, which was formulated by Diaz and Cabido (1997), was based on the idea that species can be grouped as functional types based on for instance a similar response to an environmental gradient (Gitay & Noble, 1997). The difference between the traits or absence/presence of traits (e. g. succulence) allows inter- and intra-species analysis of species and their adaptations and is not solely based on their phylogenetic origin (Díaz et al., 2004). There can be less of a difference between traits of different species belonging to the same functional type than within a species growing in different habitats that have a large plasticity. The influence of environmental drivers on species trait expressions and species distribution can be explained through the functional trait approach (Violle et al., 2007; Garnier & Navas, 2012). This way, similar ecosystems with a different species inventory can be compared in relation to the trait patterns (Kleyer et al., 2008; Kleyer & Minden, 2015).

2.2 The assembly rules

When considering a community present at a site, different mechanisms selected for this specific composition of species. Depending on the environmental gradients, the community will be composed of for instance salt tolerating species (either accreting or diluting salt) or will show a resistance to fires or flooding. This shows the filtering effect of the environment, which only allows species with specific trait expressions to survive (Keddy, 1992). The number of species can change dramatically along strong environmental gradients, because only few species might be able to survive resulting in low species diversity and low diversity in traits. This process follows the assembly rules (Weiher & Keddy, 1999), which state, that only species that are able to pass the environmental filter can establish in a habitat. This can cause species of a community to have the same trait expressions: They have to be similar enough to pass the environmental filters but different enough to co-exist (Weiher & Keddy, 1999). Therefore, this can also cause convergent traits to be favored, because species need to co-exist and thus limit similar use of resources (Bazzaz et al., 1987). The species present at a site are the most competitive species with the fitting characteristics for that environment (Scholten et al., 1987).

2.3 The response-effect framework: traits and environmental gradients

As a consequence from the assembly rules, only the species that have the suitable set of trait expressions to respond adequately to the environmental gradients are making up the community. Those specific traits are determined ‘response traits’ within the response-effect framework (Lavorel & Garnier, 2002). It differentiates traits into showing a response to the environment and/or having an effect on the environment. Response traits are those that are expressed as a response to an ecological factor (Gitay & Noble, 1997), for instance different leaf morphologies for photosynthesis. There are many different responses formed by plant species to the environmental factors in their habitat. Some plants show adaptations to salt stress like succulence or salt excretion (Minden & Kleyer, 2011), some invest into an extensive rhizome system in order to persist (Silinski et al., 2016) while another species strategy is to have an annual life-cycle, relying on its seeds for propagation.

Effect traits are those affecting the environment, for instance the decomposition rate of biomass (Díaz & Cabido, 2001) affected through the leaf dry matter content of the species present (among other things) and having an effect on soil nutrient levels (Diaz et al., 2007). Another example would be the higher decomposition rate of succulent plants (Zedler et al., 1980). Traits can be effect and response trait at the same time (Suding et al., 2008): Minden and Kleyer (2011) for instance found stem biomass, specific leaf area and C:N ratios to be effect and response traits in a saltmarsh system. The traits can be a response to one factor, e. g. flexible, short stems as a response to strong wave impact, with the effect of less aboveground biomass to dissipate wave action (Schoutens et al., 2019).

2.4 Community trait expressions

Following the mass ratio hypothesis, ecosystem functioning is controlled by trait values of dominant species that contribute most to the biomass (Grime, 1998). This finding allows the analysis based on traits of frequent species of one habitat at the community level (Minden & Kleyer, 2011). With the community level approach, a certain mean community trait expression is presumed, which is the product of the different trait values and their respective species frequency (Diaz et al., 2007; Lienin & Kleyer, 2012). Based on the concept of the assembly rules, a community weighted mean trait value would be therefore representing the selection process of that environment (Woodward & Diament, 1991; Garnier et al., 2007). Analyzing species at a community level, when it suits the research question, can have great benefits (Kleyer et al., 2012) because it allows prediction of processes at ecosystem level (Diaz et al., 2007). Hooper and Vitousek (1997) point out, that the effect of traits from abundant species can have more of an impact than the effect of a great diversity in functional traits present.

Chapter 3. Ecosystem properties and ecosystem service

3.1 Ecosystem properties

The plant traits together with the environmental drivers create the ecosystem properties as a product of both and therefore characteristic for the specific habitat (Diaz et al., 2007). Ecosystem properties encompass the aboveground biomass produced by the plant community (AGB) or its productivity (ANPP) for instance (Lavorel & Grigulis, 2012). Another ecosystem property is the decomposition rate of plant material at a site: the materials qualities and the environmental constraints influencing it simultaneously. The effect that species traits have on the environment becomes inherently obvious, when a species invasion is happening, for instance in the effect that *Impatiens glandulifera* has on riverbanks, replacing native perennial vegetation and increasing erosion risk (Greenwood et al., 2018). In many studies, the biological diversity and with it diversity in plant functional traits is seen as an insurance for ecosystem functioning (Hooper et al., 2005; Visconti et al., 2018).

3.2 Ecosystem services

Ecosystem services describe the contribution of natural systems to human benefit (Hooper et al., 2005). The idea of ecosystem services is intuitive to understand when we look at agricultural systems: A certain amount of energy, through the input of workforce, has to be put into the system. The return is higher than the input, because of the additional input of the natural system in form of water, soil nutrients, sun light and microorganisms (Hein et al., 2006). Based on the Millennium Ecosystem Assessment (MEA, 2005) and their beneficial role to humans, the above-mentioned service belongs to the category of provisioning services. The category of regulating services encompass the natural filtering effect of soils for clean drinking water or temperature regulating effects (Haines-Young & Potschin, 2013). Supporting ecosystem services are for instance pollination of crops and nutrient cycling (MEA, 2005). More abstract services and harder to quantify are effects in relation to inconsumable resources: non-extractive recreational value, information and knowledge acquisition (Haines-Young & Potschin, 2013).

The vegetation based ecosystem services provided by a functioning ecosystem can be traced back to the traits of the dominant species or the community trait means: Loreau et al. (2001) state, that from the point of view of the functioning of the ecosystem, species matter in regard to their traits and effects in stabilizing ecosystem processes (Chapin, 2003). Based on the mass ratio hypothesis (Grime 1998), the trait values of dominant species contributing most to plant biomass are determining the ecosystem functioning. Even though ecosystem services are beneficial to humans, they are in many areas threatened by exploitation and land-use practices and the lack of protection of the depending ecosystem properties (MEA, 2005). Landscape fragmentation could lead to a lack of a suitable species pool for adjustments to environmentally changing circumstances (Loreau et al., 2001; Hooper et al., 2005) and ultimately ecosystem services might no longer be delivered.

3.2.1 Wave attenuation

A valuable ecosystem service is the attenuating effect of vegetation on hydrodynamics (Leonard & Luther, 1995; Christiansen et al., 2000; Barbier et al., 2011) and the prevention of erosion (Coops and Van der Velde 1996). Wave attenuation by the vegetation is caused through friction and the drag it creates (Möller et al., 2014; Vuik et al., 2016). Even non-emergent vegetation reduces wave and flow energy (Paul & Amos, 2011). For vegetation growing on the shore, strong correlations were found for attenuation capacity and biomass present: the more standing biomass, the larger the frontal area, the more flow energy is reduced (Bouma et al., 2010; Heuner et al., 2015). Hereby, the vertical distribution of biomass is an important factor: the stems of the plants have a smaller frontal area than the part of the plant carrying leaves. Where the frontal area is larger, the plant also experiences more drag force and there is also more drag force on plants with stiffer stems (Bouma et al., 2005). This causes a trade-off between avoiding wave energy with bendy stems and a small frontal area and tolerating waves with a stiffer stem (Heuner et al., 2015). There is a twofold effect of the waves: on one hand, they are causing a zonation of species (Coops & Van Der Velde, 1996b; van Wesenbeeck et al., 2007), with the bendiest closest to the open tidal flat. Their wave attenuation is smaller, because they avoid the wave impact and move with the flow. They do, however, reduce the wave energy enough to allow species with stiffer stems to establish, with a stronger effect on wave attenuation (Heuner et al., 2015).

When considering the ecosystem service of wave attenuation by vegetation as a defense against wave energy also for instance under storm conditions, the seasonal aspect of present biomass and stem mechanics have to be taken into account. In some tidal marshes for instance, the aboveground biomass regrows every year and is largely absent in winter, with wave attenuation dramatically reduced during winter month (Schoutens et al., 2019). There is also a clear seasonal pattern in stem stiffness, which is associated with wave attenuation: after peak vegetation in midsummer, the flexibility of the stems diminishes (Coops & Van der Velde, 1996a).

3.2.2 Carbon sequestration

The storage function of soils for carbon (C) is also a major ecosystem service, because it can capture and retain atmospheric carbon over long time scales (Soussana & Lüscher, 2007; Schmidt et al., 2011). Reducing the levels of CO_2 in the atmosphere through the vegetation sequestering it can help to mitigate climate change (McLeod et al., 2011). The potential to sequester carbon varies greatly between different ecosystems (Chmura, 2013). Tidal wetlands can act as an important sink for carbon, because of the interplay of biomass production, sedimentation and anoxic conditions (Aller, 1994; Valéry et al., 2004; Duarte et al., 2005). Yet the extent of mangroves and saltmarshes for instance is shrinking with average global rates of 0.7-3 % (McLeod et al., 2011). The ability of estuarine systems to mineralize carbon highlights the importance in the coastal carbon cycle (Herrmann et al. 2015). The C cycle is intertwined with the nutrient status of the soil, through plant growth for example (Fernández-Martínez et al., 2014). Carbon is displaced and transported in form of bicarbonates and dissolved CO_2 as well as organic carbon forms (Le Quéré2013). During the process of carbon travelling from land towards the ocean, it is also sequestered in soils (Tranvik et al., 2009) or released into the atmosphere (Regnier et al., 2013). Organic matter can persist in the soil because of environmental factors hindering decomposition (Schmidt 2011).

When considering the carbon cycle of a site, the productivity of a system and the breaking-down of biomass has to be addressed. The productivity is reflected in the gain of biomass per time. The carbon captured by plants and invested into biomass represents the potential of carbon that could be stored in the soil. Therefore, highly productive systems, like tidal marshes, offer a great potential to sequester organic carbon, even though they only cover a relatively small area (Najjar et al., 2018).

The cycling of nutrients that are released from plant litter through decomposition is a principle function of the ecosystem (Swift et al., 1979). The decomposition rate is a property of the ecosystem and influenced by environmental parameters and the character of the biomass (Robertson & Paul, 2000), therefore, it is affected by litter composition and the species mix. Species tissue composition and structure was found to be a highly influential factor for decomposition rates (Freschet et al., 2012) and dominant species´ fibers have an important influence on the decomposition of the litter because of their large contribution to the biomass (Hector et al., 2000; Hooper et al., 2005). The decomposition at a site is affected by the plant material stoichiometry and texture as well (Minden et al. 2015) and traits related to structure i.e., lignin content, higher C and dry matter content, were reducing decomposability in a common-garden experiment (Freschet et al., 2012). The decomposition is controlled through the amount of nitrogen and phosphorus present via the productivity of primary and secondary producers (Teal, 1986; Hemminga & Buth, 1991; Mendelssohn et al., 1999) whereby the spatial distribution of decomposers is a crucial factor for a fast or slow decomposition process (Schmidt et al., 2011).

Another important variable in this context is the sedimentation process. The tides carry sediment into the marshes, the reduced velocities of the incoming water allow it to settle and contribute with its organic particles to the content of soil organic carbon (Hansen et al., 2017). In this process, soil salinity, temperature and inundation regimes were often shown to hamper decomposition (Hemminga & Buth, 1991; Day & Megonigal, 1993; Quintino et al., 2009).

Chapter 4. Introduction to tidal wetlands and estuaries and the Elbe estuary as s model for temperate tidal marshes

Tidal marshes are found along the coastlines and in the estuaries where the influence of the tide is still detectable. Depending on climatic conditions, the salinity of the water, wave impact and inundation regime, the plant community is characteristic for each climate zone in this highly variable environment (Hopkinson et al., 2019). Tidal marshes are very dynamic systems and are characterized by disturbance. Therefore, the vegetation is assembled by specialist species that have high tolerances and special traits to cope with the environment (Keddy, 1992). Around the world, different types of vegetation developed under these circumstances. All of them have one factor in common though: they occur in zonation. Some of the estuarine vegetation belts are kelp forests, submerged aquatic vegetation, coastal marshes, mangroves, deep-water swamps, and riverine forests. (Hopkinson et al., 2019). In tropical and subtropical regions, the typical tidal vegetation are mangroves (Davidson-Arnott, 2009).

There is pressure on tidal marshes from human activities around the world. Tidal marshes are threatened because of land-use practices, degradation, exploitation, shrimp-farming, drainage, lack of sediment supply, sea level rise and rising temperatures (Valiela et al., 2001; Barbier et al., 2011; Hopkinson et al., 2019). The valuable ecosystem services that they fulfill, in relation to wave attenuation, erosion control, nursing grounds for fish and as a filter for drinking water, are lost with them.

In north-west Europe, the vegetation close to the sea are salt marshes, with their characteristic species that are able to deal with high salinities (Odum, 1988). The driving factor determining tidal bank conditions is the elevation relative to the tide, controlling the inundation duration which in turn is important for chemical processes in the ground and oxygen availability. The elevation also affects the salinity levels, due to different inundation frequencies. Perpendicular to the shore, the hydrodynamics are impacting on the vegetation through two gradients. One is generated through the tidal regime and the hydroperiod, the other through wave action: plant species growing close to the marsh edge will have to endure long hours of water logging

(Coops & van der Velde, 1999), being submersed in sometimes turbulent water and having to withstand the drag of the waves (Denny, 1988; Coops et al., 1994).

A special form of tidal wetlands are the estuaries as the transition zones between the rivers freshwater body and the seas saltwater intrusion; their shape is funnel like (Kappenberg & Fanger, 2007). The zone of influence of two ecosystems is also referred to as an ecotone (Attrill & Rundle, 2002). In the estuaries, the vegetation ranges from brackish marshes with tall reeds and forbs, in the freshwater part also with trees, wave activity heavily influencing the species composition close to the marsh edge. The rhythm of the tide creates an environment of extremes: inundation and falling dry, sometimes strong currents or waves and varying levels of salinity. A typical feature for estuaries is the decreasing salinity upstream: with every tidal cycle, seawater is intruding up to a certain point, further inland during summer than winter. That is due to the reduced outflow in the drier summer month. With storm-surges there can be extra high floods too, bringing saline water further upstream than usual. The hydrodynamics (waves and hydroperiod) create gradients running perpendicular to the shore (Coops et al., 1994).

The Elbe and its history is a typical example for a large estuary in a temperate climate zone. With a length of 170 Km it has Germany's longest estuary, the port of Hamburg is the second biggest in Europe (HPA & WSA, 2011). The Elbe is mesotidal (Boothroyd, 1978) with a tidal range of ~2.8 m at the mouth. The upper limit of the estuary is at the lock at Geesthacht (Boehlich, 2003), which is where the tidal influence ends. The river Elbe has experienced many transformations to its riverbed and shore over the centuries. The once extensive marsh sites along the shores have been reduced (Kappenberg & Fanger, 2007), similar to the faith of many European streams (e. g. Meire et al., 2005), through the building of dikes and subsequent drainage of the former marsh. This is a process, which started in medieval times and the deepening's of the river eventually reduced the flood plains of the Elbe by 75% (Kappenberg & Fanger, 2007). Being economically highly important with the port of Hamburg 110 km inland, the Elbe's navigability is a priority for the management and many banks of the Elbe have been artificially reinforced, also of course to protect the hinterland (HPA & WSA, 2011). The deepening modifications of the river were necessary as the size and gauge of cargo ships increased but led to a higher tidal amplitude (Boehlich, 2003; HPA & WSA, 2011). This caused tidal pumping, with a higher tidal energy eroding sediments and a weaker tidal ebb, taking less sediment out of the estuary (Kerner, 2007). As a result, the estuary is acting as a sediment trap, the suspended matter also being a transport vehicle for pollutants (Kappenberg & Fanger, 2007). This has also implications for the saline water that is flowing upstream with every tide, which is reaching further upstream as a result. Beside the role of the elevation, the hydrodynamics are also influenced by the bathymetry and the wind fetch, which is a driving factor for the generation of waves. Ship waves, due to the frequent traffic occurring in the tidal Elbe, are also impacting on the vegetation. In this thesis, there was no differentiation made between wind or ship generated waves though, as the focus was on the plant species responses to the existing conditions rather than on the sources responsible for them.

The vegetation in the brackish part of the Elbe estuary consist of characteristic specialist species that can compete under highly variable conditions, due to the rhythm of the tide, the hydrodynamics and the salinity (Stiller, 2005) and the knowledge of the typical species zonation was the base for the study design of this thesis. The gradients of inundation, wave turbulence and salinity result in a twofold structuring of the plant species composition: from the mouth of the river upstream the species are composed first of salt tolerant species like *Schoenoplectus tabernaemontani* (CC. Gmel.) Palla, *Bolboschoenus maritimus* (L.) Palla or *Elymus athericus* (Link) Kerguélen. As salinity declines, other species appear, like *Phalaris arundinacea* L. or *Thypha angustifolia* L. which are more competitive under freshwater conditions (Zonneveld, 1960; Odum, 1988; Stiller, 2005).

Chapter 5. Study design, methods and material and characterization of sites

5.1 Sites

In the Elbe estuary in the Northwest of Germany, three study sites were chosen (Figure 1): Balje (53°51'30" N, 9°4'30"E), Krautsand (53°46'30"N, 9°22'0"E) and Hollerwettern (53°50'00"N, 9°22'30"E): Each site had a gradual sloped topography and relatively straight marsh edge and natural tidal bank vegetation. The climate is oceanic with an average temperature of 9.6 °C, an annual precipitation of 831 mm and 1672 hours of sunshine throughout the year (Cuxhaven, Wetterdienst 2019). The soils are sandy-silty, though in Hollerwettern influenced by deposition of sandy dredging material on higher elevations (Kappenberg & Fanger, 2007). There is no agricultural use on the sites, but the adjacent fields are used for grazing and fodder production. The elevations of the sites relative to the tidal range (Znorm=(Plot elevation-Mean Low Water)/((Mean High Water-Mean Low Water)), (Heuner 2016) are between 0.54 and 1.35 (Mean Low Water, MLW = 0, Mean High Water, MHW = 1, no units). Soil salinity varies between on average 0.2 and 4 PSU (own measurements, Figure 7).

In Balje and Krautsand, the adjacent fields are periodically grazed by cattle, in Balje additionally mowed late in the season. In Hollerwettern, the dike starts at the end of the high bank and it is grazed with sheep.

The fieldwork was carried out between March 2016 and September 2017.

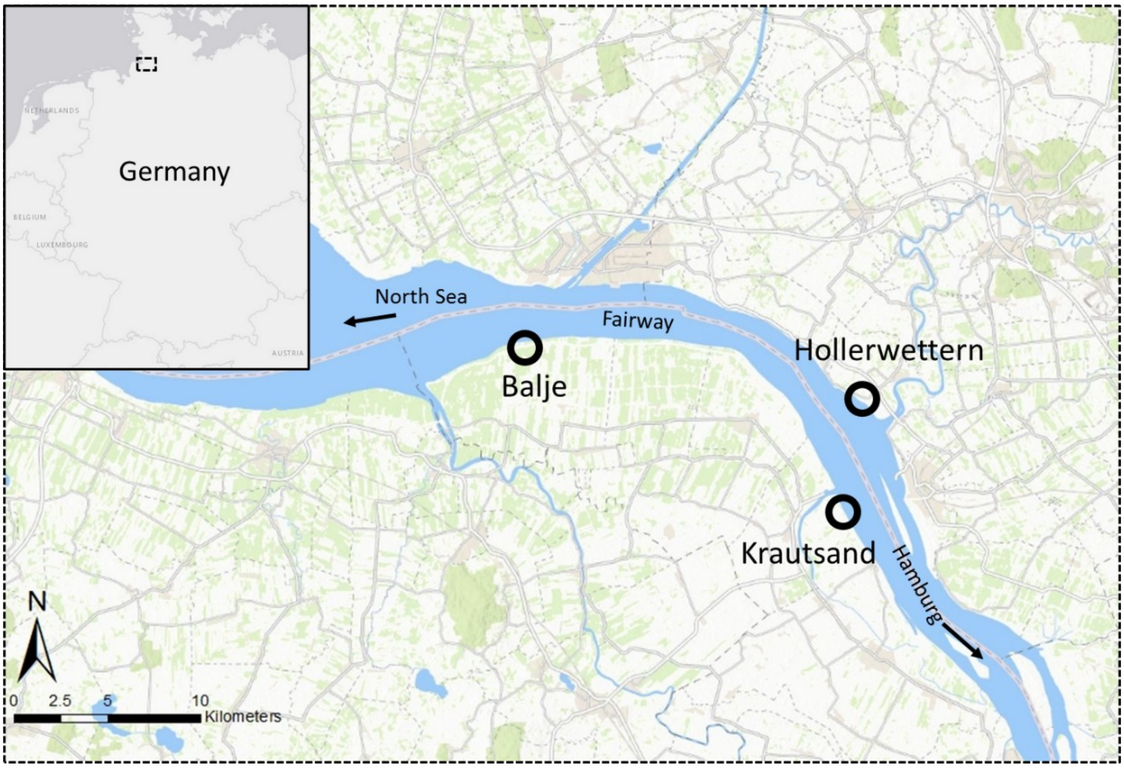


Figure 1: Position of the study sites (black circles) in Germany in the Elbe estuary. ATKIS® Base-DLM.

5.2 Plot design

Within the three sites, a total of 84 plots selected by random stratification, with 28 plots per site and 7 per vegetation zone and elevational strata. There were four different elevational strata per site and they each had a characteristic dominant species. Starting from the tidal flat, those species were *Schoenoplectus tabernaemontani, Bolboschoenus maritimus, Phragmites australis* (Cav.) Trin. ex Steud and *Phragmites australis* in mix with other species. The plots each measured 4x4 m with a distance of at least 20 m between them (to avoid interferences) and with a marker in the center and different sections within them, to avoid disruption of sampling procedures: there were four sections within the plots, in which either the plant frequency was recorded, soil, plant or biomass samples were taken.

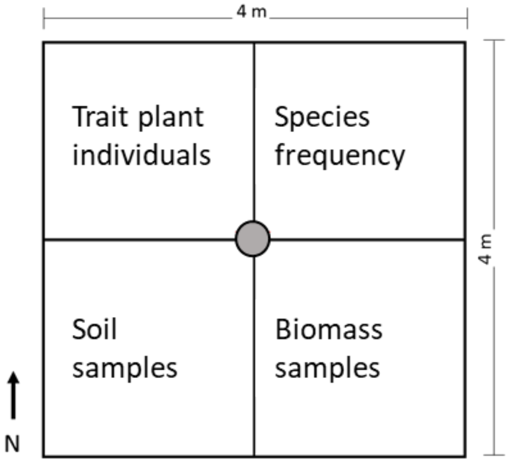


Figure 2: Design of plot with different sections. The plot center was marked with a plastic pipe and a strong magnet buried in the soil.

5.3 Species composition and vegetation zones

Species composition was recorded as a frequency (presence/absence), with a frame (50x50 cm) with 25 cells (Figure 3). By using it four times randomly, a total area of 1 m² was covered per plot (Minden et al., 2012; Cebrián-Piqueras, 2017), species were determined with Schmeil and Fitschen (2003) and Rothmaler (2007). Based on the frequency analysis, the species that made up 95% of the recorded frequencies, were selected as trait species (Cornelissen et al., 2003, suggested frequencies of 70-80 %). These were the most frequent 17 species (Figure 4) and the zones they appeared in were named after their dominant species.

Figure 3: Plant frequency recording frame. It covers an area of 1/4 m² and was used four times per plot.

Closest to the water, the zone was dominated by *Schoenoplectus tabernaemontani*, which is a bendy, leafless plant, that can exist on elevations as low as 2 m under MHW (mean tidal high water) (Kötter, 1961). The next zone on higher elevations was characterized by *Bolboschoenus maritimus*, which has a triquetorius stem that can resist wave energy. From approximately the MHW-line (starting ~0.5 m below it), *Phragmites australis* is growing in dense stands in this more sheltered environment (Ellenberg & Leuschner, 2010). At 1 m above the MHW-line, inundation frequency and duration become less and *P. australis* is less competitive; other species are able to establish. This zone has therefore been labeled *Phragmites*/mixed community-zone.

1 *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla
2 *Bolboschoenus maritimus* (L.) Palla
3 *Myosotis scorpioides* L.
4 *Typha angustifolia* L.
5 *Lythrum salicaria* L.
6 *Agrostis stolonifera* L.
7 *Lycopus eurpaeus* L.
8 *Phragmites australis* (Cav.) Trin.ex Steud
9 *Phalaris arundinacea* L.
10 *Mentha aquatica* L./*Mentha verticillata* L. s. str.
11 *Juncus gerardii* Loisel.
12 *Cirsium arvense* (L.) Scop
13 *Festuca arundinacea* Scop
14 *Elymus athericus* (Link) Kerguélen
15 *Calystegia sepium* (L.) R. Br.
16 *Scutellaria galericulata* L.

Figure 4: Schematic of the most frequent plant species found in the study sites and ordered in relation to their position in the elevational gradient. Mentha aquatica and M. verticillata are depicted as one - M. aquatica grew in Balje, M. verticillata grew its place in Hollerwettern and Krautsand.

5.4 Vegetation structure recording method

The vegetation structure was categorized through the measurement of the photosynthetically active radiation reaching the soil (PAR) and, to record the vertical distribution of the biomass, the percentages of distribution were estimated in five height classes: 0-30 cm, 30-60 cm, 60-120 cm, 120-240 cm and >240 cm.

5.5 Plant trait selection and sampling design

The aim of the plant trait analysis was to include as many trait measurements as possible and the sampling methods followed Pérez-Harguindeguy et al. (2013). The list of recorded traits can be found in Table 1. The 17 plants selected as trait plants were measured for their canopy and releasing height in the field as well as leaf chlorophyll content. At least 10 plant individuals per species were harvested and dug out (20 x 20 cm soil block). Trait measurements were done on stems, leaves, roots and rhizomes for mass per volume [$g_{fresh\ mass}$ cm^{-3}], specific density ([$g_{dry\ mass}$ cm^{-3}], specific length [mm $g^{-1}_{dry\ mass}$], dry matter content [$mg_{dry\ mass}$ $g^{-1}_{fresh\ mass}$], specific leaf area [mm^2 mg^{-1}] and total leaf area [mm^2]. From this, the mass fractions (MF) were calculated. The total dry biomass in each organ was also determined as well as seed numbers. The biomass content of each organ of C, N and P was determined analogue to the soil analysis. A selection of traits on a community base (community weighted means, Violle et al., 2007) per vegetation zone are displayed in Figure 6.

Numbers of stems per species and m² were counted and for the bending test of plant stems, fresh stem samples were taken to the NIOZ (Royal Netherlands Institute for Sea Research, Yerseke) and tested with the Instron 5942 (Figure 5,(Canton, MA, USA, Heuner et al., 2015).

Figure 5: The Instron 5942, used for the 3-point-bending test at the NIOZ. The measured force in Newton, the deformation of the stem in mm and the distance of the support-bars are recorded.

Table 1: Traits recorded from sampled individuals with abbreviations and units.

PLANT TRAITS	ABBREVIATION	UNIT
Canopy height		m
Releasing height		m
Flexural stiffness	Flex. stiff	Nmm^2
Young´s modulus		Nmm^2
Stem mass per volume		$g_{fresh\ mass}\ cm^{-3}$
Stem specific density	SSD	$g_{dry\ mass}\ cm^{-3}$
Stem specific length	SSL	
Stem dry matter content	SDMC	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Leaf specific area	SLA	$mm^2\ mg^{-1}$
Leaf chlorophyll		$\mu m\ mm^{-2}$
Total leaf area		mm^2
Leaf dry matter content	LDMC	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Root mass per volume		$g_{fresh\ mass}\ cm^{-3}$
Root specific density	RSD	$g_{dry\ mass}\ cm^{-3}$
Root specific length	RSL	$mm\ g_{dry\ mass}^{-1}$
Root dry matter content	RDMC	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Rhizome mass per volume		$g_{fresh\ mass}\ cm^{-3}$
Rhizome specific density	RHSD	$g_{dry\ mass}\ cm^{-3}$
Rhizome specific length	RHSL	$mm\ g_{dry\ mass}^{-1}$
Rhizome dry matter content	RHDMC	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Total stem mass		g
Total leaf mass		g
Total root mass		g
Total rhizome mass		g
Total seed mass		g
Seed numbers		
Nitrogen biomass	N (plant organ)	$g\ kg^{-1}$
Carbon biomass	C (plant organ)	$g\ kg^{-1}$
Phosphorus biomass	P (plant organ)	$g\ kg^{-1}$

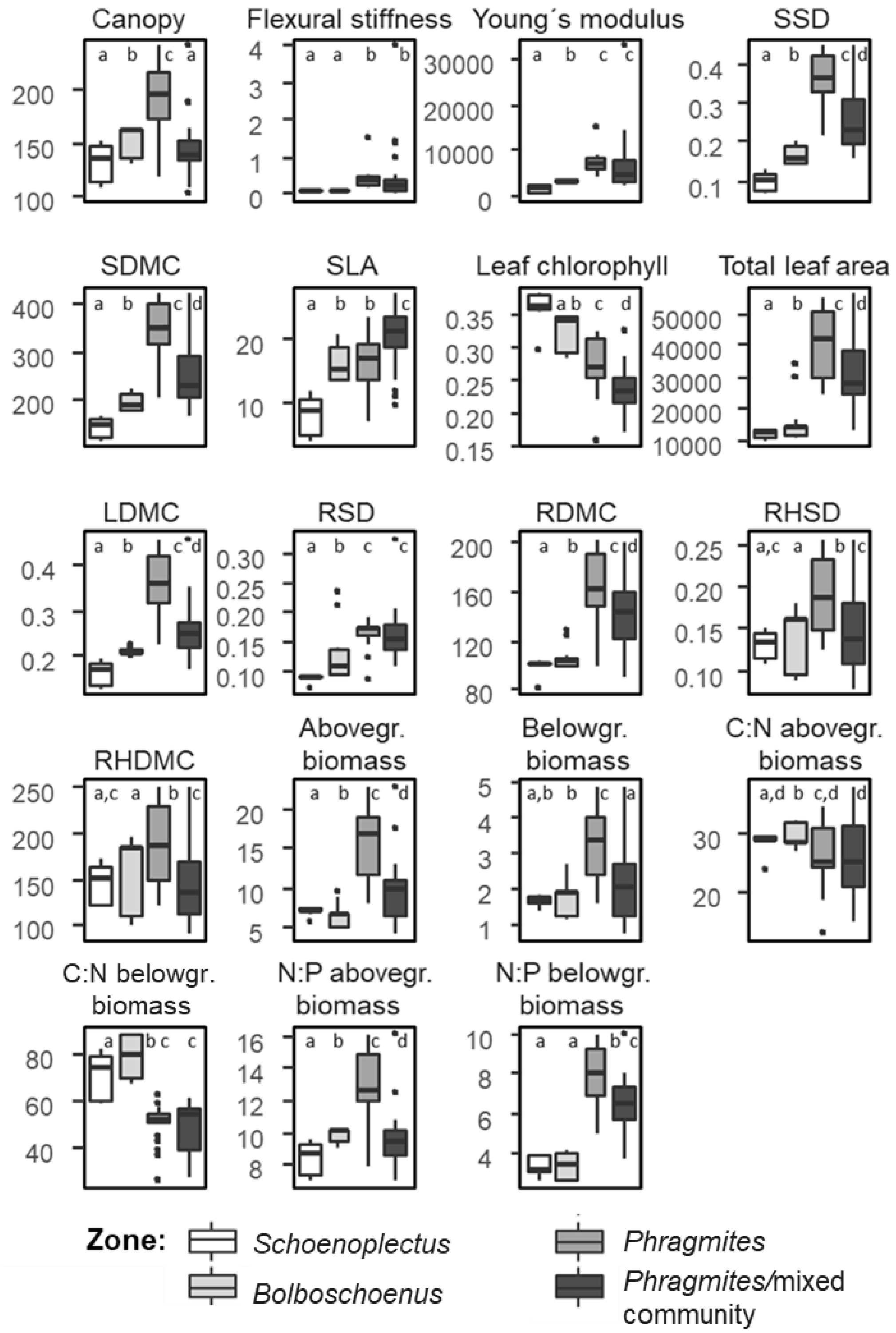


Figure 6: Community weighted means for selected trait variables. A list of mean trait values per species can be found in

Appendix 6. 9. Significant differences are indicated with different letters. Variables displayed: canopy = canopy height, flexural stiffness = stem stiffness, Young´s modulus = stem resistance to bending, SSD = stem specific density, SDMC =

stem dry matter content, SLA = specific leaf area, leaf chlorophyll = chlorophyll content per leaf area, total leaf area = leaf area per individual, LDMC = leaf dry matter content, RSD = root specific density, RDMC = root dry matter content, RHSD = rhizome specific density, RHDMC = rhizome dry matter content , aboveground biomass = abovegr. individual biomass, belowground biomass = belowgr. individual biomass, C:N and N:P are ratios for content in biomasses.

At the community level, there were clear patterns visible regarding the size of plants (canopy, aboveground biomass and total leaf area) and leaf chlorophyll content. The chlorophyll content was significantly different for each zone: it was highest in the *Schoenoplectus*-zone closest to the water, with lower values on higher elevations. The stem traits like SSD (stem specific density) and SDMC (stem dry matter content) were significantly different for every zone, with the highest values for the *Phragmites*-Zone. The stem bending properties showed a segregation into below and above MHW (flexural stiffness and Young´s modulus) as well as the specific density (RSD, RDMC). For the nutrient ratios within the biomass, there were particular patterns noticeable for the two zones below MHW (*Schoenoplectus* & *Bolboschoenus-zone*): the belowground biomass for those zones showed high C:N ratios and low N:P ratios compared to above MHW (*Phragmites* & *Phragmites*/mixed community).

5.6 Environmental parameter analysis

The analysis of the abiotic environment concentrated on soil samples taken in each soil horizon to a depth of 60 cm, where possible. The results of essential parameters are displayed in Figure 7. With the determination of the bulk density, the results of the soil analysis could be extrapolated and expressed as kg or g per m² (and calculated for a profile depth of 80 cm). Measured soil properties were salinity (measured as conductivity, Grasshoff et al., 1983), grainsize distribution was measured with the Laser Particle Sizer. The soil nutrient content of phosphorus (P) and potassium (K) were measured in the continuous flow analyzer (CFA) and the Atomic Adsorption Spectroscopy (ASS), following Egnér et al. (1960) and calcium carbonate according to Scheibler´s method (Schlichting et al., 1995). Total carbon (C) and nitrogen (N) and plant available nitrogen N_{min} were determined with the C:N-Analyzer following Allen (1989).

To record the inundation regime, pipes were inserted vertically into the ground on 24 plots (two per zone and site) and pressure loggers (Sensus Ultra, Reefnet) recorded air/water pressure every hour. The plot elevation was used to calculate inundation duration for all plots.

The mean incoming wave height was recorded along one transect per site with pressure sensors (P-Log3021-MMC, Driesen & Kern) and calculated for different water depth (<0.5 m, 0.5-1.0 m and >1.5 m, see Appendix 6. 1). The wave attenuation was the reduction in wave height in relation to the distance to marsh edge and elevation, see Appendix 8. 1 (Schoutens et al., 2019; Schoutens et al., 2020).

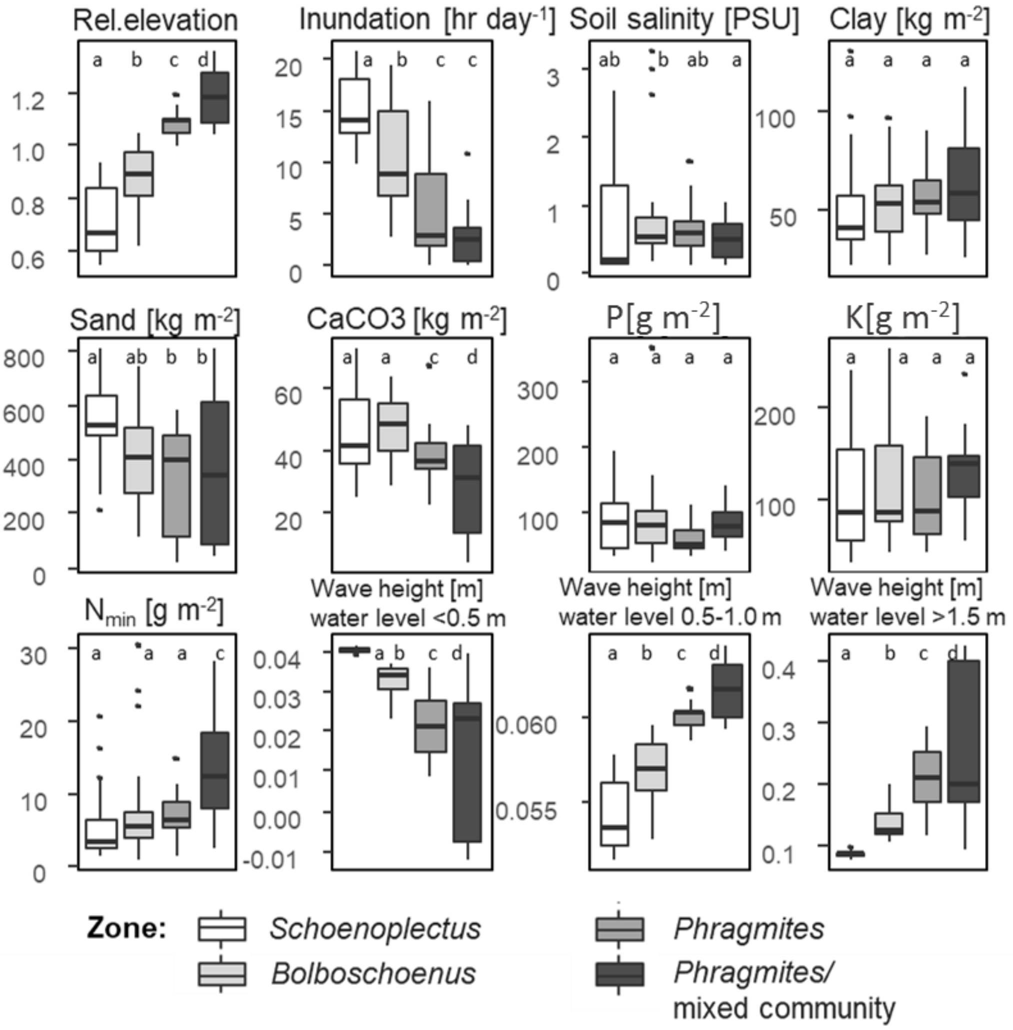


Figure 7: Environmental parameters displayed per vegetation zone. Different letters indicate significant differences ($p<0.05$).

5.7 Ecosystem parameter determination

To measure vegetation density, a SunScan (Canopy Analysis System SS1) was used, this measures the plant available sunlight reaching the ground at peak vegetation. The aboveground biomass was harvested in March and in August on ½ m² and calculated for 1 m² as the gain in biomass per month (aboveground net primary productivity, ANPP) and the peak community biomass (AGB). Decomposition was measured with samples of native biomass and standard biomass (hay) filled into mesh bags (4 g per bag, 1 mm mesh size) and left on each plot for 10 months. The decomposition rate is the material loss in % per day. The setup in the field is shown in Figure 8. The content of soil organic carbon was determined with the C:N-Analyzer (Flash 2000, Thermo Scientific). The average values for recorded ecosystem properties are displayed in Figure 9.

Figure 8: Decomposition bags fixed to the ground with coated mesh. Three bags are filled with standard litter (hay), the others with native biomass.

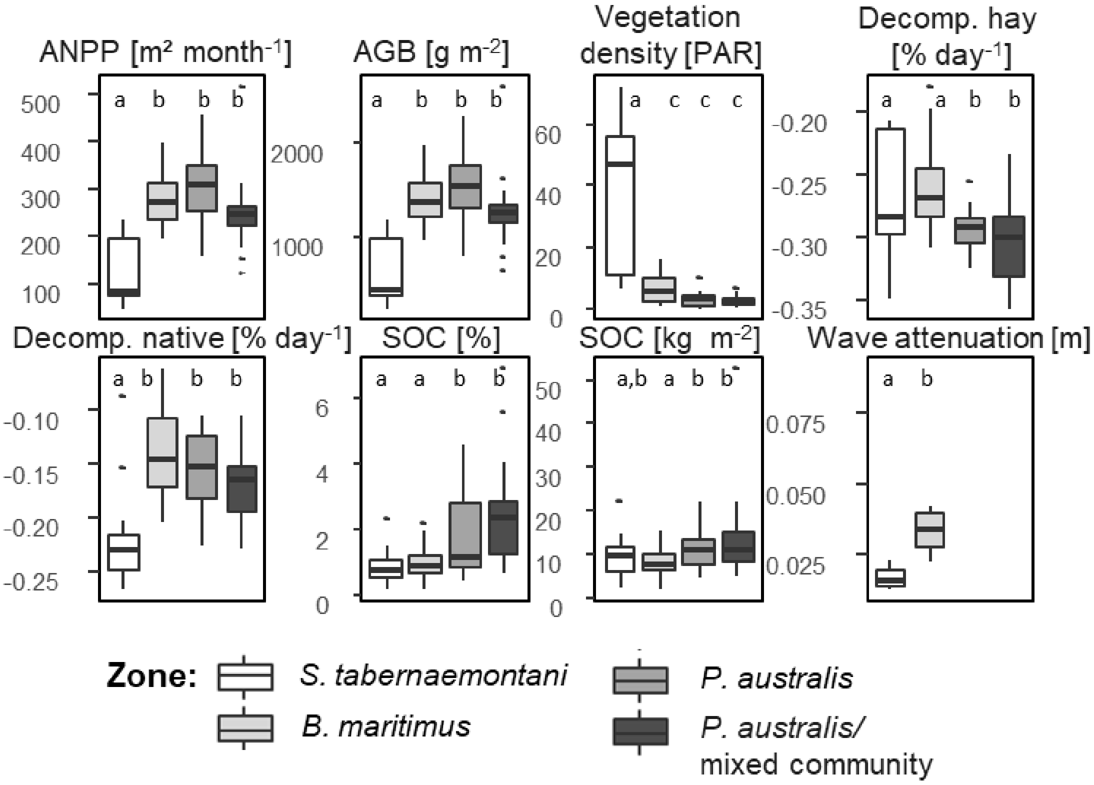


Figure 9: Boxplots for ecosystem properties, displayed per vegetation zone with different letters indicating significant differences (p<0.05).

Chapter 6. Unraveling plant strategies in tidal marshes by investigating plant traits and environmental conditions

Schulte Ostermann, Tilla; Heuner, Maike; Fuchs, Elmar; Temmerman, Stijn; Schoutens, Ken; Bouma, J. Tjeerd; Minden, Vanessa

Abstract

Tidal marsh vegetation along estuaries is exposed to strong environmental gradients that determine which species – enabled through specific traits – can establish. With these ecosystems under anthropogenic pressure, in-depth knowledge on conservation of remaining tidal wetlands and restoration potentials is needed. In this study we elaborate the habitat conditions in the natural vegetation of the Elbe estuary and analyze (1) which abiotic factors drive species composition and (2) which species-traits are key to the plants strategies in this specific ecotone.
At three sites in the Elbe estuary (river kilometer 671-703), we collected data on soil nutrients, inundation period and wave height and sampled traits of the 17 most abundant plant species, which we analyzed by RLQ (three table analysis, including environment-variables (R), species abundance and a species traits-table (Q)).

We detected a strong ˈwave-disturbance-inundation gradientˈ. This gradient separated sparsely vegetated low-lying plots receiving high wave impact and being exposed to long inundation periods from high-lying plots showing dense vegetation and aerated soils. Close to the shore, plants had low organ density and high investment into rhizomes, with a correlation of 0.72 between mass fraction of rhizome and phosphorus content of rhizome tissue. On higher elevations, traits relating to competition were detectable, like high allocation to stem biomass. Further, we found species with high leaf chlorophyll content showing low specific leaf area (SLA) values and a negative correlation with the nutrient gradient.

The results of our study are particularly relevant for restoration measures in order to re-establish healthy marsh vegetation. However, changes in the environmental conditions, for example stronger wave energies by a higher shipping frequency in the river channel and sea level

rise may trigger changes in species composition through plant trait adaptations, for example by demanding a stem flexibility beyond of what would be structurally feasible.

6.1 Introduction

Plants are affected by their abiotic and biotic environment and plant trait-expressions mirror specific adaptations towards these environments, displaying a set of traits with strong responses to the environmental constraints of a specific site (assembly rules, Keddy, 1992). Following the assembly rules, the environmental filters only allow for species that are able cope with the environmental conditions and the interspecific competition (Weiher & Keddy, 1999). For example, as an adaptation to abiotic stress such as drought or soil salinity, plants produce scleromorphic plant tissue or grow succulent (Khan et al., 2000; Read & Sanson, 2003). With the increase of biotic stress such as competition for light, traits responsible for light capture become essential. These can include high allocation of biomass to stems and leaves and high canopy height (Poorter et al., 2012). The competition between species is another driver for the different trait expressions and species composition (Weiher et al., 1998).

Across ecotones, the interface of two contrasting environments (Yarrow & Marín, 2007), trait expressions can vary strongly, depending on the extent of differences between the two adjacent systems. One such ecotone can be found in tidal marshes, which are situated along coasts and estuaries. Nowadays, tidal marshes are of high conservational value, as for instance they are home to many breeding birds, and at the same time, they face strong anthropogenic pressure as they are often alongside highly altered waterways (Eertman et al., 2002). For nature-based shoreline protection measures and the restoration of natural tidal bank vegetation (removal of stone fillings, plantation with suitable species), it is essential to understand the conditions that filter for specific traits: which are the most important environmental gradients and how do plant species respond in terms of their traits? This has been studied for the species on the low elevations (Heuner et al., 2015; Carus et al., 2017a; Schoutens et al., 2019), but research on the entire bank remains scarce.

Vegetation along the tidal bank is exposed to various environmental gradients: A disturbance gradient, caused by wave energy, is found along the elevation gradient, which decreases from the shore of the estuary to the high bank (Stiller, 2005). Perpendicular to the shore, the elevation gradient separates sites exposed to the tides with long inundation periods to less inundated, higher elevated sites on the landward side. Nutrient availability is determined by dissolved nutrients from the water body, mineralized material within the vegetation and relocated, washed in nutrients from landward sites. Depending on the extent of nutrient distribution in each of these areas, this may create a nutrient availability gradient. For salt marshes, nitrogen for example is known to be a limiting factor (Hopkinson & Giblin, 2008). Where the environmental factors create less stress (less salinity and inundation time) competition (for nutrients and light) can be the driving factor. This concept was elaborated for salt marshes by Scholten et al. (1987), see also Pennings and Callaway (1992).

Lastly, as a defining feature for marshes close to river mouths, a salt gradient runs parallel to the shore with higher salt concentrations at the river mouth and lower salt concentrations at the upstream-sites (Cloern et al., 2017). Salinity also varies depending on the elevation and inundation frequency.

The trait-based approach offers many possibilities to study plant strategies and adaptations in the field (Kleyer et al., 2008) and various studies identified plant trait responses to abiotic conditions in coastal habitats (Coops et al., 1994; Silinski et al., 2016; Carus et al., 2017a; Rupprecht et al., 2017). In a coastal salt marsh, the plant responses concern for instance traits relating to salt excretion or salt dilution by succulent growth (Flowers & Colmer, 2008). The specific impact of waves or flow velocities is also a frequent research subject: Brewer and Parker (1990) for instance studied tensile properties of stems in moving water and found them to be an important factor for plant zonation (see Coops et al., 1994 for lakeshore zonation). Plants exposed to strong wave forces often show a high flexural stiffness (Rupprecht, Möller, et al., 2015; Vuik et al., 2018). Bouma et al. (2005) have reported trade-offs between plant stiffness (withstanding waves) and experienced drag force. Adaptations to surviving long inundation periods include traits like aerenchymatic tissues or high oxygen content in rhizomes (Takahashi et al., 2014; Faußer et al., 2016). The advantage of being photosynthetically active under water is an ability found in some species like *Schoenoplectus tabernaemontani* and *Agrostis stolonifera* (Ellenberg & Leuschner, 2010).

Using the Elbe estuary in North Germany as a model system, our research questions are: (1) Which are the most important environmental factors asserting the highest effect on plant distribution and traits? (2) Which are the trait differences between the vegetation on low and high elevations? 3) Which key traits can be identified in order to comprehend the underlying plant strategies? To address these questions, we quantified a range of important abiotic parameters, such as wave height, inundation period, salt concentration in the soil and soil nutrients (nitrogen, potassium and phosphorus content, soil carbon content). Furthermore, we identified plant traits responsive to the environmental conditions in this tidal marsh as highlighted by other studies (such as bending stiffness, biomass allocation and organ stoichiometry, Poorter et al., 2012; Minden & Kleyer, 2014; Silinski et al., 2015; Carus et al., 2016). Our hypotheses are: I) Plant species growing near the marsh edge are adapted to wave strength by a low bending stiffness (thereby reducing the risk of flower and fruit destruction by shear forces). II) The inundation triggers a high investment in rhizomes and the ability to reproduce vegetatively. III) Plant species on higher elevations will show traits related to competition for nutrients and light, as they are exposed to higher competition from neighboring species. IV) Species sort into clusters based on similar adaptation patterns and resource usage. Through its effect on species composition, soil salinity has an impact on the clustering of plant strategies.

6.2 Methods and Materials

Study sites

In the Elbe estuary in the Northwest of Germany, three sites were chosen (Figure 10): Balje (53°51'30" N, 9°4'30"E), Krautsand (53°46'30"N, 9°22'0"E) and Hollerwettern (53°50'00"N, 9°22'30"E): Each site has a gradual sloped topography and relatively straight marsh edge. The climate is oceanic with an average temperature of 9.6 °C, an annual precipitation of 831 mm and 1672 hours of sunshine throughout the year (Cuxhaven, Wetterdienst, 2019). The soils are sandy-silty and in the site 'Hollerwettern' they are influenced by deposition of sandy dredging material on higher elevations (Kappenberg & Fanger, 2007). There is no agricultural use on the sites, but the adjacent fields are used for grazing and fodder production. The elevations of the sites relative to the tidal range ($Znorm = \frac{Plot\ elevation - Mean\ Low\ Water}{(Mean\ High\ Water - Mean\ Low\ Water)}$, (Heuner et al., 2019) are between 0.54 and 1.35 (Mean Low Water, MLW = 0, Mean High Water, MHW = 1). Soil salinity varies between on average 0.2 and 4 PSU (own measurements, Practical Salinity Unit, as a measure of salinity based on water conductivity).

Figure 10: Study sites in the Elbe estuary with 28 plots each in four different vegetation zones ranging from the edge of the mudflat to the high bank. The vegetation zones are illustrated for Hollerwettern, with the Schoenoplectus-zone (white circle), Bolboschoenus-zone (white triangle), Phragmites-zone (white square), Phragmites/mixed community-zone (white x) ATKIS® Base-DLM (left);©OpenStreetMap contributors (middle). © 2016 WSV, BfG, BAW (right).

Plot selection and vegetation zones

We selected 84 non-contiguous plots (4 m × 4 m) across the three sites, with 28 plots per site. Sampling was conducted between March 2016 and September 2017. Plots were selected by random stratified sampling at a minimum distance of 20 m to each other to avoid interferences, with the strata being elevation relative to the tidal range and vegetation zonation. The elevation was measured for each plot with real time kinematic GPS. Within the strata, the natural vegetation zonation consisted of three dominant species occurring in four different zones, which in the following text will be named after their dominant species. Each zone contained 7 plots per site, species accompanying the dominant species varied between sites. The *Schoenoplectus* zone was closest to the marsh edge (Pott, 1995). *Schoenoplectus tabernaemontani* can occur up to 2 m under the mean high tide level (MHW) (Kötter, 1961) and was often the only species growing on the marsh edge in the study sites. *Bolboschoenus maritimus* can be found on higher elevations (*Bolboschoenus-zone,* also often the only species present) and was followed higher up the bank by *P. australis* (Ellenberg & Leuschner, 2010). In this latter zone from about 0.5 m under MHW, *P. australis* grew in monotypic stands (*Phragmites*-zone), away from turbulent hydrodynamics, as it is sensitive to mechanical stress (Coops et al., 1994; Ellenberg & Leuschner, 2010). From 1 m above the MHW, *P. australis* is less competitive and other species, such as *Juncus gerardii* or *Mentha aquatica* were able to establish; this zone has been defined as *Phragmites*/mixed community.

Abiotic parameters

Inundation was recorded at 24 plots (two in each vegetation zone for each of the three study sites). We installed 80 cm long drainage pipes (8 cm Ø), covered with coconut to prevent sediment intrusion from the sides and covered with a cap to prevent penetration of sediment from the top. The pipes were oriented vertically in the ground and were equipped with pressure loggers (SENSUS ULTRA by Reefnet). The sensors recorded hydrostatic and atmospheric pressure hourly between March and October 2016. To record the corresponding air pressure, three additional loggers were attached to buildings nearby (Minden & Kleyer, 2014). Their measurements were used to correct for atmospheric pressure and to calculate the water depth in the submerged pipes. To extrapolate the water depths onto the other plots, a regression was made for each site separately between the elevation and the water depth. Hereby inundation period was determined as the time when the water level was above or equal to ground level and expressed as hours per day.

Wave heights were recorded on one transect per site between December 2015 and April 2017 (Schoutens et al., 2019) with nine pressure sensors (P-Log3021-MMC, Driesen & Kern). This transect spanned an elevation gradient from the shore to the high bank with measurement points (3 per transect) between the different vegetation zones. The measurements (frequency of 8 Hz) were referenced to water surface elevation by correction of atmospheric pressure. The tidal signal was separated from the wave signal, but it was not distinguished, if the waves were caused by wind or passing ships. A detailed description of the recording method for wave data can be found in Schoutens et al. (2019).

The mean wave height was used in this analysis (Heuner et al., 2015), extrapolated for all plots and calculated for each plot for three different water depth categories: <0.5 m, 0.5-1.0 m and >1.5 m. This was done because the wave height typically depends on the water depth (Schoutens et al., 2019), and the water depth varies over time (due to the tides) and spatially between the plot locations (due to different soil surface elevations). The value for wave impact in water depth category < 0.5 m for instance denotes the mean wave height in shallow water up to 0.5 m depth (description of extrapolation see Appendix 6. 1).

Soil salinity was measured in the top soil following Schlichting et al. (1995) through the determination of the conductivity: 10 g fresh soil was diluted with 25 ml H_2O, left for 30 min and conductivity measured in the excess water (WTW ph/Cond340i/SET, Tetracon 325 electrode). Then salinity was calculated using the UNESCO equation (UNESCO, 1981; Grasshoff et al., 1983). On each plot, the soil was sampled up to a depth of 60 cm and bulk density [g cm^{-3}] was determined for 200 cm^3 for each characteristic soil horizon by weighing each a fresh and dried sample (48 h at 105°C, Schlichting et al., 1995). Bulk density results were used to relate the analyzed soil parameters to volume and area at plot level, by multiplying the nutrient content with the mass per m^2 (derived from soil density multiplied by m^3 for each soil horizon). From the soil samples, grain size distribution [%] was determined with a Laser Particle Sizer (Analysette 22), using H_2O_2 to remove organic substances and subsequently relating to soil horizon depth and volume and expressed as kg m^{-2}. The Phosphorus (P) and potassium (K) content [g m^{-2}] were determined following the method of Egnér et al. (1960) and measured in the continuous flow analyzer (CFA for phosphorus) or in the Atomic Adsorption Spectroscopy (AAS for potassium). Calcium carbonate ($CaCO_3$) content [kg m^{-2}] was measured following Scheibler´s gasometric method (Schlichting et al., 1995). Ammonium (NH_4^+) and nitrate (NO_3) contents were determined using the incubation method following Gerlach (1973). The measurements were done with a Continuous Flow Analyzer (CFA) at 660 nm (ammonium) and 540 nm (nitrate). Mineral nitrogen (N_{min}), the sum of ammonium and nitrate, was expressed in g m^{-2}. Soil carbon (C) and total nitrogen (N) content was analyzed employing a C:N-Analyzer (Flash 2000, Thermo Scientific) following Allen (1989).

As a measure of vegetation density, photosynthetically active radiation (PAR) reaching the ground was recorded with a SunScan (Canopy Analysis System SS1, see Maier et al., 2010), using the mean of at least five measurements at each plot 5 cm above the ground. One additional measurement was done near the plot in full light (i.e. above the vegetation). PAR was expressed as the percentage of the total radiation (Maier et al., 2010).

Frequency analysis of plant species

The composition of plant species was determined with a frequency frame (50 x 50 cm), which contained 25 cells (each 10 x 10 cm) and was used 4 times per plot to cover an area of 1 m² (Tremp, 2005; Minden et al., 2012; Cebrián-Piqueras et al., 2017). In each cell, presence and absence of each species was recorded, species were determined by literature (Schmeil & Fitschen, 2003; Rothmaler, 2007). From the resulting species list, we selected a total of 17 species of which plant trait information was then collected. These species were selected so that they made up at least 95% of frequencies recorded (Cornelissen et al., 2003). Information on species names and their occurrence in the specific zones is provided in the supporting information (Appendix 6. 2 & Appendix 6. 4).

Trait measurements

Trait information was based on a total of 175 plant individuals (at least 10 individuals per species). The individuals were selected following Pérez-Harguindeguy et al. (2013): mature, healthy-looking and randomly picked from the suitable individuals of that plot. Sampling was conducted across the three sites, covering the largest range of elevations possible, i. e. the highest and lowest lying plot the species appeared on, see Appendix 6. 4 for details on species numbers collected. Plants were collected at the peak of their generative stage, i.e. when seeds were ripe but not yet shed (Minden et al., 2012). Individuals were dug out with a 20 x 20 cm soil volume; roots and rhizomes were cleaned with water and separated from roots belonging to other individuals with tweezers. Then plants were dissected into stems, leaves, roots and rhizomes. For the grass species, the leaf area was determined from the leaf blades, whereas the sheaths were assigned to the stems (following Yan et al., 2016). For *S. tabernaemontani*, a species that does not produce leaves, the stem was treated as an equivalent to a leaf, only the belowground part that did not produce chlorophyll was considered as stem. For species producing petioles, they were excluded from specific leaf area (SLA) measurements (Pérez-Harguindeguy et al., 2013).

Traits measured for all plant samples include: canopy height [cm] in the field (highest point on highest fully developed leaf, Weiher et al., 1999), specific leaf area measured on two leaves per individual (SLA, [mm^2 mg^{-1}]) using a Flatbed scanner (300dpi) and ImageJ-Software (Schneider et al., 2012). The chlorophyll content was measured in the field at each plant individual with a SPAD 502Plus (Konica Minolta), creating a mean of 10 measurements in 'SPAD' units, which were derived from absorbance at 650 and 940 nm (±61 SPAD) (Süß et al., 2015). To relate this to the actual chlorophyll content of trait individuals at harvest time, SPAD values of additional leaf samples were determined (at least 8 leaves per species with 20 measurements for each leaf) of other individuals of the same species. Of each of those leaves the area of 250 mg fresh leaf was determined (flatbed scanner 300dpi, ImageJ-Software), plant material was ground with acetone (80 %, 10 ml) and silica sand (Lichtentaler, 1987) and filtered. The filtrate was diluted with acetone to 25 ml of total volume (Uddling et al., 2007) and chlorophyll content was analyzed in a spectrophotometer (Genesys 10 UV, Thermo Spectronic, Braunschweig, Germany) at 646 and 663 nm (Lichtenthaler & Buschmann, 2001). Total content of chlorophyll was calculated for the dry mass of the analyzed leaf area through the establishment of a calibration curve for each species, predicting the chlorophyll content [µg mg^{-1}] for each trait plant individual and its mean SPAD value and related to the content per leaf area [µg mm^{-2}].

The bending properties of fresh stem samples were tested by sampling at least 20 stems per species across the three sites, harvested separately from the other trait measurements. Samples were kept cool and moist and bending tests completed within a few days at the Royal Netherlands Institute for Sea Research (NIOZ Yerseke, NL) with the Instron 5942 (Canton, MA, USA, Heuner et al., 2015; Rupprecht, Möller, et al., 2015). The measurement depends on the architecture of the stem and different equations were used to calculate the flexural stiffness: this is the product of the stems resistance to bending (the Young´s modulus [MPa]) and the stems cross-sectional area and expressed in Nmm^2 (Coops & Van der Velde, 1996a; Hamann & Puijalon, 2013; Heuner et al., 2015; Rupprecht, Möller, et al., 2015; Vuik et al., 2018 ,for a detailed description of calculations and summary table of equations used, see Appendix 6.3).

The mass per volume [g fresh mass cm^{-3}] and specific density [g dry mass cm^{-3}] of stems, roots, and rhizomes was determined using volumetric flasks. Root and rhizome samples (2 samples with 2 cm length each) of each trait plant were weighed fresh and measured in length and all material was finally dried and weighed (72 hr at 70°C). Specific root and rhizome length was expressed as mm per g dry mass, the dry matter content of each organ was the ratio of its dry mass to its fresh mass [mg dry mass per g fresh mass]. Plant investment into each organ was expressed as mass fraction for leaves (MF leaf), stem (MF stem), roots (MF roots) and rhizome (MF rhizome) [g organ dry mass per g total dry mass]. For each individual and plant organ, carbon (C), nitrogen (N) and phosphorus (P) content [g kg^{-1}] were determined. C and N content was analyzed by grinding the material in a mill ('pulverisette 7', Fritsch, Idar-Oberstein, Germany) and using the C:N-Analyzer analog to the soil sample treatment. P content was extracted from the milled material (7-8 mg, precision balance, CP 225 D, Sartorius, Goettingen, Germany) by heating the sample with nitric acid (95°C, 6 hr) and adding hydrogen peroxide (30%, 95°C, 4 hr).

Finally, the volume was raised to 1 ml by addition of water (bidest) and measured in the continuous flow analyzer (CFA, following Murphy and Riley (1962). For species mean trait values, see

Appendix *6. 9*.

Statistical analysis

All maps were visualized with ArcGIS (ESRI, version 10.2.1), and the statistical analyses were performed with the open source software R version 3.4.3 (R Core Team, 2017) and RStudio (RStudio Team, 2016).

To test the effects of the study sites and the different vegetation zones on the environmental variables, we applied linear models for each environmental variable with vegetation zones (four levels) and study sites (three levels) as explanatory variables. As we were only interested in the effects of vegetation zones on the measured variables, we treated the study sites as random effects (lmer(environment~zone+(1|site)), R-package 'lme4', Bates et al., 2015). To test for significant differences between the vegetation zones, we applied a post-hoc test (least squares means) to each model (R-package 'emmeans', Lenth, 2020), the degrees of freedom are based on the Kenward-Roger method, the test results shown in Appendix 6.5.

To elaborate the relations between variables, a three-table-analysis (RLQ) was performed, using the ade4 package (Delédec et al., 1996; Dray & Legendre, 2008). One table contained the environmental parameters (R-table), one the species abundance table (L-table) and one the species traits table (Q-table), for which the mean trait values for each species were used.

All environmental parameters were tested for normal distribution (Royston, 1982, R-Package stats), wave impact at water levels > 1.5 m was transformed using Box-Cox, and logit used on PAR (both with the R-package car, Fox & Weisberg, 2019), wave impact at water levels > 0.5 m was transformed to the power of 3, while log10 was used with salinity, N_{min}, clay, soil P and soil K (Becker et al., 1988, R-Package base). For the trait variables, stem flexural stiffness and total aboveground mass were log transformed, total belowground mass was Box-Cox transformed and belowground biomass specific density was transformed with log10.

Variables were aggregated if they were highly correlated and could be assigned to known concepts like allometric scaling of plant organ size (Garnier et al., 2016). Highly correlated variables showed $r>0.3$ (environmental variables) and $r>0.5$ (trait variables), as well as $p<0.05$ (Appendix 6.7). Hereby the aggregate values were the scores of the first axis of a Principal Component Analysis (PCA) performed on the variables. Environmental variables aggregated were:

sand and clay which run reciprocally (silt was only weakly correlated) as 'grainsize'. P and K correlated negatively (-soil P, +soil K). Wave impact in water levels > 0.5 m was aggregated with wave height in water levels >1.5 m (see Table 2). The measured soil C and N content were excluded from the actual analysis, as nitrogen availability was represented by soil N_{min}. However, as soil C and N delivered valuable background information for interpreting our results, they remained part of our dataset and are presented in Appendix 6. 6. Plot elevation was not included in the RLQ either, as the elevation was represented in the variables for inundation and wave impact (see Table 2 for summary of aggregated variables and Table 3 for all variables. For information on elevation and soil C:N ratio, see Appendix 6. 6).

Table 2: Variables aggregated with Principal Component Analysis (PCA) with their explained variance of the first two PCA-axes and correlation coefficients with the first two axes. Correlation coefficients between the variables were > 0.36.

Aggregated variables	**Aggregated variables with their positive or negative associations**	**Cumulative Proportion explained**		**Correlation coefficients**	
		Axis 1	**Axis2**	**Axis 1**	**Axis 2**
'grainsize'	+ sand	0.87	1.00	-0.71	0.71
	- clay			0.71	0.71
soil P, K	- soil P	0.68	1.00	-0.71	0.71
	+ soil K			0.71	0.71
Wave impact at water level >0.5 m	+ wave impact 0.5-1 m water level	0.88	1.00	0.71	0.71
	+ wave impact >1.5 m water level			0.71	-0.71
'size'	+ canopy height	0.75	0.94	0.47	0.59
	+ belowground biomass			0.55	0.11
	+ aboveground biomass			0.56	-0.04
	+ total leaf area			0.39	-0.80
'low density & high volume'	- stem specific density	0.59	0.83	-0.52	0.45
	- fresh mass/volume stem			-0.58	0.19
	- specific density belowground biomass			-0.55	-0.15
	- fresh mass/vol. belowground biomass			-0.31	-0.86
- SLA	- SLA (specific leaf area)	0.81	1.00	-0.71	-0.71

+ chlorophyll	+ chlorophyll content	0.71	-0.71

The plant traits canopy height, total belowground and aboveground biomass and total leaf area were aggregated as 'size'. Stem specific density and stem mass per volume, the specific density of belowground biomass and its volume were aggregated as 'low density and high volume'. Specific leaf area (Noble & Slatyr, 1980) and chlorophyll content were aggregated because of the relationship of SLA and photosynthesis (Leaf Economics Spectrum, Wright et al., 2004). A standard major axis regression was performed to highlight their relationship (SMA, Warton et al., 2006). This analysis can be used when similar measurement errors are associated with both variables (Cui et al., 2020). For this, the "smatr" package was used (Warton et al., 2012). Belowground biomass was represented in rhizome and root mass fraction (MF), to mirror nutrient storage and anchorage requirements. Similar to the nutrient status of the soil, the nutrient content of plant rhizome tissue was represented by phosphorus content alone, as adding plant tissue N and C did not add to the explained variance.

The aim of this study was to analyze the three tables that contain the data on species frequencies, plant traits and environmental data. For this purpose, a three table analysis (RLQ) was performed, which follows a step-wise process: In order to analyze R-, L- and Q-table together, a PCA was performed on the R and Q table each and a Canonical Correspondence Analysis (CCA) on the species table (Legendre & Legendre, 2012, R-Package vegan). Then the PCAs and CCA were analyzed simultaneously. Significance of the RLQ was tested with the randtest (Dray & Dufour, 2007, R-Package ade4). Based on the resulting species scores, the species were clustered into functional groups (Ward´s method, Wang et al., 2015), establishing the optimal grouping with the Caliński criterion (Caliński & Harabasz, 1974) and the stats package (R Core Team, 2017). The clusters highlight sets of traits that species growing under similar environmental conditions might have in common.

6.3 Results

Environmental conditions

The four zones that were categorized through species distribution differed in their environmental conditions. The relative elevation significantly increased from the *Schoenoplectus*-zone, to the *Bolboschoenus*-, to the *Phragmites*-, to the *Phragmites*/mixed community-zone (see Appendix 6. 2 & Appendix 6. 6). Accordingly, the inundation period was the longest on low elevations and differences existed between the *Schoenoplectus* & *Bolboschoenus* & *Phragmites*-zone. For the wave heights at all water levels, significant differences existed between all zones. The environmental conditions are shown in Figure 11 for the study sites with plots combined per zone, showing the range of values of that zone and significant differences between them, with the site considered as a random factor. Soil salinity varied most strongly between the sites in the *Schoenoplectus*-zone; the highest values were around 3 PSU but were mostly below 1 (Figure 11). The results yielded significant differences for soil salinity between the *Bolboschoenus*-zone & *Phragmites*/mixed-zone and for $CaCO_3$, only the *Bolboschoenus & Schoenoplectus*-zone were without significant differences. For sand content, significant differences existed between *Schoenoplectus*-zone & *Phragmites* and *Phragmites/*mixed-zone, for soil P and K there were no differences (K content showed high variances, this, like the salinity, was strongly influenced by proximity to the sea). For N_{min} there were significand differences between *Phragmites*/mixed & all other zones. For PAR, the *Schoenoplectus*-zone was significantly different from all other zones. For details on test results, see Appendix 6.5.

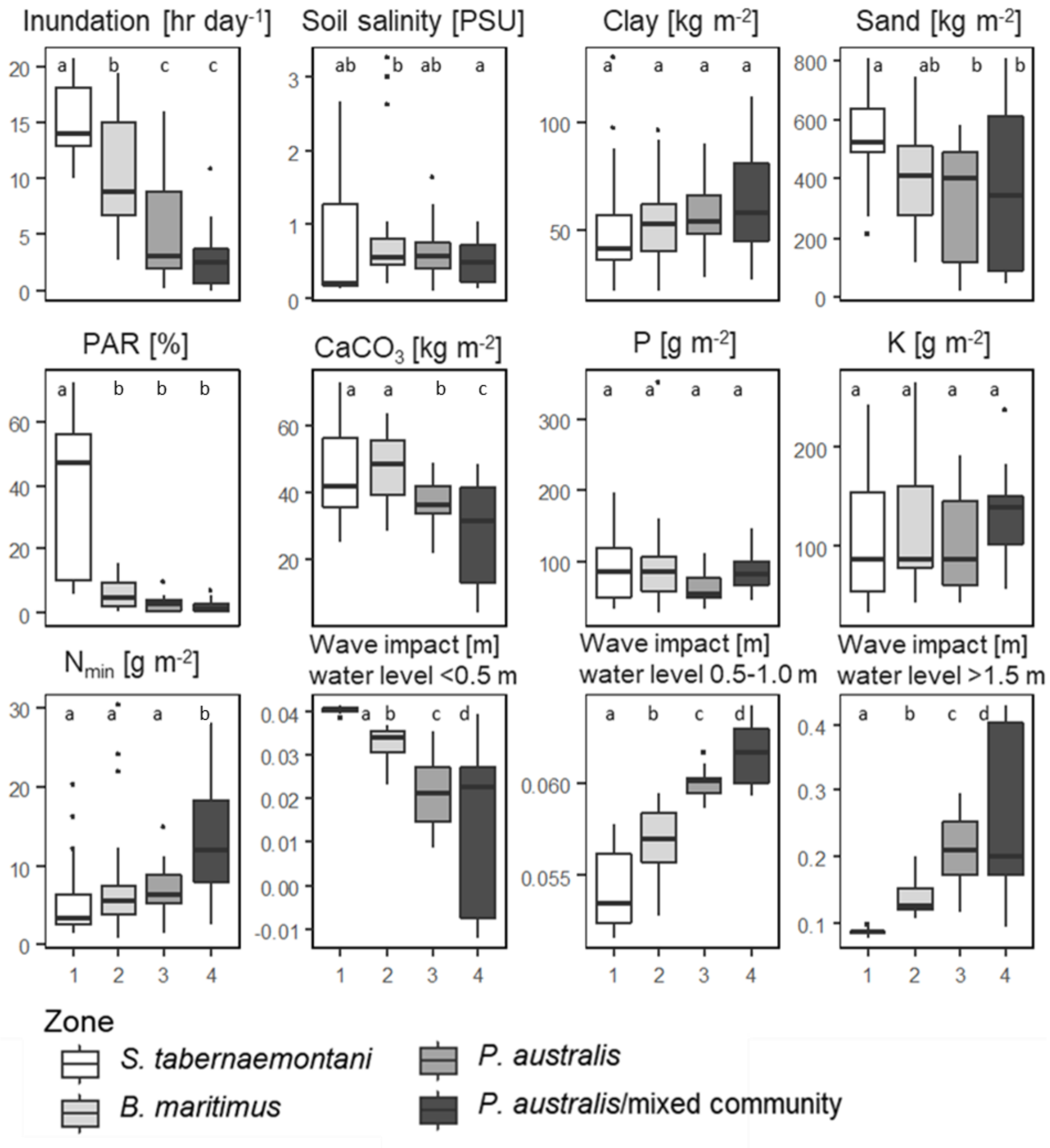


Figure 11: Environmental conditions per vegetation zone across the three study sites. Schoeonoplectus tabernaemontani occurs on the lowest elevations, followed by dominant Bolboschoenus maritimus, then Phragmites australis and on highest elevations Phragmites/mixed community occurs with a mixture of species. Significant differences between the zones are indicated with different letters, p < 0.05, for details on significance test, see Appendix 6.5. For information on species zonation, plot elevation and soil C:N ratios, see Appendix 6. 6.

Explained variances for environmental and trait Principal Component Analysis

The Principal Component Analysis (PCA) for the environmental parameters explained 42.04% on the first and 18.43% of the variance on the second axis. For the trait-PCA, the explained variance on the first axis was 50.84% and 22.75% on the second axis.

Links between environment and plant traits – RLQ Analysis

The first RLQ-axis (Figure 12, Table 3) explained 95.7% of the total variance. The second axis explained 3.35%. The analysis was significant with p<0.005. The variance of the environmental scores was preserved with 91%, and traits scores with 93% of the original PCA scores.

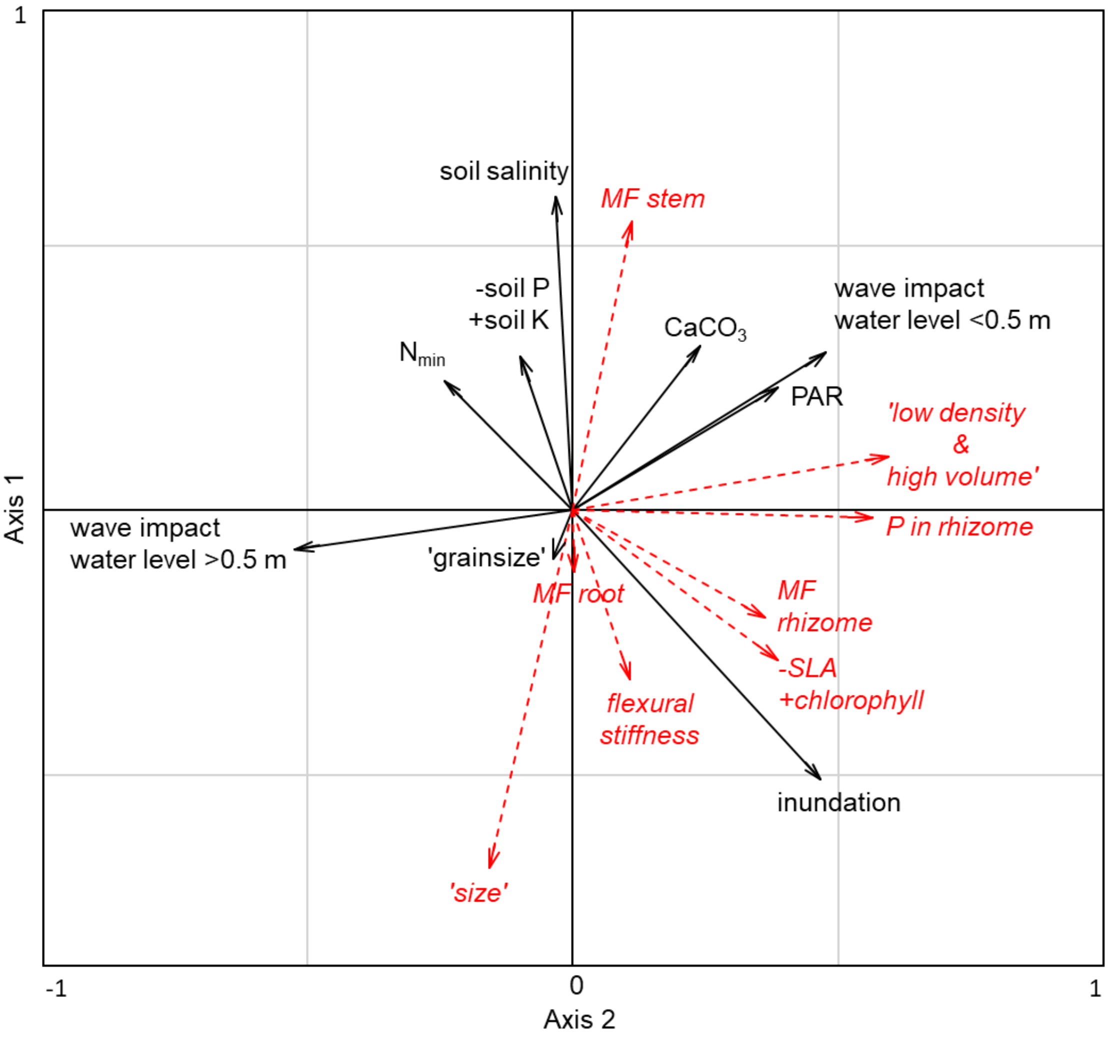


Figure 12: Ordination diagram of the RLQ-analysis displaying the environmental variables (solid lines) and the plant traits (dashed lines). For correlations with the axes, see Table 3.

- *Inundation = water > =ground level,*
- *soil salinity = salinity in topsoil,*
- *'grainsize' = aggregate - clay & + sand,*
- *$CaCO_3$=carbonate,*
- *- soil P, + soil K = aggregate phosphorus & potassium,*
- *N_{min} = plant available nitrogen,*
- *wave impact at water level <0.5 m = wave height at all water levels <0.5 m,*
- *wave impact at water levels >0.5 m = aggregate of variables for wave height >0.5 m,*
- *PAR= photosynthetically active radiation,*
- *'size' = aggregate of canopy height & above- & belowground biomass & total leaf area,*
- *'low density & high volume' = aggregate of stem and belowground biomass density & fresh mass per cm^{-3},*
- *- SLA, + chlorophyll = aggregate of specific leaf area & leaf chlorophyll,*
- *flexural stiffness = flexural bending stiffness of stem,*
- *P in rhizome = phosphorus content in rhizome,*
- *MF stem= mass fraction stem,*
- *MF rhizome= mass fraction rhizome,*
- *MF root = mass fraction root.*

The strongest environmental gradients along the first axis were wave impact at water levels > 0.5 m (correlation coefficient with the first axis -0.97); a positive correlation existed for wave impact at water levels < 0.5 m with the first axis (0.90), inundation (0.87) and photosynthetically active radiation at ground level (PAR, 0.77). As such, this set of variables spanned a 'wave disturbance-inundation gradient' along the first axis with low-lying sites receiving high wave impact and being exposed to long inundation periods. Additionally, these low-lying sites were characterized by sparse vegetation, where radiation at soil surface was high. Opposite to this, the high-lying sites showed dense vegetation and aerated soils – here, the highest wave impact was in water levels > 0.5 m.

Further, $CaCO_3$ was positively correlated with the first axis (0.53) and higher on lower-lying sites. N_{min} was significantly lower in the *Schoenoplectus*-zone and highest on high elevations with short inundation durations (Figure 7).

The second RLQ-Axis revealed a 'salinity-nutrient' gradient, with phosphorus running reciprocally to potassium and soil salinity (0.86, Table 3). Plots with high influence of sea water also contained higher potassium levels whereas the less saline sites had more soil phosphorus, which was likely due to riverine input. Grainsize showed very weak correlations with either of the first two axes (-0.10, -0.06). The accounted variance of the second axis was very small (3.35%), which suggests that the effects of nutrient availability and salt are by far of lesser importance in the studied tidal marshes than the effects of inundation and wave impact.

Table 3: Variables used in the RLQ, variables aggregated and correlations with the first and second RLQ-Axis.

Variables	**Positive or negative associations of aggregated variables**	**Unit**	**Correlation coefficients**	
Environment			**Axis 1**	**Axis 2**
Inundation		[hr day^{-1}]	0.87	-0.36
Soil salinity		[PSU]	-0.13	0.86
'grainsize'	+ sand - clay	[kg m^{-2}] [kg m^{-2}]	-0.10	-0.06
$CaCO_3$		[kg m^{-2}]	0.53	0.18
soil P, K	- soil P + soil K	[g m^{-2}] [g m^{-2}]	-0.29	0.67
N_{min}		[g kg^{-1}]	-0.53	0.26
Wave impact at water level <0.5 m		[m]	0.90	0.24
Wave impact at water level >0.5 m	+ wave impact 0.5-1 m water level + wave impact >1.5 m water level	[m]	-0.97	-0.10
PAR	(photosynthetically active radiation)	[%]	0.77	0.07
	Traits			
'size'	+ canopy height + belowground biomass + aboveground biomass + total leaf area	[cm] [g] [g] [mm²]	0.12	-0.88
'low density & high volume'	- stem specific density - fresh mass/volume stem - specific density belowground biomass - fresh mass/vol. belowground biomass	[mg dry mass cm^{-3}] [g fresh mass cm^{-3}] [mg dry mass cm^{-3}] [g fresh mass cm^{-3}]	0.91	-0.18
- SLA + chlorophyll	- SLA (specific leaf area) + chlorophyll content	[mm² mg^{-1}] [µg mm^{-2}]	0.84	-0.73
flexural stiffness		[Nmm²]	0.50	-0.80
P in rhizome		[g kg^{-1}]	0.98	-0.37
MF stem	MF=mass fraction	[$g_{(stem)}$ $g_{(all)}^{-1}$]	-0.10	0.68
MF rhizome	MF=mass fraction	[$g_{(stem)}$ $g_{(all)}^{-1}$]	0.87	-0.65
MF root	MF=mass fraction	[$g_{(stem)}$ $g_{(all)}^{-1}$]	-0.09	0.01

Connected with the 'wave disturbance-inundation' gradient, traits associated with lightweight material ('low density & high volume') were found in low-lying sites with long inundation durations (Figure 13). This aggregate only showed a high correlation with the first axis (0.91), highlighting the strong influence of the wave impact and inundation on it: plant tissue was voluminous and relatively light and plants showed a high content of phosphorus in the rhizomes, indicated by a positive correlation with the first axis (0.98). Additionally, the aggregate containing SLA and chlorophyll content showed a positive correlation with this axis ('wave disturbance-inundation', 0.84), and a negative with the second axis (-0.73, Table 3): Plots with long inundation periods were characterized by plant species with a small specific leaf area and high chlorophyll content per area (Figure 12). The relationship of chlorophyll content and SLA is highlighted in Figure 13.

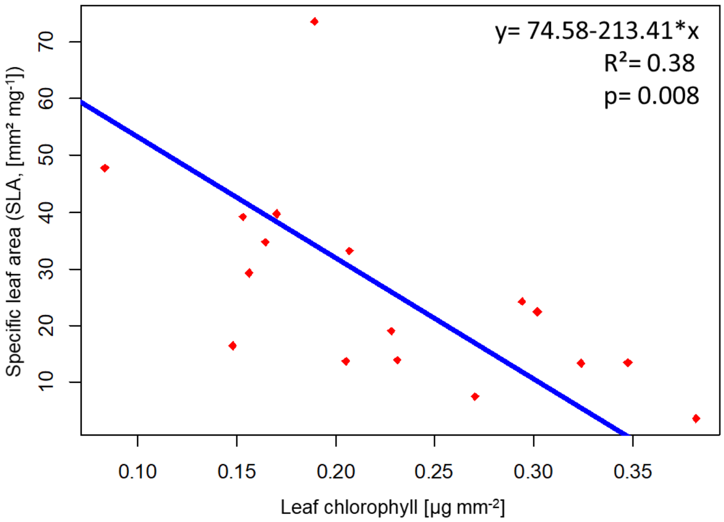


Figure 13: Standard major axis regression (SMA) of specific leaf area (SLA) and leaf chlorophyll content.

The orientation of the SLA-chlorophyll aggregate within the RLQ to plots with long inundation duration is visible in Figure 12. The 'size' gradient on the other hand strongly negatively correlated with the 'salinity-nutrient' gradient (i.e. with the second axis, -0.88), as did flexural stiffness (-0.80): tall species with a high biomass in belowground and aboveground organs showed a large total leaf area and stiff stems; the flexural stiffness increased with plant size. Stem mass fraction was highest where soil potassium was highest and inundation was lowest and showed strong correlations with the second axis ('salinity-nutrient', 0.68), opposite to the rhizome mass fraction, which showed correlations with both axes (0.87, -0.65). The root mass fraction did not show strong reactions to any of the gradients.

Species Cluster analysis

The cluster analysis yielded five stable functional groups for the trait species sampled (Figure 14 and Figure 15, clusters A to E). Cluster A encompasses one species, *Schoenoplectus tabernaemontani.* Characteristic for this species was its low tissue density and high volume of stems, rhizomes and roots, high chlorophyll content and phosphate in the rhizomes (i.e. high scores for the -SLA, +chlorophyll aggregate, Figure 15c,e) associated with the detected gradients of Figure 12. The species strongly responded to the 'wave disturbance-inundation' gradient along the first RLQ-axis (Figure 12, Figure 14, Figure 15b). *Schoenoplectus tabernaemontani* grew where the wave impact in shallow water was highest and inundation durations were long. Cluster B contained two species, *Bolboschoenus maritimus* and *Typha angustifolia*, both producing high above- and belowground biomass (ˈsizeˈ), with a very stiff stem. Those trait variables were connected to the second RLQ-axis, the 'salinity-nutrient' gradient. Further, these species had a high rhizome mass fraction which was responding the 'wave disturbance-inundation' gradient too (Figure 15a,d,g).

The species of cluster C, *Cirsium arvense, Lythrum salicaria, Calystegia sepium* and *Phragmites* were grouped through the same traits as *B. maritimus* and *T. angustifolia.* They too were similar in relation to their large size, low SLA, high chlorophyll and high flexural stiffness traits, with substantial investment into below- and aboveground biomass and a large total leaf area (ˈsizeˈ, 'salinity-nutrient' gradient). They had much denser biomass than the species of cluster B (responding to the 'wave disturbance-inundation' gradient) and showed a high root mass fraction (Figure 15a,b,h). This cluster was found on intermediate elevations, where wave impact was highest only at deep water levels (when water levels exceed vegetation height). Cluster D contained species that had intermediate trait values regarding all of the sampled traits, with species growing on the less disturbed side of the gradient compared to cluster A-C; it included *Mentha aquatica*, *Mentha verticillata*, *Juncus gerardii, Phalaris arundinacea*, *Lycopus europaeus*, *Festuca arundinacea* and *Scutellaria galericulata*. Cluster E was determined through small size of plants, high tissue density, high SLA and low chlorophyll per area, located on the other end of the 'wave disturbance-inundation' and 'salinity-nutrient' gradient compared to cluster A (Figure 15a,b,c). In our hypothesis, we expected traits typical for light and nutrient competition under these less stressful growing conditions. The cluster contained *Agrostis stolonifera*, *Myosotis scorpioides*, and *Elymus athericus* – those species were growing on higher elevations with high stem mass fractions and a relatively small investment into belowground organs (Figure 15).

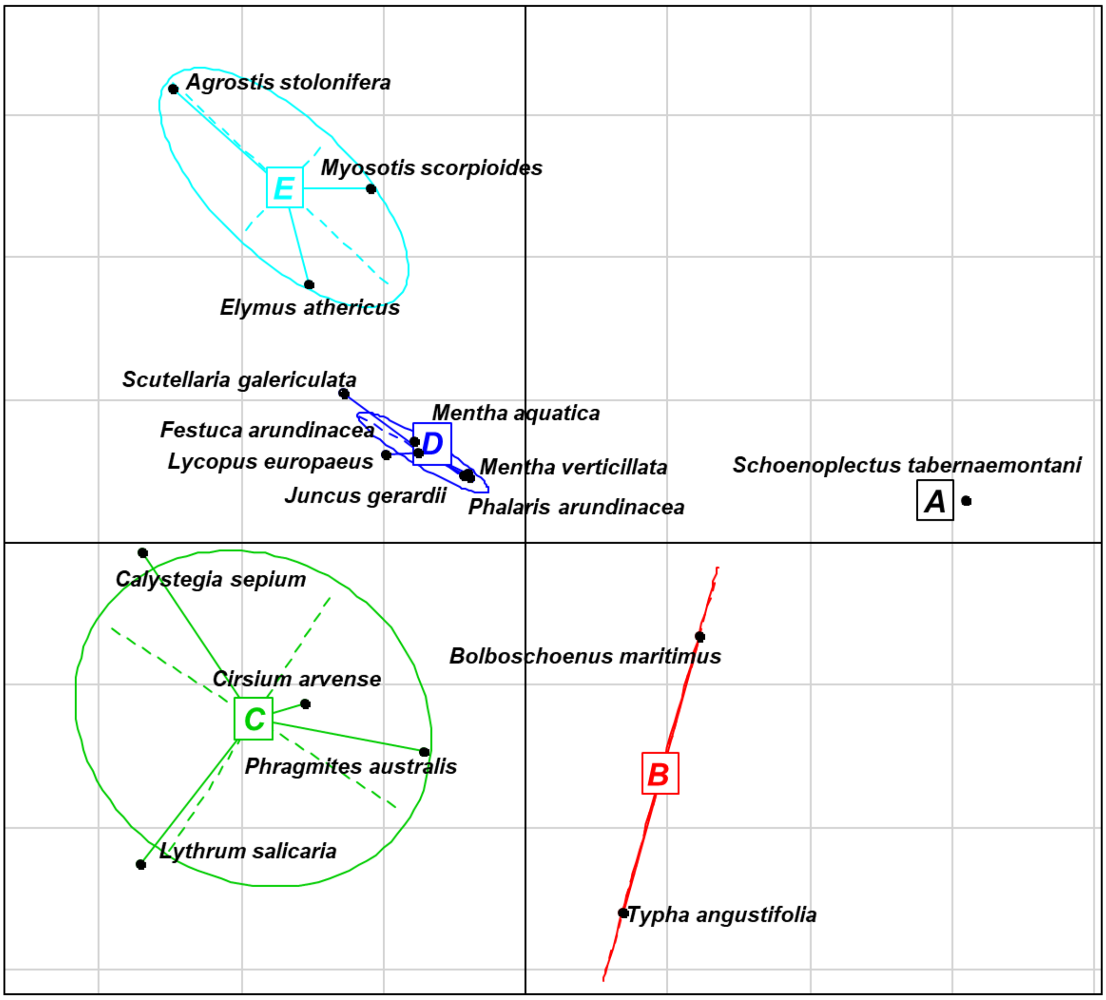


Figure 14: Species clusters (A-E) in the environment-trait space with respective species names. Clusters were based on trait scores, see boxplots in Figure 15. Ward´s method and the Caliński criterion were used to establish the clusters.

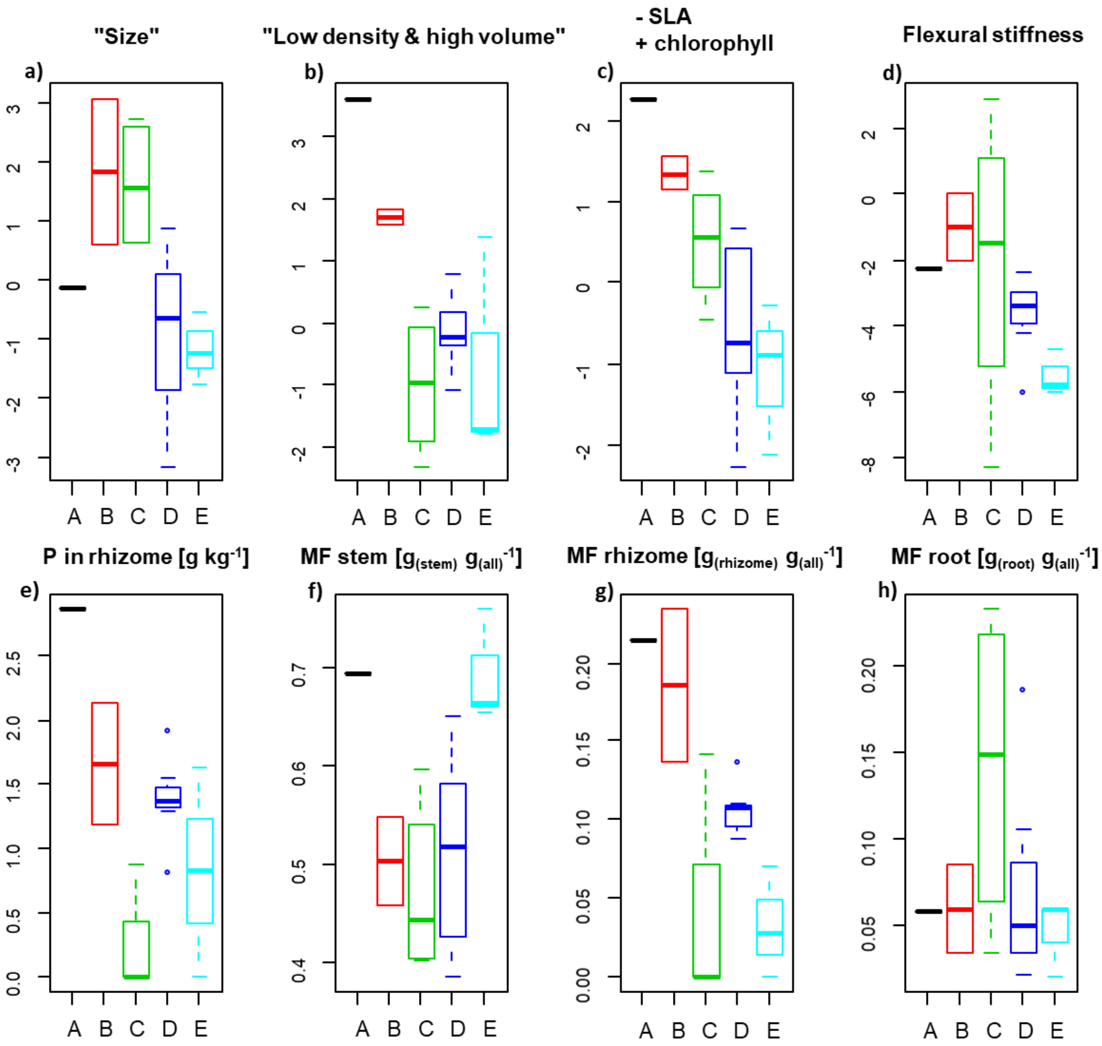


Figure 15: Boxplots a-h for trait value ranges defining species clusters of Figure 14 within the environment-trait space of the RLQ, Figure 12. The mean trait values for each species within a cluster are shown. The species clusters are named A-E, for names encompassed in the clusters, see Appendix 6. 2. For aggregated variables, the y-axis shows the PCA scores of the first axis. Flexural stiffness shows the log transformed data. For abbreviations and variables included in aggregates, see Table 2.

6.4 Discussion

Unraveling the effects of abiotic parameters on plant traits and plant zonation in tidal marshes allows the predictions of changes in environmental conditions on plant performance and the development of conservation measures to protect them. The sampling design, the selection of individuals of a trait-species growing on different elevations, might neglect to account for their possible plastic response though; therefore, the findings of the present study have to be carefully discussed, with this issue in mind. The main findings in this study are, that wave impact (height) and inundation period are by far the most important factors that determine species presence and trait expressions in the studies sites. Responses to those parameters are plant traits such as lightweight material, strong investment into rhizomes and high leaf chlorophyll content on low elevations. Contrary, on higher elevations, plants are stiffer and show a high SLA. The species plasticity as a response to environmental factors is an important aspect in this context (Carus et al., 2016; Zhu et al., 2018), but was not the focus of this study, which was based on the mean trait values of all sampled individuals per species. The results of our RLQ-analysis confirm findings of previous studies that found stem flexural stiffness and investment into rhizomes connected to hydrological gradients (wave height and inundation period). The results from our study indicate, that soil nutrients and salinity only play a minor role, gaining more importance on higher elevations that are less frequently inundated, with competition for light as a driver for species. However, in other ecosystems with a higher nutrient load of the river, nutrients may play a more important role also for plants of lower elevations.

The impact of wave height on species distribution and plant trait expressions

As a response to waves, vegetation stands at the shore show flexible stems, a reduced competitive strength and reproduction and produce less biomass (Azza et al., 2007). Wave forces acting on plants are typically highest near the water front, as waves are attenuated when propagating inside the vegetation (Koch et al., 2009) and vegetation with less dense and more flexible stems has been shown to feel less drag force from waves (Bouma et al., 2005; Heuner et al., 2015; Heuner, 2016). Flow velocities or wave height might have different intensity and impact on the vegetation, depending on site conditions, slope and exposure to wind and ship passages.

Many studies focus on wave impact and or flow velocities: Coops et al. (1994) analyzed the effect of significant wave height (i.e. the mean wave height of the highest third of waves) and found reduced tiller numbers and total biomass on exposed sites. Vuik et al. (2018) assumed in their model, that the mean of the highest one-tenth of waves was breaking the plant stems, and by this was a significant factor controlling species distribution. This is related to stem flexural stiffness as pointed out by Rupprecht, Möller, et al. (2015), who worked on biophysical properties of saltmarsh species: stems with smaller flexural stiffness can bend more easily and move along with the wave while stems that are more rigid (i.e. show higher flexural stiffness) are less able to bend (Bouma et al., 2005; Heuner et al., 2015). Often bending stiffness is determined as a key trait for species withstanding or avoiding waves (Puijalon et al., 2011; Silinski et al., 2015; Schoutens et al., 2020).

Our results also detect bending stiffness as an important trait, but the density of the tissue and the nutrient- storage function of the plant organs (high rhizome P) showed stronger correlations with the environmental gradients. The tissue density though was highly correlated with the flexural stiffness. Those findings confirm our first and second hypothesis that plants growing close to the shore show high invest into belowground organs and a low bending stiffness.

The stem stiffness can vary within species, depending on site conditions, elevation, plant height and the position within the stand (Carus et al., 2016; Zhu et al., 2019); it also varies depending on the part of the stem tested (Rupprecht, Möller, et al., 2015) and the season (Coops & Van der Velde, 1996a; Zhu et al., 2019). For instance, Vuik et al. (2018) found *B. maritimus* to have a flexural rigidity of 52.000±35.000 Nmm². In our study, bending stiffness of *B. maritimus* was found to be 136.000 Nmm², which is similar to findings from Carus et al. (2016). The geometry of the stems has to be taken into account too, the stem shape of *B. maritimus*, which is triquetrous, would lead to a smaller resistance against the currents (Kötter, 1961) and withstand higher flow velocities (Carus et al., 2017a). Regarding the wave impact on higher elevations, our results show that the impact for water levels < 0.5 m and > 0.5 m are opposite to each other, meaning that higher waves occur on the higher elevated plots only at deeper water levels. The waves are being dampened by the vegetation and are therefore usually small at higher elevations at water levels <1.5 m depth. Above this water level, dissipation effects of the vegetation could not be detected for the study sites (Schoutens et al., 2019): as the tide rises, the waves are then well above the *S. tabernaemonani*-zone, its dampening effect diminishing and therefore higher waves reaching higher elevations.

The impact of inundation period on plant trait expressions

The other major impact on the species growing on the lower elevations in the Elbe estuary are long inundation periods: inundation causes stress, such as oxygen scarcity in waterlogged soil (Colmer & Voesenek, 2009) and higher levels of toxins in the soil, such as sulfide (Adam, 1990; Lamers et al., 2013). Additional to adaptations to wave impact, plants on those low elevations allocate high amounts of chlorophyll into their photosynthetic active tissue, aiding to maintain photosynthesis during times of submergence. The SLA was negatively related to chlorophyll (per area), which means, plants with a large, thin leaves had relatively little chlorophyll per area. In relation to mass basis, the findings are in accordance with the leaf economic spectrum (LES): a high SLA with high nutrient and chlorophyll content *per mass* (Wright et al., 2004). An inverse relationship of SLA and environmental variables as expected from the LES was found in saltmarshes (Minden & Kleyer, 2015). There, leaf traits SLA and LDMC (leaf dry matter content) were more strongly constrained by salt, waterlogging and inundation than by soil nutrient availability. In our brackish tidal marsh habitats, the results revealed a similar pattern, yet due to different plant strategies. For example, in the leafless species *S. tabernaemontani*, which allocates its photosynthetic active area into its stem, a high chlorophyll content allows for effective photosynthesis on a small surface. Some species are able to do photosynthesis being submerged too, this includes *S. tabernaeomontani* and *B. maritimus* (Clevering et al., 1995; Clevering et al., 1996) .

These results point out trait-environment patterns in tidal marsh plants (see Figure 16): the traits of the species enable them to pass the strong environmental filters (such as inundation duration or wave energy).

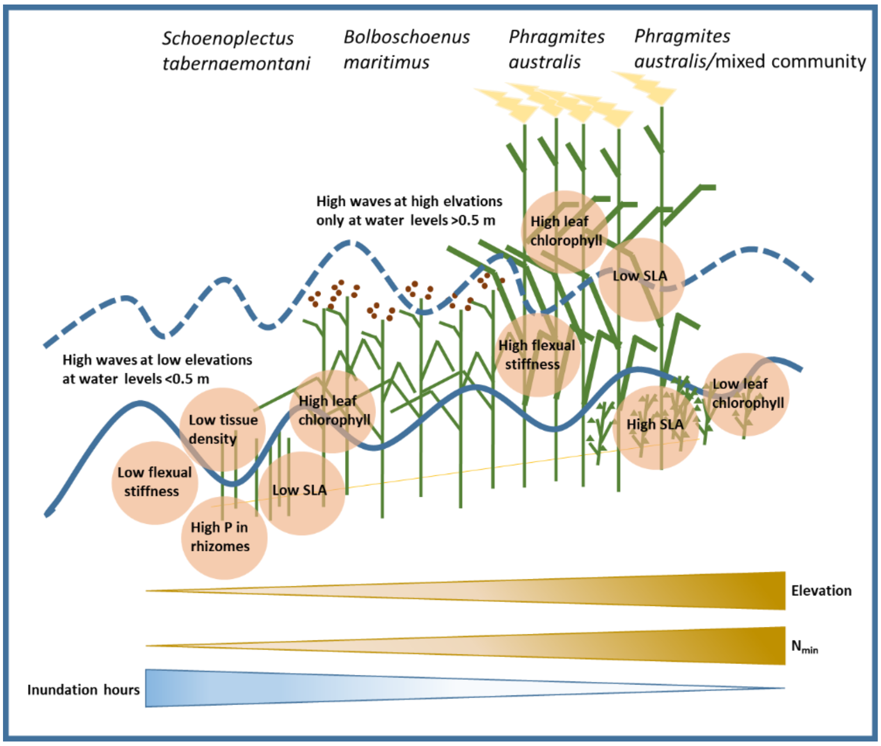


Figure 16: Schematic illustration of plant strategies in relation to the position in the tidal frame, with elevation, N_{min} (mineralized nitrogen), inundation period and wave impact in different water levels displayed as gradients. Traits shown: flexural stiffness (stem), tissue density (below- and aboveground organs), SLA (specific leaf area), P in rhizome (phosphorus content in rhizomes), leaf chlorophyll (chlorophyll content per mm² leaf). The soil salinity is a gradient from the mouth of the river upstream, shaping species inventory that ranges from species with adaptations regarding salt excretion or dilution downstream to species that can merely tolerate low salinity levels upstream.

Furthermore, we found vegetation near the marsh edge has a strong rhizome system (see also Carus et al., 2017b) to ensure nutrient storage, anchorage and growth through suckers. This relationship is in accordance with our second hypothesis and supported in our results (high allocation into belowground organs and high tissue P content with a correlation of 0.72 between rhizome mass fraction and P content, see Appendix 6.7). Relatively high investment into belowground organs is known to be connected to inundation stress (Minden et al., 2012). The importance of reproduction through rhizomes and their role as an energy storage is of major importance in this context (Granéli et al., 1992). Especially clonal integration could possibly enable species to extend their spatial range in less favorable conditions while still being connected with the parent individual (Burdick & Konisky, 2003; Silinski et al., 2016). Silinski et al.

(2016) highlighted clonal integration as a major factor for successful expansion of *B. maritimus* stands. Vegetative reproduction holds many advantages over sexual reproduction in aquatic habitats – some species are combining both for short and long distance propagation too, like *Typha angustifolia* and *P. australis* (Wetzel, 2001). As our study provides some insight into the reproductive strategies of plants from river marshes, more research is needed to further elucidate plant strategies related to reproduction in this habitat.

The impact of soil nutrients and salinity on trait expressions and plant stoichiometry

Our results show that bending stiffness is strongly connected to the size aspect of a plant, as also shown by Zhu et al. (2019), this being strongly connected to the 'salinity-nutrient' gradient, which only has a very small explanatory value in the present RLQ-analysis.

The soil nutrient contents of the study sites with phosphorus (62-92 g m^{-2}) and potassium (99-127 g m^{-2}) are sufficient for growth in every zone (Schachtschnabel et al., 1987) while N_{min} (6 and 7 g m^{-2}) is low for the *Schoenoplectus*- and the *Bolboschoenus*-zones. For the *Schoenoplectus*-zone, the sand content in the soil is significantly higher than in the other zones, which explains the reduced potential to retain N_{min} here and in turn could have a size-reducing effect on the growth of *S. tabernaemontani*. Producing slender stems in this hydro-dynamically turbulent zone is not a disadvantage though, as this helps avoiding drag forces (Puijalon et al., 2011; Heuner et al., 2015).

Following the rules of allometric scaling (Enquist & Niklas, 2002), the taller plants in this study with a large leaf area also showed a strong biomass investment into their stem (absolute, not relative). The allometric scaling model highlights the fundamental biomass partitioning rules.

Further from the shore on higher elevations with high N_{min} availability, plants show a high biomass production and a particularly high allocation to stem biomass, resulting in a dense canopy and low PAR values. In our third hypothesis, we expected values of traits related to competition such as specific leaf area or canopy height would be higher on higher elevations compared to lower elevations. The 'salinity-nutrient' (mainly P and N_{min}) gradient across the three study sites might become apparent because of the decline of the 'wave disturbance-inundation' gradient: on those higher elevations, waves are not a significant environmental factor anymore and longer inundation is rare. The species that cannot tolerate long inundation or wave activity are present here, but they still have to be salt tolerant, due to infrequent inundation with saline water.

Competition for light is probably guiding the species traits on high-lying plots. Light becomes a limiting factor, when shoots are big enough to shade out one another; the factors that influence their growth up to that point are environmental stresses and nutrient availability

(Scholten et al., 1987). Taking the plant organ analysis into account (Appendix 6.8), there is a significant difference between plant above- and belowground N:P ratios and organ N:P ratios for each species. This is due to different organ functions regarding acquisition and storage of nutrients and also environmental factors like light impacting on the plants, which can affect plant N and P similarly (Güsewell, 2004). The N:P ratios for aboveground biomass are <10 for most trait species (Appendix 6.8), which Güsewell (2004) categorize as limited by N (see also Koerselman & Meuleman, 1996). The effect of competition for light on the higher elevations could be the cause for these ratios: *Scutellaria galericulata* for instance, growing beneath *P. australis* on high elevations with very high N_{min} content, has an aboveground biomass N:P ratio of 8.16 – similar effects could be causing low ratios for *Myosotis scorpioides* and *Mentha aquatica* too, which also differed significantly from values for *P. australis*.

Summary

We could detect important plant traits which are connected to plant species distribution in the tidal marshes of the three study sites in the Elbe estuary. The hypothesis was confirmed that plants growing near the estuarine shore show stiff stems and a high investment into belowground biomass. Where waves create disturbance and plants face stress by long inundation periods, traits regarding avoiding wave energy (low flexural stiffness) and maximizing belowground storage (for vegetative reproduction) are essential. Further, as expected in hypothesis four, traits regarding competition have higher values on higher elevations and species could be grouped based on their trait scores. Regarding the spatial distribution of the three dominant species, *S. tabernaemontani*, *B. maritimus* and *P. australis*, the intensity of the wave impact in low water, and possibly also the low N_{min} content of the soil, may create the opportunity for *S. tabernaemontani* to grow in front of *B. maritimus* (Figure 16). Hereby *S. tabernaemontani* and *B. maritimus*, two species growing close to the shore, show a low specific leaf area and high chlorophyll content per area, though not per mass.

From the mean high tide level upwards, wave action is reduced enough to allow *P. australis* to thrive. On those higher elevations, where inundation stress and wave disturbance are less, traits concerning competition gain more momentum. While the low-lying plots contain extreme specialist species that passed the strong filters, the high bank is home to a mixture of species that competes regarding light acquisition. *Caltha palustris* for instance uses a temporal niche, having her cycle completed before the surrounding *P. australis* closes the light gap (Ellenberg & Leuschner, 2010). Other species, like *S. galericulata* do not have their optimal growing conditions within the *Phragmites*/mixed community-zone but are able to survive through a high investment into their stems and very slight material investment into leaves – with a large leaf area with a quick turnover rate. *Myosotis scorpioides* shows a similar ecology and, like *M. verticillata,* is able to fill gaps appearing in the canopy (due to wind and wave activity) with rapidly developing biomass.

The findings of this study are particularly relevant regarding projects to restore tidal marsh vegetation, as they highlight relationships between the different gradients that act on plants and their traits in an estuarine setting. Further research is needed to elaborate the role of the entire bank vegetation in ecosystem services such as wave attenuation and carbon sequestration. Changes in the environmental conditions, for example higher wave frequencies by more ship passages in the river channel and sea level rise may trigger changes in species composition. They may demand an even higher flexibility of the species near the shore and sea level rise will cause longer times of inundation for the vegetation on low elevations.

Acknowledgements

We would like to thank Michael Kleyer for advice and support, Hannes Sahl and Thomas Jansen for measuring the elevations with RTK and Daniela Meißner in the laboratory, Frances Pusch for working on the initial phase of the project as well as the numerous students helping with sampling and processing work. This research was conducted in cooperation with the German Federal Institute of Hydrology (BfG) in line with its R&D-Project TIBASS (Tidal Bank Science and Services).

Chapter 7. Hydrodynamics affect plant traits in estuarine ecotones with impact on organic carbon sequestration potentials

Schulte Ostermann, Tilla; Kleyer, Michael; Heuner, Maike; Fuchs, Elmar; Temmerman, Stijn; Schoutens, Ken; Bouma, J. Tjeerd; Minden, Vanessa

Abstract

Estuaries are highly productive ecosystems that play an important role in carbon fixing. The amount of carbon fixed by temperate brackish marshes depends, among others, on the biomass produced, its decomposition and the organic carbon stored in the soil. Here, we assumed that the functional trait composition of the vegetation both responded to environmental drivers and affected production, decomposition rate and soil organic carbon, in addition to direct links between environmental drivers and these ecosystem properties. We tested a set of detailed hypotheses with a partial least squares structural equation model and quantified wave height, inundation period, salinity, soil nutrients, species abundances and as traits the leaf area, specific leaf area, stem bending properties and investment per plant organ, as well as aboveground standing biomass, decomposition rate and soil organic carbon (SOC).

There was no direct relationship between environmental drivers and ecosystem properties, except with the decomposition of standard hay. All other linkages involved the functional composition of the vegetation. Increasing inundation period decreased an “aboveground” module composed of the correlated traits stem stiffness, leaf area, specific leaf area and mass fraction of stems and leaves. Total plant biomass decreased with reduced wave height. Increases in the aboveground trait module resulted in higher aboveground community biomass and SOC but decreased the decomposition of native plant material. Increasing total plant biomass also increased SOC, but not aboveground community biomass. Both the aboveground trait module and total plant biomass were response and effect traits, by responding to the environmental drivers and affecting carbon related ecosystem properties.

At lower elevation, higher inundation and higher wave height, SOC was lower than the product of standing biomass and decomposition rate, which could be a proxy of the expected SOC. This may indicate an export of dead plant material to higher elevations or further downstream.

Due to sea level rise, the area of estuarine vegetation may decrease because a fixed dike line along the river prevents landward migration. Restoration of the tidal marshes or realignment of the dikes may be necessary to protect the ecosystem properties and services of estuarine vegetation.

7.1 Introduction

Tidal marshes are highly dynamic environments, strongly affected by wave impact, inundation regime, soil salinity and nutrient supply (Broome et al., 2019). They provide important ecosystem services, such as facilitating river self-purification and trapping sediment (Kappenberg & Fanger, 2007) and are of high value for bird life. The tidal marsh vegetation protects the shores from erosion by attenuating incoming waves (Schoutens et al., 2019). Also, marshes have a remarkable potential to produce and sequester carbon (Choi & Wang, 2004). On a global scale, tidal wetlands are estimated to account for one third of the oceans carbon burial (Duarte et al., 2005). Tidal marshes ca be subdivided into salt marshes and estuarine marshes, the latter usually forming where rivers discharge fresh water into the sea. Thus, salinity stress in estuaries is not as high as in salt marshes, allowing the growth of reed stands with significantly higher aboveground biomass than salt marshes (Minden, 2010; Schoutens et al., 2019). Many estuaries are increasingly impacted by marine traffic, dredging and shoreline stabilization. Sea level rise will be an additional future impact (McLusky & Elliott, 2004). As such, it is essential to understand how ecosystem properties respond to environmental changes, to be able to predict the future delivery of ecosystem services such as carbon sequestration (Le Quéré et al., 2014).

Organic carbon sequestration is mainly mediated by biomass production, decomposition and carbon storage in soils (Grime, 1998). A component of biomass production is standing aboveground plant biomass (AGB) at the moment of peak biomass. This shows the potential of a site to sequester carbon. In tidal marshes, some part of the produced biomass will be washed away by the tides (Hansen et al., 2017) and some part will decompose in-situ. Decomposition rates of biomass produced inform on plant tissue decomposability by the microbial community and how long this process might take. Some organic carbon will not be decomposed and can, depending on site conditions, remain unmineralized and be stored in soils over long timescales (Schulze et al., 2010; Soussana et al., 2014). Also important are the chemical composition of the plant tissue and the environmental conditions that decrease decomposition rates of organic material, such as lack of oxygen in soils (Choi & Wang, 2004; Wagner et al., 2015). Studies have shown that carbon sequestration and soil organic carbon stocks are related to the high amount of biomass that tidal marshes are able to produce every growing season (McLeod et al., 2011; Elschot et al., 2015; Najjar et al., 2018).

In vegetated estuarine habitats, biomass productivity and decomposition can be directly affected by a suite of environmental factors. From eulittoral to supralittoral sites, water levels and anoxic soil conditions change strongly and continuously along with the semi-diurnal tide, making these habitats prime examples for ecotones. Apart from the change along the cross-section of a river, there is variation in tidal ranges and salinity along the longitudinal course of estuaries (Hopkinson et al., 2019). In addition and depending on size and land use intensity of the river catchment, the estuarine water can be enriched with nutrients, dissolved carbon and pollutants (McLusky & Elliott, 2004). Ship traffic and occasional storms cause waves that can disturb productivity, whereas floods can export dead plant material from the estuarine vegetation towards onshore locations or into the open sea, thus decreasing the amount of soil organic carbon stored on site.

Ecosystem properties such as biomass production and decomposition may not only be directly mediated by environmental factors, but also indirectly by plant community composition and the traits of the species (Lavorel & Grigulis, 2012; Lienin & Kleyer, 2012) . On the other hand, van der Plas et al. (2020) have shown that plants traits alone are poor predictors of ecosystem properties and need to be complemented by the assessment of direct environmental effects on ecosystem properties. In a chain running from the environment to carbon-related ecosystem properties, plant species and their traits take a central role by responding to environmental variation and affecting ecosystem properties. This chain is conceptualized in the response-effect framework (Chapin et al., 2000; Lavorel & Garnier, 2002). Some traits may either respond to the environment or affect ecosystem properties or both (Suding et al., 2008; Minden & Kleyer, 2011; Lienin & Kleyer, 2012). Given that the environmental drivers are affecting both belowground and aboveground plant parts, it is necessary to adopt a whole-plant perspective on trait responses and effects, i.e. to consider traits of all relevant plant organs (Kleyer & Minden, 2015).

Estuarine species show a range of different trait responses to the environmental conditions (Carus et al., 2017a). They differ, for instance, in their stem flexural stiffness and their investment into rhizomes (proportionally and regarding nutrient content). These responses, which may help to avoid or withstand wave forces, ensure anchorage and promote growth through suckers (Carus et al., 2017b). That is, high stem flexibility is known to reduce wave impact (Bouma et al., 2005; Puijalon et al., 2011; Hamann & Puijalon, 2013), and enables faster decomposition, because of less dense fibers (for leaf tensile properties, Cornelissen et al., 1999; Garnier et al., 2004). On the other hand, investing in a particularly thick stem and many tillers may facilitate better living conditions for neighboring con- and heterospecifics on the marsh edge (Bouma et al., 2005; Carus et al., 2016). Plants may respond to anoxic soils and salinity through aerenchyma (Takahashi et al., 2014), adapted root growth (barriers preventing oxygen-loss, Pedersen et al., 2020) and internal gas exchange (Pierik et al., 2009).

The relationship of plant traits, ecosystem properties and services has been the subject of many studies but knowledge for brackish marshes is scarce and also the simultaneous analysis of environmental gradients, traits and ecosystem properties combined (van der Plas et al., 2020). The present study is elaborating the potential of sequestration of organic carbon and the relationship with species traits, using the estuary of the Elbe river, Germany, as a model system. To this end, we applied a structural equation model (SEM), which allows the simultaneous analysis of responses and effects based on regression analysis (De Battisti et al., 2020). A SEM is the ideal tool for testing hypothesis within the effect-response framework, because it allows the construction of causal chains and requires testing specific hypothesis which we briefly describe below (see also Table 4):

Direct effects from environmental factors on ecosystem properties

Inundation should have a negative effect on decomposition, as long hours of waterlogged soil decrease microbial activity (Wang et al., 2019). Inundation, wave height and soil salinity negatively affect aboveground biomass (AGB; (Coops et al., 1994; Lillebø et al., 2003; Minden & Kleyer, 2015). Soil nutrients positively affect decomposition rates through their effects on the decomposer community (Mendelssohn et al., 1999).

Trait responses to the environment

Inundation and wave height should have a negative effect on stem flexural stiffness and total leaf area because of more surface area for drag forces to impact on. This may promote enhanced investment into belowground organs for anchorage (Cao et al., 2020).

The rules of allometric scaling (Enquist & Niklas, 2002) predict high investment into aboveground organs with a proportional investment into roots as anchoring organs, to cope with wave energy for instance (Bouma et al., 2005). Traits related to leaf structure and area are connected to biomass investment in stems and the flexural stiffness, with Young´s modulus (stress – strain relationship of a material) as a measure of it: Higher allocation to stem biomass allows physical support of a higher abundance and/or heavier leaves as well as a taller plant stature (Enquist & Niklas, 2002). As such, we expect stem flexural stiffness to be positively correlated with stem diameter and height (Niklas, 1995).

Trait effects on ecosystem properties

The structural design of stems and leaves should have positive effects on AGB (more biomass in stems and leaves, Minden & Kleyer, 2011) and also on decomposition (higher dry matter content associated with slower decomposition, Garnier et al., 2004; Pakeman et al., 2010; Minden & Kleyer, 2015), highlighting the importance of the structural composition of biomass.

Effects among ecosystem properties

Decomposition rate should positively affect AGB as rapid release of nutrients from mineralized biomass promotes fast uptake and growth of new biomass (Enríquez et al., 1993). We expect soil organic carbon (SOC) to be higher on sites with low decomposition rates (Robertson & Paul, 2000).

Table 4: Hypotheses and anticipated interactions between environment, traits and ecosystem properties to be tested for the Elbe estuary. Expected positive relationships are indicated by '+', negative relationships by '-'. Hypothesis are based on findings for other habitats or that were tested as single factors to be analyzed here simultaneously in the structural equation model (SEM), as the SEM requires specific hypothesis to be tested. For variables included in the analysis, see Table 5.

Environment	→	***Ecosystem property***	***Mechanisms***	***References***
+ Wave impact	−	Aboveground community biomass	Disturbance, uprooting	Coops et al. (1994)
+ Inundation	−	Decomposition	Hampering microorganisms	Wang et al. (2019)
+ Soil nutrients	+	Decomposition	More soil nutrients lead to faster decomposition	Mendelssohn et al. (1999)
+ Soil nutrients	+	Aboveground community biomass	More soil nutrients lead to more peak vegetation standing biomass	Więski et al. (2010) Minden and Kleyer (2015)
+ Soil salinity	−	Aboveground community biomass	Reducing survival, allocation belowground, succulence	Lillebø et al. (2003); Minden and Kleyer (2015)
Environment	→	***Traits***	***Mechanisms***	***References***
+ Inundation	−	Aboveground biomass, more allocation belowgr.	Stress induced by low oxygen	Coops et al. (1994); Coops, van den Brink, et al. (1996)
+ Wave height	−	Flexural stiffness	Where wave impact is strong, plant stems are less stiff	Schoutens et al. (2020)
+ Wave height	−	Total leaf area	Plants have less leaf area where wave impact is strong	Bouma et al. (2005); Puijalon et al. (2011); Paul et al. (2016)
+ Wave height	−	Aboveground biomass	Mechanical damage to biomass	Coops et al. (1994)
Trait	→	***Trait***	***Mechanisms***	***References***
+ Young´s modulus	+	Total leaf area	Stiffer stems with higher experienced drag-force	Heuner et al. (2015)
+ Organ mass	+	Young´s modulus, large total leaf area	Larger plants request denser material for support	Niklas (1995)
Trait	→	***Ecosystem property***	***Mechanisms***	***References***
+ Stiffer stems, larger plants	+	Aboveground community biomass	Stiffer stems associated with more biomass	Schulze et al. (2019)
+ Stiffer stems, more abovegr. biomass	−	Decomposition (native biomass)	Lignified = stiffer, decomposes more slowly	Enríquez et al. (1993)
Ecosystem property	→	***Ecosystem property***	***Mechanisms***	***References***
+ Decomp. standard	+	Decomp. native	Environmental effects visible in difference between standard and native decomposition	Robertson and Paul (2000); Guo et al. (2008)
+ Decomp. native	+	Aboveground community biomass	Nutrients promote growth	Enríquez et al. (1993)
+ Decomp. native	-	SOC	More org. C with lower rates of decomposition	Craft (2007)

7.2 Methods and Materials

Study sites

The Elbe estuary in northwest Germany is typical for Northwest-European large river estuaries, with respect to natural conditions, anthropogenic pollution, dikes and re-modeling to allow traffic of large vessels. Large parts of the Elbe estuary are part of the European Natura 2000 protection framework, with extensive reeds that are home to many bird species (Elbe Estuary Working Group, 2012). Beside its natural values and ecosystem services (defined as the part of ecosystem functioning beneficial to humans, Christiansen et al., 2000), the tidal Elbe is of high economic importance, due to the location of the Port of Hamburg 110 kilometers upstream. The economic interests for a safe and trafficable waterway led to the deepening of the Elbe and a stabilization of the bank with stone fillings and barriers. Through construction of dikes, the hinterland is protected from storm events and can be used as agricultural farmland. These transitions have led to a loss of the natural shoreline of the Elbe river by 75% (Kappenberg & Fanger, 2007). There is an ongoing demand for dredging to allow the passage of larger ships which will continue to affect the river ecosystem in the future.

Three study sites were selected in Northwest Germany in the Elbe estuary: Balje (53°51'30" N, 9°4'30"E), Krautsand (53°46'30"N, 9°22'0"E) and Hollerwettern (53°50'00"N, 9°22'30"E). The sites were characterized by unmanaged natural bank vegetation and had a gradually sloped topography and a straight marsh edge. Soil salinity varied between a maximum value of 4 PSU in Balje (closest to the sea) and a minimum of 0.2 PSU in Hollerwettern (own measurements between March and September 2016, see Figure 7, Chapter 5) where salinity is reduced by freshwater inflow from a river inlet. The salinity of open sea water is approx. 33 PSU. The climate is oceanic with an average temperature of 9.6 °C and an annual precipitation of 831 mm (Cuxhaven, Wetterdienst, 2019). The soils are sandy to silty. The elevations of the sites relative to the tidal range (dimensionless, mean high water = 1 (MHW), mean low water = 0 (MLW)) were between 0.54 and 1.35. The average tidal range is 2.8 m. Elevations were determined with a real time kinematic GPS. Field work was carried out between March 2016 and September 2017. Within each site, we selected 28 plots (4 m × 4 m) with a minimum inter-distance of 20 m to avoid strong spatial autocorrelation (84 plots in total). The plots were randomly placed with elevation relative to the tidal range as stratification criterion. Four different vegetation zones were identified and named after their dominant species: S*choenoplectus tabernaemontani* grows in a zone on the lowest elevations above the bare tidal flat (Pott, 1995). It grow up to 2 m below mean high water (Kötter, 1961; Heuner et al., 2015) and has a flexible stem (Heuner et al., 2015; Heuner et al., 2019). Landward from *S. tabernaemontani*, the next zone is characterized by *Bolboschoenus maritimus.* Starting above approximately 0.5 m under MHW level, dense, almost monospecific *Phragmites australis* stands form a third zone (Ellenberg & Leuschner, 2010). The fourth zone is on the highest elevations, the ˈ*Phragmites*/mixed communityˈ-zone, where *P. australis* occurs in communities with other species.

Abiotic parameters

To record inundation depth and duration, 80 cm long drainage pipes (8 cm Ø) were vertically inserted into the soil at 24 plots (two in each vegetation zone in each of the three study sites). Water/air pressure was recorded with pressure loggers (SENSUS ULTRA by Reefnet) on an hourly basis between March and October 2016. To determine the corresponding ambient air pressure, additional loggers were placed nearby. Ambient air pressure was used as reference to calculate the water depth above the loggers in the pipes (Minden & Kleyer, 2014). Via a regression analysis between soil surface elevation and inundation depth and duration for each logger, the inundation depth and duration could be extrapolated to all other plots, for which only soil surface elevation was measured, but no inundation. Inundation depth and duration were defined as the height of the water column and duration of inundation at and above ground level (hours per day).

Wave height was measured with three pressure sensors at each site (P-Log3021-MMC, Driesen & Kern) between December 2015 and April 2017. The measurements (8 Hz) were corrected for atmospheric pressure and the wave signal separated from the tidal signal. For a detailed description, see Schoutens et al. (2019). We used the mean incoming wave height for water depths <0.5 m, which we extrapolated from the wave measurements for all plots (for details see Appendix 7.2).

On each plot, soil samples were collected in the different soil horizons down to a depth of 60 cm. To determine salinity in the soil, conductivity was measured in the sample of the first horizon, following Schlichting et al. (1995): 10 g fresh soil, diluted with 25 ml H2O was left for 30 min, then conductivity measured in the supernatant water (WTW ph/Cond340i/SET, Tetracon 325 electrode). Conductivity was translated into PSU using the UNESCO equation (UNESCO, 1981; Grasshoff et al., 1983).

All soil samples were analyzed for bulk density [g cm^{-3}] for 200 cm^3 through weighing the fresh and dried sample (48 hr at 105°C, Schlichting et al., 1995). This allowed to express other soil parameters as mass per area (g m^{-2}). Grain size distribution [%] was measured with a Laser Particle Sizer (Analysette 22), after having removed organic substances with H_2O_2. A pH-Meter (ph 3210 WTW) was used to measure the pH, following Schlichting et al. (1995). The soil nutrients phosphorus (P) and potassium (K) were analyzed in a Continuous Flow Analyzer (CFA, P) and Atomic Adsorption Spectroscopy (AAS, K), following Egnér et al. (1960). Calcium carbonate ($CaCO_3$) was measured with the gasometric method of Scheibler (Schlichting et al., 1995), whereas ammonium (NH_4^+) and nitrate (NO_3) were measured in the Continuous Flow Analyzer (CFA) at 660nm (ammonium) and 540 nm (nitrate with the use of the incubation method following Gerlach (1973)). The sum of ammonium and nitrate is the plant available nitrogen (N_{min}).

Plant frequency analysis

We recorded presence and absence of each species on each plot in 100 squares, 10 x 10 cm each, covering an area of 1 m² (Tremp, 2005). Species were determined using Schmeil and Fitschen (2003); and Rothmaler (2007). From the recorded 34 species, we selected 17 species for trait measurements. These species covered at least 95% of all recorded frequencies (Cornelissen et al., 2003).

Trait analysis

To measure plant traits, at least 10 individuals per plant species were selected when their seeds were ripe but not yet shed (cf. Knevel et al., 2005; Minden et al., 2012), i.e. between June and September 2016 and 2017. Of each individual, a ramet was dug out (20 x 20 cm soil volume). A ramet consisted of a shoot with roots and the rhizome section that extended to the next shoot. Belowground organs were rinsed with water to remove the soil and separated with tweezers. Ramets were separated into roots, rhizomes, stems, leaves and seeds, tubers categorized as rhizomes. For the grass species, the leaf consisted only of the leaf blades and not of the petioles, the latter were defined as part of the stems (following Yan et al., 2016). *Schoenoplectus tabernaemontani* does not have leaves: here, the stem was used as an equivalent (Pérez-Harguindeguy et al., 2013). The specific density of stem biomass (SSD, $g_{dry\ mass}\ cm^{-3}$) was determined on two samples per plant individual with volumetric flasks.

Fresh mass of roots, rhizomes, stems and leaves were determined, and plant organs were subsequently dried at 70°C for 72 hours to calculate dry matter content of each organ [$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$] and total dry mass [g]. To determine biomass allocation into the specific plant organs, mass fractions (MF) were calculated for each organ [$g_{organ\ dry\ mass}\ g_{total\ dry\ mass}^{-1}$]. Specific leaf area (SLA) was measured on two leaves per individual [$mm^2\ mg^{-1}$] using a Flatbed scanner (300dpi) and ImageJ-Software (Schneider et al., 2012). To be consistent across all samples, petioles were excluded from all SLA measurements and added to stem biomass (Pérez-Harguindeguy et al., 2013). Leaves were scanned before drying.

Bending stiffness was tested on at least 20 additional fresh stem samples per species, collected across the three sites. Samples were stored under cool and moist conditions and tested within a few days after field collection at the Royal Netherlands Institute for Sea Research (NIOZ), The Netherlands, with the Instron 5942 (Canton, MA, USA, Heuner et al., 2015; Rupprecht, Möller, et al., 2015). Bending properties depended on the stem architecture and different equations were used to calculate Young´s modulus and the flexural stiffness. The support distance on the Instron was set to at least 15x the stem diameter (following Usherwood et al., 1997). The force/deflection slope $\frac{F}{D}$ was calculated (F = force used [N], D = deflection the stem experiences [m]) during the bending tests; this refers to the initial linear part of the relationship between force F and deflection D. For detailed description of the calculation procedure and used equations, we refer to Coops and Van der Velde (1996a); Usherwood et al. (1997); Rupprecht, Möller, et al. (2015).

Ecosystem properties related to carbon sequestration

Community standing biomass (AGB) was harvested in August 2016 (cf. De Leeuw et al., 1990), by cutting the vegetation on an area of 0.5 m² directly above the ground and referencing it to 1 m². The aboveground primary productivity (monthly biomass growth) was not included in the analysis explained below, because in the Elbe estuary, plants regrow after each winter from belowground buds and the growth rate is therefore represented in the AGB. The content of C [g] in AGB was calculated with the C % of aboveground biomass.

The decomposition rate of a plot was determined by using biomass filled mesh bags (1 mm wide meshes, Cebrián-Piqueras et al., 2017). For each plot, three mesh bags were filled with 4 g of native vegetation biomass which was harvested on the same plot and the exact mass noted. Only living biomass at the time of harvest was used. To compare decomposition rates across the sites, three bags filled with ˈstandard litterˈ (hay) were also left at every plot. Bags were gathered after 10 months, cleaned, dried (70°C, 72 hr) and weighed. The decomposition rate is expressed as % per day (Minden & Kleyer, 2015). The remaining C [g] content of AGB after 365 days was calculated with the initial C content and the decomposition rate of native biomass.

Soil organic carbon content ($SOC_{\%}$) was assessed as the difference between soil $CaCO_3$ and total soil carbon content (Cebrián-Piqueras et al., 2017). Soil carbon content (C, %) was determined with a C:N-Analyzer (Flash 2000, Thermo Scientific), following (Allen, 1989). The SOC stock [kg m^{-2}] is calculated with the following equation: $SOC_{kg\,m^{-2}} = bulk\ density_{g\ cm^{-3}} * SOC_{\%} * soil\ profile\ depth_{m}$ (Nipithwittaya S. & P., 2012) for a profile depth of 0.8 m.

Statistical analyses

To consider both the longitudinal gradient in salinity along the river and the perpendicular gradient from water to shore, we applied linear mixed models to all environmental variables with the sites as a random effect. For this, the R-package ˈlme4ˈ (lmer(environment~zone+(1|site)), Bates et al., 2015) was used. To test for significant differences between the zones, the post-hoc test (least squares means) with the function ˈemmeansˈ was performed (R-package 'emmeans', Lenth, 2020). The method to establish the degrees of freedom was Kenward-Roger and the p-value was adjusted with ˈmvtˈ. To test the relationships between the variables, we used partial least squares structural equation modelling (SEM) rather than a co-variance based model, because our set of causal hypotheses was to be tested exploratory, maximizing the variance explained. With reference to the hypotheses in Table 4, an initial path model (Appendix 7. 3) was constructed and relationships between variables and constructs (several related variables combined) tested with the smartPLS software (Ringle et al., 2015). Rather than confirming relationships on a co-variance base, partial least squares equation modelling takes the total variance into account and generates linear relationships, emulating principal component and canonical correlation analysis (Henseler et al., 2016).

The species trait values were weighted with the species frequency, resulting in the weighted average trait value per community/plot (community weighted mean, CWM, Garnier et al., 2007; Violle et al., 2007). As the data set was relatively small with 84 cases, some variables had to be transformed to approximate a normal distribution (Table 5). The regression between Young´s modulus and stem specific density (SSD) was calculated with a standard major axis regression (SMA, (Warton et al., 2006).

The environmental variables were constructed to be exogenous (independent, without measurement errors), while the trait variables and the ecosystem properties were endogenous, dependent variables with measurement errors that show a response to other variables. To reduce complexity, highly correlated traits were aggregated to trait modules during model construction in smartPLS. The ˈaboveground moduleˈ comprised total leaf area [mm^2], mass fraction of aboveground biomass, specific leaf area [SLA, mm^2 mg^{-1}] and Young´s modulus [MPa] as a measure for flexibility of the stem, which were all positively correlated ($r>0.69$). This was due to species with a high SLA growing on higher elevations as well as species with particularly stiff stems, like *P. australis.*

The significance of path coefficients (effects) was tested with smartPLS by bootstrapping (overall model fit) with 5000 samples (Henseler et al., 2016). Since our hypotheses made a statement about the direction of the relationship (positive or negative), we performed a one-tailed test (Cepeda-Carrión et al., 2018), with a 0.05 significance level. There are direct and indirect effects on variables: the latter indicate other variables through which an effect is directed. The effect size f^2 is the difference between the model with and without the specific variable.

Table 5: Abbreviations and units of variables used in the structural equation model and transformation to achieve normality.

VARIABLE	ABBREVIATION	UNIT	TRANSFORMATION
ENVIRONMENTAL VARIABLES			
Inundation	Inundation	hr day^{-1}	square-root
Wave height	Wave height	m	
Soil salinity	Salinity	PSU	log
Soil nitrogen	N_{min}	g m^{-2}	
Soil phosphorus	Soil P	g m^{-2}	log
Soil potassium	Soil K	g m^{-2}	square-root
PLANT TRAITS			
Specific leaf area	SLA	mm^{2} mg^{-1}	
Total leaf area	Total leaf area	mm^{2}	Tukey
Total above- and belowground biomass of an individual	Total biomass	g	
Mass fraction stem & leaves	MF aboveground		
Young´s modulus	Young´s	MPa	log
ECOSYSTEM PROPERTIES			
Aboveground community biomass	AGB	g	
Decomposition rate native	Decomp. native	% day^{-1}	
Decomposition rate standard (hay)	Decomp. standard	% day^{-1}	
Soil organic carbon content	SOC	%	log

7.3 Results

The environmental conditions differed significantly ($p<0.05$) between the four different vegetation zones in terms of elevation, distance to the marsh edge and hydroperiod, except between the *Phragmites* and *Phragmites*/mixed community-zone (Table 6). Average wave height decreased towards higher elevations, but this was again not significant between the highest two zones. Soil salinity was lowest on the higher plots but without significant differences between the zones.

Soil phosphorus was significantly lower in the *Phragmites*-zone compared to the other zones except the *Bolboschoenus*-zone, and N_{min} was lowest in the *Schoenoplectus*-zone and significantly highest in the *Phragmites*/mixed community-zone.

Table 6: Mean values and standard deviation (SD) of environmental variables analysed across all four zones, named after their dominant plant species. Significant differences are indicated with different letters, p<0.05, tested with estimated marginal means.

	ZONES NAMED AFTER DOMINANT SPECIES							
	Schoenoplectus		***Bolboschoenus***		***Phragmites***		***Phragmites/ mixed community***	
ENVIRONMENTAL VARIABLES	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**
Elevation (rel. to tidal range)	0.70^{a}	0.13	0.88^{b}	0.11	1.08^{c}	0.052	1.19^{d}	0.10
Distance to marsh edge [m]	5.7^{a}	3.0	38.1^{b}	15.1	86.6^{c}	35.2	118.1^{c}	78.4
Inundation [hr day^{-1}]	15.1^{a}	3.2	10.3^{b}	4.9	4.8^{c}	4.4	2.7^{c}	2.7
Wave height [m]	0.04^{a}	0.0004	0.03^{b}	0.003	0.02^{c}	0.008	0.01^{c}	0.02
Bulk density [g cm^{-3}]	0.58^{a}	0.22	0.53^{a}	0.24	0.49^{a}	0.14	0.48^{a}	0.12
Soil salinity [PSU]	0.76^{a}	0.82	0.89^{a}	0.90	0.68^{a}	0.42	0.50^{a}	0.3
Soil P [g m^{-2}]	89.8^{a}	46.8	$92.4^{a,b}$	70.8	62.4^{b}	22.7	$86.4^{a,c}$	29.0
Soil K [g m^{-2}]	105.5^{a}	65.4	115.6^{a}	65.3	99.4^{a}	46.0	127.0^{a}	46.3
N_{min} [g m^{-2}]	5.8^{a}	5.1	$8.1^{a,b}$	7.9	7.3^{b}	3.3	13.6^{c}	7.7

The average community weighted mean for specific leaf area (SLA) was highest at high elevations (i.e. *Phragmites*/mixed community zone), as were aboveground mass fraction, total individual plant mass, total leaf area and Young´s modulus for the *Phragmites* and *Phragmites*/mixed community-zone (Table 7, $p<0.05$). Aboveground community biomass (AGB) was highest in the *Phragmites*-zone. The decomposition rate of native biomass was lowest in the *Bolboschoenus*-zone (0.14 % day^{-1}), followed by the *Phragmites*-zone with a significantly highest decomposition in the *Schoenoplectus*-zone (0.22 % day^{-1}), whereas the decomposition rate of standard hay was lowest in the *Schoenoplectus*-zone and *Bolboschoenus*-zone (0.27 and 0.26 % day^{-1}). This means, that native plant material decomposed much better than hay in the *Schoenoplectus*-zone. Soil organic carbon (SOC %) was significantly highest in the *Phragmites* and *Phragmites*/mixed community-zone. The initial vegetation bound carbon (C) content present was lowest in the *Schoenoplectus*-zone (271.8 g), showed no significant difference between the *Bolboschoenus*- and *Phragmites*-zone and intermediate (yet significantly different) values for the *Phragmites*/mixed community-zone (553.2 g). Remaining C content in biomass after 365 days showed a similar pattern, with the lowest values for the *Schoenoplectus*-zone (52.6 g) and highest values for the *Bolboschoenus*- and *Phragmites*-zone (310.5 and 269.9 g respectively).

Table 7: Average community weighted means and ecosystem properties for the four zones, named after their dominant plant species. The 'aboveground module' combines the variables SLA, total leaf area, Young's modulus and aboveground biomass fraction. Total biomass (dry mass) is a separate single variable. Ecosystem properties: aboveground community biomass (AGB), C content of AGB initially and after 365 days, decomposition rate of native and standard litter and soil organic carbon (SOC) content (%) and SOC density (kg m^{-2}). SD = standard deviation, significant differences have different letters, $p<0.05$, tested with t-test for trait variables and estimated marginal means for ecosystem properties. Soil organic C kg m^2 represent the carbon stock present; this variable is not included in the SEM and displayed here as additional information, as well as the details on C content of AGB.

	ZONES NAMED AFTER DOMINANT SPECIES							
	Schoenoplectus		***Bolboschoenus***		***Phragmites***		***Phragmites/ mixed community***	
TRAIT & ECOSYSTEM PROPERTY VARIABLES	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**	**mean**	**SD**
Specific leaf area (SLA) [mm² mg^{-1}]	7.76^{a}	3.09	16.19^{b}	3.13	16.26^{b}	3.84	22.40^{c}	3.97
Total leaf area [cm²]	117.97^{a}	45.10	157.32^{b}	71.28	480.83^{c}	286.59	309.52^{d}	106.69
Young´s modulus [MPa]	1555.9^{a}	763.8	2848.8^{b}	587.9	7857.1^{c}	3174.4	8556.1^{c}	6597.5
Mass fraction aboveground [$g_{leaves\ \&\ stem}\ g_{all}^{-1}$]	0.68^{a}	0.02	0.70^{b}	0.05	0.74^{c}	0.07	0.75^{c}	0.04
Total biomass [g]	7.13^{a}	2.94	7.86^{a}	1.96	22.39^{c}	10.42	13.55^{b}	6.73
Abovegr. community biomass (AGB) [g m^{-2}]	620.7^{a}	322.4	1386.9^{b}	286.8	1519.6^{b}	334.1	1272.0^{b}	381.9
C Abovegr. Community biomass at peak vegetation [g]	271.8^{a}	139.5	611.5^{b}	126.1	660.4^{b}	143.2	553.2^{c}	165.4
C Abovegr. Community biomass left after 365 days [g]	52.6^{a}	41.3	310.5^{b}	140.4	269.9^{b}	98.8	210.8^{c}	79.9
Decomposition rate native [% day^{-1}]	0.22^{a}	0.04	0.14^{b}	0.04	0.16^{b}	0.04	0.17^{b}	0.04
Decomposition rate standard [% day^{-1}]	0.27^{a}	0.04	0.26^{a}	0.03	0.30^{b}	0.02	0.30^{b}	0.03
Soil organic carbon [%]	0.85^{a}	0.49	1.01^{a}	0.60	1.92^{b}	1.36	2.54^{b}	1.60
Soil organic carbon [kg m^{-2}, 0.8 m soil profile]	$9.14^{a,b}$	4.80	8.07^{a}	3.97	11.27^{b}	5.08	13.38^{b}	10.13

The hypotheses (Table 4) led to the construction of an initial model (see Appendix 7. 3) which was refined in an exploratory way. For instance, the bootstrapping procedure revealed significant pathways for all relationships except for soil N_{min}, and soil phosphorus (P) which showed no significant contribution to explaining any other variable. These parameters were thus excluded from the final model. The final PLS-SEM (Figure 17, Table 8) showed an adequate model fit in the standardized root mean square residual (SRMR, Henseler et al., 2016) with a cutoff of 0.08 (Hu & Bentler, 1999). Other parameters indicating a good model fit were: average variance extracted (AVE) >0.66, Cronbach´s alpha >0.88, Dijksra and Henseler`s rho >0.90, variance inflation factors (VIF) <5. VIF values should be lower than five to rule out collinearity. The Heterotrait-Monotrait Ratio (HTMT) for discriminant validity was <0.85 (Henseler et al., 2015).

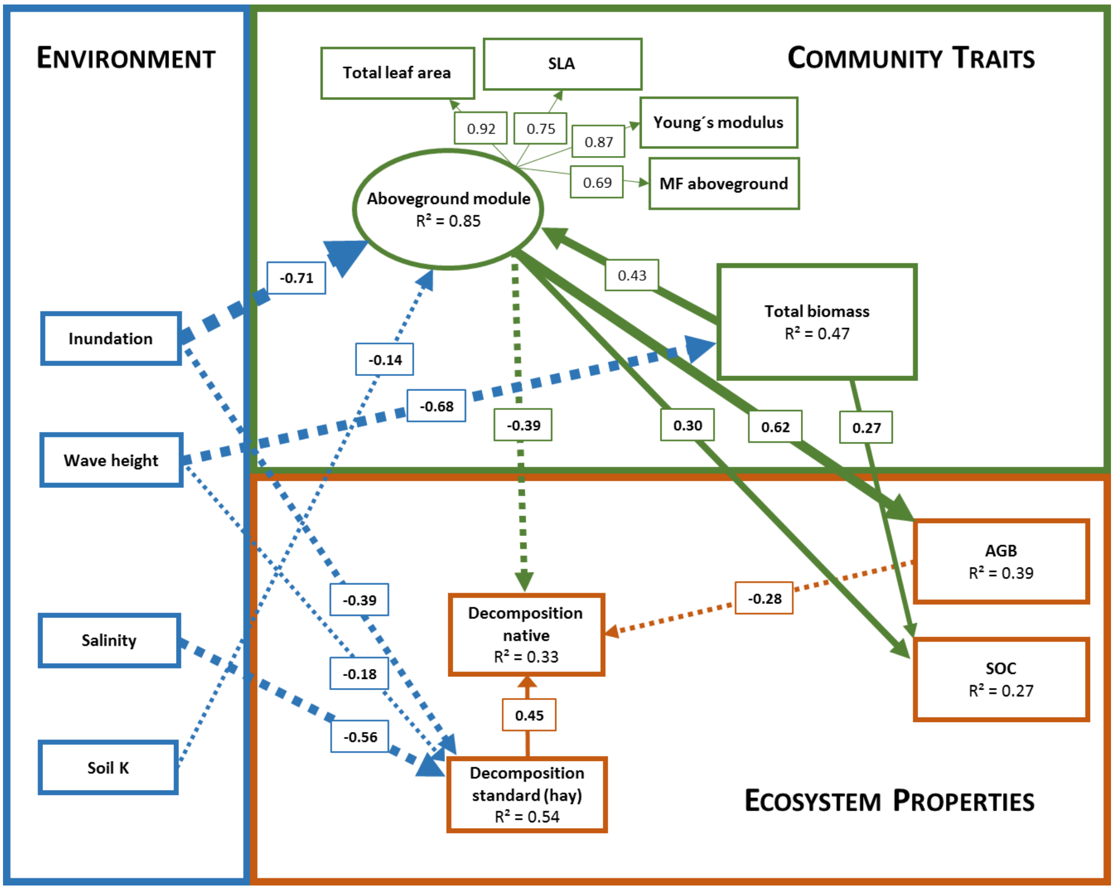


Figure 17: Partial least squares structural equation model (PLS-SEM) calculating the relationships of environment, traits and ecosystem properties. Variables displayed are: Wave impact (mean wave height at water depth <0.5 m [m]), inundation (water level at ground level or above [hr day^{-1}]), soil salinity [PSU], soil K (soil potassium content [g m^{-2}]), construct (combined related variables) ˈaboveground moduleˈ with indicator variables and their correlation coefficients: total leaf area (total leaf area per plant individual [mm^2]), specific leaf area (SLA, mm^2 mg^{-1}), Young´s modulus (for the plant stems [MPa]), MF aboveground (mass fraction of leaves & stem). Single item trait variable: total plant biomass [g], AGB (abovegr. community biomass [g m^{-2}]), Decomposition of native biomass (decomp. rate [% day^{-1}]), Decomposition of standard biomass (hay) [% day^{-1}], SOC (soil organic carbon content [%]). p<0.05 for all paths shown with regression coefficients for direct effects in small rectangles. For indirect effects and effect sizes see Table 8. Solid lines indicate positive relationships, dashed lines indicate negative relationships, line width indicates strength of relationship.

Inundation period negatively affected the 'aboveground module' (Table 8). Wave height also exerted a strong indirect negative effect on this construct (constructed from the four related indicator variables, Figure 17) and a direct negative effect on the total biomass. Large effect sizes (f^2) highlight the surmount importance of the direct effects of these drivers. As for soil potassium (K), there was a low negative effect on the 'aboveground module'.

Regarding the trait-trait interactions, the total plant biomass and 'aboveground module' were strongly correlated: plant individuals with high biomass showed strong investment into structural components of stems and leaves (total leaf area, specific leaf area (SLA) and Young´s modulus). Young´s modulus also showed a strong positive correlation with the stem specific density (SSD, Figure 18): stiffer stems were constructed with denser biomass.

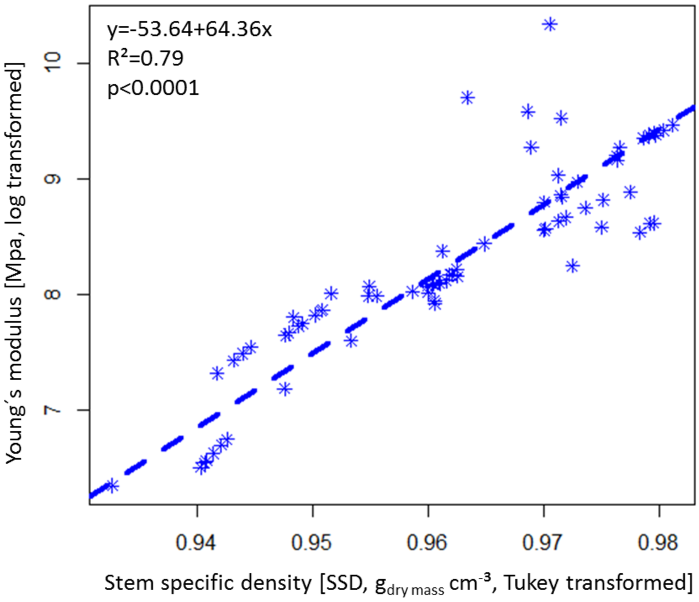


Figure 18: Standard major axis regression of Young´s modulus (log transformed) vs stem specific density (Tukey transformed) for the community weighted means per plot.

Regarding the ecosystem properties, decomposition was negatively affected by the 'aboveground module' through direct and indirect effects via aboveground community biomass (AGB): stiffer and denser stems were decomposing more slowly. Total plant biomass had an indirect positive effect on AGB and a negative effect on decomposition. AGB and soil organic carbon (SOC) were directly positively connected to the 'aboveground module' and the total biomass. A direct negative relationship existed between AGB and decomposition of native material, a positive one between the decomposition of the standard material (hay) and the native materials decomposition.

Direct negative effects of environmental variables on ecosystem properties were: inundation, wave height and salinity on the decomposition of standard hay with a moderate, weak and large effect size respectively.

Table 8: Total, indirect and direct effects (path coefficients) of the variables of Figure 17 on each other. All effects shown were significant with p<0.05. The effect size f² for direct effects is strong >0.35, moderate >0.15 and weak >0.02 (Henseler et al., 2016). For details regarding variables units and variables encompassed in the 'aboveground module', see Table 5 and Table 7.

	ENVIRONMENT															
	Inundation				Wave height				Salinity				Soil K			
	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2
Abovegr. module	-0.7	-0.7		2.6	-0.3		-0.3						-0.1	-0.1		0.1
Total biomass					-0.7	-0.7		0.9								
AGB	-0.4		-0.4		-0.2		-0.2						0.09		0.09	
Decomp. native	0.2		0.2						-0.3		-0.3		0.08		0.08	
Decomp. standard	-0.4	-0.4		0.2	-0.2	-0.2		0.04	-0.6	-0.6		0.5				
SOC	-0.2		-0.2		-0.3		-0.3									

	COMMUNITY TRAITS								**ECOSYSTEM PROPERTIES**							
	Abovegr. module				Total biomass				AGB				Decomp. standard (hay)			
	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2	Tot.	Dir.	Ind.	f^2
Abovegr. module					0.4	0.4		1.1								
Total biomass																
AGB	0.6	0.6		0.6	0.3		0.3									
Decomp. native	-0.6	-0.4	-0.2	0.1	-0.3		-0.3		-0.3	-0.3		0.07	0.5	0.5		0.2
Decomp. standard																
SOC	0.3	0.3		0.07	0.4	0.3	0.1	0.06								

7.4 Discussion

Our model proved an overall indirect relationship between environment and organic carbon-related ecosystem properties via the functional traits of the vegetation. The effect sizes were not particularly high but still much higher than in the recent study by van der Plas et al. (2020), contradicting their statement that plant traits alone are poor predictors of ecosystem properties. The reason of this contradiction is most probably related to scale: while the study by van der Plas et al. (2020) dealt with random species subsets of a single grassland community and almost absent environmental variation, our study included clear environmental gradients and multiple communities that result from species sorting based on trait response to these gradients (see also Minden & Kleyer, 2011).

Our final model differed considerably from the initial model as many literature-based relationships between environment, traits and ecosystem were insignificant and had to be dropped from the final model. This highlights the fact that response – effect relationships are not easily transferable across ecosystems.

Direct environmental effects on ecosystem properties

Most hypothesized environmental effects on ecosystem properties were not significant, except for wave height, inundation and salinity on decomposition of standard hay. The decomposition of standard hay was explicitly meant to show the direct effect of the direct environment on decomposition, excluding the traits of the native species. Beside long inundation durations, also salinity hindered decomposition, with moderate and strong effect sizes, which is in line with Stagg et al. (2017). Long hydroperiods exert pressure on the decomposer community (Wang et al., 2019); where oxygen is scarce, microbes need more time to recycle plant fibers and therefore anaerobic decomposition is much less efficient (Choi & Wang, 2004).

On the other hand, we could neither confirm any direct comparable environmental effects on the decomposition of native plant material nor any significant effect of decomposition on the promotion of aboveground community biomass (AGB) or a decrease of soil organic carbon (SOC). The decomposition of native biomass was controlled by the characteristics of that biomass. The second assumption was probably not confirmed because nutrients were plentiful in the eutrophic estuary, the third, because dead biomass is often re-deposited on higher elevations by flooding, overriding detectable effects of in-situ decomposition.

All other links between environmental factors and ecosystem properties were indirect, i.e. mediated by plants and their traits. This underlines the relevance of the vegetation in determining carbon-related ecosystem processes (Chmura, 2013).

Trait responses to environmental drivers

In line with our initial model, strongly correlated aboveground traits such as total leaf area and Young´s modulus decreased with increasing inundation duration and wave height. Both traits respond to the drag forces imposed by these drivers: The larger the leaf area or frontal area, the higher the drag forces exerted by waves and tides that impact on a species (Bouma et al., 2005). Plants follow either a strategy to withstand drag forces by investing into stiff stems or to avoid them by, for example, a flexible, stream-lined shape (Puijalon et al., 2011), like the leafless *S. tabernaemontani* in places with strong velocities; Young´s modulus, as a measure of resistance of the stem to bending, mirrors this response. The structural design to allow flexibility is reflected in the elemental composition: *P. australis,* for instance, has a high lignin content (Ágoston-Szabó & Dinka, 2008) and *B. maritimus* has a high silica content to strengthen the stem, as compared to the more flexible *S. tabernaemontani* growing at the water front (Heuner et al. 2015). Where conditions in the study sites are more benign (i.e. less influence of wave height and shorter inundation hours), competition for light becomes important (Poorter et al., 2012). On these sites, plants allocate more biomass to aboveground than to belowground organs. The anchoring and resource acquisition aspect, to match the larger aboveground drag-force area, is reflected in the composite trait 'total biomass' as a result of an equally extensive root and rhizome system (Enquist & Niklas, 2002). Altogether, inundation, wave exposure and salinity decreased stem stiffness (and with it stem tissue density) and total species biomass. That is, plants were on average smaller, more bendy and had less dense stems at the shore as compared to the landward zones dominated by *Phragmites australis*. Vegetation zonation is thus reflecting a trait zonation with increasing stem flexibility as well as decreasing leaf area and plant biomass towards the waterfront (Silinski et al., 2016; Carus et al., 2017a).

Contrary to our initial model, neither soil nutrients (except a slight effect of K) nor soil salinity had a strong effect on the traits measured, in contrast to other findings in salt marshes (van Wijnen & Bakker, 1999; Pennings et al., 2002). This is probably due to the overall high nutrient levels in the eutrophic estuarine system where inundation and wave activity override any nutrient related effects. Similarly, Minden and Kleyer (2015) found that inundation had a stronger effect on leaf structural composition than soil nutrients in a salt marsh. The soil salinity of the study sites is very low compared to levels for salt marshes (Minden et al., 2012), which is probably why there is no detectable effects on traits. Although salinity does affect species composition, the dominant species were the same in the three study sites. The salt-tolerant species occurring in Balje (e.g. *Elymus athericus*) and non-tolerating species in Hollerwettern (like *Solanum dulcamara*) were not very abundant and did not strongly affect the community weighted trait means. This indicates that the increase in salinity along the river towards the sea was not strong enough to drive community composition into a salt marsh state.

Indirect, vegetation mediated effects on ecosystem properties

There is a lack of knowledge about which traits are strongly responding to the environment but are not affecting ecosystem properties (Suding et al., 2008). Traits that are not responding to environmental impacts but have a strong effect on ecosystem properties are characterising the overall systems structure and continuity of estuarine habitats as compared to other habitats. An example would be stem stiffness of *Phragmites australis* that can grow at different salinity levels and would thus deliver similar biomass texture for decomposition in different abiotic settings. On the other hand, traits that both respond to the environment and affect ecosystem properties determine the resilience and tolerance of the ecosystem and are most relevant to understand the indirect effects of the environment on ecosystem properties (Díaz et al., 1999). Responses of plant traits to environmental drivers translated into effects on ecosystem properties, corresponding to the response – effect framework (Suding et al., 2008).

Here, we found that all traits were both response and effect traits. For instance, waves increased the decomposition of native biomass via the ˈaboveground moduleˈ, as opposed to what we found for standard hay. This had two aspects to it: the stem biomass of the native species on the wave exposed marsh was on the one hand less stiff (and less dense) and on the other hand there was also more physical pressure on the material, which combined could speed up the fragmentation and decomposition of dead plant material. It is also possible, that solely the trait response in form of less stiff and less dense stem material resulted in a faster decomposition. Species´ tissue qualities were often shown to have an important influence on litter decomposition (Odum, 1988; Wardle et al., 2002). Nitrogen and lignin content of tissues were found to respectively speed up and slow down decomposition rates (Hemminga & Buth, 1991). We also know from salt marshes that plant traits such as leaf dry matter content, succulence, lignin content and stoichiometric make-up have a profound influence on decomposition dynamics (Simões et al., 2011; Minden & Kleyer, 2015), with succulent plants decomposing faster than non-succulent ones (Zedler et al., 1980).

The community aboveground biomass (AGB) increased towards higher elevations, where *P. australis* is dominant. This illustrates the important impact of *P. australis:* Plant mass fraction was shifted towards longer stems (response to light competition, Poorter et al., 2012). *P. australis* stems are strongly lignified, the higher lignin content in stiffer stems (Ágoston-Szabó & Dinka, 2008; Schoelynck et al., 2010; Heuner et al., 2015) would result in a slower decomposition of biomass (Hodson et al., 1984; Simões et al., 2011). This result was in line with findings for salt marsh systems where AGB was negatively related to decomposition rates (Minden & Kleyer, 2015).

In the present study, the ˈaboveground moduleˈ was clearly the most influential in relation to decomposition rates, albeit with a rather small effect size. The ˈaboveground moduleˈ and the total biomass of plant individuals also positively affected the SOC content, again not with strong effect sizes though. This could be attributed to the belowground biomass: Rasse et al. (2005) found soil C to be largely influenced by root carbon content. In contrast to dead aboveground biomass, belowground biomass is not at risk to be flushed away during winter. Elschot et al. (2015) for instance hypothesized for a saltmarsh system, that the increased organic carbon input in fact resulted because of increased belowground biomass production. Hansen et al. (2017) found SOC to be negatively influenced by salinity through less biomass production. This way, the allocation of biomass to specific organs can strongly influence SOC (Jobbágy & Jackson, 2000).

Implications for organic carbon sequestration

Carbon storage is one of the essential ecosystem services of tidal marshes (for salt marshes and US estuaries, Chmura et al., 2003; Najjar et al., 2018). That is because of the sedimentation processes and carbon burial (Duarte et al., 2005) and the accumulation through the vegetation (Hansen et al., 2017). Sedimentation was not in the focus of this study but has a surmount importance by accreting organic and inorganic material (Hughes, 1997; Kirwan & Megonigal, 2013) and the rising of the marsh surface (Hopkinson et al., 2019). Elschot et al. (2015) found that total organic carbon increased with marsh age whereas the carbon sequestration rate decreased with marsh age, resulting in the highest rates on young marshes. For more SOC to get stored, the chemical composition of the vegetation (i. e. lignin content, Williams & Rosenheim, 2015), its structure and the amount of produced biomass is essential.

We found 8.07-13.38 kg organic carbon per m^2 (0.8 m profile), with more carbon content above the mean high water level. Van de Broek et al. (2016) reported carbon stocks for brackish marshes in the Scheldt estuary of 18.63±0.71 to 19.63±0.27 kg m^{-2} (0.6 m depth). Around 16 kg m^{-2} (0.6 m depth) were estimated for salt marshes (Northern US, Drake et al., 2015) whereas much higher carbon stocks were reported for mangroves (31 kg m^{-2}, 1.0 m profile, Weiss et al., 2016).

In our study, the C content of the aboveground biomass revealed a production of 611.5 and 660.4 g C per m^2 at peak vegetation for the *Bolboschoenus*- and *Phragmites*-zone, respectively. Considering the decomposition rate, 310.5 and 269.9 g C respectively would theoretically remain after one year, indicating almost similar fluxes of aboveground C to the SOC stock. However, this was not reflected in the actual SOC stock, which was significantly higher in the *Phragmites*-zone at higher elevations. Apparently, the potential C pool was not stored where it was produced. Biomass removal was created through waves and ice, which broke or clipped stems and subsequently flushed them away. In our study sites, large amounts of plant material were thus transported inland with the flowing water during high flood events and deposited in thick layers in the high marsh (Hansen et al., 2017). Here they decomposed in relatively dry and aerated conditions. This loss of biomass may explain the relatively low SOC levels of the study sites, compared to findings for other marshes (Drake et al., 2015). Belowground biomass was not exposed to waves and may probably be more strongly connected to local SOC.

Concluding management recommendations

Our study showed that carbon related ecosystem properties of eutrophic estuaries are mainly controlled by the functional composition of the vegetation, specifically the total biomass, organ biomass and stiffness of stems and leaves. These traits responded mainly to wave action and inundation period as the main drivers of the estuarine system. Direct effects from environmental factors on ecosystem properties were found for the decomposition of standard hay which served as a control to assess whether such effects could be found. For the native conditions, however, plant traits were better predictors of ecosystem properties than direct environmental effects. Predicting ecosystem processes with functional traits can thus be a valuable tool in this regard because it allows to dissect the response of the vegetation to environmental changes and its effects on estuarine ecosystem properties.

With future sea level rise, the estuarine vegetation may be threatened by coastal squeeze, i.e. the prevention of landward migration by dikes constructed alongside the river Elbe. If the vegetated space were to become narrower, species adapted to stronger hydrodynamics would grow on higher elevations, taking the space of the species with stiffer, denser biomass that have a larger potential to fix and store carbon. In order to keep the carbon stocks provided by the estuarine vegetation, new defence strategies against future storm surges are necessary that can include the managed realignment of dikes or building sluices that allow tides to flow through the dikes in order to restore tidal marshes in the hinterland (Chmura, 2013; Temmerman et al., 2013). Therefore, the management focus should be on preserving the remaining marshes in order to secure their carbon stock (McLeod et al., 2011) and where needed, providing space for marsh migration with sea level rise (Chmura, 2013) in order to preserve the whole species range with their species-specific services.

Acknowledgements

We would like to thank Hannes Sahl and Thomas Jansen for measuring the elevations with RTK and Daniela Meißner in the laboratory, Frances Pusch for working on the initial phase of the project as well as the numerous students helping with sampling and processing work. This research was conducted in cooperation with the German Federal Institute of Hydrology (BfG) in line with its R&D-Project TIBASS (Tidal Bank Science and Services).

Chapter 8. Identifying key traits driving wave attenuation and carbon sequestration potential of tidal marsh vegetation

Schulte Ostermann, Tilla; Heuner, Maike; Fuchs, Elmar; Temmerman, Stijn; Schoutens, Ken; Bouma, J. Tjeerd; Minden, Vanessa

Abstract

Wave attenuation and carbon sequestration are increasingly recognized as key essential ecosystem services provided by tidal marsh vegetation in estuaries. Here, we aim to identify which plant traits and ecosystem properties are most important for the delivery of essential ecosystem services. For this, the Elbe estuary was used as a case study, the traits of the most abundant plant species were studied for the marsh zone below the mean high tide water level (MHW) and above MHW. The focus was on the following traits: stem bending properties, stem, leaf and belowground organ specific density and dry matter content, biomass investment per plant organ, canopy height and leaf N:P and C:N ratios. Analyzed ecosystem properties included aboveground community biomass (AGB), decomposition rates and soil organic carbon (SOC) content and stocks. The traits were analyzed on a community base and aggregated if they were strongly correlated. Multiple linear regression was used to evaluate the relationship between environmental variables, trait aggregates and ecosystem properties and standard major axis regression for trait-trait relationships.

Our results for the marsh zone below MHW show, that stem mass per volume, stem resistance to bending, stem specific density and stem dry matter content (stem trait aggregate) and aggregated leaf leaf traits (leaf dry matter content and total leaf area) had a positive relationship with wave attenuation, while only the leaf traits had a positive relationship with soil organic carbon content. We further highlighted that the delivery of the ecosystem service of wave attenuation for the marsh zone below MHW was dependent on high aboveground community biomass and the character of that biomass (i. e. high stem bending resistance and large leaf area).

The ecosystem service of carbon sequestration above MHW was governed mainly by inundation duration through the decomposition rates, with intermediate values for the aggregated stem traits showing the highest decomposition rates.

Implication of present findings for preserving these services under rising sea levels and the management implications to promote and secure these functions are discussed.

8.1 Introduction

Tidal estuaries are typically hotspots of valuable ecosystems, such as tidal marshes, and of human activities, such as development of ports, cities, and agricultural areas (Mitsch & Gosselink, 2000). In the past, human land use development has often resulted in the loss of tidal marsh ecosystems. But nowadays there is an increasing demand for conservation and restoration of tidal marsh ecosystems, as they provide valuable ecosystem services that can support the sustainability of human activities along estuaries. In many estuaries, human land use development is enabled by the construction of embankments and dikes to avoid flooding of the human infrastructure, but maintenance of artificial embankments is labour and cost intensive and – with the issue of raising sea levels (SLR) – additional works, such as heightening of the dikes will demand for further investments. As such and where possible, a vegetation-based protection of estuarine shorelines is favoured in front of artificial embankments, since natural vegetation acts as a sediment trap (Coops, Geilen, et al., 1996), attenuates waves (Gedan et al., 2010; Barbier et al., 2011), reduces flow velocities (Leonard & Luther, 1995) and is potentially able to keep up with the rising sea levels (Kirwan & Megonigal, 2013; Temmerman & Kirwan, 2015). Furthermore, the carbon sequestration function by the vegetation could play a role in climate change mitigation – the potential of coastal and tidal wetlands in this context is the focus of several studies (McLeod et al., 2011; Najjar et al., 2018).

The attenuation of waves and carbon storage are relevant ecosystem services of the tidal marsh vegetation, which are delivered through the properties of this specific ecosystem. An ecosystem service is defined as an ecosystem function that is of benefit to human welfare (MEA, 2005; UN, 2015). The provision of firewood by vegetation is an example for a vegetation based ecosystem service (Riis et al., 2020), which depends on biomass production, which is an ecosystem property (Lavorel & Grigulis, 2012). The in-situ decomposition rates of biomass are another example for an ecosystem property (Schmidt et al., 2011), and are a product of both specific plant traits and environmental factors (i. e. waterlogged soils decreasing decomposition, Wang et al., 2019). Ecosystem properties (such as biomass productivity) in general are strongly influenced by plant species traits, which themselves are affected by environmental conditions (Díaz et al., 2006; Diaz et al., 2007). Plant traits, like for example the bending stiffness of plant stems, characterize the ecosystem properties by for instance slow decomposition of fibres. One plant trait explaining a particular ecosystem property may not be relevant for another (Hooper et al., 2005). Therefore, identifying key plant traits that strongly influence ecosystem properties is beneficial for understanding ecosystem services delivered by tidal marsh vegetation.

The delivery of plant related ecosystem services is dependent on and affected by the abiotic conditions of a specific site. Tidal marshes are characterized by strong environmental gradients, such as inundation regime, currents, wave action and fluctuating salinity levels. The last two affect the tidal marsh vegetation with a descending magnitude from the low-elevation tidal flat up to the high-elevation riverbank. The salinity levels create an additional gradient from the mouth of the river upstream.

The focus of our study was on the relationship between plant traits and the delivery of the ecosystem services of wave attenuation and soil carbon sequestration in tidal marshes and the Elbe estuary was used as a case study area.

We analysed the role of plant traits in affecting ecosystem properties and their respective relationships with wave attenuation and soil organic carbon stocks. For the analysis, we distinguished between a zone below mean tidal high-water level (below MHW) and above mean tidal high-water level (above MHW). The separation of these two zones is motivated by the strong differences in both the environmental influence and the resulting ecosystem services between these different parts of the bank.

The zone below MHW has a higher salinity and is inundated very regularly. Plants of this zone either show flexible stems to avoid drag forces (where wave energy is high) or have a lignified, robust stem to withstand them (where wave energy is lower, Heuner et al., 2015). Further, they are exposed to long times of inundation and potentially oxygen scarcity around their roots (Caudle & Maricle, 2012; Carus et al., 2017a). The upper zone, above MHW, is irregularly inundated with salt water, mainly during springtides or storm surges. In this zone, competition for light is a key interspecific driver (Coops, van den Brink, et al., 1996; Craine et al., 2013; Carus et al., 2017a). The abovementioned ecosystem services, wave attenuation and carbon sequestration, are delivered by the two zones below and above MHW in different degrees. Wave attenuation is one of the major ecosystem services of the lower marsh and analysing the role of the vegetation in detail an urgent matter, as energy cost to maintain and upgrade artificial bank protections rises (Temmerman & Kirwan, 2015). The wave- and flow-reducing effect of plants has been the focus of many studies for species growing within water bodies (Bouma et al., 2005; Reidenbach & Thomas, 2018), through salt marshes (Leonard & Luther, 1995; Bouma et al., 2010), brackish marshes (Schoutens et al., 2020) and mangroves

(Horstman et al., 2014). For example, Schoutens et al. (2019) found wave height reductions of up to 50 % in *Bolboschoenus maritimus* dominated vegetation below MHW.

The zone above the MHW is characterized by an extensive production of biomass and thus holds a considerable potential for carbon sequestration (Najjar et al., 2018), which is an essential ecosystem service of tidal marshes (Chmura et al., 2003), but research on temperate brackish marshes in that context is scarce yet. The dominant species above MHW in the studied Elbe marshes is *Phragmites australis,* which grows taller than 3.5 m. The biomass production, particularly belowground, has a strong impact on the carbon cycle (Rasse et al., 2005). The process of carbon sequestration is strongly connected to the sedimentation dynamics, i. e. carbon is buried by sedimentation and hence stored at increasing depth (also organic sedimentation, Chmura et al., 2003; Mudd et al., 2009), and is related to the decomposition of biomass and the species traits as well (Wardle et al., 2002).

The traits included in the analysis are bending stiffness of plant stems, and associated traits like stem biomass density (Chapter 7) and dry matter content (Hamann & Puijalon, 2013; Vuik et al., 2018). They represent the adaptation to hydrodynamic stress (either being bendy or stiff – avoiding or withstanding wave engergy, Heuner et al., 2015; Schoutens et al., 2020) and strongly influence decomposition, with stiffer and denser material being more resistant to mineralization (for leaf toughness, Cornelissen & Thompson, 1997).

Because total leaf area is affected by strong waves and currents (larger frontal area results in higher experienced drag-force, Puijalon et al., 2011) we also analysed leaf traits and leaf nutrient ratios, as they affect decomposability (White et al., 2004).

Traits of belowground organs give information on plant strategies regarding resource usage (Kong et al., 2019) and were often found to be connected to carbon cycling (Faucon et al., 2017). The ecosystem properties analysed were aboveground community biomass (AGB), decomposition rates and soil organic carbon content (SOC).

In the analysis, we focus on the ecosystem services of wave attenuation and carbon sequestration for the zone below MHW. For the zone above MHW, the incoming waves are already attenuated, we therefore focus on aspects of the carbon cycle, i.e. biomass production, decomposition and soil organic carbon content. The objective of this study is to assess the differences in the delivery of ecosystem services between the two zones.

Specifically, the questions asked to fill knowledge gaps are: What impact do environmental factors have on the ecosystem properties? How are plant traits related to each other and to ecosystem properties in this estuarine setting? Finally, the aim of the analysis it to establish, which traits and ecosystem properties correlate most strongly with a) the ecosystem service of wave attenuation and b) the service of organic carbon sequestration?

8.2 Methods

Study sites

The river Elbe is one of the busiest and economically most important waterways of Germany. 66 thousand ships navigate the tidal part of the River Elbe connecting the port of Hamburg with the North Sea every year, 90 % of them are seagoing vessels with an increasing number of particularly large ships (WSA, 2011; HPA, 2019). The ships create high-frequency waves (Hofmann et al., 2008) which, additionally to the naturally created wind waves, enhance the strain on both naturally vegetated tidal banks and artificially constructed dike reinforcements (Silinski et al., 2015). The deepening of the river bed led to less bottom friction, faster tidal waves and a higher tidal amplitude (Boehlich, 2003), due to increased mean high water and decreased mean low water levels (Butzeck et al., 2016). This dynamic caused an increased transport of sediment into the system, as the tidal inflow is faster than the outgoing tidal ebb (Kerner, 2007). As a result, the maintenance of the waterway may be more laborious as more dredging is necessary to relocate the incoming sediment. Furthermore, higher sedimentation rates and changed inundation durations may affect the tidal marsh vegetation with effects on species composition and/or ecosystem service deliveries.

Three sites were chosen as replicate sites in the Elbe estuary (Northwest Germany: Balje (53°51'30" N, 9°4'30"E), Krautsand (53°46'30"N, 9°22'0"E) and Hollerwettern (53°50'00"N, 9°22'30"E) (for more details, see Chapter 5 or Schoutens et al., 2019). They all have a gradually sloping topography and straight marsh edge. The climate at the sites is oceanic, the average temperature is 9.6 °C with an annual precipitation of 831 mm (Cuxhaven, Wetterdienst, 2019). The soils are sandy-silty and agricultural activity is nearby, yet not directly at the sites. The elevations, relative to the tidal range ($Znorm = \frac{Plot\ elevation - Mean\ Low\ Water}{(Mean\ High\ Water - Mean\ Low\ Water)}$, (Heuner, 2016) are between 0.54 and 1.35 (Mean Low Water, MLW = 0, Mean High Water, MHW = 1) and soil salinity ranges between an average of 0.2 and 4 PSU (own measurements).

Plot selection and vegetation zones

The sampling period was March 2016 to September 2017. By random stratified sampling, a total of 84 non-contiguous plots (4 m x 4 m) were distributed across the three sites, with 24 plots per site with a minimum distance of 20 m. The strata were elevation relative to the tidal range and vegetation zonation. The elevation was measured at each plot with real time kinematic GPS. The zones were differentiated as a zone above mean tidal high water level (MHW) and below MHW. In the study sites, three different plant species grew almost in monodominant stands parallel to the river, with only few other accompanying species (Figure 19). Closest to the water edge, the salt tolerant, leafless and bendy species *Schoenoplectus tabernaemontani* can be found up to 2 m under mean high water (Kötter, 1961), followed next in landward direction by *Bolboschoenus maritimus*, a stiffer and taller sedge, still below MHW. *Phragmites australis* can establish near the MHW level and dominates in dense stands, distant to wave action because it is sensitive to mechanical stress (Coops et al., 1994; Ellenberg & Leuschner, 2010). From 1 m above MHW, *P. australis* grows in a mix with other species, such as *Mentha aquatica* and *Juncus gerardii* (Figure 19).

Frequency analysis of plant species

To record vegetation composition, a frequency frame (50 x 50 cm) was used. It contained 25 cells (each 10 x 10 cm) and was used four times per plot to cover a total area of 1 m² (Tremp, 2005; Minden et al., 2012; Cebrián-Piqueras, 2017). In each cell, the presence or absence of a species was recorded. Species were determined by literature (Schmeil & Fitschen, 2003; Rothmaler, 2007). From all recorded species, 17 species were selected from which plant trait information was then collected (Figure 19). These species were selected to represent at least 95% of frequencies recorded (Cornelissen et al., 2003). Information on species names and their position below or above MHW is provided in Figure 19.

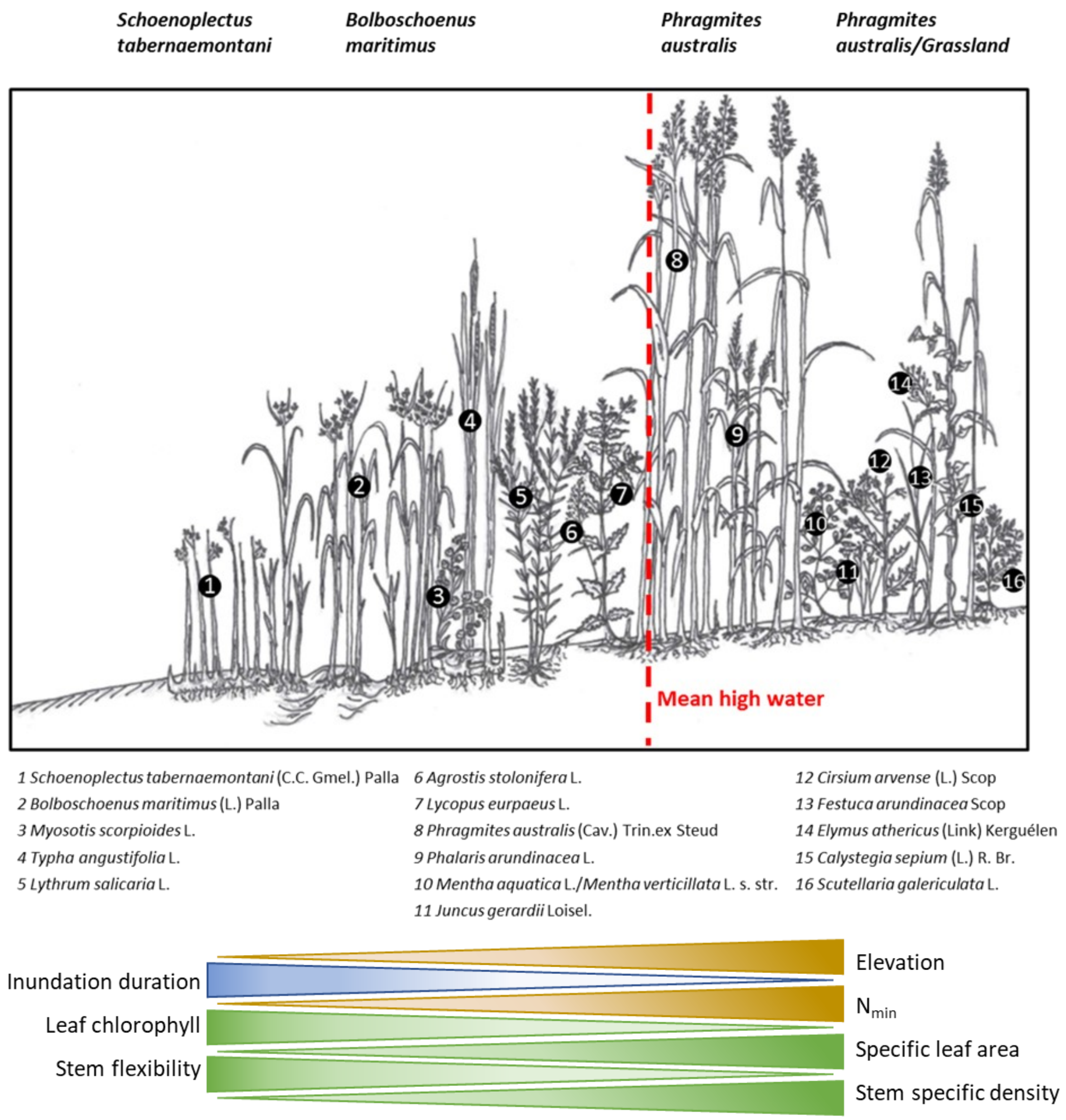


Figure 19: Schematic of the species of the study sites, sorted based on their occurrence along the elevational gradient. The zone below mean tidal high water level (MHW) is dominated by S. tabernaemontani and B. maritimus. The zone above MHW is dominated by P. australis growing in monotypic stands close to MHW and in a mix with species on higher elevations. The numbers refer to the species names. M. aquatica and M. verticillata are depicted as one. Gradients directions and trait patterns are indicated with arrows (Chapter 6).

Trait measurements

A total of 175 plant individuals (at least 10 individuals per species) were collected at the peak of their development, i.e. when seeds were ripe but not yet shed (Minden et al., 2012). Plants were dug out with a 20 x 20 cm soil volume. Roots and rhizomes were cleaned with water and separated from those of other plant individuals. Seeds, stems, leaves, roots and rhizomes were sorted, dried for 72 hours at 70 °C and weighed. For the grass species, the leaf area was measured as the leaf blades, the petioles were assigned to the stem part (following Yan et al., 2016). For *S. tabernaemontani*, a leafless species, the stem was used as an equivalent to the leaf; only the belowground part that did not produce chlorophyll was treated as stem. The petioles of species were excluded from specific leaf area (SLA) measurements (Pérez-Harguindeguy et al., 2013).

Traits measured were: canopy height (cm) in the field (Weiher et al., 1999) and specific leaf area measured on two leaves per plant sample (SLA, (mm^2 mg^{-1})) with a Flatbed scanner (300dpi) and ImageJ-Software (Schneider et al., 2012). From this, the total leaf area (mm^2) could be calculated. The stem bending properties of fresh samples were tested for at least 20 stems per species across the three sites. Samples were stored cool and moist with testing completed within a few days after harvest at the Royal Netherlands Institute for Sea Research (NIOZ Yerseke, NL) with the Instron 5942 (Canton, MA, USA, Heuner et al., 2015; Rupprecht, Möller, et al., 2015). The Young´s modulus (MPa) describes the resistance of a stem to bending (with higher values indicating stiffer stems), as the slope of its stress-strain curve (Hamann & Puijalon, 2013). Different equations were used to calculate the bending properties (Coops & Van der Velde, 1996a; Hamann & Puijalon, 2013; Vuik et al., 2018), for a detailed description, see Appendix 8. 2.

For the mass per volume ($g_{\text{fresh mass}}$ cm^{-3}) and specific density ($g_{\text{dry mass}}$ cm^{-3}) of stems, roots, and rhizomes, volumetric flasks were used. Samples of the roots and rhizomes (~2 cm per organ sample) of each collected trait plant individual were freshly weighed, measured exactly in length and all material was finally dried and weighed (72 hr at 70°C). Specific root and rhizome length (mm $g_{\text{dry mass}}^{-1}$) and the dry matter content of each organ ($mg_{\text{dry mass}}$ $g_{\text{fresh mass}}^{-1}$) was determined. For each plant individual and organ, carbon (C), nitrogen (N) and phosphorus (P) content (g kg^{-1}) were analyzed. C and N content was determined by grinding the material in a mill ('pulverisette 7', Fritsch, Idar-Oberstein, Germany) and using the C:N-Analyzer (Flash 2000, Thermo Scientific) following Allen (1989). P content was extracted from the pulverized material (7-8 mg, precision balance, CP 225 D, Sartorius, Goettingen, Germany) by heating the sample with nitric acid (95°C, 6 hr) and then adding hydrogen peroxide (30%, 95°C, 4 hr). The volume was then raised to 1 ml with water (bidest) and measured in the continuous flow analyzer (CFA), following Murphy and Riley (1962).

Abiotic parameters

Soil salinity of the top soil was determined following Schlichting et al. (1995): 10 g fresh soil, diluted with 25 ml H_2O was left for 30 min and conductivity measured in the excess water (WTW ph/Cond340i/SET, Tetracon 325 electrode). The salinity was calculated with the UNESCO equation (UNESCO, 1981; Grasshoff et al., 1983). For every plot, the soil samples were taken up to a depth of 60 cm and extrapolated to a depth of 80 cm. Bulk density (g cm^{-3}) was determined for 200 cm^3 for each soil horizon by weighing each fresh and dried sample (48 h at

105°C, Schlichting et al., 1995). The bulk density results were related to other soil parameters, by multiplying the nutrient content with the mass per m² (derived from soil density and multiplied by m³ for each soil horizon). Calcium carbonate ($CaCO_3$) content (kg m^{-2}) was measured following Scheibler´s gasometric method (Schlichting et al., 1995). Ammonium (NH_4^+) and nitrate (NO_3) contents were determined using the incubation method following Gerlach (1973). The measurements were done with a Continuous Flow Analyzer (CFA) at 660 nm (ammonium) and 540 nm (nitrate). Grain size distribution (%) was determined with a Laser Particle Sizer (Analysette 22), with H_2O_2 added to remove organic substances, then related to soil horizon depth and volume and expressed as kg m^{-2}. Mineral nitrogen (N_{min}) is the sum of ammonium and nitrate, expressed in g m^{-2}. Soil phosphorus (P) and potassium (K) content (g m^{-2}) were determined following the method of Egnér et al. (1960) and measured in the continuous flow analyzer (CFA for phosphorus) or in the Atomic Adsorption Spectroscopy (AAS for potassium). Soil carbon (C) content was analyzed with the C:N-Analyzer (Flash 2000, Thermo Scientific) following Allen (1989).

To record inundation, 80 cm long drainage pipes (8 cm Ø) were installed at two plots per zone and site. The pipes were placed vertically in the ground and equipped with pressure loggers (SENSUS ULTRA by Reefnet). The loggers recorded the pressure (hydrostatic and/or atmospheric) every hour between March and October 2016. Three additional loggers were positioned on each site on buildings nearby, to record the corresponding air pressure (Minden & Kleyer, 2014). A regression was made for each site separately for elevation and the water depth. The inundation period was set as the time when the water level was at ground level or above and expressed as hours per day.

Wave heights were recorded at each site on one transect between December 2015 and April 2017 (Schoutens et al., 2019) with nine pressure sensors (P-Log3021-MMC, Driesen & Kern). The transect followed the elevation gradient from the shore to the high marsh with measurements between the different vegetation zones. By correction of atmospheric pressure, the measurements (frequency of 8 Hz) were referenced to water surface elevation. The tidal signal could be separated from the wave signal, but wind or ship generated waves were not distinguishable. A detailed description of the recording method can be found in Schoutens et al. (2019).

In this study, the wave attenuation was extrapolated for all plots for water depth <0.5 m, the water depth varies over time (due to the tides) and between the plot locations. For details on this process, see Appendix 8. 1. The wave attenuation is the difference in wave height between two measurement points (Schoutens et al., 2020), this was measured only for the zone below MHW.

Ecosystem properties

The aboveground biomass (AGB) was cut at the start of the growing season in March 2016 and again in August 2016 (De Leeuw et al., 1990). The vegetation was cut on 0.5 m² at ground level and sorted into dead and living biomass (Scurlock et al., 2002), subsequently dried, weighed and calculated for 1 m². The photosynthetically active radiation reaching the soil surface was (PAR) detected with a SunScan (Canopy Analysis System SS1, see Maier et al., 2010). This acts as a measure of the vegetation density: at least five measurements were taken at each plot, 5 cm above the ground. To relate this to the radiation above the vegetation, one measurement was taken in full light. PAR was expressed as the percentage of the total radiation.

The decomposition rate on plot level was determined by preparing mesh bags for each plot (1 mm wide meshes, Cebrián-Piqueras et al., 2017). Each bag was filled with 4 g of biomass from the same plot, the exact weight was noted. To compare the decomposition rate across the sites, three bags per plot were filled with "standard litter" (hay). The bags were placed on top of the soil in each plot with the vegetation removed, fixed with mesh and collected after 10 months, cleaned, dried and weighed. The decomposition rate was expressed as % per day (Minden & Kleyer, 2015).

With the C:N-Analyzer (Flash 2000, Thermo Scientific), the content of soil carbon (C, %) was determined (Allen, 1989). Soil organic carbon (SOC) is the difference between the $CaCO_3$ and the total carbon content (Cebrián-Piqueras et al., 2017). The soil organic carbon stock (SOC stock) present was calculated with the percentage of SOC and the bulk density for each horizon, which gives a measure of SOC per kg and m². For details on ecosystem properties above MHW and below, see Figure 20.

Statistical analysis

The statistical analysis was conducted with the open source software R (R Core Team, 2017) and RStudio (RStudio Team, 2016). To test the significant differences between the environmental and ecosystem property variables, we used linear mixed effects models for each variable with the vegetation zones (two levels, below MHW and above MHW) and the study sites (three levels) as explanatory variables. As the focus of this study was on the zones above and below MHW, the study sites were treated as random effects (lmer(environment~zone+(1|site)), R-package 'lme4', Bates et al., 2015). A pairwise test was done between the vegetation zones (least squares means) for each model (R-package 'emmeans', Lenth, 2020), the degrees of freedom are based on the Kenward-Roger method, the p-value adjusted with 'mvt'.

To obtain the community weighted mean per plot, the trait values were weighted with the frequency analysis (community weighted mean, CWM, Violle et al., 2007; Cebrián-Piqueras et al., 2017). Variables were transformed to conform to a normal distribution ('stats' package, Royston, 1982), see Table 9.

As some plant traits were strongly correlated, they were aggregated by a principal component analysis (PCA, "stats" package), and the scores of the first PCA axis were used in the remaining analyses. This procedure helped to avoid collinearity issues. The aggregated traits were: Young´s Modulus, stem mass per volume, stem specific density (SSD) and stem dry matter content (SDMC), which were summarized as 'stem traits'. As 'leaf traits', total leaf area and leaf dry matter content were aggregated. Combined as 'mass' were total biomass of stem, leaf, root and rhizomes (g). As 'belowground traits' we aggregated root & rhizome dry matter content (RDMC, RHDMC), root & rhizome specific density (RSD, RHCD), and with inverted values root & rhizome specific length (RSL, RHSL), see Table 9 and Table 10 for units, abbreviations and details on aggregates. Leaf biomass ratios of N:P and C:N were aggregated as ˈleaf stoichiometryˈ, those traits were negatively correlated.

To explore the relationship between different trait variables, standard major axis regressions (SMA, Warton et al., 2006) were performed. This type of analysis is appropriate, when similar measurement errors are associated with both variables (Cui et al., 2020). The SMA minimizes the error of both variables and was performed with the "smatr" package (Warton et al., 2012).

Multiple linear regression (MLR) was used to explore the relationship of environmental variables, plant traits and ecosystem properties together. To meet the model assumptions, some variables had to be transformed, see Table 9. To find the best predictor for the ecosystem properties and ecosystem services, a stepwise selection was used to choose the best performing model with the lowest Akaike Information Criterion (AIC, Venables & Ripley, 2002).
The wire graphs (Figure 24 & Figure 26) were constructed with the "lattice" package (Sarkar, 2008). The relationship between AGB and wave attenuation in the zone below MHW was shown in a scatterplot ("graphics" package, R Core Team, 2017).

Table 9: Environmental variables, plant traits and ecosystem properties with abbreviations and transformations used and units. For the plant traits, the aggregates are indicated. For details on aggregates, see Table 10.

VARIABLE		ABBREVIATION	TRANSFORMATION	UNIT
ENVIRONMENTAL VARIABLES				
Inundation			square root	hr day^{-1}
Soil salinity				PSU
Soil carbonate		CaCO3		kg m^{-2}
Clay content				kg m^{-2}
Sand content				kg m^{-2}
Plant available nitrogen		N_{min}		g m^{-2}
Soil phosphorus content		Soil P		g m^{-2}
Soil potassium content		Soil K		g m^{-2}
PLANT TRAITS	**AGGREGATE**	**ABBREVIATION**	**TRANSFORMATION**	**UNIT**
Stem mass to volume	**Stem traits**			$g_{fresh\ mass}$ cm^{-3}
Young´s modulus			log	MPa
Stem specific density		SSD	Tukey	$g_{dry\ mass}$ cm^{-3}
Stem dry matter content		SDMC	log	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Leaf dry matter content	**Leaf traits**	LDMC	Tukey	$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Total leaf area			log	mm²
Total stem	**Mass**		log	g
Total leaves			log	g
Total root			log	g
Total rhizome			log	g
Root dry matter content	**Belowground traits**	RDMC		$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Rhizome dry matter content		RHDMC		$mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$
Root specific density		RSD	square root	$g_{dry\ mass}$ cm^{-3}
Rhizome specific density		RHSD	log	$g_{dry\ mass}$ cm^{-3}
Root specific length		RSL	log	mm $g_{dry\ mass}^{-1}$
Rhizome specific length		RHSL	log	mm $g_{dry\ mass}^{-1}$
N:P ratio leaf	**Leaf stoichiometry**	N:P leaf		
C:N ratio leaf		C:N leaf	Tukey	
Canopy height			log	m
ECOSYSTEM PROPERTIES		**ABBREVIATION**	**TRANSFORMATION**	**UNIT**
Aboveground community bio-		AGB		g m^{-2}
Photosynthetically active radi-		PAR		%
Wave attenuation				m
Decomposition standard hay		decomp. hay		% day^{-1}
Decomposition native biomass		decomp. native		% day^{-1}
Soil organic carbon content		SOC (%)	log	%
Soil organic carbon stock		SOC(kg m^{-2})		kg m^{-2}

8.3 Results

Abiotic conditions and ecosystem properties below and above mean high tide water level

For the abiotic conditions of the tidal marsh below MHW and above MHW, only clay content, soil P and K yielded non-significant results. All other factors differed significantly: salinity (p=0.04) was higher below MHW, soil content of carbonate (p<0.0001) was lower below MHW, sand content (p=0.002) was higher below MHW and plant available nitrogen (N_{min}, p=0.02) was lower below MHW (Figure 20). Due to the difference in elevation between the vegetation zones (p<0.0001), the inundation duration was also significantly different.

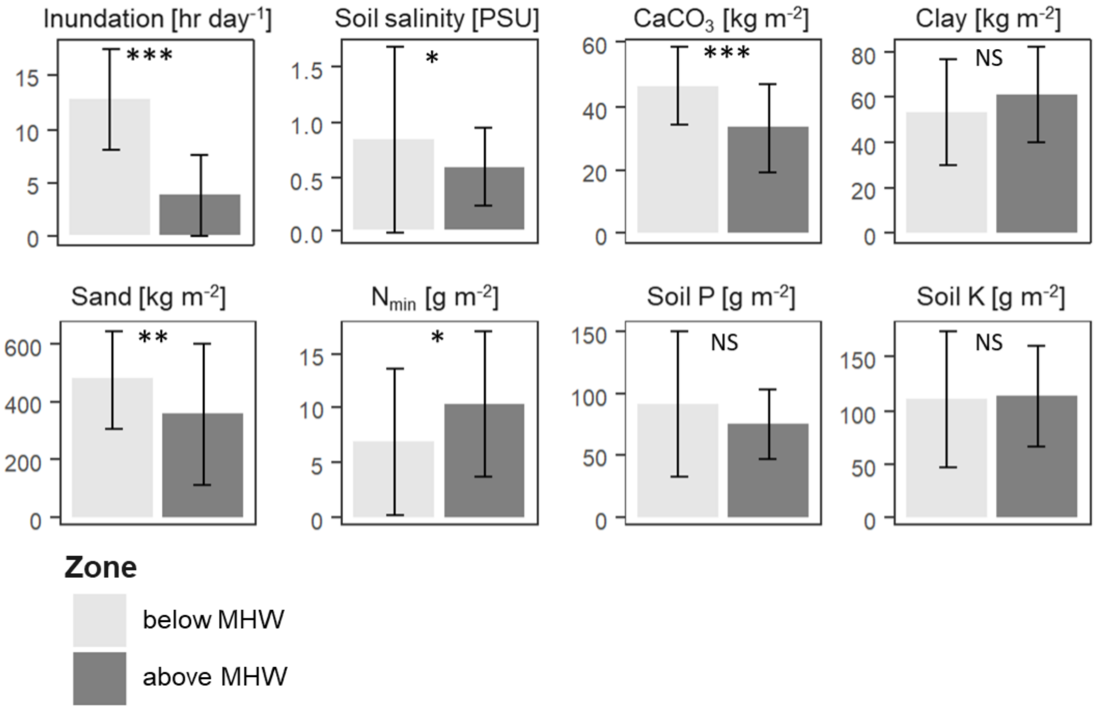


*Figure 20: Environmental variables for the tidal marsh zone below mean high water (below MHW, light grey bars) and above MHW (dark grey bars) with standard deviation. Significant differences are indicated with * p<0.05, ** p<0.01 and ***p<0.001, tested with t-test. Non-singnificant differences are indicated with NS.*

Regarding the ecosystem properties, significant differences existed in the AGB between the zones (p=0.0001, both higher for the zone above MHW) as well as for density of the vegetation (p<0.0001, expressed as photosynthetically active radiation (PAR) reaching the ground). The decomposition of standard litter (hay) was smaller below MHW (p<0.0001), while the decomposition of native biomass in contrast showed no significant difference between the two zones. The soil organic C content (SOC %) was significantly higher above MHW than below and so was the soil organic carbon stock (kg m^{-2}).

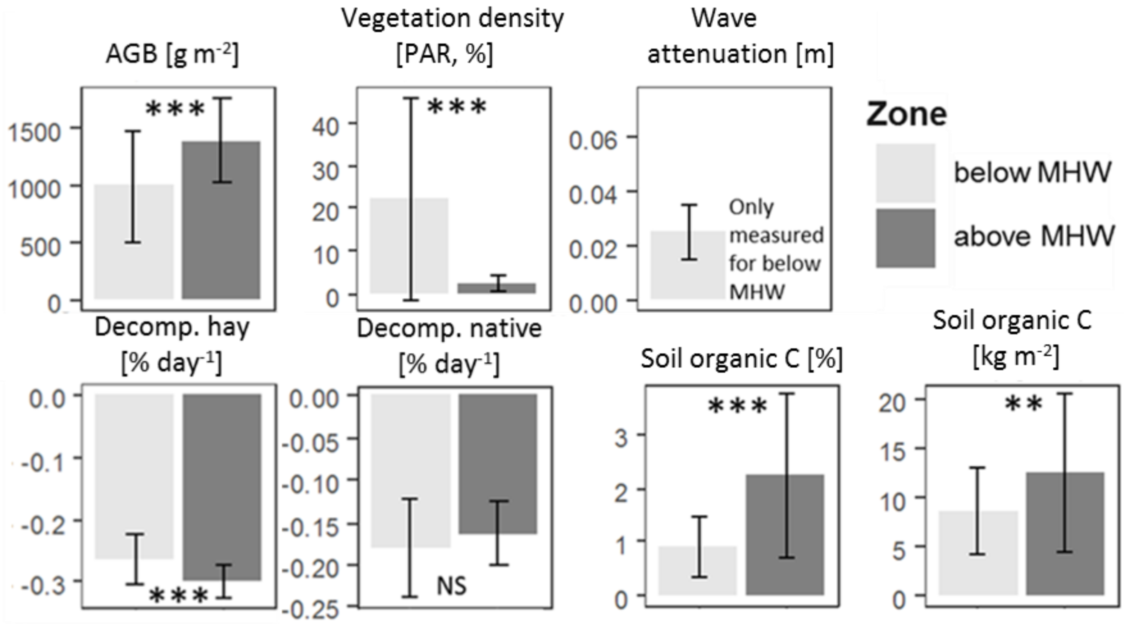


*Figure 21: Ecosystem properties for the tidal marsh zone below mean high water (below MHW, light grey bars) and above MHW (dark grey bars) with standard deviation. Significant differences are indicated with * $p<0.05$, ** $p<0.01$ and ***$p<0.001$, tested with t-test. Non-significant differences are indicated with NS.*

Relationships of traits and trait aggregates analysed with standard major axis regression (SMA) and PCAs

The results of the PCAs showed highly positively correlated traits for stem and leaf variables, biomass investment and stoichiometric composition of leaves (Table 10, the PCAs are shown in Appendix 8. 3 - Appendix 8. 7). An example of highly correlated traits is Young´s modulus (a measure for stem resistance to bending) and stem specific density (SSD), see Figure 22. Those two traits were encompassed in the ˈstem traitsˈ aggregate. The SMA of ˈstem traitsˈ versus ˈleaf traitsˈ for the zone below MHW (Appendix 8. 9) highlighted the strong relationship between these traits: higher SSD and Young´s modulus were positively related with the support of a larger leaf area.

Table 10: Aggregates of variables and explained variances. The variables were aggregated with a Principal Component Analysis (PCA) for the community weighted means of the vegetation below mean tidal high-water level (MHW) and above MHW. All PCAs were significant at p<0.05, their explained variances were between 53-96%. The variances explained by the first and second axis are shown.

AGGREGATE	**VARIABLES COMBINED**	**VEGETATION-ZONE**	**VARIANCE EXPLAINED AXIS 1**	**VARIANCE EXPLAINED AXIS 2**
'Stem traits'	Stem $g_{fresh\ mass}$ cm^{-3}, Young´s modulus, SSD, SDMC	below MHW	0.91	0.07
		above MHW	0.72	0.16
'Leaf traits'	LDMC, total leaf area	below MHW	0.77	0.23
		above MHW	0.81	0.19
'Mass'	total biomass of stems, leaves, roots, rhizomes	below MHW	0.66	0.27
		above MHW	0.77	0.17
'Belowground traits'	RDMC, RHDMC, RSD, RHSD, -RSL, -RHSL	below MHW	0.53	0.32
		above MHW	0.61	0.24
'Leaf stoichiometry'	N:P leaf, - C:N leaf	below MHW	0.96	0.03
		above MHW	0.82	0.18

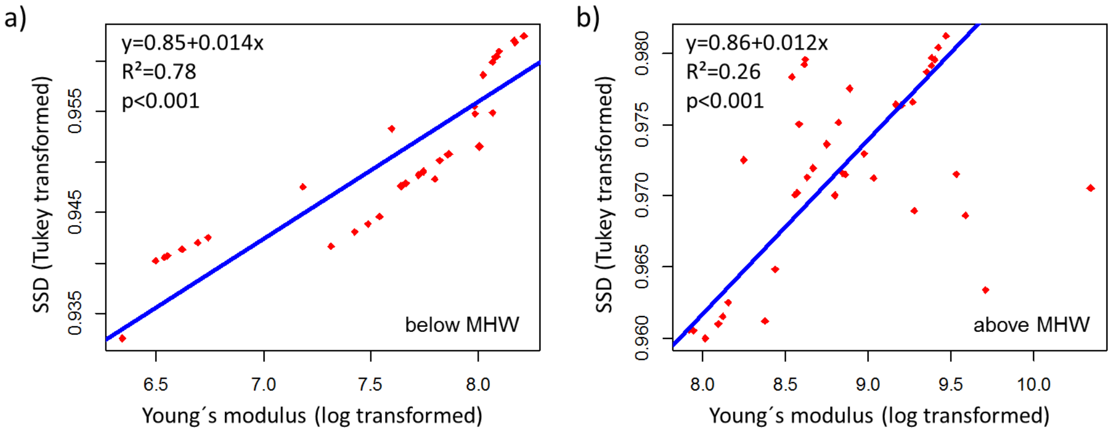


Figure 22: a) SMA (standard major axis regression) of Young´s modulus (stem resistance to bending, original unit = MPa) and SSD (stem specific density, original unit = $g_{dry\ mass}$ cm^{-3}*) for the community weighted means for the zone below MHW, and b) above MHW with equations for linear regression lines and R² values; p <0.001. Both variables displayed are part of the 'stem traits' aggregate, Appendix 8. 3, Table 9 and Table 10.*

Other SMAs showing significant relationships between stem traits, canopy height and leaf stoichiometry can be found in the supplementary information (Appendix 8. 10 & Appendix 8. 11):

A higher canopy was positively related to denser and stiffer support structures. The nutrient ratios within the leaves were positively related to the leaf traits aggregates: higher N:P ratios and lower C:N ratios were associated with a larger leaf area and higher dry matter content. For the zone above MHW, strong correlations existed between the 'leaf traits' and 'stem traits' with higher values for leaf area and dry matter content associated with stiffer and denser structure of the stem (Appendix 8. 9b). The relationship of leaf stoichiometry and leaf traits was similar to the zone below MHW (Appendix 8. 11b).

Relationships of community weighted means of traits, ecosystem properties and environmental variables analysed with multiple linear regression models

For the trait aggregates for mass, belowground and leaf stoichiometry, no significant relationships to the measured ecosystem properties of AGB (aboveground community biomass), decomposition rates, SOC % and SOC stock could be shown with multiple linear regression (MLR) for the zones above mean high water level (MHW) or below.

The vegetation zone below the mean high tide water level

Wave attenuation for the zone below MHW showed an almost linear relationship with AGB (Figure 23, Figure 24a, Table 11). The attenuation of waves (i.e. calculated here as the reduction in wave height over the distance to the marsh edge and corrected for plot elevation) was higher where there was more AGB present. The range of reduction in wave height at plot level (dependant on distance to marsh edge and plot elevation) was between 0.01-0.05 m.

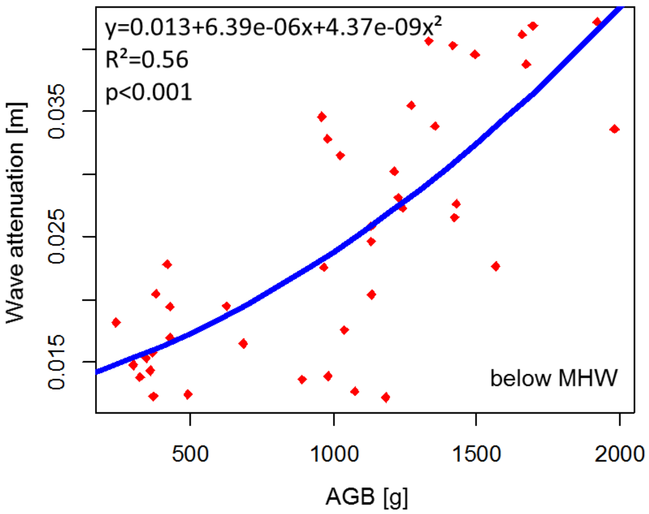


Figure 23: Scatterplot for wave attenuation vs AGB (aboveground community biomass) for the zone below MHW. The quadratic equation and R^2 value is shown, $p<0.001$.

Wave attenuation increased both linearly with the stem traits aggregate and exponentially with the aboveground community biomass (AGB, Figure 24a, Table 11). AGB itself increased with ‘leaf traits’ and ‘stem traits’ (Figure 24b), meaning that there was more AGB where stems were stiffer and supported lager leaf sizes. Low soil organic carbon (SOC) was associated with low ˈstem traitˈ values (i. e. less dense material, lower Young´s modulus) and showed a negative relationship with the inundation duration (Figure 24). The highest amounts of SOC were predicted for the combination of intermediate ˈstem traitsˈ (stem specific density, fresh mass per volume, Young´s modulus and dry matter content, Figure 24c) and low inundation.

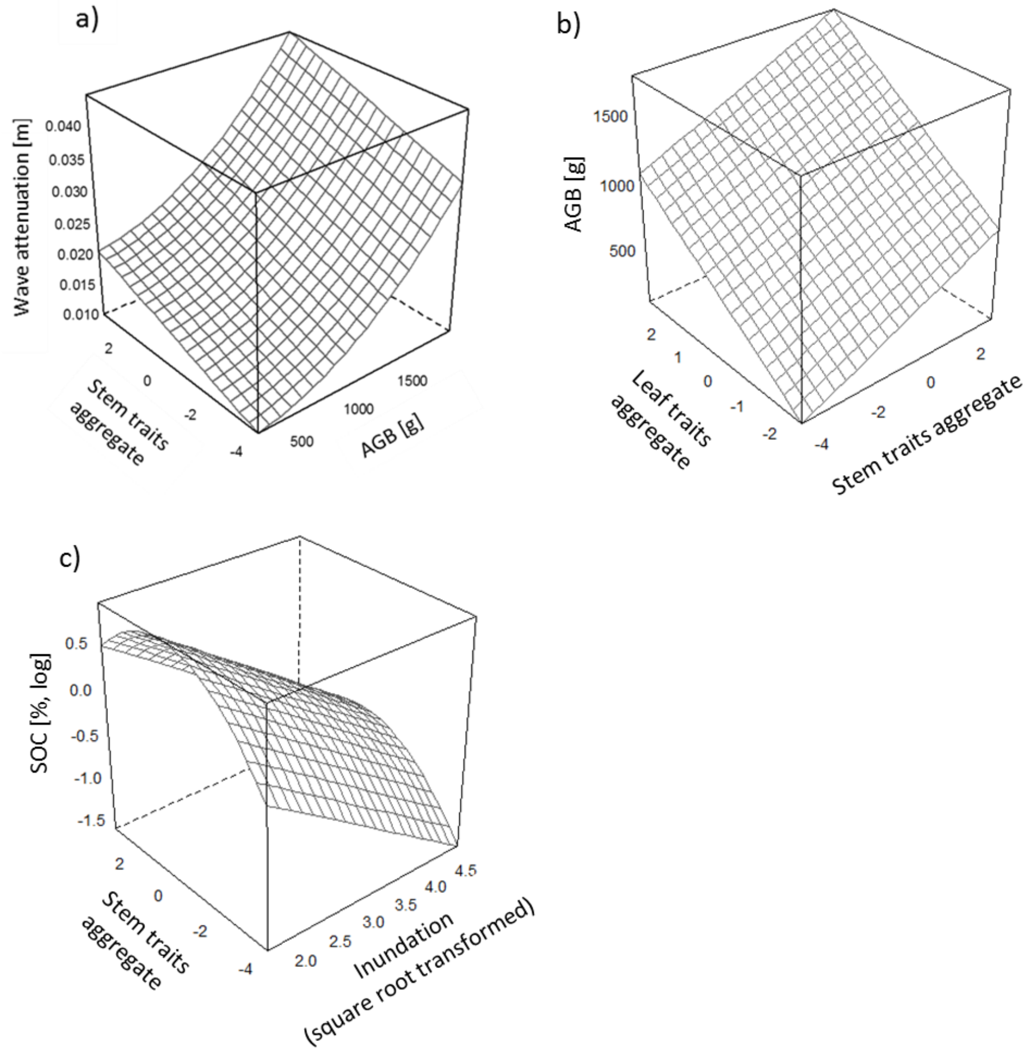


Figure 24: Results for multiple linear regression (MLR). All graphs show the zone below MHW a) Variables displayed are wave attenuation [m], AGB (aboveground community biomass [g m^{-2}]), PCA scores ˈstem traitsˈ (SSD, SDMC, fresh mass per volume, Young´s modulus). b) AGB (aboveground community biomass [g m^{-2}]), PCA scores ˈstem traitsˈ (SSD, SDMC, fresh mass per volume, Young´s modulus) and ˈleaf traitsˈ (total leaf area, LDMC). c) SOC (soil organic carbon [%]), inundation duration (square root transformed), PCA scores ˈstem traitsˈ (SSD, SDMC, fresh mass per volume, Young´s modulus). The stepwise analysis of the relationship between trait aggregates, environmental variables and ecosystem properties for the zone below MHW revealed significant relationships (Table 11), the p-value for the F-test was below 0.05. The variances explained for the different models were between 22 and 68%.

Table 11: Results of the multiple linear regression model for wave attenuation, AGB, stem traits, SOC, leaf traits and decomposition rate for the zone below MHW. Given are estimates, standard error, t-values, and significance levels. Significant p-values at α = 0.05 are shown in bold. Measures of model performance are shown additionally.

	ESTIMATE	**SE**	**t**	**p**	
Vegetation zone below the mean high-water level					
a)					
Intercept wave attenuation	1.59e-02	2.15e-03	7.41	**7.02e-09**	***
AGB^2	6.14e-09	1.29e-09	4.78	**2.67e-05**	***
'stem traits'	1.48e-03	7.03e-04	2.11	**0.04**	*
Adj. $R^2 = 0.60$; variance explained: 63%; $F(3,38) = 21.67$, $p < 0.001$					
Vegetation zone below the mean high-water level					
b)					
Intercept AGB	1003.77	43.83	22.90	**< 2e-16**	***
'stem traits'	96.19	39.57	2.431	**0.01975**	*
'leaf traits'	194.88	60.78	3.21	**0.0027**	**
Adj. $R^2 = 0.67$; variance explained: 68%; $F(2,39) = 41.77$, $p < 0.001$					
Vegetation zone below the mean high-water level					
c)					
Intercept SOC %	1.77616	0.67071	2.648	**0.01172**	*
inundation	-0.52791	0.17736	-2.976	**0.00505**	**
'stem traits'^2	-0.05294	0.02599	-2.037	**0.04868**	*
Adj. $R^2 = 0.15$; variance explained: 22%; $F(3,38) = 3.50$, $p = 0.02$					

The vegetation zone above mean high tide water level

For the vegetation zone on the higher elevations, above MHW and dominated by *Phragmites australis*, the decomposition rate of native plant material was strongly negatively related to inundation duration (Figure 25, Figure26a, Table 12). This was the strongest effect for the zone above MHW created by the inundation duration: with longer inundation, the decomposition rates of the native biomass were significantly lower (Figure 25 & Figure 26a).

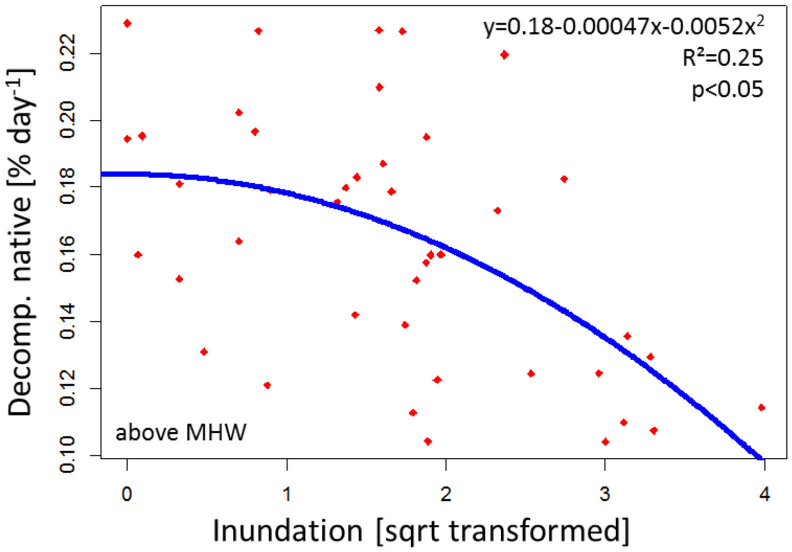


Figure 25: Quadratic regression of decomposition rates of native biomass vs inundation duration (original unit = h day^{-1}) for the zone above MHW.

The relationship of decomposition rates, inundation duration and 'stem traits' analysed together showed, that the decomposition was highest for short inundation duration and intermediate 'stem trait' values (Figure 26a).

The SOC stock (soil organic carbon, kg m^{-2}) was analysed depending on decomposition rates and the stem traits aggregate and shown in Figure 26b. This analysis revealed a bathtub-shaped relationship with 'stem traits': the SOC stock was lowest, where the vegetation showed intermediate values for Young´s modulus, dry matter content and density. The SOC stock was almost linearly positively correlated with the decomposition rate of native biomass (Figure 26b) for the zone above MHW.

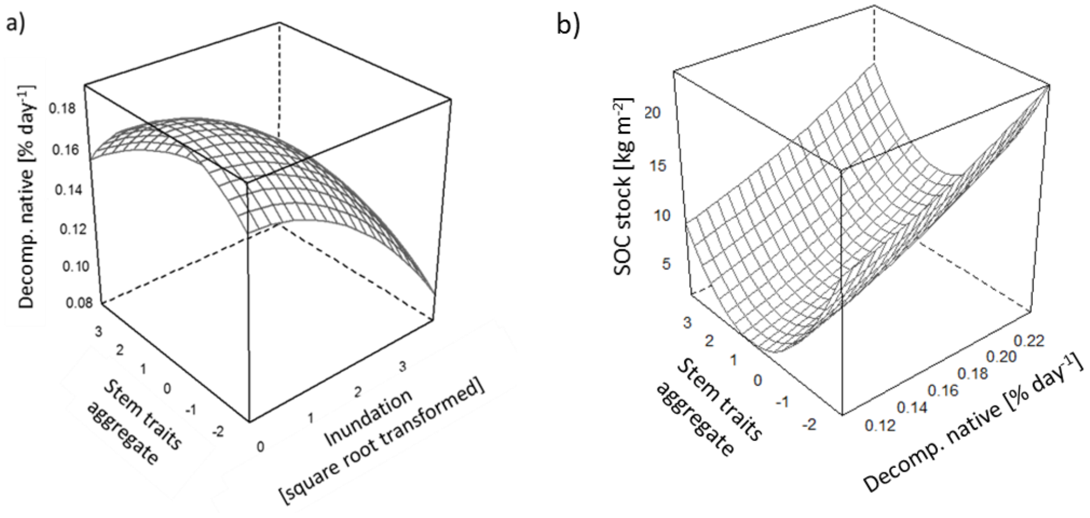


Figure 26: Both graphs show results of MLR for the zone above MHW. a) Variables displayed are decomposition rate [% day^{-1}], inundation [hr day^{-1}, square root transformed], PCA scores ˈstem traitsˈ (SSD, SDMC, Young´s Modulus). b) SOC stock (soil organic carbon stock [kg m^{-2}]), decomposition rate [% day^{-1}], PCA scores 'stem traits'. The stepwise analysis of the relationship between trait aggregates, environmental variables and ecosystem properties for the zone above MHW revealed significant relationships (Table 12), the p-value for the F-test was below 0.05. The variances explained for the different models were between 20 and 36%.

Table 12: Results of the multiple linear regression model for inundation duration, decomposition rates, 'stem traits' and soil organic carbon stock for the zone above MHW. Given are estimates, standard error, t-values, and significance levels. Significant p-values at α = 0.05. Measures of model performance are shown additionally.

	ESTIMATE	**SE**	**t**	**P**	
Vegetation zone above the mean high tide water level					
a)					
Intercept SOC stock	0.19	0.0074	25.57	**< 2e-16**	***
Inundation^2	-0.0048	0.0013	-3.59	**0.00093**	***
ˈstem traitsˈ^2	-0.0031	0.0015	-2.11	**0.042**	**
Adj. R^2 = 0.32; variance explained: 36%; *F*(2,39) = 10.85, *p* < 0.001					
Vegetation zone above the mean high tide water level					
b)					
Decomp. native^2	216.78	101.76	2.13	**0.04**	*
ˈstem traitsˈ	-1.78	0.78	-2.28	**0.028**	*
ˈstem traitsˈ^2	1.1119	0.4152	2.678	**0.0109**	*
Adj. R^2 = 0.14; variance explained: 20%; *F*(3,38) = 3.22, *p* < 0.05					

8.4 Discussion

Understanding the relationships between species traits, ecosystem properties, and ecosystem services is important to develop effective measures of ecosystem management that contribute to optimal delivery of ecosystem services. In this paper, we identified such relationships for two ecosystem services that are considered highly valuable in tidal marsh ecosystems, i.e. (1) wave attenuation, which contributes to nature-based mitigation of shoreline erosion and flood risks (Coops, Geilen, et al., 1996; Möller et al., 2014; Schoutens et al., 2019), and (2) soil carbon storage, which contributes to nature-based mitigation of climate warming (IPCC, 2007; Hansen et al., 2017; Najjar et al., 2018). Our study revealed that the ecosystem service of wave attenuation was most strongly affected by AGB (aboveground community biomass) and the 'stem' and 'leaf traits' of that biomass whereas soil organic carbon was influenced by the 'stem traits' and inundation in the tidal marsh zone below MHW (mean high tide water level), the ˈstem traitsˈ aggregate and decomposition rates in the zone above MHW, which were reactive to inundation too. We detected strong differences in the delivery of ecosystem services between the vegetation zones above and below MHW which highlights that a) the delivery of ecosystem services is not necessarily equally spread across one habitat type and b) ecosystem management should be optimized in order to maximize the ecosystem services delivery potential of the different zones.

Ecosystem Services in the lower tidal marsh zone (below MHW)

In the lower tidal marsh zone (below MHW), plant species diversity is relatively low. This is because the species here need to adapt to more harsh environmental conditions such as salt (we found significantly higher salinity than above MHW), submersion and soil oxygen scarcity (Odum, 1988; Weiher & Keddy, 1999; Takahashi et al., 2014). Other hydrodynamic stress, such as strong waves, influence species composition, which is well known for various types of shoreline vegetation (van Wesenbeeck et al., 2007), where the type of vegetation present was determined by the level of hydrodynamic forcing. This in turn, through other traits of the species (e.g. small statue under strong wave exposure, Coops et al., 1994) may affect the ecosystem service of wave attenuation.

For the zone below MHW, we found correlations of Young´s modulus (higher stem resistance to bending) with higher wave attenuation (Augustin et al., 2009; Möller et al., 2014; Schoutens et al., 2019). Young´s modulus was part of the 'stem traits' aggregate and this showed a relationship between Young´s modulus and stem specific density (SSD). This is an intriguing finding, as SSD is easier to determine, with less laboratory equipment needed and therefore could offer a good alternative to determining stem bending properties. Investment into a stiffer stem leads to a trade-off as it also means a higher experienced drag-force resulting from waves (Bouma et al., 2005) and therefore more risk of breakage or buckling of the stems under the influence of the waves. For the ecosystem services provided by the lower tidal marsh zone, these mechanisms are of great significance: through its roughness and therefore enlarged surface area and more friction, the vegetation reduces the wave energy (for wave experiments and salt marsh species, see Möller et al., 1999). We could proof this for an estuarine ecosystem with the effect that the 'leaf traits' aggregate had on wave attenuation. Also, we could highlight the relationship between wave attenuation, on the one hand, and 'stem traits' and aboveground biomass together, on the other hand. Aboveground community biomass (AGB) and wave attenuation were almost linearly correlated. Heuner et al. (2015) also found strong correlations between aboveground biomass and wave attenuation (see also Rupprecht, Möller, et al., 2015). Schoutens et al. (2019) found for the Elbe estuary, that waves (mean significant height of 0.09 m) were attenuated up to 50% over a 10 m stretch of vegetation. In other habitats, AGB was shown to be strongly positively influenced by soil fertility and negatively by incoming waves, inundation and salinity (Lillebø et al., 2003; Crain, 2007; van Wesenbeeck et al., 2007; Minden & Kleyer, 2015). The only detectable difference in soil nutrient content in this study was found for N_{min}, with less available nitrogen below MHW, but this was not correlated with AGB.

As we could show in a previous study (Chapter 7), the wave impact, through the influence on species traits, had an impact on the decomposition rates of AGB, with denser and stiffer biomass decomposing more slowly. It has been shown that salinity levels have a negative effect on biomass production, as the species resources, rather than in growth, are invested into actively dealing with the salinity (succulent growth or excretion of salt from their tissues, Flowers & Colmer, 2008). For example, biomass production in salt marshes was determined at 466,99 g m^{-2} (Minden, 2010, similar results were found by Rupprecht, Möller et al., 2015), compared to an average of 700-900 g m^{-2} for brackish marshes on low elevations (Schoutens et al., 2019). Succulent growth has been shown to be related to plant tissue decomposability too (succulent plants decompose more rapidly, Zedler et al., 1980). This may have repercussions on the carbon cycling and possibly carbon sink function of the ecosystem. The present analysis highlights that the decomposition on elevations below MHW in the study area is mainly governed by the inundation regime, possibly through the effects on the microbial community (Wang et al., 2019). The inundation affects the belowground traits with less dense organs and less dry matter content produced (Chapter 6). This, combined with effects of soil salinity on AGB and ramet height (Carus et al., 2017a) could explain the relatively low soil organic carbon concentrations below MHW: there is less biomass and dry matter content present. The carbon stock ranged between ~8 and 9 kg C m^{-2} for the zone below MHW (Chapter 8), soil C content was between 0.85 ±0.49 % and 1.01 ±0.60 %.

On these elevations, another important factor is that especially the dead and decaying vegetation is often broken off and washed away (Hansen et al., 2017) and therefore not physically present to add to the carbon stock.

Ecosystem services in the high marsh zone (above MHW)

Although species diversity above MHW was much higher than on elevations below MHW, Hooper and Vitousek (1997) point out, that soil processes are primarily influenced by dominant species' functional characteristics. The acquisition and investment of resources through plants is affecting species composition and ecosystem functions (Chapin et al., 2000; Loreau et al., 2001). For the zone above MHW, the focus of this study was on SOC stock, plant traits and decomposition rates.

The potential of tidal marshes to sequester carbon is the subject of various studies. Chmura et al. (2003) found C accumulation rates of ~210 g C m^{-2} year^{-1} for mangrove swamps and salt marshes, which is considerably higher than estimated values of 20-30 g C m^{-2} year^{-1} for peatlands (Roulet, 2000). Chmura et al. (2003) analyzed research on carbon sequestration in tidal saline wetlands and found that carbon density or accumulation rates vary within wetlands, for example due to differences in suspended sediment supply. Megonigal and Neubauer (2019) estimated carbon burial rates of 229 g C m^{-2} year^{-1} for a fresh water marsh (with C input from sediment making up one third) and Neubauer et al. (2002) found rates of ~517 g C m^{-2} year^{-1} of carbon accumulation in an US fresh tidal marsh.

In the present study, soil carbon content in the zone below MHW was low (~1 %), it was twice as high in the zone above MHW; for an 80 cm soil profile, this relates to SOC stock values of ~9-13 kg C m^{-2}. Van de Broek et al. (2016) found carbon stocks in the brackish part of the Scheldt estuary of 18.63-19.63 kg C m^{-2} and Hansen et al. (2017) found carbon stocks of 14.11 kg C m$^{−2}$ to 22.58 kg C m$^{−2}$ for 100 cm soil profiles for sites close to our study area. The SOC stock was positively related to intermediate values for the 'stem traits' aggregate: it was highest on the highest elevations, where a species mix exists, with differently structured biomass. For AGB (aboveground community biomass), no significant relationship to the SOC stock could be shown for the zone above MHW. Regarding the potential carbon storage, the belowground biomass is essential (Rasse et al., 2005; Chmura, 2013), which is away from physical deterioration and less likely to be flushed away. SOC is influenced by plant organ biomass allocation, especially to belowground organs (Jobbágy & Jackson, 2000; Rasse et al., 2005). In this study, we could not establish a relationship between the 'belowground trait' aggregate and SOC stocks though. A higher SOC stock in the plots above MHW was related to higher decomposition rates, which seems contradictive, as the decomposition process would break down organic material (Robertson & Paul, 2000).

The hampering effects of inundation on decomposition rates could be clearly shown for this zone, though unexpectedly we could not relate decomposition to leaf stoichiometry. Higher N:P ratios of leaf biomass could promote decomposition, which was found previously (Güsewell & Verhoeven, 2006; Liu et al., 2016). For a subarctic flora, Cornelissen et al. (2004) found lignin/N leaf concentrations to be correlated with decomposability while Freschet et al. (2012) found traits related to structure (lignin, dry matter content and C) to control decomposition. Possibly the inundation effect is overriding the effect of leaf chemical impacts in our study. The leaf economics spectrum (LES) highlights the connection between a short life span, high SLA and photosynthetic capacity as well as high nitrogen concentrations (Wright et al., 2004). Species with high leaf C:N ratio and low LDMC (leaf dry matter content) showed high allocations to aboveground biomass in a saltmarsh (Minden & Kleyer, 2015). We also found high leaf C:N ratios connected to low LDMC and low N:P ratios. In our study, this was highly correlated with the total leaf area the plants produced too, which was part of the 'leaf traits' aggregate.

Implications for management of tidal marshes

The plant traits analysed in the present study showed strong correlations with each other, following the concept of allometric scaling and this was similar in the tidal marsh zones below and above MHW. For the two ecosystem services that were focussed on in this study, we found that the involved traits below and above MHW differed: the ecosystem service of wave attenuation was strongly influenced by stem and leaf traits while the service of carbon storage was dependent on biomass characteristics and inundation as a controlling factor of decomposition. Additional to the changes that climate change may induce to plant species zonation in estuarine systems, the Elbe estuary and its tidal wetlands are also facing challenges due to the deepening of the riverbed and reduced space of floodplains by construction of embankments (HPA & WSA, 2011). The natural floodplains have been reduced by 75 % since 1902 (Kappenberg & Fanger, 2007). The deepening of the Elbe river in 1999 produced a decrease by 25 % in the outflow velocities during low tide, which in turn affected the upstream directed sediment transport and increased it by 120 % in the fresh water part and 20 % in Hamburg harbor (Kerner, 2007). An important threat to the tidal marsh vegetation is sea level rise (SLR), which will affect species zonation and reduce the size of the flood plain further (Reise, 2005; Zhu et al., 2019). Many studies have shown that the elevation of a site relative to MHW can be used as a key predictor for the distribution of a species (Zonneveld, 1960; Bertness & Ellison, 1987;

Bockelmann et al., 2002; Suchrow & Jensen, 2010). Although studies have shown that marshes can keep up with sea level rise (Temmerman & Kirwan, 2015; Kirwan, Temmerman, et al., 2016), they erode and eventually drown if the water table rises too quickly (Chmura et al., 2003). This is reducing their potential to attenuate waves and results in a higher necessary investment for artificial bank enforcements. As Temmerman and Kirwan (2015) pointed out, nature-based solutions will be more sustainable especially with rising energy cost for artificial structures (see also Temmerman et al., 2013).

For the service of wave attenuation, we found in this study that the AGB was essential. The zonation of species in the study sites for the marsh zone below MHW shows the smaller and more flexible *S. tabernaemontani* on the lowest elevations closest to the river channel, with *B. maritimus* on higher elevations, with more biomass and higher effect on wave attenuation. For the carbon sequestration, the biomass production of *P. australis* on higher elevations, with short inundation duration was important, as it creates large plants with dense fibres and makes up most of the biomass present. There could be an opportunity in many sites to allow the extension of the *P. australis* zone into the agriculturally used grasslands adjacent. There are now many projects for restoring salt marshes, allowing for more flooding space (Wolters et al., 2005; Meine, 2011). A key aspect of future management of the tidal marsh will have to be allowing for sufficient space inland in order to sustain the functioning of the lower and higher marsh zones. This will also depend on the supply of sediment, land use practises upstream, SLR and the species response to climate change (Kirwan & Megonigal, 2013).

Acknowledgements

We would like to thank Michael Kleyer for advice and support, Hannes Sahl and Thomas Jansen for measuring the elevations with RTK and Daniela Meißner in the laboratory, Frances Pusch for working on the initial phase of the project as well as the numerous students helping with sampling and processing work. This research was conducted in cooperation with the German Federal Institute of Hydrology (BfG) in line with its R&D-Project TIBASS (Tidal Bank Science and Services).

Chapter 9. Synthesis

9.1 General remarks

This thesis is an analysis of the mediating role of the estuarine tidal bank vegetation. The aim was, to elaborate the factors driving the brackish tidal marsh species zonation, plant trait responses to environmental drivers and interactions of traits as well as the effects on ecosystem properties that translate to ecosystem services.

The analyses were approached first through exploring the mean species trait values and therefore with the focus on the species basis, with the species frequency of occurrence and the abiotic factors of each plot in a three-table-analysis (RLQ). This gave an overview of the environmental drivers, the species zonation and essential traits and the direction for the further analysis. It also highlighted the species position with their specific traits and strategies in the environmental space. Then traits were analyzed at the community level which revealed the impact of the environmental drivers on traits and trait aggregates and direct or indirect effects (through the traits) on ecosystem properties. The community weighted means for traits reflected the impact of the vegetation on ecosystem properties because the specific traits of the species were weighted with their abundance and thus their contribution to the total biomass present. In a further step, the community weighted trait mean was analyzed in two separate sections of the tidal bank: the vegetation below and above mean high water (MHW). This was due to the very different habitat and community structure of these zones and the surmount importance of the inundation regime as the essential driver detected from the previous analyses.

Abiotic factors and traits of present plant species are determining the distribution of species and traits and with it the ecosystem properties and the resulting ecosystem services (Díaz et al., 2004). The abiotic conditions in an estuary represent strong filters that allow the establishment of only a small set of species, depending on those environmental conditions. These abiotic drivers therefore determine which trait expressions are the fitting ones for the successful establishment and survival of the species. The traits of the species are then affecting the ecosystem properties of biomass production and decomposition for instance. These are eventually translating into ecosystem services (Diaz et al., 2007). There are many ecosystem services that the coast and the estuaries deliver, for instance as a breeding habitat for fish, a filter system for drinking water or for recreational purposes (MEA, 2005). Two important ecosystem services were in the focus of this thesis, they were wave attenuation of the lower bank and the resulting protection of the tidal bank and the carbon sequestration potential of the entire bank and the high bank especially, capturing carbon dioxide and helping to mitigate the greenhouse effect (IPCC, 2007). On the high bank, waves were already attenuated, therefore this service could not be assessed above MHW.

In the next sections, the results of the separate analyses are discussed together, the overarching context and questions from the aim of this thesis elaborated and consequences and challenges for future management highlighted. Finally, further possible directions for research are outlined.

9.2 Environmental gradients driving vegetation zonation

Tidal marshes are associated with strong hydrological gradients, like severe wave impact for instance (van Wesenbeeck et al., 2007; Horstman et al., 2014). In the brackish tidal marsh study sites in the Elbe estuary, the distribution of species was clearly driven by the hydrological gradients too (Figure 12, Chapter 6 & Figure 17, Chapter 7 & Figure 24, Chapter 8). Many studies have elaborated the reasons for plant zonation (Coops et al., 1994; Coops & van der Velde, 1999; Rupprecht, Wanner, et al., 2015; Moffett & Gorelick, 2016; Silinski et al., 2016). Carus et al. (2017a), who were researching the stand characteristics of *B. maritimus* and *P. australis* in the Elbe estuary, found flow velocities to be the most important factor determining their distribution as well as inundation levels and durations.

In the study sites there was a very clear and distinct zonation visible. The clear gradients that were connected to species zonation in this study were related to hydroperiod and wave height (Chapter 6), which was both a function of the elevations and the distance to the marsh edge. Because of the strong gradients, there was only a small set of species present (Keddy, 1992), in the study sites the gradients were inundation regime and wave impact. This is in accordance with findings from van Wesenbeeck et al. (2007) who pointed out, that hydrodynamic stress can influence community structures and species zonation (Hopkinson et al., 2019). For all incoming waves and their height at different water depth (for which we chose the water levels from <0.5 m, 0.5-1.0 m and >1.5 m), there were significant differences for all zones. Starting from the open tidal flat, the very slender and widely spaced *Schoenoplectus* *tabernaemontani* was growing. Then the much taller and densely growing *Bolboschoenus maritimus* followed with only some other species dotted here and there, like *Lythrum salicaria* or *Phalaris arundinacea*. From around mean high water, *Phragmites australis* took over, growing much taller and with other, still very few species mixed in, like *Caltha palustris* or *Solanum dulcamara* L..

Heuner et al. (2015) hypothesized, that *S. tabernaemontani* has a niche in front of *B. maritimus*, where hydrodynamics are severe, and that it is facilitating the latter species (Brooker et al., 2008). For the sites of Balje and Hollerwettern, the zonation was abrupt and clear between the species growing on the lowest elevations *S. tabernaemontani* and *B. maritimus*, whereas in Krautsand, the *Schoenoplectus*-zone was very narrow and more mixed with *B. maritimus*. For all three sites, the transition from *B. maritimus* to *P. australis* was a clear cut and, when aerial photos were consulted, coincided quite accurately with the line of the mean high tide water level (MHW). Carus et al. (2017a) pointed out, that ranges for *B. maritimus* and *P. australis* overlap regarding the site elevation and that inundation duration therefore is not the only determining factor for the zonation. All of the dominant species and indeed many of the species found rely on a strong rhizome system, which is an essential characteristic in this habitat (Carus et al., 2017b). The gradients that were found in and across the four vegetation zones named after their dominant species partly depended on the zones analyzed together: soil salinity was significantly higher in the zones below mean high water (MHW), which were the *Schoenoplectus*-zone and the *Bolboschoenus*-zone, compared to above MHW but there was only a significant difference in salinity between the *Bolboschoenus* and *Phragmites*/mixed community-zone when all four zones were compared. The salinity levels found in all three sites were relatively low though, compared to levels for salt marshes (Minden et al., 2012). Therefore, the effect of salinity was not strongly detectable in the vegetation zonation. There were some salt-indicating species in the most seaward site Balje (*Elymus athericus, Triglochin maritima*), but with relatively low frequencies. Examples for species of freshwater marshes were found in Hollerwettern (intermediate site) on high elevations, for example *Solanum dulcamara*.

The nutrient status of the soil allowed no clear interpretation of the influence on species zonation. The gradient for calcium carbonate ($CaCO_3$) ran perpendicular to the shore, with the zones above MHW having significantly lower values. The sites, due to their different position along the river, had different levels of phosphate (P) which was highest in Krautsand, the most upstream site. Potassium (K) was highest in Balje, the most seaward site, whereas plant available nitrogen (N_{min}) differed based on elevation and was lower below MHW. The nutrient dynamic of P is known to be governed by riverine input (Beeftink et al., 1977), whereas K is owed to the high K content of water from the North Sea. The N_{min} content in this study was connected to the disturbance of the soil, namely the inundation regime either allowing decomposition and microbes recycling nitrogen or hampering this process. Therefore, this was dependent on the elevation, which was different between each vegetation zone – and the inundation period was different for the lower-lying zones of *Schoenoplectus* and *Bolboschoenus* compared to the *Phragmites* and *Phragmites*/mixed community-zone.

9.3 Environmental conditions, plant trait responses and trait-trait interactions

Species distribution along the environmental gradients was a function of their trait responses to the strong changes in abiotic conditions (Chapter 6, Figure 12). The soil salinity was influencing the species community composition and through this slightly the distribution of trait values. *Triglochin maritima* as an example was present in Balje (most seaward site) which shows succulence as a response to soil salinity. There are possible responses to salinity, which were noticeable on an intra-specific level. *Phragmites australis* for instance, formed much more slender stems in the study site Balje, were salinity was highest and the same was noticeable for *S. tabernaemontani* (own observation). Lillebø et al. (2003) found a negative impact of salinity on biomass of *B. maritimus*. The present study showed that nutrient availability did not drive trait expressions in the study area (Figure 7, Chapter 6). Nutrient availability gradients were not as strong as the other abiotic drivers (Figure 17, Chapter 7). Additionally, the measured soil nutrient contents indicated, that the plant communities in these areas are probably not nutrient limited (Schachtschnabel et al., 1987). The main drivers for the distribution of traits were incoming wave height and inundation duration (Chapter 6 and Chapter 7).

In relation to adaptation to long hydroperiods, the RLQ-analysis revealed, that the leaf chlorophyll content was much higher in leaves of plants on plots with longer inundation periods, as it was strongly correlated to the elevational gradient (Chapter 6). This could be an important advantage, when the time for assimilation is short and the ability of photosynthesis under water is known for some species (Clevering et al., 1996).

The schematic in Figure 27 shows the most essential trait responses, to either high waves and long inundation periods or, on higher elevations as a response to competition, to short inundation duration and already dissipated waves. The hydrodynamic drivers were strong, salinity and soil nutrient content of less importance (Figure 27 and Chapter 6).

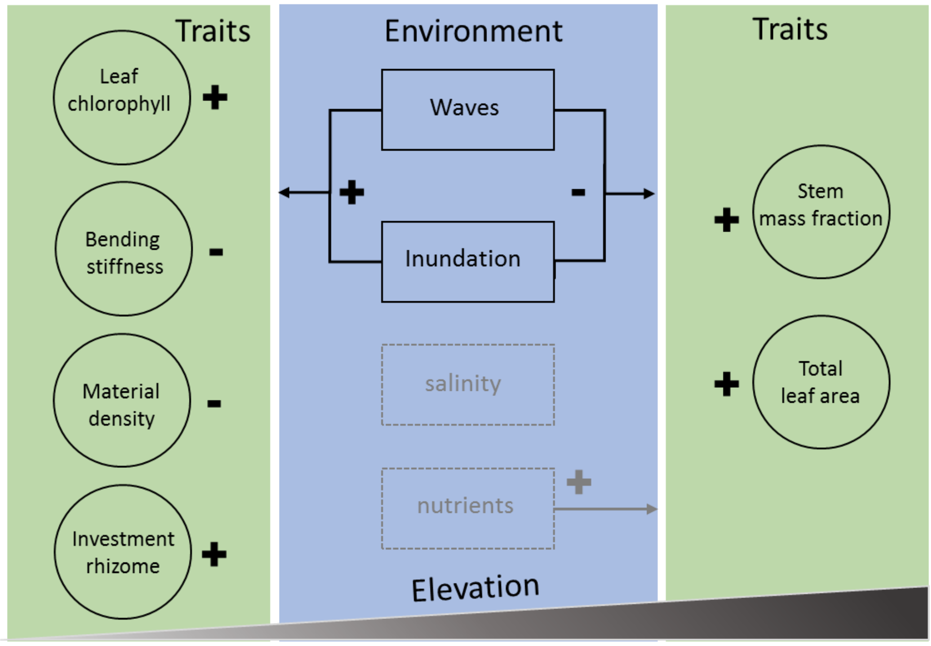


Figure 27: Schematic of the most important environmental drivers and plant trait responses. Salinity and soil nutrients played only a minor role and are depicted in light grey.

As a consequence of wave impact, the bendy *S. tabernaemontani* grew closest to the open tidal flat, followed by *B. maritimus* in still (but slightly less so) turbulent water (Figure 12, Chapter 6 & Figure 24, Chapter 8). Rather than bending with the wave action, the latter species was withstanding the currents or more accurately: it could thrive, where its stems could resist the drag-force (Heuner et al., 2015). Brewer and Parker (1990) found mechanical properties of stems were an essential aspect for plant zonation of a lake shore (see also Coops et al., 1994). Confirming this for the Elbe estuary, the specific density of the stem material was correlated to the incoming wave height in this study, the stems either avoiding or withstanding the wave energy (Figure 28). Stem bending properties were shown to be strongly correlated with stem density (Figure 18, Chapter 7). Strong impact of wave height was also executed on the leaf traits aggregate, which contained total leaf area and leaf dry matter content (LDMC). Here, the influence of waves and higher velocities and dragging impact on the vegetation became obvious (Figure 17, Chapter 7): plants with a larger exposed area would feel more drag-force (Bouma et al., 2005; Puijalon et al., 2011). Heuner et al. (2015) found *B. maritimus* to experience twice the amount of drag-force than *S. tabernaemontani*.

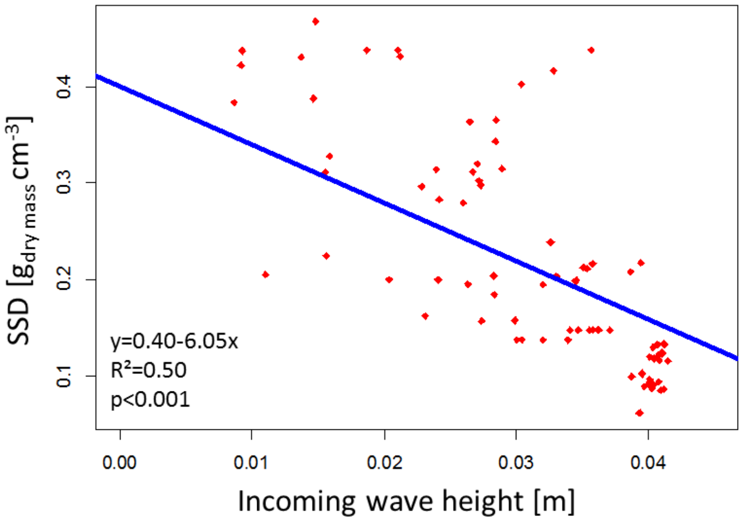


Figure 28: Regression of community weighted mean for SSD (stem specific density) and its relationship to incoming wave height across all elevations.

There are also known responses of plants to water depth regarding higher investment into belowground biomass (Coops, van den Brink, et al., 1996). The results of this study showed, that the mass fraction (MF) of rhizome was larger, were the inundation period was long (Figure 12). Larger rhizome MF could have the advantage of reducing the impact of loss of above-ground biomass and also highlights that clonal integration is an essential factor for the species at the extreme end of the gradient (Carus et al., 2017b). The dominant three species *S. tabernaemontani, B. maritimus* and *P. australis* all had an extensive rhizome system. There were also high concentration of P in the rhizomes on low elevations as a considerable energy storage (Figure 12, Chapter 6). At the same time, the density of organs below- and aboveground was less where inundation duration was long (Figure 34 & Figure 29). There could be two mechanism responsible for this: on one hand, less dense roots and rhizomes might enable a better oxygen exchange (Armstrong et al., 2006) which would be essential in times of long inundation periods. On the other hand, it could also be a factor of similar structural biomass make-up of below- and aboveground biomass as there was also a relationship between stem flexural stiffness and stem specific density (Figure 29 & Figure 30).

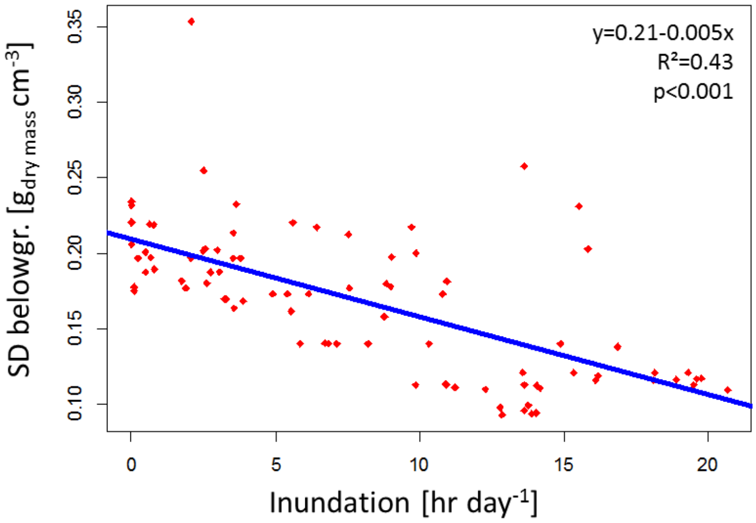


Figure 29: Regression for the community weighted mean of SD (specific density) of belowground biomass and inundation duration across all elevations.

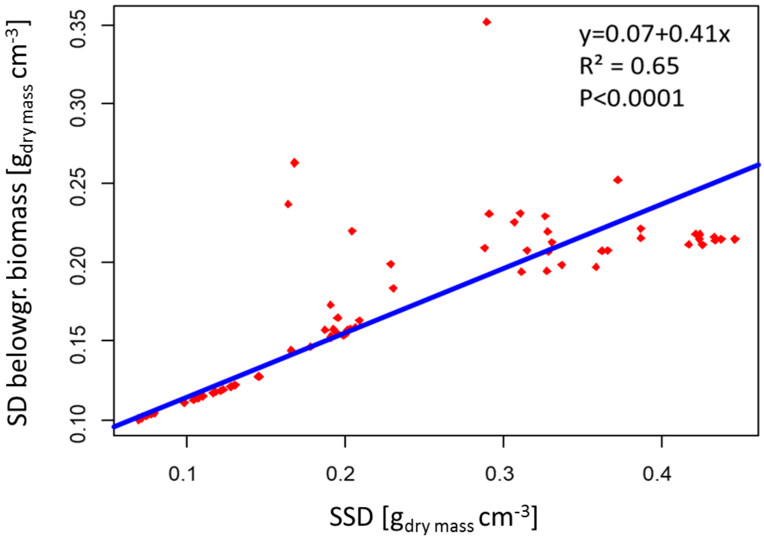


Figure 30: SMA (standard major axis regression) for the community weighted mean for SSD (stem specific density) and density of belowground biomass (roots & rhizomes) across all elevations.

The effect of wave height is of course connected to the inundation duration: where there is a long hydroperiod, waves have a bigger impact on the vegetation (Figure 31). At the mean high tide water level (MHW) then, waves were attenuated and the mechanically sensitive *P. australis* was able to compete. On those higher elevations, the stem MF was larger, possibly as a consequence of for competition for light on this less stressful side of the environmental gradients of inundation and wave impact (Figure 12, Chapter 6). The theory of the 'functional equilibrium' (Brewer & Parker, 1990; Poorter et al., 2012) states that plants invest more intensively into the organ that is most essential to capturing a scarce resource, which on the higher bank in this study is the resource ˈlightˈ. Some species invest into a very stiff, dense stem and grow just in front of the *Phragmites*-zone or in patches in the *Bolboschoenus*-zone, which are for example *Typha angustifolia* or *Lythrum salicaria*. Because of growing in relatively high ground though, at the higher end of the *Bolboschoenus*-zone, the wave height is already largely reduced (Schoutens et al., 2019).

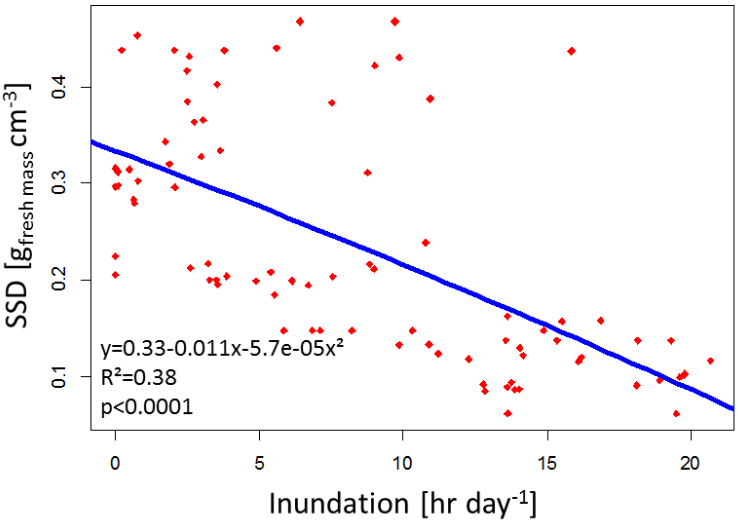


Figure 31: Regression of community weighted mean for SSD (stem specific density) and inundation duration across all elevations.

Many plant traits were connected to each other, which was clearly shown in the PCAs for the trait aggregates (Appendix 8. 3-Appendix 8. 7) for the species growing below and above MHW. Díaz et al. (2004) pointed out that trade-offs between plant design exist that either allow fast uptake of resources or their conservation (Reich, 2014) and that correlated traits exist, with positive and negative associations between characteristics of plants. To show the relationship between the most important findings in trait-trait interactions, the schematic network in Figure 32 was created. This shows the cascade effect of one trait responding to an environmental gradient and the suit of traits that are connected to it.

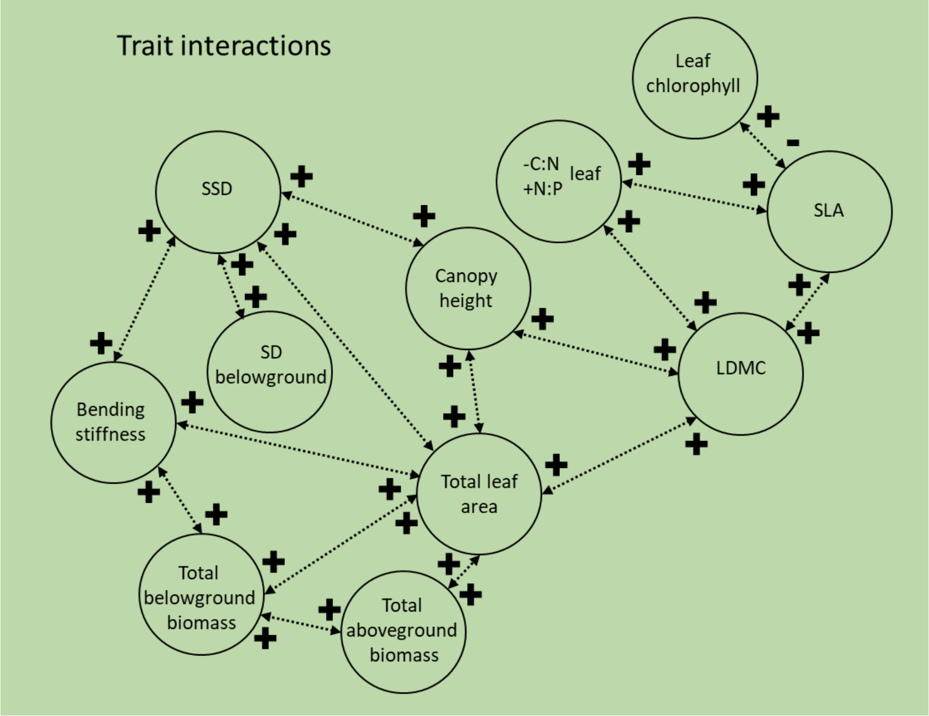


Figure 32: Schematic of the most important trait-trait relationships found. + and – indicate positive or negative relationships (e. g. lower SLA, more leaf chlorophyll). Displayed traits include SSD (stem specific density), SD belowground (specific density of roots and rhizomes), stem bending stiffness, total below- and aboveground biomass, total leaf area, canopy height, LDMC (leaf dry matter content), C:N and N:P ratio in leaf biomass, SLA (specific leaf area), leaf chlorophyll content.

In Kleyer et al. (2019) a trait correlation network was analyzed and trait modules found: in the present study, there were also modules found (for instance for leaf and stem traits) and correlations between traits of different organs. Similar to their study, there was a 'size' cluster, which incorporated correlated mass related traits. The biomass investment into each organ was scaled proportionally (Appendix 8. 4). Correlations between organ investments is known to exist across a vast range of ecosystems (Niklas, 2004; Freschet et al., 2013). In this study, the total leaf area was larger with higher stem bending stiffness as well as with more belowground mass (Figure 33). This highlights the trade-off between the investment into a large leaf area accompanied with the need for a stiffer stem (higher energy investment, Heuner et al., 2015). Stem traits relating to density and dry matter content were strongly correlated to bending properties (Figure 18), which was also suggested by (Kleyer et al., 2019), as they found stem specific length to be a hub trait, strongly connected to many other traits. This highlights how a change in one trait provokes changes in possibly a whole range of traits (Kleyer et al., 2019). The stem density in this study for instance was also strongly correlated with the species canopy height: growing tall to capture the available sunlight is a key trait for plants growing in more benign conditions above the mean high tide level. The 'size' aggregate in the RLQ-analysis therefore showed correlations with the flexural stiffness: large plants need a stiffer stem to support their biomass. Larger aboveground biomass also requires an essential belowground anchorage (Figure 33), to withstand drag forces for instance (Bouma et al., 2005).

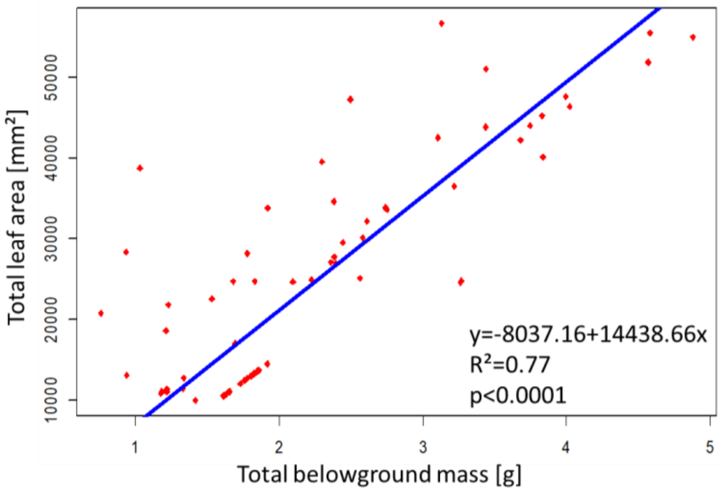


Figure 33: SMA for total leaf area and the relationship with total belowground mass across all elevations. Dots represent community weighted means per plot.

There were correlations between leaf chlorophyll content and specific leaf area too (SLA, Figure 13), which is connected to the structural design of the leaves. The construction of leaves and nutrient partitioning was also responding to wave impact with drag forces being higher for larger leaf areas. This had consequences for the nutrient composition of the leaves, with lower C:N ratios and higher N:P ratios connected to higher dry matter content (Figure 34, see also Kleyer et al. (2019)). The different strategies of species became apparent here: they either invested into robust and thick leaves, that would last throughout the growing season, with a low SLA and high C:N ratio. This was described as the conservation of resources by Díaz et al. (2004). Or the species constructed large and thin leaves (found on the higher elevations, away from hydrodynamic turbulence) with a high SLA and a high N:P ratio. This meant relatively little material investment and a short leaf-life span, and these species were the acquisitive type (Díaz et al., 2004). Those species were the smaller species which were growing beneath the dominant species of either *B. maritimus* or *P. australis* and would be able to fill gaps that occurred in the canopy rapidly. Examples for species with this strategy would be *Mentha aquatica* or *Myosotis scorpioides.*

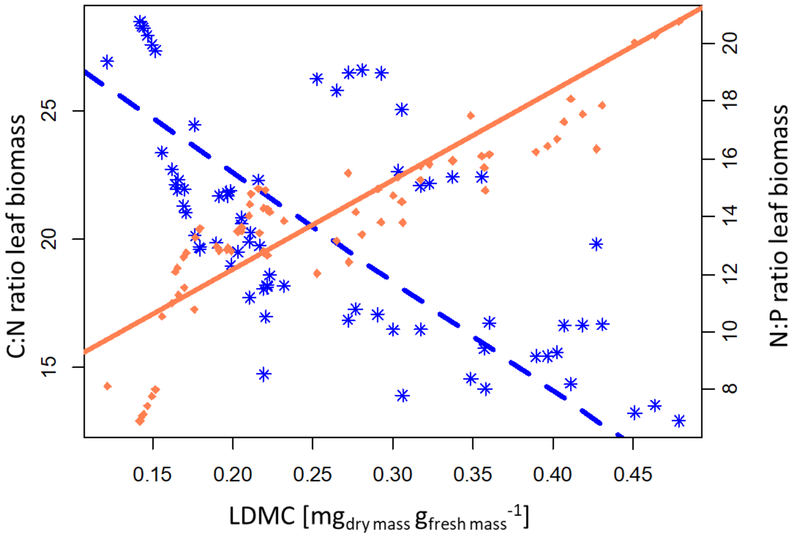


Figure 34: SMA of weighted means for C:N (carbon:nitrogen) across all elevations (stars and dotted line) and N:P (nitrogen:phosphorus) ratios of leaf biomass (dots and solid line) in relation to LDMC (leaf dry matter content). C:N vs LDMC is displayed with stars and a dotted regression line ($y=31.16-42.70x$, $R^2=0.43$, $p<0.0001$). N:P vs LDMC is displayed with dots and a solid regression line ($y= 5.98+30.93x$, $R^2=0.75$, $p<0.0001$).

9.4 Environmental drivers and plant species traits affecting ecosystem properties

The only direct links between environmental drivers and ecosystem properties could be found for inundation and salinity with a negative effect on the decomposition of standard hay, when the four different zones based on the dominant species were analyzed. The decomposition rates of standard hay reflected the influence of the environment, taking the variation of the native biomass out of the equation. When only the zone above mean high water (MHW) was analyzed, which included the *Phragmites*- and *Phragmites*/mixed community-zone (Chapter 7), a negative effect of inundation on decomposition of native biomass could also be shown. For this zone, there was also a negative effect of inundation on soil organic carbon detectable. All other environmental effects on ecosystem properties were mediated by species traits, they were indirect.

This highlighted that plant traits affecting the environment can have a substantial impact through the ecosystem properties (Zak et al., 2003; Lavorel & Grigulis, 2012; Freschet et al., 2013). For the ecosystem properties in this study, the measure for vegetation density (PAR) showed, that the *Schoenoplectus*-zone had significantly more plant available radiation reaching the ground. The corresponding property of aboveground community biomass (AGB) showed significantly more biomass for the zone above MHW. From the structural equation model (SEM), it could be shown that the plant traits combined in the aboveground module (total leaf area, aboveground MF, Young´s modulus and SLA) had a positive impact on AGB (Chapter 7). Encompassed in the AGB in the studied ecosystem is the aboveground net primary productivity (ANPP), as the species regrow every growing season. At the same time, the RLQ-Analysis (Chapter 6) showed, that species response to inundation included the construction of less dense biomass (Figure 35). Combined, these relationships had an impact on several ecosystem properties: there was less AGB, because there was less biomass created per individual plant with low tissue density and lower tiller numbers per m² (Figure 36, see also Coops et al. (1994)). This had also consequences for the decomposition rate, which was faster for less dense biomass than for denser material. In this context Windham (2001) found high C:N ratios to reduce decomposition and high N in turn was found to be connected to the higher breakability of stems (Sloey & Hester, 2018). Representing the aboveground potential of carbon produced in-situ that could be stored on site, was the AGB with its carbon content. This was probably also responsible for the low soil organic carbon content in the *Schoenoplectus*-zone, next to the open tidal flat (Chapter 7). The *Schoenoplectus*-zone had the lowest C content with only 272 g m^{-2} of initial carbon in the aboveground biomass. The highest initial C content in aboveground biomass was 660 g C per m² in the *Phragmites*-zone at peak vegetation. Interestingly, concerning the decomposition of the native material, it was found to decompose most rapidly on the low elevations where the standard hay in contrast decomposed most slowly. This means, that the environmental conditions on low elevations were hampering decomposition in comparison to conditions on higher elevations, but the material structure and composition of *S. tabernaemontani* was allowing for faster decomposition despite this effect. Decomposition rates for native biomass were as a result highest in the *Schoenoplectus*-zone.

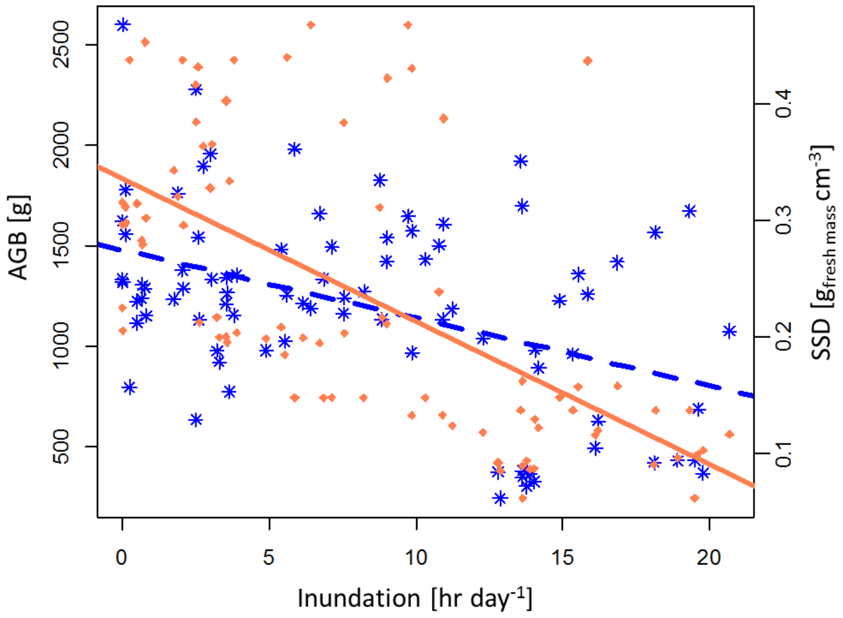


Figure 35: Inundation duration in relation to AGB (aboveground community biomass) and SSD (stem specific density) across all elevations. Inundation vs AGB is displayed with stars and a dotted regression line ($y=1475.96-33.63x$, $R^2=0.18$, $p<0.0001$) and inundation vs SSD is displayed with dots and solid regression line ($y=0.33-0.011x-5.7e-05x^2$, $R^2=0.38$, $p<0.0001$).

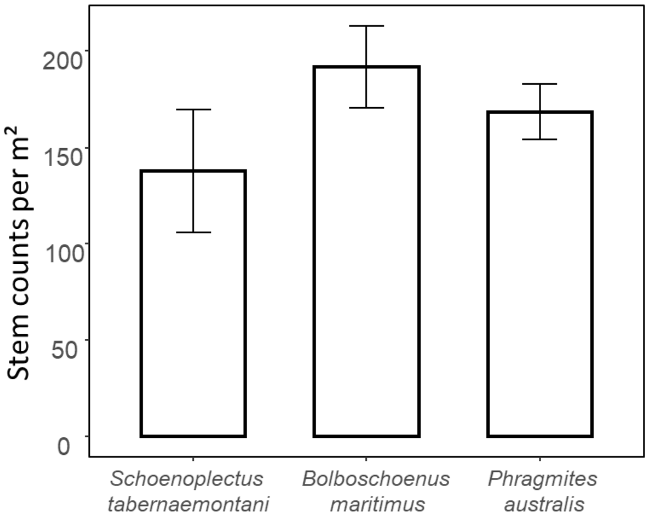


Figure 36: Stem counts per m² for the dominant three species with error bars.

Regarding the ecosystem property of soil organic carbon (SOC), the question is, how the potential carbon that is present in the plant material on site translates into carbon stocks present. There are two different measurements of SOC used in this thesis: the carbon stock describes the carbon content in kg m^{-2} for a soil profile of 0.8 m depth. The SOC in % is a measure of the average percentage of carbon in the soil samples of all horizons per plot. The SEM showed a positive effect from the aboveground module on SOC %, thus the percentage was higher, where plants were stiffer with larger leaf areas. The theoretically still present C content of native biomass after 365 days was 211 g m^{-2} for the *Phragmites/*mixed community-zone and 311 g m^{-2} for the *Bolboschoenus*-zone, which was the highest potential of the four zones. This could potentially be stored in the soil over long time periods (Chapter 7). The actual carbon stock found in the sites was relatively low though, the reasons are probably mainly the low material density of biomass and dislocation of aboveground biomass (Chapter 9.5.2.). In the carbon cycle in the Elbe estuary, the redistribution of litter with the tide was found to have a substantial influence on carbon dynamics (Hansen et al., 2017).

9.5 Ecosystem services determined by ecosystem properties, mediated by plant traits

9.5.1 Wave attenuation in dependence of aboveground biomass and plant mechanical traits

The effect of vegetation attenuating waves has been the subject of many studies (Bouma et al., 2010; Gedan et al., 2010; Barbier et al., 2011; Carus et al., 2016). Hereby, the roughness that the surface of the vegetation creates was found to be a key factor for wave attenuation (Möller et al., 1999). Those effects can be large, as Carus et al. (2016) found, flow velocities were reduced more than half when entering the vegetated zone; Schoutens et al. (2019) found similar results. During winter month, hence without vegetation, this rate fell to 10 % in their study. Wave attenuation is an essential ecosystem service by the marsh vegetation and fulfilled under strong dynamics: the average maximum recorded wave height for the analyzed study sites was 0.30 m (Schoutens et al., 2019). Essentially, which are the factors that determine the dissipation of this wave energy? The marsh vegetation, through the friction that it creates, is reducing the flow velocities of the water and can through this effect hinder erosion and contribute to the stabilization of the tidal bank (Hopkinson et al., 2019), with the belowground biomass contributing to soil stability (Zonneveld, 1960). The relationship of stem resistance to bending (Young´s modulus) and AGB and their effect on the reduction of wave height could clearly be shown in the present analysis (Figure 37). This is in line with findings Heuner et al. (2015) (brackish tidal marsh) and Koch et al. (2009) (for mangroves and seagrass ecosystem) as well as Schulze et al. (2019) (saltmarsh).

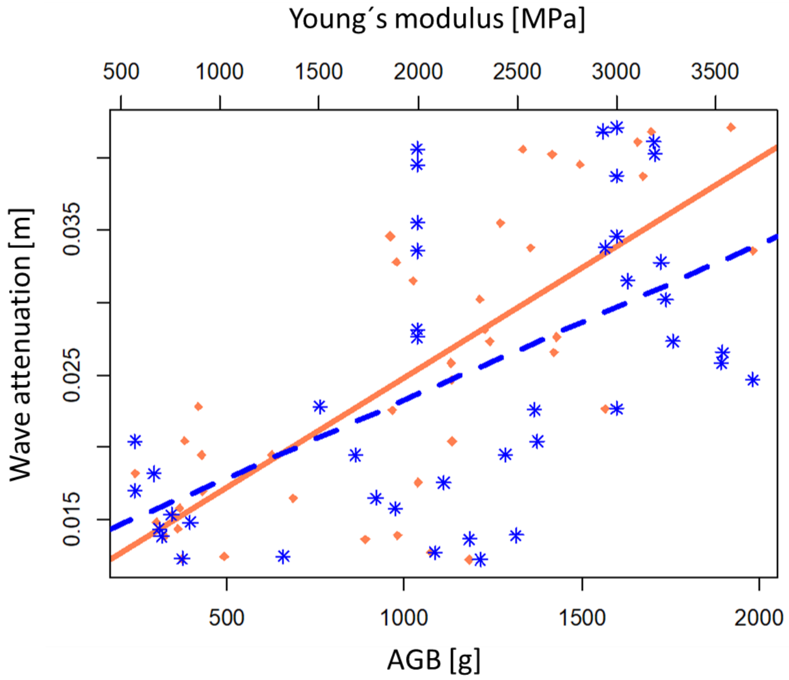


Figure 37: Regression of wave attenuation (of mean wave height at water levels <0.5 m) in relation to AGB (above-ground community biomass) and community weighted means for Young´s modulus (stem resistance to bending) for the zones below mean high water (Schoenoplectus and Bolboschoenus-zone). Wave attenuation vs Young´s modulus is displayed as stars, the regression line is dotted (y=0.012+6.01e-06, R²=0.31, p<0.0001). Wave attenuation vs AGB is displayed as dots, the regression line is solid (y=0.0096+1.5e-05x, R²=0.56, p<0.0001).

The strong relationship of AGB and the potential to attenuate waves had consequences for the ecosystem functioning and the protection of the tidal bank: for the plants on the lowest elevations, just after the open tidal flat, it was essential to be bendy and slender – this produced comparatively small individuals, constructed with lightweight material. As a result, the AGB was smaller, there was less friction created and the reduction in wave height was less (Bouma et al., 2005; Heuner et al., 2015). Where plant stems were stiffer and denser (Figure 37), on higher elevations with substantially more AGB, the reduction in wave height was bigger too. The waves at this point were of course already attenuated to some degree (through attenuation by vegetation and bottom friction on the tidal slope (Möller et al., 1999; Le Hir et al., 2000)), which made it possible for the species with stiffer stems to grow there in the first place. The intra-specific plasticity was of great importance in this regard: *B. maritimus* for instance showed strong morphological differences, when it is growing on the fringe of its populations – it stays much shorter, with a wider diameter (Carus et al., 2016). Adaptations to flow stress are known from several species, including for instance *M. aquatica* (Puijalon et al., 2008).

Knowing and using the potential of these species and the service that they provide will be of increasing urgency: the ecosystem service of wave attenuation will gain more value, because of rising sea levels, causing the need to invest more into flood management with at the same time rising energy costs for artificial constructions (Temmerman & Kirwan, 2015).

9.5.2 Carbon sequestration and the relationship with traits, ecosystem properties and environmental drivers

Simultaneously to reducing the water velocities through friction, the vegetation is also reducing the speed of the dissolved organic matter and sediment within the water body (Mudd et al., 2010). The carbon contained in the native biomass is only one source of organic carbon that can get sequestered in the soil. During the formation process of soils, an increasing content of clay is accreting simultaneously to increasing content of organic matter (Zonneveld, 1960; Beeftink et al., 1977). As regards to carbon burial, wetlands were estimated to deliver a third of the ocean´s carbon burial (Duarte et al., 2005). Tidal marshes are known to accumulate chlorophyll and organic particles (Craft, 2007; Neubauer, 2008). In this study, an important factor for the delivery of the ecosystem service of carbon sequestration was also the amount of biomass present (Figure 38) and thus the initial potential of carbon in the plant biomass. Elschot et al. (2015) found, that total organic carbon increased with marsh age and the carbon sequestration rate decreased with marsh age, leaving young marshes with the best rates. This change might also be a result of the changed species composition as the marsh ages (Davy et al., 2011), and highlighted, that the type of vegetation through its allocation pattern can affect the content of carbon in the soil. In this line, Elschot et al. (2015) hypothesized that the increased organic carbon input resulted because of increased belowground biomass production. Carbon that originated from roots was found to get stored to a higher percentage than aboveground material also by Rasse et al. (2005). Schmidt et al. (2011) suggested, that the physical separation of decomposer and biomass is a factor for long-lasting deep soil organic matter, they name nutrient limitation for microbial activity, energy scarcity e. g. Aller (1994) points to the lack of oxygen that reduce the rate of mineralization in soils. The high potential of marsh soils to sequester carbon is due to the hampered decomposition in water saturated soils and the substantial biomass production (Choi and Wang 2004). This influence could also be shown for the studied ecosystem (Figure 38). The carbon stocks determined for the study sites were highest in the *Phragmites*/mixed community-zone with 13 kg m^{-2} and lowest in the *Bolboschoenus*-zone with 8 kg m^{-2}, despite the high initial potential of this zone. For mangroves, the carbon stock can be around 31 kg m^{-2} (1.0 m profile) (Weiss et al., 2016) for temperate forests this was estimated at 17.4 ± 10.8 kg m^{-2} (Jobbágy & Jackson, 2000). For peatland this figure is much higher, but varies greatly with the depth of the peat: Akumu and McLaughlin (2014) found 100 ± 17 kg C m^{-2} for an average soil profile depth of 2.26 ± 0.36 m, which is similar to findings from Holden and Connolly (2011). Thus, the actual carbon stock found in this study was comparatively quite low. Taking into account the large areas though, that the brackish marshes along the Elbe estuary cover, they do have a considerable carbon storage function on a regional and national scale (Hansen et al., 2017).

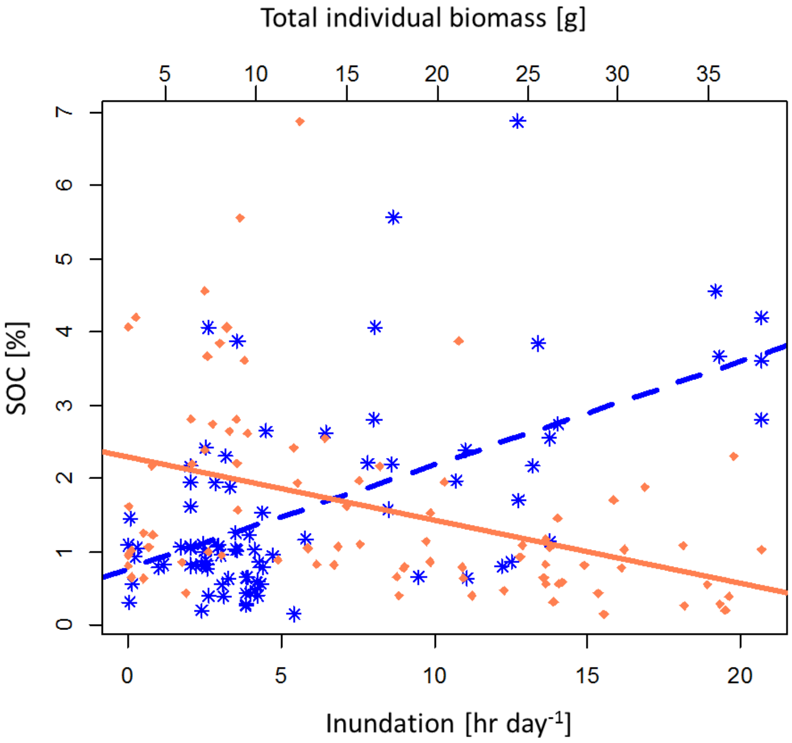


Figure 38: Soil organic carbon in relation to total individual biomass (community weighted mean) and inundation duration. Total individual biomass vs SOC is displayed as stars, the regression line is dotted ($y= 0.51+0.08x$, $R^2=0.32$, $p<0.0001$). Inundation vs SOC is displayed as dots, the regression line is solid ($y=2.29-0.09x$, $R^2=0.16$, $p<0.0001$).

The carbon production and distribution is discussed in Chapter 7 and Chapter 8: in the study sites, the strong dynamics created by waves and currents lead to this carbon potential often being flushed to other places. It is deposited in thick layers during particularly high floods and an unknown amount could be washed into the open sea too. Najjar et al. (2018) point out that estuaries provide a big input of carbon to adjacent waters too and play an important role in the carbon budget.

9.6 Outlook and future challenges

Coastal systems and estuaries are among the most threatened ecosystems worldwide: 50 % of saltmarshes were lost or degraded, mainly due to drainage, intensified agriculture, coastal development, climate change and sea level rise (SLR) (Barbier et al., 2011). For the mangroves, the lucrative business of growing prawns in aquaculture along the coast is a considerable threat and since the 1970s, approximately 35 % of mangrove forests have been lost globally (Valiela et al., 2001).

For the major estuaries in Europe, pressure is coming from the construction of infrastructure and cities and the associated need for flood protection and deepening of the riverbed for ship passages (Meire et al., 2005). This, as well as the input of nutrients and pollutants through land use and industries, represents the pressure and threat that the anthropogenic demands place on estuaries. For the Elbe estuary, the deepening and artificial embankments have led to a loss of zones of shallow water (Kappenberg & Fanger, 2007). Connected to this is the issue of landscape fragmentation, which, beside consequences for the hydrology and nutrient cycles, can reduce the available suitable species pool (Loreau et al., 2001), which might be needed for adjustments to changed environmental circumstances.

The findings of the present thesis highlight, that there is only a small set of species characterizing the ecosystem properties and delivering the ecosystem services. That makes the system potentially sensitive to changes, because if one species fails, it could have a knock-on effect on the others too, due to, for instance, facilitation effects (e. g. *S. tabernaemontani* for *B. maritimus,* Heuner et al., 2015*).* Those two species were fulfilling the ecosystem service of wave attenuation – *Phragmites australis* can only establish around the mean high tide level in the study sites, as it is sensitive to mechanical disturbance (Ellenberg & Leuschner, 2010).

Threatening to the performance of species and affecting their delivered ecosystem service could be the suite of climate change, as it causes higher air and water temperatures and an accelerated SLR (IPCC, 2007). Higher temperatures can have an effect on the species life cycle and competitive ability (Short et al., 2016). It could also create an opportunity for species from other climatic zones to invade: species with different trait expressions and life cycles and thus different effects on ecosystem properties and services (Chapin et al., 2000). As the results of the mediating role of the vegetation between environmental drivers and ecosystem properties in this thesis showed, changes in species traits could change for instance the amount of aboveground biomass, with repercussions on wave attenuation and carbon sequestration.

There is also the possibility of more extreme weather events as a consequence from climate change like drought or excessive rain and a higher frequency of storm surges for instance. Storm events could lead to increased stem breakage (Rupprecht et al., 2017), which could affect species fitness.

Climate change of course is also the engine for the major threat that our coasts and estuaries are facing, which is sea level rise (SLR). This is already changing coastlines dramatically in other parts of the world (Kirwan & Megonigal, 2013). For the Elbe estuary, the sea level rise could cause higher salinity levels further upstream, with consequences for plant zonation (Carus et al., 2017a) and therefore changes in the distribution of functional traits important for carbon sequestration. Hansen et al. (2017) for instance found lower stocks of soil organic carbon with higher soil salinities and hypothesized, that the carbon stock in the Elbe estuary might be reduced because of the shift in salinity levels. The ability of our tidal marshes to rise with the rising sea level (which they have done before, Hopkinson et al., 2019) is partly dependent on the supply of sediment to build up the new bank elevation. The sediment supply is declining in some estuarine systems (MEA, 2005), which can pose a problem for raising the marsh surface. With SLR, the other way for the tidal marshes to persist is to "migrate" inland (Kirwan, Walters, et al., 2016); this is only an option were enough space exists between the water and the dike or seawall (Bouma et al., 2014). Thus, tidal marshes can get wedged between the water and the flood defense structures ("Coastal Squeeze", Reise, 2005).

The findings of this thesis are relevant in this context, because the species have restricted areas, of where they can grow: a change in salinity levels and inundation period would cause a shift in species for instance (Zhu et al., 2019). It could clearly be shown that the hydrological gradients of inundation and wave impact were driving species zonation, structural composition of stems and leaves, biomass produced and decomposition processes. The species niches and with this their trait dependent delivered ecosystem services are potentially at risk if the marsh surface is not raising fast enough. Otherwise it could result in greater water depth and therefore higher waves impacting. Schoutens et al. (2020) showed, that *S. tabernaemontani* and *B. maritimus* could exist at similar elevations, but incoming wave height and flow velocities were higher where *S. tabernaemontani* was established.

Beside all efforts to reduce the drivers of climate change, direct management intervention for the brackish tidal marshes in the Elbe estuary might therefore have to be undertaken. In some places there would be an opportunity to allow the tidal bank vegetation to extend into the adjacent agricultural lands. It might also be a possibility to retract and modify the dike line in suitable places and allow salt and brackish marshes to reclaim ground (ecosystem-based engeneering, Temmerman & Kirwan, 2015). This has been put into practice in some projects and can be a suitable option for highly populated areas because flood protection is not impacted.

9.7 Suggestions for future research

Regarding future alleys for research, looking into the species plastic adaptations would be of interest, since in monotypic zonation, they largely contribute to differences in ecosystem properties (De Battisti et al., 2020). In the present thesis, the three different study sites were treated as a random factor in the analysis. There were noticeable differences within the species (Carus et al., 2017a) and between the sites though and an analysis of intra-specific variations and responses to the salinity, inundation and wave gradient could bring valuable information (Puijalon et al., 2008) and extend the knowledge on the effect of those trait variations on ecosystem properties.

To be able to predict the effects of rising air and water temperatures, experiments with the dominant three species (*S. tabernaemontani, B. maritimus* and *P. australis*) responses under field conditions (strong environmental drivers of salinity, wave height and inundation) would be interesting. Similar analyses have been done for saltmarshes (Gedan & Bertness, 2009). Mimicking climate change could generate helpful information regarding future management objectives because species changed distribution and characteristics would be more predictable.

In relation to the distribution and tolerance to wave impact, experiments with shelters would be of interest (see for example van Wesenbeeck et al., 2007). Species could be planted behind shelters and their performance measured and some areas could be monitored for self-establishment of species behind shelters as well.

The erosion and sedimentation dynamics in relation to plant traits would be an interesting study: which species in the Elbe estuary contributes most to the sedimentation process? What traits are the most essential in this context? De Battisti et al. (2019) for instance showed root traits to be important in erosion dynamics in a salt marsh ecosystem.

Since the decomposition process of plant biomass is known to be non-linear (Robertson & Paul, 2000), it would provide precious information to analyze the decomposition rates in the Elbe estuary over long timescales (Freschet et al., 2012). It could answer questions concerning which trait expressions are effective for long-term sequestration of carbon.

Studying the carbon cycle in temperate tidal marshes in detail would also be helpful to be able to adapt management practice. In addition to knowing the carbon stock on a site, it would be of use to know the rate of carbon accumulation per year. Peatlands for instance have a great carbon stock, but the actual sequestration rate per year is relatively small (Roulet, 2000).

In relation to the carbon cycle, extensive sampling of belowground biomass would add information regarding the role of belowground biomass. The sampling of belowground biomass could be done with a core cutter (Schoutens et al., 2019), this would also allow estimations of biomass from roots and rhizomes from previous years that would not be reflected in the belowground sampling of trait individuals.

References

Adam, P. (1990). Coping with the environment. In Saltmarsh Ecology. (Cambridge Studies in Ecology, pp. 207-308). Cambridge: Cambridge University Press.

Ágoston-Szabó, E. & Dinka, M. (2008). Decomposition of Typha angustifolia and Phragmites australis in the littoral zone of a shallow lake. *Biologia, 63*(6), 1104—1110.

Akumu, C. E. & McLaughlin, J. W. (2014). Modeling peatland carbon stock in a delineated portion of the Nayshkootayaow river watershed in Far North, Ontario using an integrated GIS and remote sensing approach. *Catena, 121*, 297–306.

Allen, S. E. (1989). Chemical analysis of ecologicalmaterials. Blackwell Scientific, Oxford,UK.

Aller, R. C. (1994). Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chemical Geology, 114*, 331-345.

Armstrong, J., Jones, R. E. & Armstrong, W. (2006). Rhizome phyllosphere oxygenation in Phragmites and other species in relation to redox potential, convective gas flow, submergence and aeration pathways. *New Phytologist, 172* 719–731.

Attrill, M. J. & Rundle, S. D. (2002). Ecotone or Ecocline: Ecological Boundaries in Estuaries. *Estuarine, Coastal and Shelf Science, 55*(6), 929-936. doi:https://doi.org/10.1006/ecss.2002.1036

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

Azza, N., van de Koppel, J., Denny, P. & Kansiime, F. (2007). Shoreline vegetation distribution in relation to wave exposure and bay characteristics in a tropical great lake, Lake Victoria. *Journal of Tropical Ecology, 23*, 353-360.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C. & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs, 81*(2), 169-193. doi:10.1890/10-1510.1

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1–48.

Bazzaz, F. A., Chiariello, N. R., Coley, P. D. & Pitelka, L. F. (1987). Allocating Resources to Reproduction and Defense. *BioScience, Vol., 37*(1), 58-67.

Becker, R. A., Chambers, J. M. & Wilks, A. R. (1988). The New S Language. Wadsworth & Brooks/Cole.

Beeftink, W. G., Daane, M. C., Van Liere, J. M. & Nieuwenhuize, J. (1977). Analysis of estuarine soil gradients in salt marshes of the southwestern Netherlands with special reference to the Scheldt estuary. *Hydrobiologia, 52*(1), 93-106.

Bertness, M. D. & Ellison, A. M. (1987). Determinants of Pattern in a New England Salt Marsh Plant Community. *Ecological Monographs, 57*(2), 129-147. doi:10.2307/1942621

Bockelmann, A.-C., Bakker, J. P., Neuhaus, R. & Lage, J. (2002). *Aquatic Botany, 73* 211–221.

Boehlich, M. J. (2003). Tidedynamik der Elbe. *Mitteilungsblatt der Bundesanstalt für Wasserbau, 86*, Karlsruhe: Bundesanstalt für Wasserbau. p. 55-60.

Boothroyd, J. C. (1978). *Mesotidal Inlets and Estuaries. In: Davis R.A. (eds) Coastal Sedimentary Environments. Springer, New York, NY.*

Bouma, T. J., De Vries, M. B. & Herman, P. M. (2010). Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. *Ecology, 91*(9), 2696-2704.

Bouma, T. J., De Vries, M. B., Low, E., Peralta, G., Ta, I. C. & Herman, P. M. (2005). Trade-Offs Related to Ecosystem Engineering: a Case Study on Stiffness of Emerging Macrophytes. *Ecology, 86*(8), 2187-2199.

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

Brewer, C. A. & Parker, M. (1990). Adaptations of macrophytes to life in moving water: upslope limits and mechanical properties of stems. *Hydrobiologia, 194*, 133-142.

Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, G., Liancourt, P., TielbÖRger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C. L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology, 96*, 18-34. doi:10.1111/j.1365-2745.2007.01295.x

Broome, S. W., Craft, C. B. & Burchell, M. R. (2019). Chapter 22 - Tidal Marsh Creation. *Coastal Wetlands*, 789-816.

Burdick, D. M. & Konisky, R. A. (2003). Determinants of expansion for Phragmites australis, common reed, in natural and impacted coastal marshes. *Estuaries and Coasts, 26*(2B), 407-416.

Butzeck, C., Schröder, U., Oldeland, J., Nolte, S. & Jensen, K. (2016). Vegetation succession of low estuarine marshes is affected by distance to navigation channel and changes in water level. *Journal of Coastal Conservation, 20*(3), 221-236. doi:10.1007/s11852-016-0432-1

Caliński, T. & Harabasz, J. (1974). A Dendrite Method for Cluster Analysis. *Communications in Statistics, 3*, 1-27.

Cao, H., Zhu, Z., James, R., Herman, P. M. J., Zhang, L., Yuan, L. & Bouma, T. J. (2020). Wave effects on seedling establishment of three pioneer marsh species: survival, morphology and biomechanics. *Annals of Botany*(125), 345–352.

Carus, J., Heuner, M., Paul, M. & Schröder, B. (2017a). Plant distribution and stand characteristics in brackish marshes: Unravelling the roles of abiotic factors and interspecific competition. *Estuarine, Coastal and Shelf Science, 196*, 237-247. doi:10.1016/j.ecss.2017.06.038

Carus, J., Heuner, M., Paul, M. & Schröder, B. (2017b). Which factors and processes drive the spatio-temporal dynamics of brackish marshes?—Insights from development and parameterisation of a mechanistic vegetation model. *Ecological Modelling, 363*, 122-136. doi:10.1016/j.ecolmodel.2017.08.023

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. *Ecology and Evolution, 6*(6), 1579-1589. doi:10.1002/ece3.1904

Caudle, K. L. & Maricle, B. R. (2012). Effects of flooding on photosynthesis, chlorophyll fluorescence, and oxygen stress in plants of varying flooding tolerance. *Transactions of the Kansas Academy of Science, 115*(1/2), 5-18.

Cebrián-Piqueras, M. A. (2017). *Trade-offs and synergies between forage production, species conservation and carbon stocks in temperate coastal wet grasslands. An ecosystem services and process-based approach.* Dissertation. University of Oldenburg, Oldenburg.

Cebrián-Piqueras, M. A., Trinogga, J., Grande, C., Minden, V., Maier, M. & Kleyer, M. (2017). Interactions between ecosystem properties and land use clarify spatial strategies to optimize trade-offs between agriculture and species conservation. *International Journal of Biodiversity Science, Ecosystem Services & Management, 13*(2), 53-66. doi:10.1080/21513732.2017.1289245

Cepeda-Carrión, G. A., Nitzl, C. & Roldán, J. L. (2018). *Mediation Analyses in Partial Least Squares Structural Equation Modeling. Guidelines and Empirical Examples. In H. Latan & R. Noonan (Eds.), Partial Least Squares Structural Equation Modeling: Basic Concepts, Methodological Issues and Applications*: Heidelberg: Springer.

Chapin, F. S., 3rd. (2003). Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Ann Bot, 91*(4), 455-463. doi:10.1093/aob/mcg041

Chapin, S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D., Lavorel, S., Sala;´, O. E., Hobbie, S. E., Mack, M. C. & Díaz, S. (2000). Consequences of changing biodiversity. *Nature, 405*, 234-242.

Chmura, G. L. (2013). What do we need to assess the sustainability of the tidal salt marsh carbon sink? *Ocean & Coastal Management, 83*, 25-31. doi:10.1016/j.ocecoaman.2011.09.006

Chmura, G. L., Anisfeld, S. C., Cahoon, D. R. & Lynch, J. C. (2003). Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles, 17*(4), n/a-n/a. doi:10.1029/2002gb001917

Choi, Y. & Wang, Y. (2004). Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Global Biogeochemical Cycles, 18*(4), n/a-n/a. doi:10.1029/2004gb002261

Christiansen, T., Wiberg, P. L. & Milligan, T. G. (2000). Flow and Sediment Transport on a Tidal Salt Marsh Surface. *Estuarine, Coastal and Shelf Science, 50*(3), 315-331. doi:10.1006/ecss.2000.0548

Clevering, O. A., Blom, C. W. P. M. & Van Vierssen, W. (1996). Growth and morphology of Scirpus lacustris and S. maritimus seedlings as affected by water level and light availability. *Functional Ecology*(10), 289-296.

Clevering, O. A., Van Vierssen, W. & Blom, C. W. P. M. (1995). Growth, photosynthesis and carbohydrate utiHzation in submerged Scirpus maritimus L. during spring growth. *New Phytologist*(130), 105-116.

Cloern, J. E., Jassby, A. D., Schraga, T. S., Nejad, E. & Martin, C. (2017). Ecosystem variability along the estuarine salinity gradient: Examples from long-term study of San Francisco Bay. *Limnology and Oceanography, 62*, 272–291.

Colmer, T. D. & Voesenek, L. A. C. J. (2009). Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology, 36*, 665-681.

Coops, H., Geilen, N. & van der Velde, G. (1994). Distribution and growth of the helophyte species Phragmites australis and Scirpus lacustris in water depth gradients in relation to wave exposure. *Aquatic Botany, 48*, 273-284.

Coops, H., Geilen, N., Verheij, H. J., Boeters, R. & van der Velde, G. (1996). Interactions between waves, bank erosion and emergent vegetation: an experimental study in a wave tank. *Elsevier, 53*, 187-198.

Coops, H., van den Brink, F. W. D. & van der Velde, G. (1996). Growth-and-morphological-responses-of-four-helophyte-species-in-an-experimental-water-depth-gradient. *Aquatic-Botany*(54), 11-24.

Coops, H. & Van der Velde, G. (1996a). Effects of waves on helophyte stands: mechanical characteristics of stems of Phragmites australis and Scirpus lacustris. *Aquatic Botany, 53*(3), 175-185. doi:https://doi.org/10.1016/0304-3770(96)01026-1

Coops, H. & Van Der Velde, G. (1996b). Impact of hydrodynamic changes in the zonation of helophytes. *Netherlands Journal of Aquatic Ecology*, 30-165.

Coops, H. & van der Velde, G. (1999). Helophyte Zontation in Two Regulated Estuarine Areas in the Netherlands: Vegetation Analysis and Relationships with Hydrological Factors. *Estuaries, 22*(3A), 657-668.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G. & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany, 51*, 335-380.

Cornelissen, J. H. C., Pérez-Harguindeguy, N., Diaz, S., Grime, J. P., Marzano, B., Cabido, M., Vendramini, F. & Cerabolini, B. (1999). Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist, 143*, 191 - 200.

Cornelissen, J. H. C., Quested, H. M., Gwynn-Jones, D., Van Logtestijn, R. S. P., De Beus, M. A. H., Kondratchuk, A., Callaghan, T. V. & Aerts, R. (2004). Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *FunctionalEcology*(18), 779–786.

Cornelissen, J. H. C. & Thompson, K. (1997). Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist, 135*, 109-114.

Craft, C. B. (2007). Freshwater input structures soil properties, vertical accretion, and nutrient accumulation of Georgia and U.S. tidal marshes. *Limnology and Oceanography, 52*(3), 1220–1230.

Crain, C. M. (2007). Shifting Nutrient Limitation and Eutrophication Effects in Marsh Vegetation Across Estuarine Salinity Gradients. *Estuaries and Coasts, 30*(1), 26-34.

Craine, J. M., Dybzinski, R. & Robinson, D. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology, 27*(4), 833-840. doi:10.1111/1365-2435.12081

Cui, E., Weng, E., Yan, E. & Xia, J. (2020). Robust leaf trait relationships across species under global environmental changes. *Nature Communitcations, 11*(2999).

Davidson-Arnott, R. (2009). Saltmarshes and mangroves. In Introduction to Coastal Processes and Geomorphology (pp. 325-368). Cambridge: Cambridge University Press.

Davy, A. J., Brown, M. J. H., Mossman, H. L. & Grant, A. (2011). Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. *Journal of Ecology, 99*, 1350-1357.

Day, F. P. & Megonigal, J. P. (1993). The relationship between variable hydroperiod, production allocation, and belowground organic turnover in forested wetlands. *Wetlands, 13*(2), 115-121. doi:10.1007/BF03160871

De Battisti, D., Fowler, M., Jenkins, S., Skov, M., Bouma, T., Neyland, P. & Griffin, J. (2020). Multiple trait dimensions mediate stress gradient effects on plant biomass allocation, with implications for coastal ecosystem services. *Journal of Ecology, 108*, 1227–1240.

De Battisti, D., Fowler, M. S., Jenkins, S. R., Skov, M. W., Rossi, M., ,, Bouma, T. J., Neyland, P. J. & Griffin, J. N. (2019). Intraspecific Root Trait Variability Along Environmental Gradients Affects Salt Marsh Resistance to Lateral Erosion. *Frontiers in Ecology and Evolution, 7*(150). doi:10.3389/fevo.2019.00150

De Leeuw, J., Olff, H. & Bakker, J. P. (1990). Year-to-year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. *Aquatic Botany, 36*, 139-151.

Delédec, S., Chessel, D., ter Braak, C. & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics, 3*, 143-166.

Denny, M. (1988). Biology And The Mechanics Of The Wave-Swept Environment. Princeton University Press.

Diaz, S. & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science, 8*, 463-474.

Díaz, S. & Cabido, M. (2001). Vive la différence: plant functionaldiversity matters to ecosystemprocesses. *TRENDS in Ecology & Evolution, 16*(11), 646-655.

Díaz, S., Cabido, M. & Casanoves, F. (1999). Functional implications of trait–environment linkages in plant communities. E. Weiher and P. Keddy. Cambridge, UK, Cambridge University Press: 338-392.

Díaz, S., Fargione, J., Chapin, I. F. S. & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biology, 4*, 1300–1305.

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science, 15*(3), 295. doi:10.1658/1100-9233(2004)015[0295:tpttde]2.0.co;2

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci U S A, 104*(52), 20684-20689. doi:10.1073/pnas.0704716104

Drake, K., Halifax, H., Adamowicz, S. C. & Craft, C. B. (2015). Carbon Sequestration in Tidal Salt Marshes of the Northeast United Stated. *Environmental Management, 56*, 998-1008.

Dray, S. & Dufour, A. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software, 22*(4), 1-20.

Dray, S. & Legendre, P. (2008). Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology, 89*, 3400-3412.

Duarte, C. M., Middelburg, J., J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*(1), 173–180.

Eertman, R. H. M., Kornman, B. A., Stikvoort, E. & Verbeek, H. (2002). Restoration of the Sieperda Tidal Marsh in the Scheldt Estuary, The Netherlands. *Restoration Ecology, 10*(3), 438–449.

Egnér, H., Riehm, H. & Domingo, W. R. (1960). Untersuchungen über die Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes des Bodens. II. Chemische Extraktionsmethoden zur Phosphor- und Kaliumbestimmung. *Kungliga Lantbrukshögskolans Annualer 26*, 199-215.

Elbe Estuary Working Group. (2012). Integrated management plan for the Elbe Estuary. URL: https://www.natura2000-unterelbe.de/english.php (accessed: 31.03.2019).

Ellenberg, H. & Leuschner, C. (2010). *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht* (6. Auflage ed.). Stuttgart: Ulmer.

Elschot, K., Bakker, J. P., Temmerman, S., van de Koppel, J. & Bouma, T. J. (2015). Ecosystem engineering by large grazers enhances carbon stocks in a tidal salt marsh. *Marine Ecology Progress Series, 537*, 9-21. doi:10.3354/meps11447

Enquist, B. J. & Niklas, K. J. (2002). Global Allocation Rules for Patterns of Biomass Partitioning in Seed Plants. *Science, 295*, 1517-1520.

Enríquez, S., Duarte, C. M. & Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C :N :P content. *Oecologia*(94), 457-471.

Faucon, M. P., Houben, D. & Lambers, H. (2017). Plant Functional Traits: Soil and Ecosystem Services. *Trends in Plant Science, 22*(5), 385-394.

Faußer, A. C., Dušek, J., Čížková, H. & Kazda, M. (2016). Diurnal dynamics of oxygen and carbon dioxide concentrations in shoots and rhizomes of a perennial in a constructed wetland indicate down-regulation of below ground oxygen consumption. *AoB Plants, 8:plw025*.

Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., Chapin Iii, F. S., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F. & Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change, 4*(6), 471-476. doi:10.1038/nclimate2177

Flowers, T. J. & Colmer, T. D. (2008). Salinity tolerance in halophytes. *New Phytol, 179*(4), 945-963. doi:10.1111/j.1469-8137.2008.02531.x

Fox, J. & Weisberg, S. (2019). An R Companion to Applied Regression. Third Edition, Sage.

Freschet, G. T., Aerts, R. & Cornelissen, J. H. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology*(26), 56-65.

Freschet, G. T., Cornwell, W. K., Wardle, D. A., Elumeeva, T. G., Liu, W., Jackson, B. G., Onipchenko, V. G., Soudzilovskaia, N. A., Tao, J. & Cornelissen, J. H. C. (2013). Linking litter decomposition of above- and below-ground organs to plant–soil feedbacks worldwide. *Journal of Ecology, 101*(4), 943-952. doi:https://doi.org/10.1111/1365-2745.12092

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecography, 85*(9), 2630-2637.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J. P., Thebault, A., Vile, D. & Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann Bot, 99*(5), 967-985. doi:10.1093/aob/mcl215

Garnier, E., Navas, M.-L. & Grigulis, K. (2016). *Plant functional diversity: Organism traits, community structure, and ecosystem properties*: Oxford University Press.

Garnier, E. & Navas, M. L. (2012). A trait-based approach to comparative functionalplant ecology: concepts, methods and applicationsfor agroecology. A review. *Agronomy for Sustainable Development*(32), 365–399.

Gedan, K. B. & Bertness, M. D. (2009). Experimental warming causes rapid loss of plant diversity in New England salt marshes. *Ecology Letters, 12*, 842–848.

Gedan, K. B., Kirwan, M. L., Wolanski, E., Barbier, E. B. & Silliman, B. R. (2010). The present and future role of coastal wetland vegetation in protecting shorelines: answering recent challenges to the paradigm. *Climatic Change, 106*(1), 7-29. doi:10.1007/s10584-010-0003-7

Gerlach, A. (1973). *Methodische Untersuchungen zur Bestimmung der Stickstoffnettomineralisation. Scripta Geobotanica 5*: Verlag Erich Goltze KG, Göttingen.

Giller, P. S. (1984). Community structure and the niche. Outline Studies in Ecology. Chapman and Hall, London and New York.

Gitay, H. & Noble, I. R. (1997). What are funtional types and how should we seek them? In: Smith TM, Shugart HH, Woodward FI (eds) Plant funtional types. Their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, pp. 3-19.

Granéli, W., Weisner, S. E. B. & Sytsma, M. D. (1992). Rhizome dynamics and resource storage in Phragmites australis. *Wetlands Ecology and Management, 1*(4), 239-247.

Grasshoff, K., Ehrhardt, M. & Kremling, K. (1983). *Methods of Seawater Analysis* (3rd ed.). Weinheim: Verlag Chemie: WILEY-VCH.

Greenwood, P., Baumann, P., Pulley, S. & Kuhn, N. J. (2018). The invasive alien plant, Impatiens glandulifera (Himalayan Balsam), and increased soil erosion: causation or association? Case studies from a river system in Switzerland and the UK. *Journal of Soils and Sediments*(18), 3463–3477.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology, 86*, 902-910.

Guo, X., Lu, X., Tong, S. & Dai, G. (2008). Influence of environment and substrate quality on the decomposition of wetland plant root in the Sanjiang Plain, Northeast China. *Journal of Enviornmental Sciences*(20), 1445–1452.

Güsewell, S. (2004). N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist, 164*, 243-266.

Güsewell, S. & Verhoeven, J. T. A. (2006). Litter N:P ratios indicate whether N or P limits the decomposability of graminoid leaf litter. *Plant Soil, 287*, 131–143.

Haines-Young, R. & Potschin, M. (2013). CommonInternational Classification of Ecosystem Services (CICES): Consultation on Version 4, August-December 2012. EEA Framework Contract No EEA/IEA/09/003.

Hamann, E. & Puijalon, S. (2013). Biomechanical responses of aquatic plants to aerial conditions. *Annals of Botany, 112*(9), 1869-1878. doi:10.1093/aob/mct221

Hansen, K., Butzeck, C., Eschenbach, A., Gröngröft, A., Jensen, K. & Pfeiffer, E. M. (2017). Factors influencing the organic carbon pools in tidal marsh soils of the Elbe estuary (Germany). *J Soils Sediments, 17*, 47–60.

Hector, A., Beale, A. J., Minns, A., Otway, S. J. & Lawton, J. H. (2000). Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos, 90*(2), 357-371. doi:https://doi.org/10.1034/j.1600-0706.2000.900217.x

Hein, L., van Koppen, K., de Groot, R. S. & van Ierland, E. C. (2006). Spatial Scales, Stakeholders and the Valuation of Ecosystem Services. *Ecological Economics*(57), 209–228.

Hemminga, M. A. & Buth, G. J. C. (1991). Decomposition in salt marsh ecosystems of the S.W. Netherlands: the effects of biotic and abiotic factors. *Vegetatio*(92), 73-83.

Henseler, J., Hubona, G., , & Ray, P. A. (2016). Using PLS path modeling in new technology research: updated guidelines. *Industrial Management & Data Systems, 116*(1), 2-20.

Henseler, J., Ringle, C. M. & Sarstedt, M. (2015). A new criterion for assessing discriminant validity in variance-based structural equation modeling. *Journal of the Academy of Marketing Science*(43), 115–135.

Heuner, M. (2016). *Key ecosystem engineers in estuarine vegetation.* Dissertation. University of Berlin, Berlin.

Heuner, M., Schröder, B., Schröder, U. & Kleinschmit, B. (2019). Contrasting elevational responses of regularly flooded marsh plants in navigable estuaries. *Ecohydrology and Hydrobiology, 19*, 38–53.

Heuner, M., Silinski, A., Schoelynck, J., Bouma, T. J., Puijalon, S., Troch, P., Fuchs, E., Schröder, B., Schröder, U., Meire, P. & Temmerman, S. (2015). Ecosystem Engineering by Plants on Wave-Exposed Intertidal Flats is Governed by Relationships between Effect and Response Traits. *PLoS One, 10*(9), e0138086. doi:0138010.0131371/journal.pone.0138086. doi:10.1371/journal.pone.0138086

Hodson, R. E., Christian, R. R. & Maccubbin, A. E. (1984). Lignocellulose and lignin in the salt marsh grass Spartina alterniflora: initial concentrations and short-term, post-depositional changes in detrital matter. *Marine Biology*(81), 1-7

Hofmann, H., Lorke, A. & Peeters, F. (2008). The relative importance of wind and ship waves in the littoral zone of a large lake. *Limnol. Oceanogr., 53*(1), 368–380.

Holden, N. M. & Connolly, J. (2011). Estimating the carbon stock of a blanket peat region using a peat depth inference model. *Catena, 86*, 75–85.

Hooper, D. & Vitousek, P. (1997). The Effects of Plant Composition and Diversity on Ecosystem Processes. *Science, 277*, 1302-1305.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. & Wardle, D. A. (2005). Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs, 75*(1), 3-35. doi:10.1890/04-0922

Hopkinson, C. S. & Giblin, A. E. (2008). Chapter 22 - Nitrogen Dynamics of Coastal Salt Marshes. In *Nitrogen in the Marine Environment (2nd Edition)* (pp. 991-1036).

Hopkinson, C. S., Wolanski, E., Cahoon, D. R., Perillo, G. M. E. & Brinson, M. M. (2019). Coastal Wetlands. 1-75. doi:10.1016/b978-0-444-63893-9.00001-0

Horstman, E. M., Dohmen-Janssen, C. M., Narra, P. M. F., van den Berg, N. J. F., Siemerink, M. & Hulscher, S. J. M. H. (2014). Wave attenuation in mangroves: A quantitative approach to field observations. *Coastal Engineering, 94*, 47-62.

HPA. (2019). Hamburg Port Authority: Taking action. Creating values. Sustainability 2018 at the Port of Hamburg.

HPA & WSA. (2011). Hamburg Port Authority and Federal Waterways and Shipping Administration: River Elbe River Engineering and Sediment Management Concept. Review of sediment management strategy in the context of other European estuaries from a morphological perspective.

Hu, L. & Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives,. *Structural Equation Modeling: A Multidisciplinary Journal, 6*(1), 1-55.

Hughes, F. M. R. (1997). Floodplain biogeomorphology. *Progress in Physical Geography, 21*(4), 501-529.

IPCC. (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assess-ment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A.(eds.)]. IPCC, Geneva, Switzerland, 104 pp.

Jobbágy, E. G. & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications, 10*(2), 423-436.

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

Keddy, P. (1992). Assembly and Response Rules: Two Goals for Predictive Community Ecology. *Journal of Vegetation Science, 3*(2), 157-164.

Kerner, M. (2007). Effects of deepening the Elbe Estuary on sediment regime and water quality. *Estuarine, Coastal and Shelf Science, 75*(4), 492-500. doi:10.1016/j.ecss.2007.05.033

Khan, M. A., Ungar, I. A. & Showalter, A. M. (2000). The effect of salinity on the growth, water status, and ion content of a leaf succulent perennialhalophyte,Suaeda fruticosa (L.) Forssk. *Journal of Arid Environment, 45*, 73–84.

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

Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R. & Fagherazzi, S. (2016). Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change, 6*(3), 253-260. doi:10.1038/nclimate2909

Kirwan, M. L., Walters, D. C., Reay, W. G. & Carr, J. A. (2016). Sea level driven marsh expansion in a coupled model of marsh erosion and migration. *Geophysical Research Letters, 43*(9), 4366-4373.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. G., Jackel, A. K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. J., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C., Eriksson, O., Garnier, E. & Peco, B. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology, 96*(6), 1266-1274. doi:10.1111/j.1365-2745.2008.01430.x

Kleyer, M., Dray, S.,, de Bello, F., Lepsˇ, J., Pakeman, R. J., Strauss, B., Thuiller, W. & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science, 23* 805–821.

Kleyer, M. & Minden, V. (2015). Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology*(16), 1-9.

Kleyer, M., Trinogga, J., Cebrián-Piqueras, M. A., Trenkamp, A., Fløjgaard, C., Ejrnæs, R., Bouma, T. J., Minden, V., Maier, M., Mantilla-Contreras, J., Albach, D. C. & Blasius, B. (2019). Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. *Journal of Ecology*(107), 829-842.

Knevel, I. C., Bekker, R. M., Kunzmann, D., Stadler, M. & Thompson, K. E. (2005). The LEDA Traitbase collecting and measuring standards of life-history traits of the northwest European flora. LEDA Traitbase project. University of Groningen, The Netherlands.

Koch, E. W., Hacker, S. D., Barbier, E. B., Granek, E. F., Benjamin S Halpern, B. S., Silliman, B. R., Primavera, J. H., Kennedy, C. J., Reed, D. J., Kappel, C. V., Muthiga, N., Perillo, G. M. E., Polasky, S. & Wolanski, E. (2009). Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment, 7*(1), 29-37.

Koerselman, W. & Meuleman, A. F. M. (1996). Nutrient N:P ratio: a new tool to detect the nature limitation. *Journal of Applied Ecology, 33*, 1441-1450.

Kong, D., Wang, J., Wu, H., Valverde-Barrantes, O. J., Wang, R., Zeng, H., Kardol, P., Zhang, H. & Feng, Y. (2019). Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communitcations, 10:2203*.

Kötter, F. (1961). Die Pflanzengesellschaften im Tidegebiet der Unterelbe in: Ohle, W., Elster, H.-J. (Eds.), Elbe-Aestuar. (Stuttgart), pp. 106-184.

Lamers, L. P., Govers, L. L., Janssen, I. C., Geurts, J. J., Van der Welle, M. E., Van Katwijk, M. M., Van der Heide, T., Roelofs, J. G. & Smolders, A. J. (2013). Sulfide as a soil phytotoxin-a review. *Frontiers in Plant Science, 4*, 1-14. doi:10.3389/fpls.2013.00268

Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007). Plant functional types: are we getting any closer to the holy grail? In 'Terrestrial ecosystems in a changing world'. (Ed. PD Canadell JG, Pitelka L) Springer-Verlag, Berlin, pp. 149–160

Lavorel, S. & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Ecology*(16), 545-556.

Lavorel, S. & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology, 100*(1), 128-140. doi:10.1111/j.1365-2745.2011.01914.x

Le Hir, P., Roberts, W., Cazaillet, O., Christie, M., Bassoullet, P. & Bacher, C. (2000). Characterization of intertidal flat hydrodynamics. *Continental Shelf Research, 20*, 433–459.

Le Quéré, C., Peters, G. P., Andres, R. J., Andrew, R. M., Boden, T. A., Ciais, P., Friedlingstein, P., Houghton, R. A., Marland, G., Moriarty, R., Sitch, S., Tans, P., Arneth, A., Arvanitis, A., Bakker, D. C. E., Bopp, L., Canadell, J. G., Chini, L. P., Doney, S. C., Harper, A., Harris, I., House, J. I., Jain, A. K., Jones, S. D., Kato, E., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Koven, C., Lefèvre, N., Maignan, F., Omar, A., Ono, T., Park, G. H., Pfeil, B., Poulter, B., Raupach, M. R., Regnier, P., Rödenbeck, C., Saito, S., Schwinger, J., Segschneider, J., Stocker, B. D., Takahashi, T., Tilbrook, B., van Heuven, S., Viovy, N., Wanninkhof, R., Wiltshire, A. & Zaehle, S. (2014). Global carbon budget 2013. *Earth System Science Data, 6*(1), 235-263. doi:10.5194/essd-6-235-2014

Legendre, P. & Legendre, L. (2012). Numerical Ecology. 3rd English ed. Elsevier.

Lenth, R. (2020). Emmeans: Estimated Marginal Means, Aka Least-squares Means. R Package Version 1.5.0.

Leonard, L. & Luther, M. (1995). Flow hydrodynamics in tidal marsh canopies. *Limnol. Oceanogr., 40*(8), 1474-1484.

Lichtentaler, H. K. (1987). Chlorophylls and Carotenoids: Pigments of Photosynthetic Biomembranes. *Methods in Enzymology, 148*, 350-382.

Lichtenthaler, H. K. & Buschmann, C. (2001). Chlorophylls and Carotenoids: Measurement and Characterization by UV-VIS Spectroscopy. *Current Protocols in Food Analytical Chemistry*, F4.3.1-F4.3.8.

Lienin, P. & Kleyer, M. (2012). Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology, 13*(4), 301-311. doi:10.1016/j.baae.2012.05.002

Lillebø, A. I., Pardal, M. A., Neto, J. M. & Marques, J. C. (2003). Salinity as the major factor affecting Scirpus maritimus annual dynamics Evidence from field data and greenhouse experiment. *Aquatic Botany, 77*, 111–120.

Liu, G., Sun, J., Tian, K., Xiao, D. & Yuan, X. (2016). Long-term responses of leaf litter decomposition to temperature, litter quality and litter mixing in plateau wetlands. *Freshwater Biology, 62*(1), 178–190.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Schmid, B., Grime, J. P., Tilman, D., Hector, A., Hooper, D. U. & Wardle, D. A. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Chanllenges. *Science, 294*(5543), 804-808.

Maier, M., Schwienheer, J., Exo, K.-M. & Stahl, J. (2010). Vegetation structure of TMAP vegetation types on mainland salt marshes. *Wadden Sea Ecosystem, 26*, 105-110.

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H. & Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and the Environment, 9*(10), 552-560. doi:10.1890/110004

McLusky, D., S., & Elliott, M. (2004). *The Estuarine Ecosystem. Ecology, Threats and Management*: Oxford University Press.

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

Megonigal, J. P. & Neubauer, S. C. (2019). Biogeochemistry of Tidal Freshwater Wetlands. *Coastal Wetlands*, 641–683.

Meine, M. (2011). The TIDE Project. Hamburg Port Authority, Humber Estuary Conference, 2011.

Meire, P., Ysebaert, T., Damme, S. V., Bergh, E. V. d., Maris, T. & Struyf, E. (2005). The Scheldt estuary: a description of a changing ecosystem. *Hydrobiologia, 540*(1), 1-11. doi:10.1007/s10750-005-0896-8

Mendelssohn, I. A., Sorrell, B. K., Brix, H., Schierup, H. H., Lorenzen, B. & Maltby, E. (1999). Controls on soil cellulose decomposition along a salinity gradient in a Phragmites australis wetland in Denmark. *Aquatic Botany, 64*, 381–398.

Minden, V. (2010). *Functional traits of salt marsh plants: responses of morphology- and elemental- based traits to environmental constraints, trait-trait relationships and effects on ecosystem properties.* Oldenburg, Oldenburg. https://plus.orbis-oldenburg.de/permalink/f/126s6ph/49GBVUOB_ALMA51213924230003501.

Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. (2012). Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts. *Perspectives in Plant Ecology, Evolution and Systematics, 14*(3), 183-192. doi:10.1016/j.ppees.2012.01.002

Minden, V. & Kleyer, M. (2011). Testing the effect–response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science*(22), 387-401.

Minden, V. & Kleyer, M. (2014). Internal and external regulation of plant organ stoichiometry. *Plant Biology, 16*(5), 897-907. doi:10.1111/plb.12155

Minden, V. & Kleyer, M. (2015). Ecosystemmultifunctionality of coastalmarshes is determined by key plant traits. *Journal of Vegetation Science, 26*, 651–662.

Mitsch, W. & Gosselink, J. (2000). The value of wetlands: importance of scale and landscape setting. *Elsevier, 35*(200), 25-33.

Moffett, K. B. & Gorelick, S. M. (2016). Alternative stable states of tidal marsh vegetation patterns and channel complexity. *Ecohydrology, 9*(8), 1639-1662. doi:10.1002/eco.1755

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. (2014). Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience, 7*(10), 727-731. doi:10.1038/ngeo2251

Möller, I., Spencer, T., French, J. R., Leggett, D. J. & Dixon, M. (1999). Wave Transformation Over Salt Marshes: A Field and Numerical Modelling Study from North Norfolk, England. *49*(3), 411–426.

Mudd, S. M., D'Alpaos, A. & Morris, J. T. (2010). How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and hydrodynamic controlson biologically mediated sedimentation. *Journal of Geophysical Research, 115*, F03029.

Mudd, S. M., Howell, S. & Morris, J. T. (2009). Impact of the dynamic feedback between sedimentation, sea level rise, and biomass production on near surface marsh stratigraphy and carbon accumulation. *Estuarine, Coastal and Shelf Science, 82*, 377–389.

Murphy, J. & Riley, J. (1962). A modified single solution method for the determination pf phosphate in natural waters. *Analytica Chimica Acta, 27*, 36-39.

Najjar, R. G., Herrmann, M., Alexander, R., Boyer, E. W., Burdige, D. J., Butman, D., Cai, W. J., Canuel, E. A., Chen, R. F., Friedrichs, M. A. M., Feagin, R. A., Griffith, P. C., Hinson, A. L., Holmquist, J. R., Hu, X., Kemp, W. M., Kroeger, K. D., Mannino, A., McCallister, S. L., McGillis, W. R., Mulholland, M. R., Pilskaln, C. H., Salisbury, J., Signorini, S. R., St-Laurent, P., Tian, H., Tzortziou, M., Vlahos, P., Wang, Z. A. & Zimmerman, R. C. (2018). Carbon Budget of Tidal Wetlands, Estuaries, and Shelf Waters of Eastern North America. *Global Biogeochemical Cycles, 32*(3), 389-416. doi:10.1002/2017gb005790

Neubauer, S. C. (2008). Contributions of mineral and organic components to tidal freshwater marsh accretion. *Estuarine, Coastal and Shelf Science, 78*, 78-88.

Neubauer, S. C., Anderson, I. C., Constantine, J. A. & Kuehl, S. A. (2002). Sediment deposition and accretion in a mid-Atlantic (U.S.A.) tidal freshwater marsh. *Estuarine, Coastal and Shelf Science, 54*, 713-727.

Niklas, K. J. (1995). Plant Height and the Properties of Some Herbaceous Stems. *Annals of Botany, 75*, 133-142.

Niklas, K. J. (2004). Plant allometry: is there a grand unifying theory? *Biol. Rev., 79*, 871–889.

Nipithwittaya S. & P., S. (2012). Estimation of Soil Organic Carbon Concentration accumulated in Mangrove Forest Filtration System. *Research Journal of Chemistry and Environment, 16*(3).

Noble, I. R. & Slatyr, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio, 43*, 5-21.

Odum, W. (1988). Comparative Ecology of Tidal Freshwater and Salt Marshes. *Ann. Rev. Ecol. Syst., 19*, 147-176.

Pakeman, R. J., Eastwood, A. & Scobie, A. (2010). Leaf dry matter content as a predictor of grassland litter decomposition: a test of the 'mass ratio hypothesis'. *Plant Soil*(342), 49–57.

Paul, M. & Amos, C. L. (2011). Spatial and seasonal variation in wave attenuation over *Zostera noltii*. *Journal of Geophysical Research*, C08019.

Paul, M., Rupprecht, F., Möller, I., Bouma, T. J., Spencer, T., Kudella, M., Wolters, G., van Wesenbeeck, B. K., Jensen, K., Miranda-Lange, M. & Schimmels, S. (2016). Plant stiffness and biomass as drivers for drag forces under extreme wave loading: A flume study on mimics. *Coastal Engineering, 117*, 70–78.

Pedersen, O., Sauter, M., Colmer, T. D. & Nakazono, M. (2020). Regulation of root adaptive anatomical and morphological traits during low soil oxygen. *New Phytologist*.

Pennings, S. C. & Callaway, R. M. (1992). Salt Marsh Plant Zonation: The Relative Importance of Competition and Physical Factors. *Ecology, 73*(2), 681-690.

Pennings, S. C., Stanton, L. E. & Brewer, J. S. (2002). Nutrient Effects on the Composition of Salt Marsh Plant Communities along the Southern Atlantic and Gulf Coasts of the United States. *Estuaries, 25*(6), 1164-1173.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S. & Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*(3), 167. doi:10.1071/bt12225

Pierik, R., van Aken, J. M. & Voesenek, L. A. C. J. (2009). Is elongation-induced leaf emergence beneficial for submerged Rumex species? *Annals of Botany*(103), 353–357.

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P. & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol, 193*(1), 30-50. doi:10.1111/j.1469-8137.2011.03952.x

Pott, R. (1995). Die Pflanzengesellschaften Deutschlands. *Ulmer, Stuttgart, 2. Auflage*.

Puijalon, S., Bouma, T. J., Douady, C. J., van Groenendael, J., Anten, N. P., Martel, E. & Bornette, G. (2011). Plant resistance to mechanical stress: evidence of an avoidance-tolerance trade-off. *New Phytol, 191*(4), 1141-1149. doi:10.1111/j.1469-8137.2011.03763.x

Puijalon, S., Bouma, T. J., Van Groenendael, J. & Bornette, G. (2008). Clonal Plasticity of Aquatic Plant Species Submitted to Mechanical Stress: Escape versus Resistance Strategy. *Annals of Botany*(102), 989-996.

Quintino, V., Sangiorgio, F., Ricardo, F., Mamede, R., Pires A., Freitas, R., Rodrigues, A. M. & Basset, A. (2009). In situ experimental study of reed leaf decomposition along a full salinity gradient. *Estuarine, Coastal and Shelf Science, 85*, 497–506.

R Core Team. (2017). R: A Language and Environment for Statistical Computing. URL https://www.r-project.org/ (last access 8.10.2017).

Rasse, D. P., Rumpel, C. & Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil, 269*(1-2), 341-356. doi:10.1007/s11104-004-0907-y

Raunkiær, C. (1905). Types biologiques pour la géographie botanique. Oversigt over Det Kongelige Danske Videnskabernes Selskabs Forhandlinger, 1905, 1347-1438.

Read, J. & Sanson, G. D. (2003). Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytologist, 160*, 81–99.

Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F. T., Gruber, N., Janssens, I. A., Laruelle, G. G., Lauerwald, R., Luyssaert, S., Andersson, A. J., Arndt, S., Arnosti, C., Borges, A. V., Dale, A. W., Gallego-Sala, A., Goddéris, Y., Goossens, N., Hartmann, J., Heinze, C., Ilyina, T., Joos, F., LaRowe, D. E., Leifeld, J., Meysman, F. J. R., Munhoven, G., Raymond, P. A., Spahni, R., Suntharalingam, P. & Thullner, M. (2013). Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nature Geoscience, 6*(8), 597-607. doi:10.1038/ngeo1830

Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology, 102*(2), 275-301. doi:10.1111/1365-2745.12211

Reidenbach, M. A. & Thomas, E. L. (2018). Influence of the Seagrass, Zostera marina, on Wave Attenuation and Bed Shear Stress Within a Shallow Coastal Bay. *Frontiers in Marine Science, 5*(397). doi:10.3389/fmars.2018.00397

Reise, K. (2005). Coast of change: habitat loss and transformations in the Wadden Sea. *Helgoland Marine Research, 59*(1), 9-21. doi:10.1007/s10152-004-0202-6

Riis, T., Kelly-Quinn, M., Aguiar, F., C.,, Manolaki, P., Bruno, D., Bejarano, M. D., Clerici, N., Fernandes, M. R., Franco, J. C., Pettit, N., Portela, A. P., Tammeorg, O., Tammeorg, P., Rodríguez-González, P. M. & Dufour, S. (2020). Global Overview of Ecosystem Services Provided by Riparian Vegetation. *BioScience*(70), 501-514.

Ringle, C. M., Wende, S. & Becker, J. M. (2015). SmartPLS 3., Bönningstedt: SmartPLS. Retrieved from http://www.smartpls.com.

Robertson, G. P., , & Paul, E. A. (2000). *Decomposition and Soil Organic Matter Dynamics. In: Sala O.E., Jackson R.B., Mooney H.A., Howarth R.W. (eds) Methods in Ecosystem Science. Springer, New York, NY*.

Rothmaler, W. (2007). Exkursionsflora von Deutschland. Gefäßpflanzen: Atlasband. *Elsevier GmbH, München*(11. Auflage).

Roulet, N. T. (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: Prospects and significance for Canada. *Wetlands, 20*(4), 605-615. doi:10.1672/0277-5212(2000)020[0605:pcsgga]2.0.co;2

Royston, P. (1982). An extension of Shapiro and Wilk's W test for normality to large samples. *Applied Statistics, 31*, 115-124.

RStudio Team. (2016). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Rupprecht, F., Möller, I., Evans, B., Spencer, T. & Jensen, K. (2015). Biophysical properties of salt marsh canopies — Quantifying plant stem flexibility and above ground biomass. *Coastal Engineering, 100*, 48-57. doi:10.1016/j.coastaleng.2015.03.009

Rupprecht, F., Möller, I., Paul, M., Kudella, M., Spencer, T., van Wesenbeeck, B. K., Wolters, G., Jensen, K., Bouma, T. J., Miranda-Lange, M. & Schimmels, S. (2017). Vegetation-wave interactions in salt marshes under storm surge conditions. *Ecological Engineering, 100*, 301-315. doi:10.1016/j.ecoleng.2016.12.030

Rupprecht, F., Wanner, A., Stock, M., Jensen, K. & Middleton, B. (2015). Succession in salt marshes - large-scale and long-term patterns after abandonment of grazing and drainage. *Applied Vegetation Science, 18*(1), 86-98. doi:10.1111/avsc.12126

Sarkar, D. (2008). *Lattice: Multivariate Data Visualization with R*: Springer, New York.

Schachtschnabel, P., Blume, H.-P., Hartge, K.-H., Schwertmann, U., Brümmer, G. & Renger, M. (1987). *Lehrbuch der Bodenkunde* (11 ed.). Stuttgart: Ferdinand Enke Verlag.

Schlichting, E., Blume, H. P. & Stahr, K. (1995). Bodenkundliches Praktikum. Blackwell.

Schmeil, O. & Fitschen, J. (2003). *Flora von Deutschland und angrenzender Länder* (W. Rauh & K. Senghas Eds.): Quelle & Meyer Verlag, Wiebelsheim.

Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kogel-Knabner, I., Lehmann, J., Manning, D. A., Nannipieri, P., Rasse, D. P., Weiner, S. & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature, 478*(7367), 49-56. doi:10.1038/nature10386

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods, 9*, 671-675.

Schneider, K. J. (1998). *Bautabellen für Ingenieure*. (13. Auflage). Düsseldorf: Werner Verlag.

Schoelynck, J., Bal, K., Backx, H., Okruszko, T., Meire, P. & Struyf, E. (2010). Silica uptake in aquatic and wetland macrophytes: a strategic choice between silica, lignin and cellulose? . *New Phytologist, 186*, 385–391.

Scholten, M., Blaauw, P. A., Stroetenga, M. & Rozema, J. (1987). The impact of competitive interactions on the growth and distribution of plant species in salt marshes. In: Huiskes, A.H.L., Blom, C.W.P.M., Rozema, J. (Eds.), Vegetation Between Land and Sea. Dr. W. Junk, pp. 270-283.

Schoutens, K., Heuner, M., Fuchs, E., Minden, V., Schulte-Ostermann, T., Belliard, J. P., Bouma, T. J. & Temmerman, S. (2020). Nature-based shoreline protection by tidal marsh plants depends on trade-offs between avoidance and attenuation of hydrodynamic forces. *Estuarine, Coastal and Shelf Science, 236*. doi:Urn:Nbn:Nl:Ui:10-1874-395996

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J.-P. & Temmerman, S. (2019). How effective are tidal marshes as nature-based shoreline protection throughout seasons? *Limnology and Oceanography*. 9999, 1-13. doi:10.1002/lno.11149

Schulze, D., Rupprecht, F., Nolte, S. & Jensen, K. (2019). Seasonal and spatial within-marsh differences of biophysical plant properties: implications for wave attenuation capacity of salt marshes. *Aquatic Sciences*, 81-65.

Schulze, E. D., Ciais, P., Luyssaert, S., Schrumpf, M., Janssens, I. A., Thiruchittampalam, B., Theloke, J., Saurat, M., Bringezu, S., Lelieveld, J., Lohila, A., Rebmann, C., Jung, M., Bastviken, D., Abril, G., Grassi, G., Leip, A., Freibauer, A., Kutsch, W., Don, A., Nieschulze, J., Börner, A., Gash, J. H. & Dolman, A. J. (2010). The European carbon balance. Part 4: integration of carbon and other trace-gas fluxes. *Global Change Biology, 16*(5), 1451-1469. doi:10.1111/j.1365-2486.2010.02215.x

Scurlock, J. M. O., Johnson, K. & Olson, R. J. (2002). Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology, 8*, 736-753.

Shipley, B., Vile, D., , & Garnier, E. (2006). From Plant Traits to Plant Communities: A Statistical Mechanistic Approach to Biodiversity. *Science, 314*, 812-814.

Short, F. T., Kosten, S., Morgan, P. A., Malone, S. & Moore, G. E. (2016). Impacts of climate change on submerged and emergent wetland plants. *Aquatic Botany, 135*, 3-17.

Silinski, A., Heuner, M., Schoelynck, J., Puijalon, S., Schroder, U., Fuchs, E., Troch, P., Bouma, T. J., Meire, P. & Temmerman, S. (2015). Effects of wind waves versus ship waves on tidal marsh plants: a flume study on different life stages of Scirpus maritimus. *PLoS One, 10*(3), e0118687. doi:10.1371/journal.pone.0118687

Silinski, A., van Belzen, J., Fransen, E., Bouma, T. J., Troch, P., Meire, P. & Temmerman, S. (2016). Quantifying critical conditions for seaward expansion of tidal marshes: A transplantation experiment. *Estuarine, Coastal and Shelf Science, 169*, 227-237. doi:10.1016/j.ecss.2015.12.012

Simberloff, D. & Dayan, T. The Guild Concept and the Structure of Ecological Communities. *Annual Review of Ecology and Systematics, 22*, 115-143.

Simões, M. P., Calado, M. L., Madeira, M. & Gazarini, L. C. (2011). Decomposition and nutrient release in halophytes of a Mediterranean salt marsh. *Aquatic Botany, 94*, 119–126.

Sloey, T. M. & Hester, M. W. (2018). Impact of nitrogen and importance of silicon on mechanical stem strength in Schoenoplectus acutus and Schoenoplectus californicus: applications for restoration. *Wetlands Ecology and Management, 26*(3), 459-474. doi:10.1007/s11273-017-9586-3

Soussana, J.-F., Klumpp, K. & Ehrhardt, F. (2014). The role of grassland in mitigating climate change. *Grassland Science in Europe,, 19*, 75-86.

Soussana, J.-F. & Lüscher, A. (2007). Temperate grasslands and global atmospheric change: a review. *Grass and Forage Science, 62*, 127–134.

Stagg, C. L., Schoolmaster, D. R., Krauss, K. W., Cormier, N. & Conner, W. H. (2017). Causal mechanisms of soil organic matter decomposition: Deconstructing salinity and flooding impacts in coastal wetlands. *Ecology, 0*(0), 1–16.

Stiller, G. (2005). Bewertungsverfahren für die Qualitätskomponenten Makrophyten und Angiospermen in der Tideelbe gemäß EU Wasserrahmenrichtlinie. Sonderaufgabenbereich Tideelbe - Wassergütestelle Elbe, Hamburg.

Suchrow, S. & Jensen, K. (2010). Plant Species Responses to an Elevational Gradient in German North Sea Salt Marshes. *Wetlands, 30*(4), 735–746.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldeberg, D., Hooper, D. U., Jackson, S. T. & Navas, M. L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*(14), 1125-1140.

Süß, A., Danner, M., Obster, C., Locherer, M., Hank, T. & Richter, K. (2015). Measuring Leaf Chlorophyll Content with the Konica Minolta SPAD-502Plus – Theory, Measurement, Problems, Interpretation. EnMAP Field Guides Technical Report, GFZ Data Services.

Swift, M., Heal, O. & Anderson, J. (1979). Decomposition in Terrestrial Ecosystems. *Studies in Ecology, 5*.

Takahashi, H., Yamauchi, T., Colmer, T. D. & Nakazono, M. (2014). Aerenchyma Formation in Plants. In J. T. van Dongen & F. Licausi (Eds.), *Low-Oxygen Stress in Plants: Oxygen Sensing and Adaptive Responses to Hypoxia* (pp. 247-265). Vienna: Springer Vienna.

Teal, J. M. (1986). The ecology of regularly flooded salt marshes of New England: a community profile. U.S. Fish and Wildlife Service, Biological Report 85 (87.84).

Temmerman, S. & Kirwan, M. L. (2015). Building land with a rising sea. Cost-efficient nature-based solutions can help to sustain coastal societies. *Science, 349*(6248), 588-589.

Temmerman, S., Meire, P., Bouma, T. J., Herman, P. M., Ysebaert, T. & De Vriend, H. J. (2013). Ecosystem-based coastal defence in the face of global change. *Nature, 504*(7478), 79-83. doi:10.1038/nature12859

Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R. G., Ballatore, T. J., Dillon, P., Finlay, K., Fortino, K., Knoll, L. B., Kortelainen, P. L., Kutser, T., Larsen, S., Laurion, I., Leech, D. M., McCallister, S. L., McKnight, D. M., Melack, J. M., Overholt, E., Porter, J. A., Prairie, Y., Renwick, W. H., Roland, F., Sherman, B. S., Schindler, D. W., Sobek, S., Tremblay, A., Vanni, M. J., Verschoor, A. M., von Wachenfeldt, E. & Weyhenmeyer, G. A. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography, 54*(6, part 2), 2298-2314.

Tremp, H. (2005). Aufnahme und Analyse vegetationsökologischer Daten. Stuttgart: Ulmer.

Uddling, J., Gelang-Alfredsson, J., Piikki, K. & Pleijel, H. (2007). Evaluating the relationship between leaf chlorophyll concentration and SPAD-502 chlorophyll meter readings. *Photosynth Res, 91*(1), 37-46. doi:10.1007/s11120-006-9077-5

UN. (2015). *The Millennium Development Goals Report*: United Nations, New York, USA.

UNESCO. (1981). International Oceanographic Tables. *Unesco Technical Papers in Marine Science, 3*(No. 39).

Usherwood, J. R., Ennos, A. R. & Ball, D. J. (1997). Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments. *Journal of Experimental Botany, 48*(No. 312), 1469-1475.

Valéry, L., Bouchard, V. & Lefeuvre, J.-C. (2004). Impact of the invasive native species Elymus athericus on carbon pools in a salt marsh. *Wetlands, 24*(2), 268-276. doi:10.1672/0277-5212(2004)024[0268:IOTINS]2.0.CO;2

Valiela, I., Bowen, J. L. & York, J. K. (2001). Mangrove forests: one of the world's threatened major tropical environments. *BioScience*(51), 807–815.

Valiela, I., Kinney, E., Culbertson, J., Peacock, E. & Smith, S. (2009). Global losses of mangroves and salt marshes: magnitudes, causes and consequences. In: Global loss of coastal habitats: rates, causes, and consequences (C. Duarte, ed.), pp. 107– 138. Spain Fundación BBVA, Bilbao, Spain.

Van de Broek, M., Temmerman, S., Merckx, R. & Govers, G. (2016). Controls on soil organic carbon stocks in tidal marshes alongan estuarine salinity gradient. *Biogeosciences*(13), 6611–6624.

van der Meulen, M. J., van der Spek, A. J. F., de Lange, G., Gruijters, S. H. L. L., van Gessel, S. F., Nguyen, B.-L., Maljers, D., Schokker, J., Mulder, J. P. M. & van der Krogt, R. A. A. (2007). Regional Sediment Deficits in the Dutch Lowlands:Implications for Long-Term Land-Use Options. *J Soils Sediments, 7*(1), 9 – 16.

van der Plas, F., Schröder-Georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R. L., Buchmann, N., de Kroon, H., Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., Hildebrandt, A., Koller-France, E., Leimer, S., Milcu, A., Mommer, L., Niklaus, P. A., Oelmann, Y., Roscher, C., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Schmid, B., Schulze, E.-D., Temperton, V., Tscharntke, T., Voigt, W., Weisser, W., Wilcke, W. & Wirth, C. (2020). Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution, 4*, 1602–1611.

van Wesenbeeck, B. K., Crain, C. M., Altieri, A. H. & Bertness, M. D. (2007). Distinct habitat types arise along a continuous hydrodynamic stress gradient due to interplay of competition and facilitation. *Marine Ecology Progress Series, 349*, 63-71. doi:10.3354/meps07051

van Wijnen, H. J. & Bakker, J. P. (1999). Nitrogen and phosphorus limitation in a coastal barrier salt marsh] the implications for vegetation succession. *Journal of Ecology*(87), 265-272.

Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Vol. fourth edition): 4th edition. Springer, New York.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007). Let the concept of trait be functional! *Oikos, 116*(5), 882-892. doi:10.1111/j.0030-1299.2007.15559.x

Visconti, P., Elias, V., Sousa Pinto, I., Fischer, M., Ali-Zade, V., Báldi, A., Brucet, S., Bukvareva, E., Byrne, K., Caplat, P., Feest, A., Guerra, C., Gozlan, R., Jelić, D., Kikvidze, Z., Lavrillier, A., Le Roux, X., Lipka, O., Petrík, P., Schatz, B., Smelansky, I. & Viard, F. (2018). Chapter 3: Status, trends and future dynamics of biodiversity and ecosystems underpinning nature's contributions to people., In IPBES. The IPBES regional assessment report on biodiversity and ecosystem services for Europe and Central Asia. Rounsevell, M., Fischer, M., Torre-Marin Rando, A. and Mader, A. (eds.). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 187-382.

Vuik, V., Jonkman, S. N., Borsje, B. W. & Suzuki, T. (2016). Nature-based flood protection: the efficiency of vegetated foreshores for reducing wave loads on coastal dikes. *Coastal Engineering*(116), 42-56.

Vuik, V., Suh Heo, H. Y., Zhu, Z., Borsje, B. W. & Jonkman, S. N. (2018). Stem breakage of salt marsh vegetation under wave forcing: A field and model study. *Estuarine, Coastal and Shelf Science, 200*, 41-58. doi:10.1016/j.ecss.2017.09.028

Wagner, D., Eisenhauer, N. & Cesarz, S. (2015). Plant species richness does not attenuate responses of soil microbialand nematode communities to aflood event. *Soil Biology & Biochemistry*(89), 135-149.

Wang, B., Zhang, G. & Duan, J. (2015). Relationship between topography and the distribution of understory vegetation in a Pinus massoniana forest in Southern China. *International Soil and Water Conservation Research*(3), 291-304.

Wang, F., Kroeger, K. D., Gonneea, M., E.,, Pohlman, J. W. & Tang, J. (2019). Water salinity and inundation control soil carbon decomposition during salt marsh restoration: An incubation experiment. *Ecology and Evolution*(9), 1911-1921.

Wardle, D. A., Bonner, K. I. & Bakker, G. M. (2002). Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology*(16), 585–595.

Warton, D. I., Duursma, R. A., Falster, D. S. & Taskinen, S. (2012). smatr 3 - an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution, 3*(2), 257-259.

Warton, D. I., Wright, I. J., Falster, D. S. & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biol. Rev., 81*, 259–291.

Weiher, E., Clarke, G. D. P. & Keddy, P. A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos, 81*, 309–322.

Weiher, E. & Keddy, P. (1999). *Assembly rules as general constraints on community composition. In E. Weiher & P. Keddy (Eds.), Ecological Assembly Rules: Perspectives, Advances, Retreats (pp. 251-271)*: Cambridge: Cambridge University Press.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science, 10*(5), 609-620.

Weiss, C., Weiss, J., Boy, J., Iskandar, I., Mikutta, R. & Guggenberger, G. (2016). Soil organic carbon stocks in estuarine and marine mangrove ecosystems are driven by nutrient colimitation of P and N. *Ecology and Evolution, 6*(14), 5043– 5056.

Wetterdienst, D. (2019). Mean Climate Values for the Period 1981 to 2010. https://www.dwd.de/DE/wetter/wetterundklima_vorort/niedersachsen_bremen/cuxhaven/_node.html (accessed: 21.05.2019).

Wetzel, R. G. (2001). Land-water interfaces: larger plants. Limnology (Third Edition), Academic Press, pp. 527-575.

White, T. A., Barker, D. J. & Moore, K. J. (2004). Vegetation diversity, growth, quality and decomposition in managed grasslands. *Agriculture, Ecosystems & Environment, 101*(1), 73-84. doi:10.1016/s0167-8809(03)00169-5

Węski, K., Guo, H., Craft, C. B. & Pennings, S. C. (2010). Ecosystem Functions of Tidal Fresh, Brackish, and Salt Marshes on the Georgia Coast. *Estuaries and Coasts, 33*, 161–169.

Williams, E. K. & Rosenheim, B. E. (2015). What happens to soil organic carbon as coastal marsh ecosystems change in response to increasing salinity? An exploration using ramped pyrolysis. *Geochemistry, Geophysics, Geosystems*(16), 2322-2335.

Windham, L. (2001). Comparison of biomass production and decomposition between Phragmites australis (Common Reed) and Spartina patens (Salt Hay Grass) in brackish tidal marshes of New Jersey, USA. *Wetlands, 21*(2), 179-188.

Wolters, M., Garbutt, A. & Bakker, J. P. (2005). Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. *Biological Conservation*(123), 249–268.

Woodward, F. & Diament, A. (1991). Functional Approaches to Predicting the Ecological Effects of Global Change. *Functional Ecology, 5*(2), 202-212.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. & Villar, R. (2004). The worldwide leaf economics spectrum. *Nature, 428*, 821-827. doi:10.1038/nature02403

WSA. (2007). Fahrrinnenanpassung Unter- und Außenelbe. Projektbüro Fahrrinnenanpassung, Wasser- und Schifffahrtsamt Hamburg.

WSA. (2011). Wasserstraßen- und Schifffahrtsamt Hamburg. Statistik. http://www.wsa-hamburg.wsv.de/schifffahrt/Nautik/Statistik/index.html (acceced on: 02.10.2020).

Yan, B., Ji, Z., Fan, B., Wang, X., He, G., Shi, L. & Liu, G. (2016). Plants adapted to nutrient limitation allocate less biomass intostems in an arid-hot grassland. *New Phytologist, 211*, 1232-1240.

Yarrow, M. M. & Marín, V. H. (2007). Toward Conceptual Cohesiveness: a Historical Analysis ofthe Theory and Utility of Ecological Boundaries and Transition Zones. *Ecosystems, 10*, 462–476.

Zak, D. R., Holmes, W. E., White, D. C., Peacock, A. D. & Tilman, D. (2003). Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology, 84*(8), 2042-2050.

Zedler, J. B., Winfield, T. & Williams, P. (1980). Salt marsh productivity with natural and altered tidal circulation. *Oecologia, 44*(2), 236–240.

Zhu, G., Yuan, C., Di, G., Zhang, M., Ni, L., Cao, T., Fang, R. & Wu, G. (2018). Morphological and biomechanical response to eutrophication and hydrodynamic stresses. *Sci Total Environ, 622-623*, 421-435. doi:10.1016/j.scitotenv.2017.11.322

Zhu, Z., Yang, Z. & Bouma, T. J. (2019). Biomechanical properties of marsh vegetation in space and time: effects of salinity, inundation and seasonality. *Annals of Botany*(XX), 1-13.

Zonneveld, I. (1960). De Brabantse Biesbosch. *Centrum voor Landbouwpublikaties. Wageningen*.

Appendices

List of figures

List of tables

Appendix Chapter 6

Appendix 6. 1 Description of extrapolation of wave measurements to all plots

For the locations where wave heights were measured, mean wave heights were calculated for classes with different water depths (<0.5 m, 0.5-1.0 m, 1.0-1.5 m and >1.5 m). For each water depth class, the mean wave heights calculated for the different measuring locations were tested for significant regressions in relation to normalized elevation of the measuring locations or distance to marsh edge of the locations. No significant regressions were found for wave heights in the water depth class of 1.0-1.5 m. For the water depth class >1.5 m, significant relationships were found with the distance from marsh edge ($R^2=0.97$, $p=0.02$). For the water depth class between 0.5-1.0 m, the mean wave height was significantly related to the normalized elevation ($R^2=0.33$, $p=0.05$), while for shallow water levels (0-0.5 m), it was significantly related to the distance from marsh edge ($R^2=0.96$, $p<0.001$). The resulting regression equations were used to calculate the mean wave height (Hmean) for the three water depth classes on plot basis:

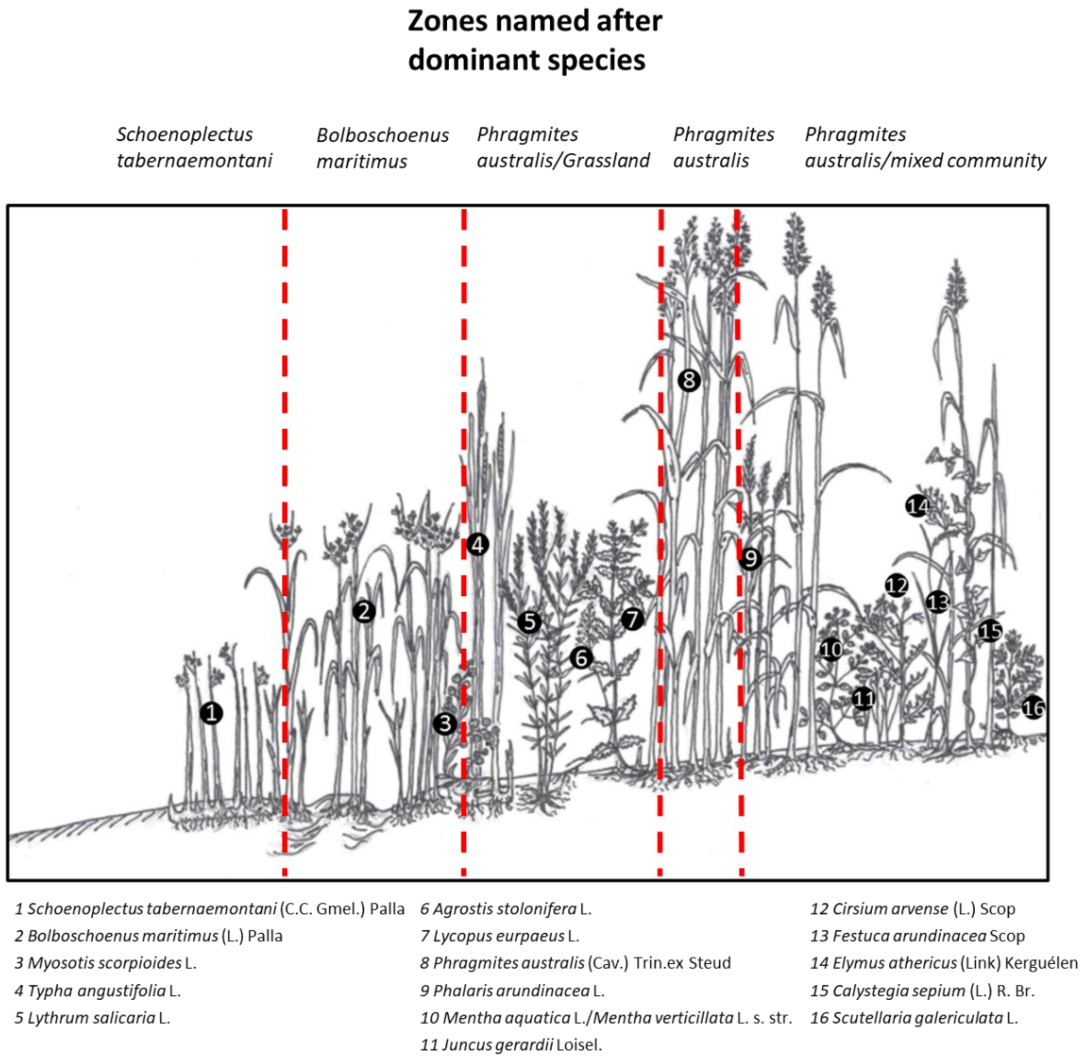
Hmean water level >1.5 m = 0.0015295*distance to marsh edge + 0.0768710

Hmean water level 0.5-1.0 m = 0.015331*normalized elevation + 0.043411

Hmean water level 1.0-1.5 not significant

Hmean water level <0.5 m = 0.0002325*distance to marsh edge + 0.04165

In the RLQ-analysis, the mean wave height in the water depth classes 0.5-1.0 m and >1.5 m correlated strongly and was combined using a PCA and its scores on the first axis.



Appendix 6. 2: Selected plant species and their position along the elevational gradient, classified in vegetation zones based on their highest frequency. Mentha aquatica and M. verticillata grew in the Phragmites/mixed community-zone and were depicted as one species. ©T. Schulte Ostermann

Appendix 6. 3: Overview of equations used to calculate flexural stiffness and Young´s modulus for different stem geometries. For more information see (Coops & Van der Velde, 1996a; Schneider, 1998; Hamann & Puijalon, 2013; Rupprecht, Möller, et al., 2015; Vuik et al., 2018).

	CIRCULAR, FILLED STEMS	CIRCULAR, HOLLOW STEMS	TRIANGULAR STEMS	SQUARE STEMS
SECOND MOMENT OF AREA	$I = \pi * \frac{d^4}{64}$	$I = \frac{\pi}{4} * ({r_{out}}^4 - {r_{inn}}^4)$	$I \ = \frac{\sqrt{3}}{96} * bv^4$	$I = \frac{b * b^3}{12}$
d = diameter	r_{out} = outer stem radius	r_{inn} = inner stem radius	bv = basal triangle lenght	b= side length of the stem

FLEXURAL STIFFNESS ALL STEMS	$EI = \frac{s^3}{48} * \frac{F}{D}$	s = support distance $\frac{F}{D}$ = force/deflection slope
YOUNGS MODULUS ALL STEMS	$E = \frac{EI}{I}$	

The second moment of area I for round hollow stems (such as *P. australis*) is calculated as $I = \frac{\pi}{4} * (r_{out}^4 - r_{inn}^4)$ where r = radius, out = outer and inn = inner. For round filled stems (like *S. tabernaemontani*) the second moment of area is calculated through $I = \pi * \frac{d^4}{64}$, with d being the diameter. For triangular stems (like *B. maritimus)* the equation is: $I = \frac{\sqrt{3}}{96} * bv^4$ where bv is the basal length of the triangle. For square stems (such as *M. aquatica*) the second moment of area is calculated as $I = b * \frac{b^3}{12}$, with b being the side length. The flexural stiffness *EI* can be calculated for all stems as: $EI = \frac{s^3}{48} * \frac{F}{D}$, with s being the support distance set on the Instron (which was set to at least 15x stem diameter, following Usherwood et al., 1997) and $\frac{F}{D}$ the force/deflection slope calculated during the bending tests; this refers to the initial straight part of the slope. Young´s modulus can then be derived for all stems with this equation: $= \frac{EI}{I}$.

Appendix 6. 4: Table containing information on trait plant species, numbers of individuals collected per zone and site. The vegetation zones are based on and named after their dominant species. *Balje = BAL, Hollerwettern = HW, Krautsand = KS*

Phragmites australis/ mixed community	*Phragmites australis*	*Bolboschoenus maritimus*	*Schoenoplectus tabernaemontani*	Number of trait plant individuals collected per site	Zone (named after dominant species)	Trait species
3 KS, 3 BAL	3 BAL	2 KS			*Agrostis stolonifera*	
		3 KS, 4 BAL, 4 HW			*Bolboschoenus maritimus*	
2 KS, 2 BAL, 2 HW	2 KS, 1 BAL, 1 HW				*Calystegia sepium*	
8 BAL	3 BAL				*Cirsium arvense*	
10 BAL					*Elymus athericus*	
9 BAL	2 BAL				*Festuca arundinacea*	
7 BAL	3 BAL				*Juncus gerardii*	
5 KS, 5 BAL					*Lycopus europaeus*	
4 HW		6 HW			*Lythrum salicaria*	
7 BAL					*Mentha aquatica*	
7 KS					*Mentha verticillata*	
10 KS					*Myosotis scorpioides*	
2 KS, 3 BAL	2 KS	3 HW			*Phalaris arundinacea*	
1 BAL, 1 HW	3 KS, 3 HW, 2 BAL				*Phragmites australis*	
		2 KS	4 KS, 7 BAL, 5 HW		*Schoenoplectus tabernaemontani*	
10 HW					*Scutellaria galericulata*	
6 KS	4 HW				*Typha angustifolia*	

*Appendix 6. 5: Details for linear mixed models with the site as a random effect. Number of obs: 84, groups: site, 3, degrees of freedom determined with Kenward-Roger-method, confidence level 95%, adjustment method for p value = mvt, p=0.05. Displayed are standard deviation, standard error, t-values, significance levels (*p < 0.05, **p < 0.01, ***p < 0.001) and degrees of freedom.*

Soil salinity							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	0.24	0.49					
Residual	0.27	0.52					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	0.89	0.30	2.49	2.94	0.08	.	
Vegeation zone							
Phragmites	-0.21	0.16	78	-1.33	0.19		
Phragmites/mixed	-0.39	0.16	78	-2.44	0.02	*	
Schoenoplectus	-0.13	0.16	78	-0.80	0.43		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	0.89	0.30	2.49	-0.80	2.58		
Phragmites	0.68	0.30	2.49	-1.01	2.37		
Phragmites/mixed	0.50	0.30	2.49	-1.19	2.19		
Schoenoplectus	0.76	0.30	2.49	-0.93	2.45		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	0.21	0.16	78	1.33	0.55
Bolboschoenus	-	*Phragmites/mixed*	0.39	0.16	78	2.44	0.08
Bolboschoenus	-	*Schoenoplectus*	0.13	0.16	78	0.80	0.85
Phragmites	-	*Phragmites/mixed*	0.18	0.16	78	1.11	0.68
Phragmites	-	*Schoenoplectus*	-0.08	0.16	78	-0.53	0.95
Phragmites/mixed	-	*Schoenoplectus*	-0.26	0.16	78	-1.64	0.36
$CaCO_3$							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	87.33	9.35					
Residual	94.44	9.72					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	46.57	5.80	2.47	8.03	0.008	**	
Vegeation zone							
Phragmites	-8.33	3.0	78	-2.78	0.007	**	
Phragmites/mixed	-18.61	3.0	78	-6.20	2.47E-08	***	
Schoenoplectus	-1.15	3.0	78	-0.38	0.70		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	46.6	5.8	2.47	14.24	78.9		
Phragmites	38.2	5.8	2.47	5.91	70.6		
Phragmites/mixed	28	5.8	2.47	-4.37	60.3		
Schoenoplectus	45.4	5.8	2.47	13.09	77.8		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	8.33	3	78	2.78	0.03
Bolboschoenus	-	*Phragmites/mixed*	18.6	3	78	6.20	<.0001
Bolboschoenus	-	*Schoenoplectus*	1.15	3	78	0.38	0.98
Phragmites	-	*Phragmites/mixed*	10.28	3	78	3.43	0.006
Phragmites	-	*Schoenoplectus*	-7.18	3	78	-2.39	0.09
Phragmites/mixed	-	*Schoenoplectus*	-17.46	3	78	-5.82	<.0001
Clay							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	10.77	3.28					
Residual	489.44	22.12					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	54.88	5.19	14.99	10.58	2.38E-08	***	

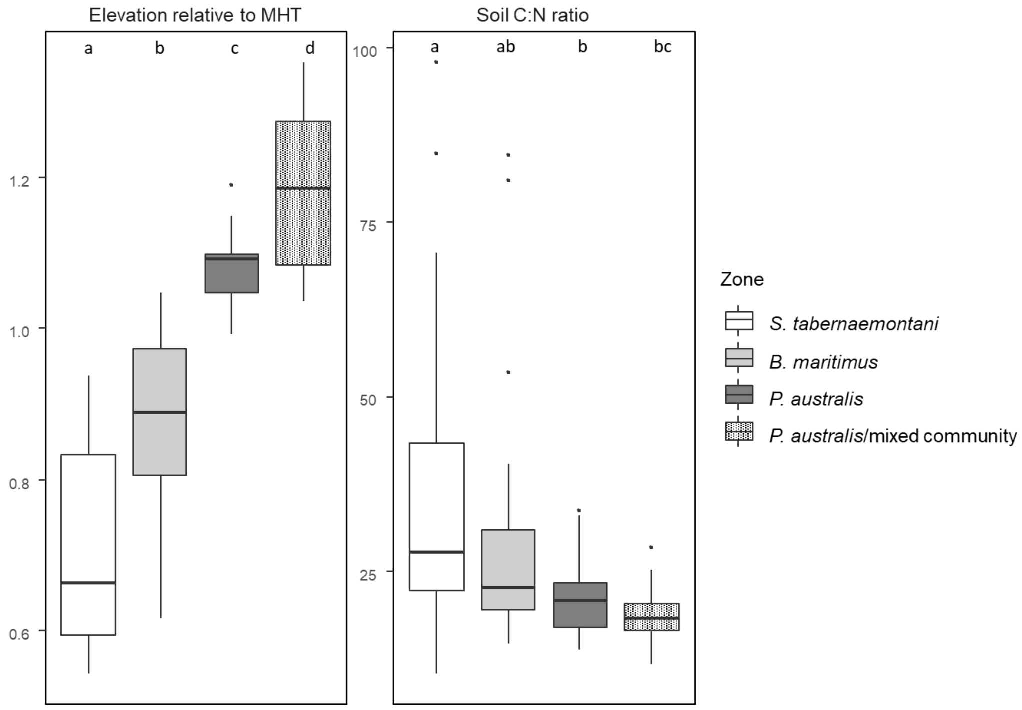
Vegeation zone							
Phragmites	2.84	6.83	78	0.42	0.68		
Phragmites/mixed	9.73	6.83	78	1.43	0.16		
Schoenoplectus	-2.87	6.83	78	-0.42	0.68		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	54.9	5.19	15	40.4	69.4		
Phragmites	57.7	5.19	15	43.2	72.2		
Phragmites/mixed	64.6	5.19	15	50.1	79.1		
Schoenoplectus	52	5.19	15	37.5	66.5		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	-2.84	6.83	78	-0.415	0.98
Bolboschoenus	-	*Phragmites/mixed*	-9.73	6.83	78	-1.426	0.49
Bolboschoenus	-	*Schoenoplectus*	2.87	6.83	78	0.42	0.98
Phragmites	-	*Phragmites/mixed*	-6.9	6.83	78	-1.01	0.74
Phragmites	-	*Schoenoplectus*	5.7	6.83	78	0.835	0.84
Phragmites/mixed	-	*Schoenoplectus*	12.6	6.83	78	1.846	0.26
Sand							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	19094	138.2					
Residual	28603	169.1					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	407.44	87.90	2.65	4.64	0.02	*	
Vegeation zone							
Phragmites	-87.52	52.19	78	-1.68	0.10	.	
Phragmites/mixed	-26.29	52.19	78	-0.50	0.62		
Schoenoplectus	130.42	52.19	78	2.50	0.01	*	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	407	87.9	2.65	-96.5	911		
Phragmites	320	87.9	2.65	-184	824		
Phragmites/mixed	381	87.9	2.65	-122.8	885		
Schoenoplectus	538	87.9	2.65	33.9	1042		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	87.5	52.2	78	1.68	0.34
Bolboschoenus	-	*Phragmites/mixed*	26.3	52.2	78	0.50	0.96
Bolboschoenus	-	*Schoenoplectus*	-130.4	52.2	78	-2.50	0.07
Phragmites	-	*Phragmites/mixed*	-61.2	52.2	78	-1.17	0.65
Phragmites	-	*Schoenoplectus*	-217.9	52.2	78	-4.18	0.0005
P.australi/mixed	-	*Schoenoplectus*	-156.7	52.2	78	-3.00	0.02
Soil P							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	584.9	24.19					
Residual	1730.1	41.59					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	92.37	16.65	3.30	5.55	0.009	**	
Vegeation zone							
Phragmites	-29.99	12.84	78	-2.34	0.02	*	
Phragmites/mixed	-5.99	12.84	78	-0.47	0.64		
Schoenoplectus	-2.62	12.84	78	-0.20	0.84		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	92.4	16.7	3.3	20.96	164		
Phragmites	62.4	16.7	3.3	-9.03	134		
Phragmites/mixed	86.4	16.7	3.3	14.97	158		
Schoenoplectus	89.8	16.7	3.3	18.34	161		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	29.99	12.8	78	2.34	0.10
Bolboschoenus	-	*Phragmites/mixed*	5.99	12.8	78	0.47	0.97

Bolboschoenus	-	*Schoenoplectus*	2.62	12.8	78	0.20	1.0
Phragmites	-	*Phragmites/mixed*	-24	12.8	78	-1.87	0.25
Phragmites	-	*Schoenoplectus*	-27.37	12.8	78	-2.13	0.15
Phragmites/mixed	-	*Schoenoplectus*	-3.37	12.8	78	-0.26	0.99
Soil K							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	2492	49.92					
Residual	1457	38.17					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	115.62	30.00	2.25	3.85	0.05	.	
Vegeation zone							
Phragmites	-16.21	11.78	78	-1.38	0.17		
Phragmites/mixed	11.42	11.78	78	0.97	0.34		
Schoenoplectus	-10.15	11.78	78	-0.86	0		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	115.6	30	2.25	-42.9	274		
Phragmites	99.4	30	2.25	-59.2	258		
Phragmites/mixed	127	30	2.25	-31.5	286		
Schoenoplectus	105.5	30	2.25	-53.1	264		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	16.21	11.8	78	1.38	0.52
Bolboschoenus	-	*Phragmites/mixed*	-11.42	11.8	78	-0.97	0.77
Bolboschoenus	-	*Schoenoplectus*	10.15	11.8	78	0.86	0.82
Phragmites	-	*Phragmites/mixed*	-27.63	11.8	78	-2.35	0.10
Phragmites	-	*Schoenoplectus*	-6.07	11.8	78	-0.52	0.96
Phragmites.mixed	-	*Schoenoplectus*	21.56	11.8	78	1.83	0.27
$\mathrm{N}_{\mathrm{min}}$							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	3.54	1.88					
Residual	37.13	6.09					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	8.06	1.72	6.50	4.69	0.003	**	
Vegeation zone							
Phragmites	-0.80	1.88	78	-0.43	0.67		
Phragmites/mixed	5.49	1.88	78	2.92	0.005	**	
Schoenoplectus	-2.31	1.88	78	-1.23	0.22		
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	8.06	1.72	6.5	2.37	13.7		
Phragmites	7.26	1.72	6.5	1.57	12.9		
Phragmites/mixed	13.55	1.72	6.5	7.86	19.2		
Schoenoplectus	5.75	1.72	6.5	0.06	11.4		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	0.80	1.88	78	0.43	0.97
Bolboschoenus	-	*Phragmites/mixed*	-5.49	1.88	78	-2.92	0.02
Bolboschoenus	-	*Schoenoplectus*	2.31	1.88	78	1.23	0.61
Phragmites	-	*Phragmites/mixed*	-6.29	1.88	78	-3.34	0.007
Phragmites	-	*Schoenoplectus*	1.51	1.88	78	0.8	0.85
Phragmites/mixed	-	*Schoenoplectus*	7.79	1.88	78	4.15	0.0004
PAR							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	58.22	7.63					
Residual	102.35	10.12					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	5.80	4.93	2.77	1.18	0.33		
Vegeation zone							

Phragmites	-3.00	3.12	78	-0.96	0.34		
Phragmites/mixed	-3.58	3.12	78	-1.15	0.26		
Schoenoplectus	32.63	3.12	78	10.45	<2e-16	***	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	5.8	4.93	2.77	-14.5	26.1		
Phragmites	2.79	4.93	2.77	-17.5	23.1		
Phragmites/mixed	2.22	4.93	2.77	-18.1	22.5		
Schoenoplectus	38.43	4.93	2.77	18.2	58.7		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	3.00	3.12	78	0.96	0.77
Bolboschoenus	-	*Phragmites/mixed*	3.58	3.12	78	1.15	0.66
Bolboschoenus	-	*Schoenoplectus*	-32.63	3.12	78	-10.45	<.0001
Phragmites	-	*Phragmites/mixed*	0.58	3.12	78	0.19	1.0
Phragmites	-	*Schoenoplectus*	-35.63	3.12	78	-11.41	<.0001
Phragmites/mixed	-	*Schoenoplectus*	-36.21	3.12	78	-11.60	<.0001
Inundation							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	9.54	3.09					
Residual	8.56	2.93					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	10.33	1.89	2.39	5.45	0.021	*	
Vegeation zone							
Phragmites	-5.58	0.90	78	-6.19	2.67E-08	***	
Phragmites/mixed	-7.61	0.90	78	-8.43	1.38E-12	***	
Schoenoplectus	4.72	0.90	78	5.22	1.42E-06	***	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	10.33	1.89	2.39	-0.09	20.8		
Phragmites	4.75	1.89	2.39	-5.68	15.2		
Phragmites/mixed	2.72	1.89	2.39	-7.70	13.1		
Schoenoplectus	15.05	1.89	2.39	4.62	25.5		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	5.58	0.903	78	6.19	<.0001
Bolboschoenus	-	*Phragmites/mixed*	7.61	0.903	78	8.43	<.0001
Bolboschoenus	-	*Schoenoplectus*	-4.72	0.903	78	-5.22	<.0001
Phragmites	-	*Phragmites/mixed*	2.03	0.903	78	2.25	0.1202
Phragmites	-	*Schoenoplectus*	-10.3	0.903	78	-11.41	<.0001
Phragmites/mixed	-	*Schoenoplectus*	-12.32	0.903	78	-13.65	<.0001
Wave height at water level >1.5 m							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	0.003	0.05					
Residual	0.003	0.05					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	0.14	0.03	2.42	4.25	0.04	*	
Vegeation zone							
Phragmites	0.07	0.02	78	4.72	1.01E-05	***	
Phragmites/mixed	0.12	0.02	78	7.79	2.38E-11	***	
Schoenoplectus	-0.05	0.02	78	-3.16	0.002	**	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	0.14	0.03	2.42	-0.04	0.31		
Phragmites	0.21	0.03	2.42	0.03	0.39		
Phragmites/mixed	0.26	0.03	2.42	0.08	0.43		
Schoenoplectus	0.09	0.03	2.42	-0.09	0.26		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	-0.07	0.02	78	-4.72	0.0001
Bolboschoenus	-	*Phragmites/mixed*	-0.12	0.02	78	-7.79	<.0001
Bolboschoenus	-	*Schoenoplectus*	0.05	0.02	78	3.16	0.012

Phragmites	-	*Phragmites/mixed*	-0.05	0.02	78	-3.07	0.02
Phragmites	-	*Schoenoplectus*	0.12	0.02	78	7.88	<.0001
Phragmites/mixed	-	*Schoenoplectus*	0.17	0.02	78	10.95	<.0001
Wave height at water level 0.5-1.0 m							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	5.99E-07	0.0008					
Residual	2.14E-06	0.001					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	0.06	0.0005	3.57	103.68	2.39E-07	***	
Vegeation zone							
Phragmites	0.003	0.0005	78	6.78	2.06E-09	***	
Phragmites/mixed	0.005	0.0005	78	10.32	3.11E-16	***	
Schoenoplectus	-0.003	0.0005	78	-6.10	3.81E-08	***	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	0.06	0.0005	3.57	0.06	0.06		
Phragmites	0.06	0.0005	3.57	0.06	0.06		
Phragmites/mixed	0.06	0.0005	3.57	0.06	0.06		
Schoenoplectus	0.05	0.0005	3.57	0.05	0.06		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	-0.003	0.0005	78	-6.78	<.0001
Bolboschoenus	-	*Phragmites/mixed*	-0.005	0.0005	78	-10.32	<.0001
Bolboschoenus	-	*Schoenoplectus*	0.003	0.0005	78	6.10	<.0001
Phragmites	-	*Phragmites/mixed*	-0.002	0.0005	78	-3.54	0.004
Phragmites	-	*Schoenoplectus*	0.006	0.0005	78	12.88	<.0001
Phragmites/mixed	-	*Schoenoplectus*	0.007	0.0005	78	16.42	<.0001
Wave height at water level 0.0- 0.5 m							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	6.15E-05	0.008					
Residual	5.99E-05	0.008					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	0.03	0.005	2.42	6.79	0.01	*	
Vegeation zone							
Phragmites	-0.01	0.002	78	-4.72	1.01E-05	***	
Phragmites/mixed	-0.02	0.002	78	-7.79	2.38E-11	***	
Schoenoplectus	0.008	0.002	78	3.16	0.002	**	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	0.03	0.005	2.42	0.006	0.06		
Phragmites	0.02	0.005	2.42	-0.005	0.05		
Phragmites/mixed	0.01	0.005	2.42	-0.01	0.04		
Schoenoplectus	0.04	0.005	2.42	0.01	0.07		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	0.01	0.002	78	4.72	<.0001
Bolboschoenus	-	*Phragmites/mixed*	0.02	0.002	78	7.79	<.0001
Bolboschoenus	-	*Schoenoplectus*	-0.008	0.002	78	-3.16	0.01
Phragmites	-	*Phragmites/mixed*	0.007	0.002	78	3.07	0.02
Phragmites	-	*Schoenoplectus*	-0.02	0.002	78	-7.88	<.0001
Phragmites/mixed	-	*Schoenoplectus*	-0.03	0.002	78	-10.95	<.0001
Rel.elevation							
Random effects:							
Groups Name	**Variance**	**Std.Dev.**					
Site (Intercept)	0.003	0.051					
Residual	0.009	0.095					
Fixed effects:	**Estimate**	**Std. Error**	**df**	**t value**	**Pr(>|t|)**		
(Intercept)	0.88	0.036	3.575	24.63	4.04e-05	***	
Vegeation zone							
Phragmites	0.12	0.029	78	6.78	2.06e-09	***	

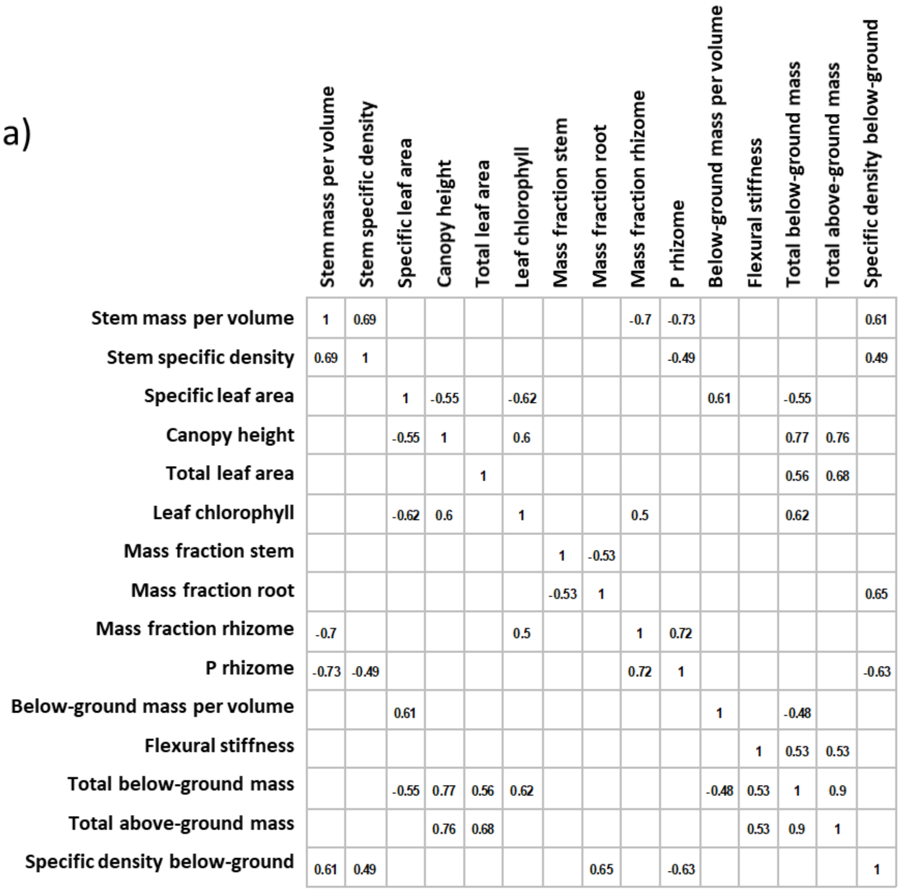
Phragmites/mixed	0.30	0.029	78	10.32	3.11e-16	***	
Schoenoplectus	-0.18	0.029	78	-6.10	3.81e-08	***	
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	0.88	0.036	3.57	0.73	1.04		
Phragmites	1.08	0.036	3.57	0.93	1.24		
Phragmites/mixed	1.19	0.036	3.57	1.03	1.34		
Schoenoplectus	0.70	0.036	3.57	0.55	0.86		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	-0.2	0.029	78	-6.78	<.0001
Bolboschoenus	-	*Phragmites/mixed*	-0.30	0.029	78	-10.32	<.0001
Bolboschoenus	-	*Schoenoplectus*	0.18	0.029	78	6.10	<.0001
Phragmites	-	*Phragmites/mixed*	-0.10	0.029	78	-3.54	0.004
Phragmites	-	*Schoenoplectus*	0.38	0.029	78	12.88	<.0001
Phragmites/mixed	-	*Schoenoplectus*	0.48	0.029	78	16.42	<.0001
C/N soil							
Coefficients:	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**			
(Intercept)	30.84	3.34	9.22	3.20E-14	***		
Vegeation zone							
Phragmites	-9.56	4.73	-2.02	0.046	*		
Phragmites/mixed	-12.03	4.73	-2.55	0.013	*		
Schoenoplectus	7.00	4.73	1.48	0.143			
Estim. marginal means	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**		
Bolboschoenus	30.8	3.34	80	22.3	39.3		
Phragmites	21.3	3.34	80	12.8	29.8		
Phragmites/mixed	18.8	3.34	80	10.3	27.3		
Schoenoplectus	37.8	3.34	80	29.3	46.3		
Pairwise differences of contrast			**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Bolboschoenus	-	*Phragmites*	9.56	4.73	80	2.02	0.19
Bolboschoenus	-	*Phragmites/mixed*	12.03	4.73	80	2.55	0.06
Bolboschoenus	-	*Schoenoplectus*	-7	4.73	80	-1.48	0.46
Phragmites	-	*Phragmites/mixed*	2.47	4.73	80	0.52	0.96
Phragmites	-	*Schoenoplectus*	-16.56	4.73	80	-3.50	0.004
Phragmites/mixed	-	*Schoenoplectus*	-19.03	4.73	80	-4.03	0.0008



Appendix 6. 6: Relative elevation (normalized by the tidal range) and soil C:N ratios of the four zones: Schoenoplectus, Bolboschoenus, Phragmites and Phragmites/mixed community. Different letters indicate significant differences, p<0.05 (t-test).

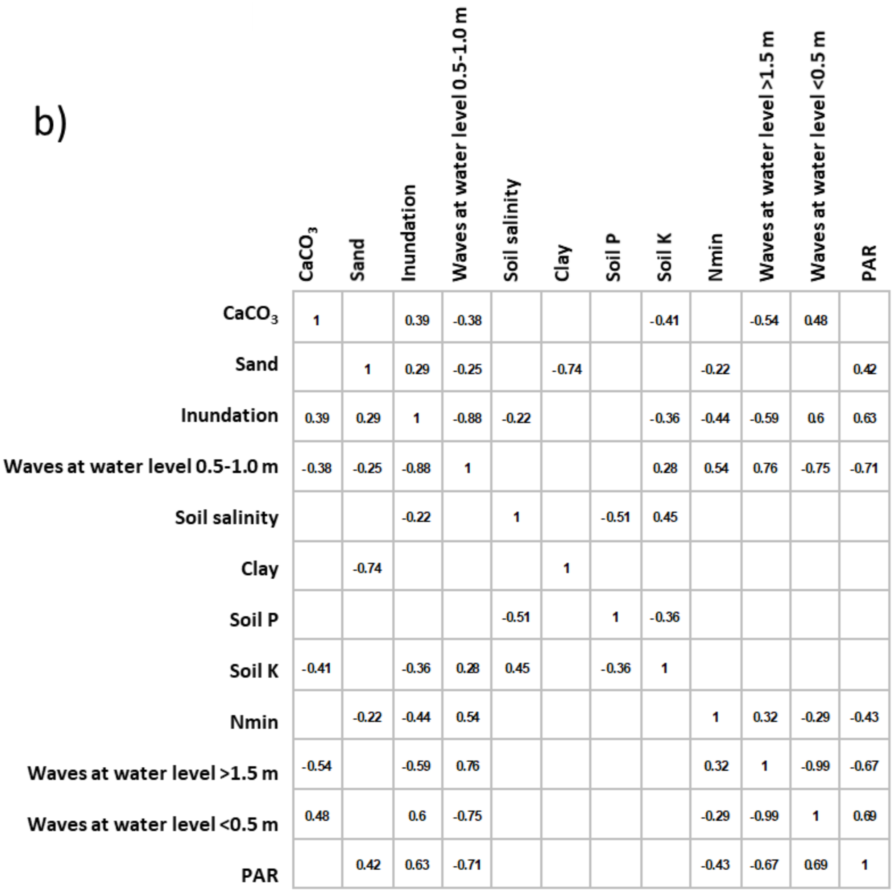
Appendix 6. 7: Correlations of a) mean trait variables (per species), b) environmental variables.

a)



	Stem mass per volume	Stem specific density	Specific leaf area	Canopy height	Total leaf area	Leaf chlorophyll	Mass fraction stem	Mass fraction root	Mass fraction rhizome	P rhizome	Below-ground mass per volume	Flexural stiffness	Total below-ground mass	Total above-ground mass	Specific density below-ground
Stem mass per volume	1	0.69							-0.7	-0.73					0.61
Stem specific density	0.69	1								-0.49					0.49
Specific leaf area			1	-0.55		-0.62					0.61		-0.55		
Canopy height			-0.55	1		0.6							0.77	0.76	
Total leaf area					1								0.56	0.68	
Leaf chlorophyll			-0.62	0.6		1			0.5				0.62		
Mass fraction stem							1	-0.53							
Mass fraction root							-0.53	1							0.65
Mass fraction rhizome	-0.7					0.5			1	0.72					
P rhizome	-0.73	-0.49							0.72	1					-0.63
Below-ground mass per volume			0.61								1		-0.48		
Flexural stiffness												1	0.53	0.53	
Total below-ground mass			-0.55	0.77	0.56	0.62					-0.48	0.53	1	0.9	
Total above-ground mass				0.76	0.68							0.53	0.9	1	
Specific density below-ground	0.61	0.49						0.65		-0.63					1

b)



	$CaCO_3$	Sand	Inundation	Waves at water level 0.5-1.0 m	Soil salinity	Clay	Soil P	Soil K	Nmin	Waves at water level >1.5 m	Waves at water level <0.5 m	PAR
$CaCO_3$	1		0.39	-0.38				-0.41		-0.54	0.48	
Sand		1	0.29	-0.25		-0.74			-0.22			0.42
Inundation	0.39	0.29	1	-0.88	-0.22			-0.36	-0.44	-0.59	0.6	0.63
Waves at water level 0.5-1.0 m	-0.38	-0.25	-0.88	1				0.28	0.54	0.76	-0.75	-0.71
Soil salinity			-0.22		1		-0.51	0.45				
Clay		-0.74				1						
Soil P					-0.51		1	-0.36				
Soil K	-0.41		-0.36	0.28	0.45		-0.36	1				
Nmin		-0.22	-0.44	0.54					1	0.32	-0.29	-0.43
Waves at water level >1.5 m	-0.54		-0.59	0.76					0.32	1	-0.99	-0.67
Waves at water level <0.5 m	0.48		0.6	-0.75					-0.29	-0.99	1	0.69
PAR		0.42	0.63	-0.71					-0.43	-0.67	0.69	1

Appendix 6. 8: Species mean N:P ratios in leaves, stems, above- and belowground biomass.

SPECIES	N:P LEAF	N:P STEM	N:P ABOVE-GROUND BIOMASS	N:P BELOW-GROUND BIOMASS
Agrostis stolonifera	14.64	4.19	9.03	5.99
Bolboschoenus maritimus	14.79	5.06	10.16	2.54
Calystegia sepium	10.76	3.77	6.85	7.55
Cirsium arvense	9.15	2.26	4.48	5.70
Elymus athericus	9.16	3.54	6.19	8.62
Festuca arundinacea	9.31	2.80	5.92	7.49
Juncus gerardii	12.17	5.93	8.81	5.39
Lycopus europaeus	7.52	2.87	5.15	8.46
Lythrum salicaria	13.62	6.06	10.93	7.89
Mentha aquatica	6.59	2.22	4.31	7.78
Mentha verticillata	8.76	3.85	6.45	6.52
Myosotis scorpioides	8.42	6.20	7.61	10.22
Phalaris arundinacea	15.39	5.65	10.46	6.79
Phragmites australis	18.31	11.77	16.18	10.03
Schoenoplectus tabernaemontani	7.31	7.31	3.66	3.86
Scutellaria galericulata	13.82	3.92	8.16	9.17
Typha angustifolia	16.31	8.72	13.56	7.29

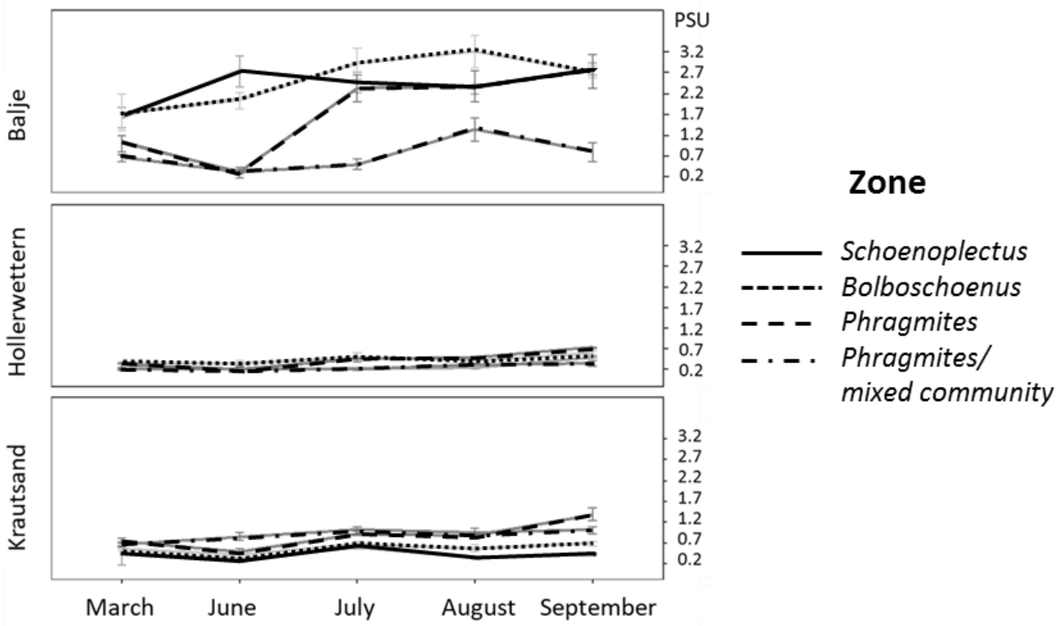
Appendix 6. 9: Species mean trait values with standard deviation and unit sorted alphabetically by variable name and species.

Mentha verticillata	*Mentha aquatica*	*Lythrum salicaria*	*Lycopus europaeus*	*Juncus gerardii*	*Festuca arundinacea*	*Elymus athericus*	*Cirsium arvense*	*Calystegia sepium*	*Bolboschoenus maritimus*	*Agrostis stolonifera*	Species		
1.02	1.13	1.23	1.54	1.1	1.08	1.1	1.05	1.16	0.91	1.74	Mean	belowground mass per volume	Trait variable
0.12	0.3	0.29	1.19	0.16	0.17	0.09	0.04	0.21	0.06	0.77	SD	$\mathrm{g_{fresh\ mass}\ cm^{-3}}$	Unit
105.43	60.43	127	95.3	48.8	97.73	110.3	94.5	126.4	161.9	110.1	Mean	canopy height	Trait variable
19.81	14.8	33.35	32.26	9.67	17.81	14.02	9.69	47.49	23.3	16.35	SD	cm	Unit
0.16	0.15	0.3	0.17	-	0.23	0.15	0.21	0.21	0.35	0.16	Mean	chlorophyll	Trait variable
0.01	0.02	0.05	0.03	-	0.06	0.05	0.04	0.03	0.12	0.03	SD	µg mm^{-2}	Unit
14.72	33.1	110.69	26.51	-	41.03	8.98	18401.2	0.26	135.84	2.49	Mean	flexural stiffness	Trait variable
8.52	13.63	82.34	24.28	-	14.59	5.65	11112.2	0.21	53.27	1.37	SD	N mm²	Unit
0.08	0.11	-	0.1	0.14	0.1	0.07	-	-	0.14	-	Mean	mass fraction (MF) rhizome	Trait variable
0.02	0.03	-	0.04	0.04	0.05	0.03	-	-	0.05	-	SD		Unit
0.02	0.07	0.21	0.05	0.19	0.11	0.06	0.1	0.24	0.09	0.06	Mean	mass fraction (MF) root	Trait variable
0.01	0.03	0.2	0.02	0.05	0.06	0.02	0.02	0.13	0.03	0.04	SD		Unit
0.57	0.4	0.41	0.5	0.38	0.6	0.66	0.48	0.38	0.53	0.75	Mean	mass fraction (MF) stem	Trait variable
0.06	0.05	0.1	0.08	0.06	0.07	0.03	0.04	0.1	0.07	0.08	SD		Unit
1.92	1.37	-	1.36	1.55	0.82	0.82	-	-	2.14	-	Mean	P content in rhizome	Trait variable
0.8	0.51	-	0.35	0.57	0.12	0.3	-	-	1.5	-	SD	g kg^{-1}	Unit
0.99	1	-	1	1.03	1.07	1.09	-	-	0.86	-	Mean	rhizome mass per volume	Trait variable
0.02	0.09	-	0.04	0.04	0.09	0.08	-	-	0.08	-	SD	$\mathrm{g_{fresh\ mass}\ cm^{-3}}$	Unit
0.15	0.18	0.78	0.31	0.34	0.15	0.25	0.17	0.25	0.09	0.22	Mean	root specific density	Trait variable
0.05	0.1	1.54	0.4	0.15	0.04	0.07	0.05	0.05	0.02	0.13	SD	$\mathrm{mg_{dry\ mass}\ cm^{-3}}$	Unit
1.05	1.26	1.23	2.08	1.17	1.08	1.12	1.05	1.16	0.96	1.74	Mean	root mass per volume	Trait variable
0.24	0.55	0.29	2.38	0.3	0.27	0.2	0.04	0.21	0.08	0.77	SD	$\mathrm{g_{fresh\ mass}\ cm^{-3}}$	Unit
0.13	0.17	0.78	0.22	0.31	0.22	0.33	0.17	0.25	0.13	0.22	Mean	specific density belowground	Trait variable
0.03	0.06	1.54	0.2	0.09	0.07	0.04	0.05	0.05	0.02	0.13	SD	g	Unit
29.28	39.14	22.41	39.66	13.95	19.04	16.45	13.71	33.21	13.54	34.7	Mean	specific leaf area	Trait variable
7.33	12.49	6.61	6.59	2.29	3.65	2.04	1.76	8.56	1.16	7.91	SD	mm^{2} mg^{-1}	Unit
0.19	0.16	0.26	0.18	0.27	0.24	0.36	0.19	0.18	0.15	0.32	Mean	stem specific density	Trait variable
0.03	0.02	0.04	0.03	0.04	0.03	0.05	0.02	0.01	0.01	0.04	SD	$\mathrm{mg_{dry\ mass}\ cm^{-3}}$	Unit
0.94	0.95	1.06	0.92	1.04	1.01	1.07	1	1.04	0.81	1.03	Mean	stem mass per volume	Trait variable
0.06	0.05	0.03	0.08	0.05	0.02	0.02	0.07	0.04	0.07	0.09	SD	$\mathrm{g_{fresh\ mass}\ cm^{-3}}$	Unit
9.85	1.3	19.52	3.74	0.27	3.55	2.13	10.4	4.92	6.7	1.77	Mean	total aboveground biomass	Trait variable
6.5	0.52	6.34	1.51	0.09	1.22	0.58	2.02	3.03	2.03	0.7	SD	g	Unit
1.28	0.28	5.9	0.7	0.13	0.91	0.32	1.08	1.26	1.92	0.11	Mean	total belowground biomass	Trait variable
1.11	0.15	7.33	0.38	0.03	0.31	0.1	0.22	0.52	0.45	0.07	SD	g	Unit
11.14	1.58	25.42	4.44	0.4	4.45	2.44	11.49	6.18	8.62	1.88	Mean	total biomass	Trait variable
7.58	0.64	6.01	1.83	0.11	1.31	0.64	2.14	3.1	2.32	0.71	SD	g	Unit
67149.11	17837.3	108378.	32525.12	883.65	6910.13	3832.48	61313.6	61282.61	14492.24	7036.14	Mean	total leaf area	Trait variable
48354.3	9244.29	63045.6	11972.34	239.27	3423.08	1169.36	11012.8	52135.95	4872.77	4927.54	SD	mm²	Unit

Continuing table Appendix 6.9

Typha angustifolia	*Scutellaria galericulata*	*Schoenoplectus tabernaemontani*	*Phragmites australis*	*Phalaris arundinacea*	*Myosotis scorpioides*	Species		
1.04	1.63	0.9	0.95	1.03	0.9	Mean	belowground mass per volume	Trait variable
0.07	0.7	0.11	0.06	0.14	0.23	SD	g$_{\text{fresh mass}}$ cm^{-3}	Unit
222.1	42.6	113.32	240.8	176	64.9	Mean	canopy height	Trait variable
16.57	17.91	38.87	32.11	17.08	19.28	SD	cm	Unit
0.27	0.19	0.38	0.32	0.29	0.08	Mean	chlorophyll	Trait variable
0.07	0.02	0.05	0.05	0.06	0.03	SD	µg mm^{-2}	Unit
1010.32	-	107.74	508.82	65.33	-	Mean	flexural stiffness	Trait variable
366.68	-	107.28	406.98	49.77	-	SD	N mm^{2}	Unit
0.24	0.12	0.22	0.15	0.09	0.03	Mean	mass fraction (MF) rhizome	Trait variable
0.04	0.07	0.09	0.03	0.05	0.02	SD		Unit
0.04	0.03	0.07	0.04	0.05	0.02	Mean	mass fraction (MF) root	Trait variable
0.01	0.02	0.04	0.03	0.03	0.01	SD		Unit
0.45	0.41	0.69	0.6	0.65	0.66	Mean	mass fraction (MF) stem	Trait variable
0.02	0.05	0.08	0.04	0.05	0.06	SD		Unit
1.18	1.39	2.86	0.87	1.29	1.62	Mean	P content in rhizome	Trait variable
0.24	0.42	0.78	0.17	0.39	0.34	SD	g kg^{-1}	Unit
1.05	0.98	0.92	1.02	1.03	1.03	Mean	rhizome mass per volume	Trait variable
0.05	0.07	0.05	0.03	0.05	0.04	SD	g$_{\text{fresh mass}}$ cm^{-3}	Unit
0.13	0.38	0.09	0.17	0.15	0.11	Mean	root specific density	Trait variable
0.03	0.27	0.02	0.03	0.06	0.11	SD	mg$_{\text{dry mass}}$ cm^{-3}	Unit
1.04	2.28	0.88	0.88	1.04	0.77	Mean	root mass per volume	Trait variable
0.15	1.35	0.2	0.12	0.27	0.45	SD	g$_{\text{fresh mass}}$ cm^{-3}	Unit
0.17	0.26	0.1	0.21	0.2	0.11	Mean	specific density belowground bi-	Trait variable
0.03	0.14	0.02	0.02	0.04	0.07	SD	g	Unit
7.5	73.55	3.63	13.36	24.24	47.83	Mean	specific leaf area	Trait variable
0.95	15.94	0.6	1.6	4.23	13.2	SD	mm^{2} mg^{-1}	Unit
0.13	0.12	0.07	0.45	0.23	0.13	Mean	stem specific density	Trait variable
0.02	0.03	0.02	0.04	0.05	0.03	SD	mg$_{\text{dry mass}}$ cm^{-3}	Unit
0.79	0.95	0.57	1.06	1.01	0.98	Mean	stem mass per volume	Trait variable
0.04	0.08	0.1	0.09	0.04	0.03	SD	g$_{\text{fresh mass}}$ cm^{-3}	Unit
38.56	1.12	4.31	22.78	6.39	5.42	Mean	total aboveground biomass	Trait variable
13.22	0.95	2.53	8.45	2.12	3.53	SD	g	Unit
14.13	0.17	1.61	4.88	0.99	0.28	Mean	total belowground biomass	Trait variable
4.71	0.14	1.02	1.82	0.48	0.18	SD	g	Unit
52.7	1.29	5.93	27.66	7.38	5.7	Mean	total biomass	Trait variable
17.35	1.07	3.37	9.4	2.06	3.63	SD	g	Unit
49747.89	31709.66	10542.36	55053.87	24911.74	57983.71	Mean	total leaf area	Trait variable
9068.01	17493.79	5492.1	29618.35	6580.54	47879.84	SD	mm^{2}	Unit

Appendix Chapter 7

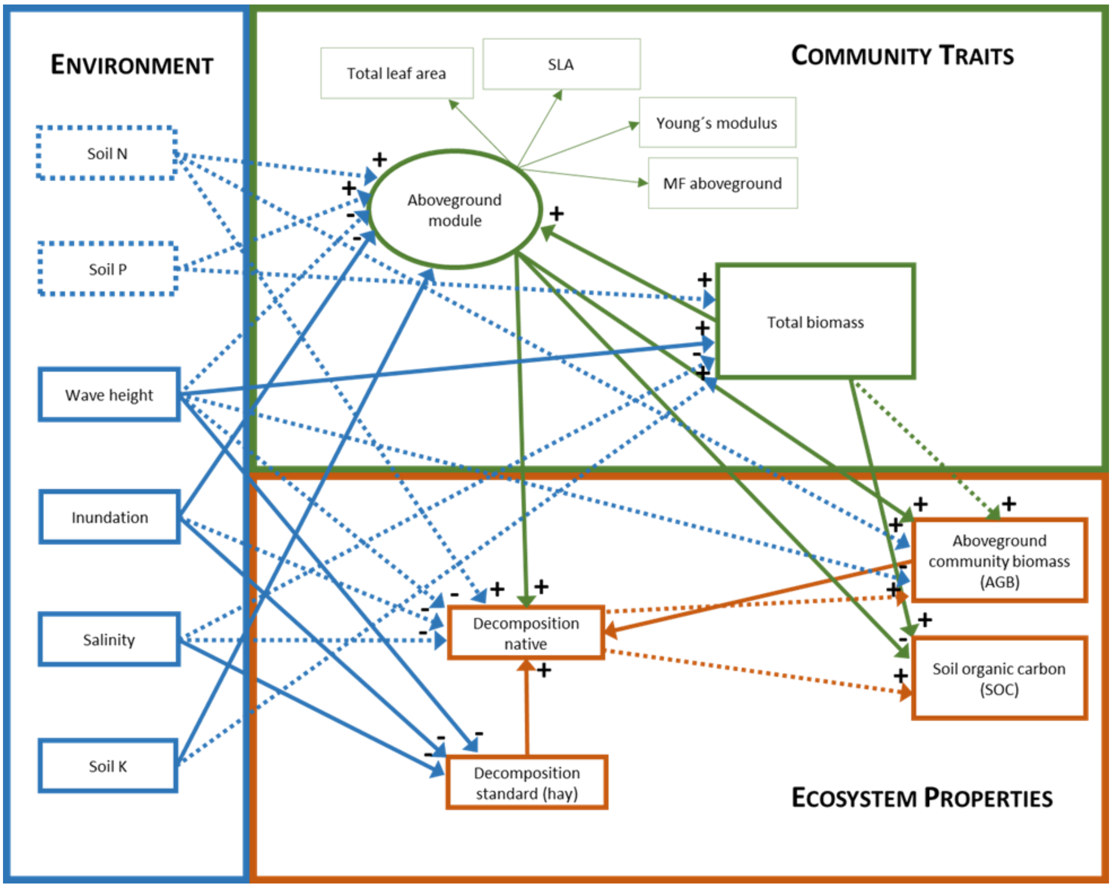


Appendix 7. 1: Salinity in the topsoil of the three study sites from March to September 2016 for the four different vegetation zones. The unit is practical salinity unit (PSU).

Appendix 7. 2: Extrapolation method for wave heights.

The mean wave height was calculated for water depth <0.5 m for all measurement points. For the different locations, test for significant regressions in relation to normalized elevation of the measuring locations or distance to marsh edge were perfomed. The shallow water levels (0-0.5 m) were significantly related to the distance from marsh edge ($R^2=0.96$, $p<0.001$). The resulting regression equation was used to calculate the mean wave height (Hmean) on plot basis:

Hmean water level 0-0.5 m = 0.0002325*distance to marsh edge + 0.04165



Appendix 7. 3: Initial partial least squares structural equation model (PLS-SEM). Dashed lines show relationships that proofed not to be significant in the final model as well as non-significant variables. Variables displayed are: Wave impact (mean wave height in water levels <0.5 m [m]), Inundation (water=> ground level [hr day^{-1}]), Soil N$_{min}$ (plant available nitrogen [g m^{-2}]), Soil P (plant available phosphorus [g m^{-2}]), Soil K (soil potassium content [g m^{-2}]), soil salinity [PSU], total leaf area (total leaf area per plant individual [mm^2]), SLA (specific leaf area [mm^2 mg^{-1}], Young´s modulus [MPa], MF aboveground (mass fraction of leaves and stems), AGB (aboveground community biomass [g m^{-2}]), Decomposition native (decomposition rate of native biomass [% day^{-1}]), Decomposition standard (decomposition rate of standard hay [% day^{-1}]). $p<0.005$ for all solid paths.

Appendix Chapter 8

Appendix 8. 1: Calculation of wave attenuation for the zone below the mean high tide level.

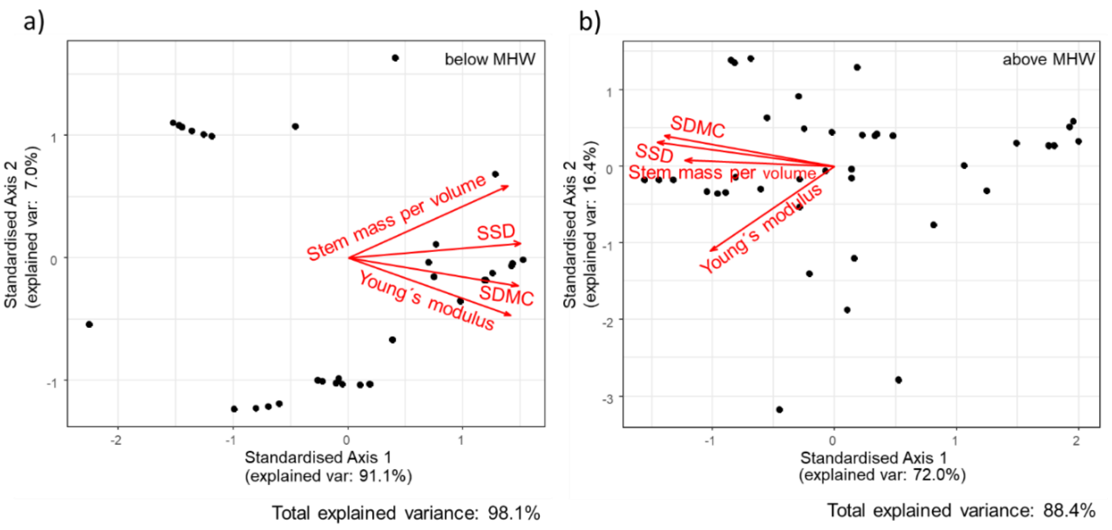
For the estimation of wave height reduction (attenuation), the mean wave height was used for water depth <0.5 m for all measurement points in the *Schoenoplectus*- and *Bolboschoenus*-zone and thus below the mean high tide water level. Test for significant regressions were perfomed for the different sites. The attenuation is the difference in incoming wave height and height after a certain distance and at a higher elevation. Used was the following regression equation for wave attenuation (AttenHmean) and adjustment for plot elevation (znorm_diff):

AttenHmean = 0.093670 * znorm_diff + 0.010679

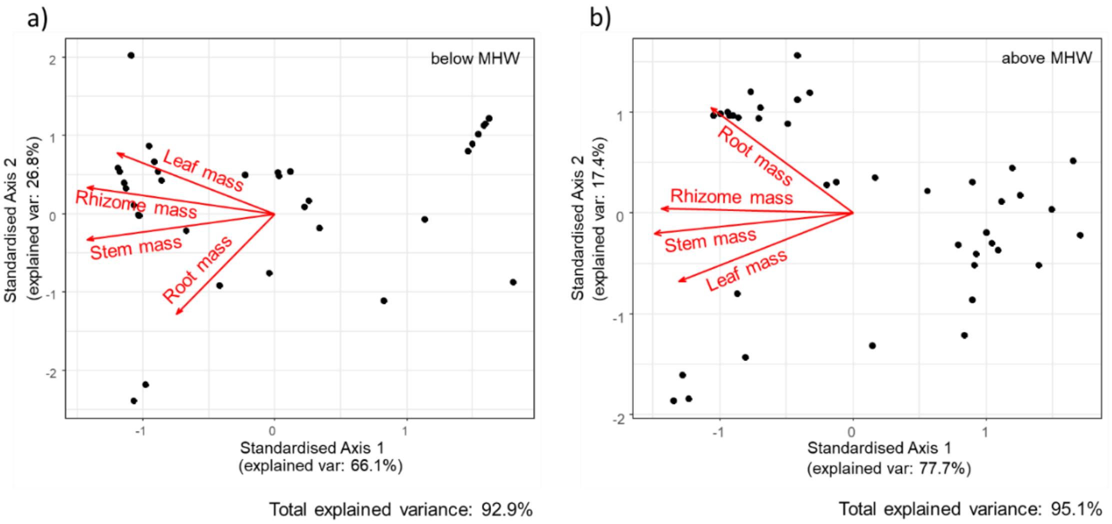
Appendix 8. 2: Equations used for the calculation of Young´s modulus.

The equation needed for the calculation of Young´s modulus is: $= \frac{EI}{I}$. The elements needed are:

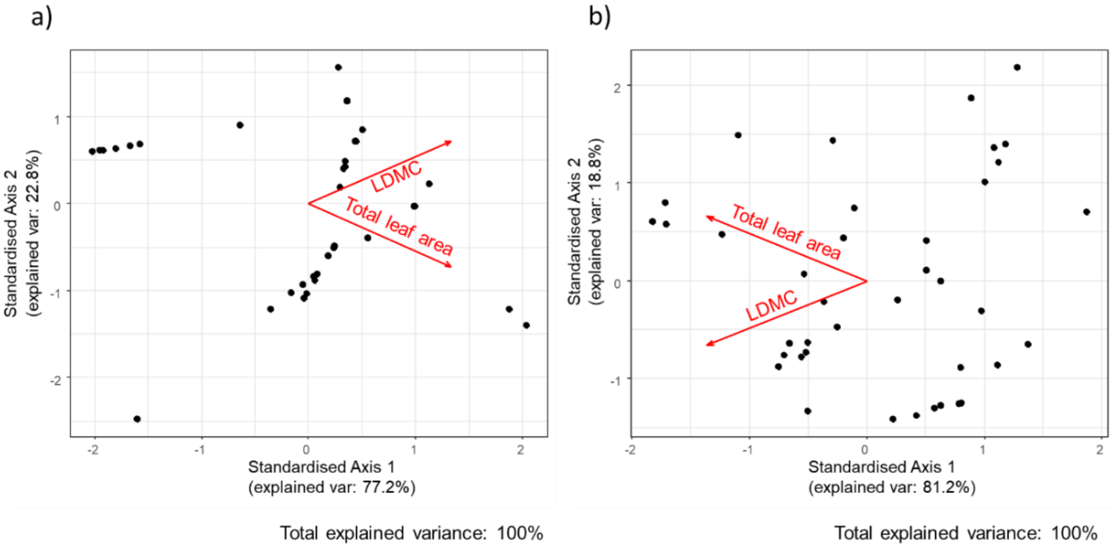
- Flexural stiffness *EI,* which can be calculated for all stem shapes as: $EI = \frac{s^3}{48} * \frac{F}{D}$. s is the support distance set on the Instron (at least 15x stem diameter, see Usherwood et al., 1997) and $\frac{F}{D}$ is the force/deflection slope, derived from the bending tests.
- The second moment of area I: for round hollow stems (such as *P. australis*) this is calculated as $I = \frac{\pi}{4} * (r_{out}^4 - r_{inn}^4)$ where r = radius, out = outer and inn = inner. For round filled stems (like *S. tabernaemontani*) this is calculated through $I = \pi * \frac{d^4}{64}$, with d being the diameter. For triangular stems (like *B. maritimus)* the calculation is: $I = \frac{\sqrt{3}}{96} * bv^4$ where bv is the basal length of the triangle. For square stems (such as *M. aquatica*) the equation for the second moment of area is: $I = b * \frac{b^3}{12}$, with b being the side length.



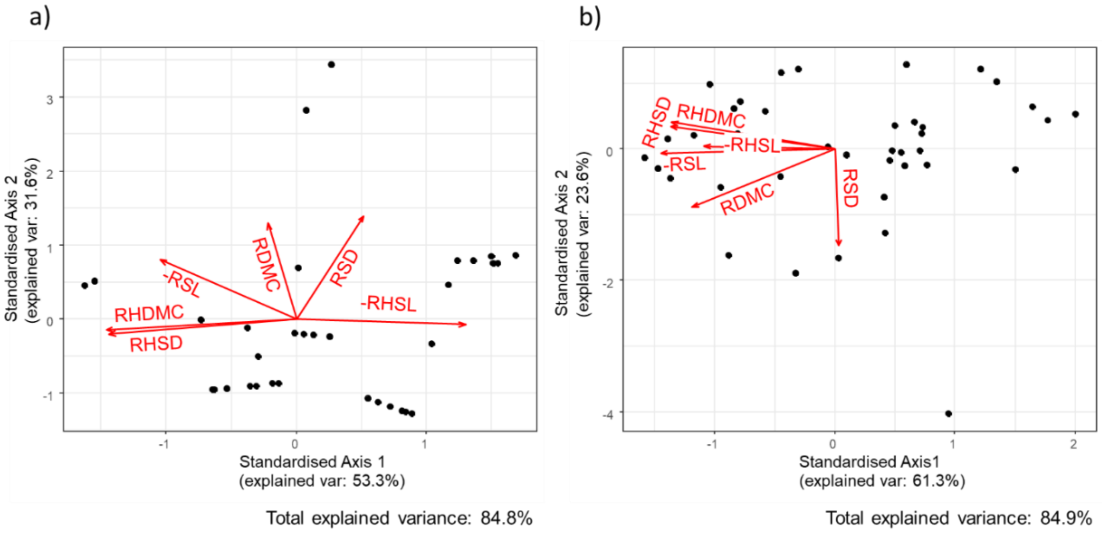
Appendix 8. 3: a) PCA for the aggregate 'stem traits' for the zone below MHW. b) For the zone above MHW. Points represent community weighted means per plot. Variables displayed: Stem mass per volume = stem $g_{fresh\ mass}$ cm³, SSD = stem specific density ($g_{fresh\ mass}$ cm^{-3}), SDMC = stem dry matter content ($mg_{dry\ mass}\ g_{fresh\ mass}^{-1}$), Young´s modulus = stem resistance to bending (MPa).



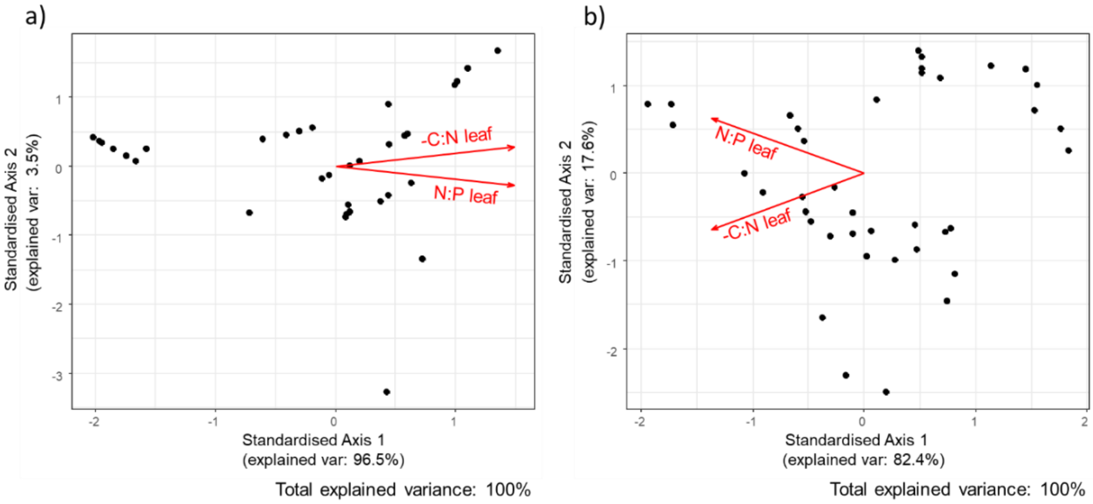
Appendix 8. 4: a) PCA for the aggregate 'mass' for the zone below MHW. b) For the zone above MHW. Points represent community weighted means per plot. Variables displayed: dry mass for leaves (g), rhizomes (g), stems and roots (g).



Appendix 8. 5: a) PCA 'leaf traits' zone below MHW (mean high water). b) PCA 'leaf traits' zone above MHW. Points represent community weighted means per plot. Variables displayed: LDMC = leaf dry matter content (mg$_{dry\ mass}$ g$_{fresh\ mass}$$^{-1}$) and total leaf area (mm²).



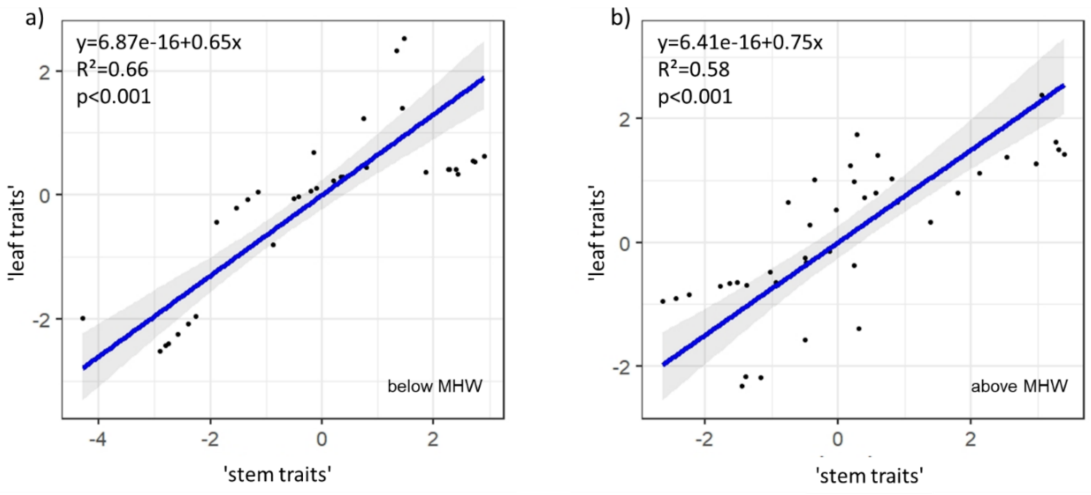
Appendix 8. 6: PCA 'belowground traits' zone below MHW (mean high water). b) PCA 'belowground traits' zone above MHW. Points represent community weighted means per plot. Variables displayed: RHSD = rhizome specific density (g$_{fresh\ mass}$ cm^{-3}), RHDMC = rhizome dry matter content (mg$_{dry\ mass}$ g$_{fresh\ mass}$$^{-1}$), RSL = root specific length (mm g$_{dry\ mass}$$^{-1}$), RDMC = root dry matter content (mg$_{dry\ mass}$ g$_{fresh\ mass}$$^{-1}$,, RSD = root specific density (g$_{fresh\ mass}$ cm^{-3}), RHSL = rhizome specific length (mm g$_{dry\ mass}$$^{-1}$).



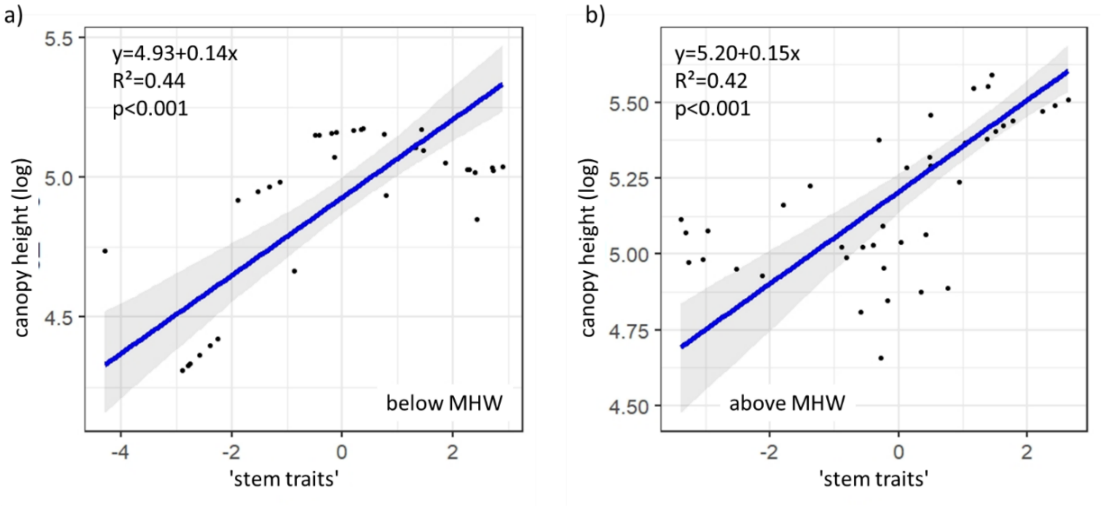
Appendix 8. 7: a) PCA leaf stoichiometry for the zone below MHW. b) PCA leaf stoichiometry zone above MHW. Points represent community weighted means per plot. Variables displayed: C:N leaf = carbon/nitrogen ratio of leaf biomass, N:P leaf = nitrogen/phosphorus ratio of leaf biomass.

Appendix 8. 8: Standard major axis regression (SMA) for trait aggregates above and below mean high water (MHW) with correlation, p-value, R² and associated intercepts and slopes.

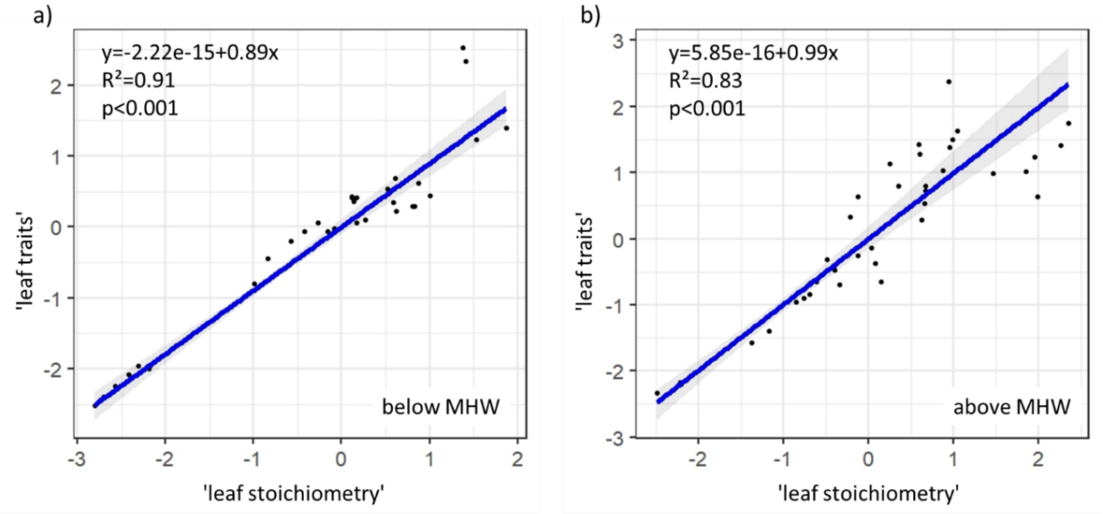
Zone	Trait 1	Trait 2	Corre-lation	p	R²	inter-cept	slope
below MHW	'leaf traits'	'stem traits'	0.81	<0.001	0.66	-6.87e-16	0.65
above MHW	'leaf traits'	'stem traits'	0.76	<0.001	0.58	6.41e-16	0.75
below MHW	'stem traits'	'mass'	-0.05	0.8	0.002	-	
above MHW	'stem traits'	'mass'	0.59	<0.001	0.36	-1.66e-15	0.96
below MHW	'belowground traits'	'stem traits'	-0.10	0.6	0.01	-	
above MHW	'belowground traits'	'stem traits'	0.89	<0.001	0.80	1.97e-15	1.13
below MHW	'leaf stoichiometry'	'stem traits'	0.81	<0.001	0.67	-1.72e-15	0.73
above MHW	'leaf stoichiometry'	'stem traits'	0.52	<0.001	0.28	5.75e-17	0.76
below MHW	'leaf traits'	'mass'	-0.43	0.004	0.19	-5.48e-16	-0.76
above MHW	'leaf traits'	'mass'	0.92	<0.001	0.74	-6.08e-16	0.72
below MHW	'leaf traits'	'belowground traits'	-0.38	0.01	0.14	-8.29e-16	-0.69
above MHW	'leaf traits'	'belowground traits'	0.82	<0.001	0.68	-0.68e-16	0.66
below MHW	'leaf traits'	'leaf stoichiometry'	0.96	<0.001	0.91	-2.22e-15	0.89
above MHW	'leaf traits'	'leaf stoichiometry'	0.91	<0.001	0.83	5.85e-16	0.99
below MHW	'mass'	'belowground traits'	0.04	0.01	0.001	3.68e-16	0.91
above MHW	'mass'	'belowground traits'	0.75	<0.001	0.56	-8.28e-16	0.92
below MHW	'mass'	'leaf stoichiometry'	-0.36	0.02	0.12	2.19e-15	-1.17
above MHW	'mass'	'leaf stoichiometry'	0.85	<0.001	0.73	1.65e-15	1.37
below MHW	'belowground traits'	'leaf stoichiometry'	-0.54	0.0002	0.29	2.00e-15	-1.29
above MHW	'belowground traits'	'leaf stoichiometry'	0.71	<0.001	0.50	1.89e-15	1.50
below MHW	canopy (log)	'stem traits'	0.66	<0.001	0.44	4.93	0.14
above MHW	canopy (log)	'stem traits'	-0.65	<0.001	0.42	5.20	-0.15



Appendix 8. 9: a) SMA of 'leaf traits' vs 'stem traits' with 95 % confidence intervals for zone below MHW and b) above MHW. For variables combined in trait aggregates and units of variables, see Table 9.



Appendix 8. 10: SMA of 'stem traits' vs canopy height with 95 % confidence intervals for zone below MHW and b) above MHW. For variables combined in trait aggregates and units of variables, see Table 9.



Appendix 8. 11: SMA of 'leaf stoichiometry' vs 'leaf traits' with 95 % confidence intervals for zone below MHW and b) above MHW. For variables combined in trait aggregates and units of variables, see Table 9.

Acknowledgments

I would like to thank Vanessa Minden and Michael Kleyer for being my supervisors and helping me through the process of making manuscripts, solving questions and coming up with new ones! I also would like to thank Boris Schröder-Esselbach for investing the time to be the second scientific referee for my thesis! A special thanks to Maike Heuner, Stijn Temmerman, Ken Schoutens and Elmar Fuchs for their participation, scientific advice and all the time invested into working out ideas! And thank you also to Tjeerd Bouma, for the valuable comments on the manuscripts and that I could use the Instron at the NIOZ in Yerseke!

For all the help in the many hours spent in the laboratory a great thanks to Daniela Meißner! I would also like to thank all the students for their help with field and laboratory work!

For all the help with administrative issues, my thanks go to Brigitte, Helga and Jutta!

I would like to thank the entire Landscape Ecology Working group of the University of Oldenburg for knowing how to solve all those statistical issues (special thanks to Cord Peppler-Lisbach!) and how to tame R. And also, for all the nice coffee breaks and chats we had: Thank you Julia, Celia, Nadine, Hawa, Angelika, Rolf and Lisa! A special thanks to Kertu Lõhmus, for the time invested in reading and commenting!

I actually had not expected I would be doing a PhD. The chance to do it came as a surprise and I am very glad it did! During the past 4 ½ years, I learned many new things in programming and statistics. And about fieldwork, which sometimes was quite a struggle. A struggle with the elements, the rain that seemed to come from all sides, the tides that kept me on my toes and the fantastic and partly almost impenetrable thick vegetation cover in the Elbe estuary that did its best to stop me from going anywhere. I managed to wrest my sample plants away from the estuary, but I could not have put in all this energy without the help of my sister Carlotta, taking care of my son Jos. Thank you for that! I also wish to thank Jos, for being patient with me, bearing things being covered in mud at times and sharing me with all this “nature stuff”!

I would like to thank Noel for the support of this new phase of my life in Germany!

A special thanks to my parents, for all the support and advice!

And thank you Markus, for listening, helping to structure thoughts and being there!

CURRICULUM VITAE

PERSONAL DATA

Name	Tilla Schulte Ostermann
Date of birth	4. August 1982
E-mail	tilla.schulte.ostermann@uni-oldenburg.de

EDUCATION

May 2016 – June 2020	**Scientific staff and PhD student, Environmental Sciences, Landscape Ecology** Working Group, University of Oldenburg. Thesis: Plant traits and ecosystem properties in the Elbe estuary
June 2010 – August 2015	**Ecological advisor, Cuilleann Forestry Services, Newtown Cashel, Ireland** Site evaluation, surveys, digitising, planting
May 2010	**Degree in Landscape Ecology, Westfälische Wilhelmsuniversität Münster, Germany** Degree work on the control of *Equisetum palustre* in a wet grassland
June 2007	**Birth of my son Jos**
May – September 2006	**Practical training, Killarney National Park, Ireland** Testing clearance methods for *Rhododenron ponticum*
September 2005 – April 2006	**Foreign Studies, Université de Dijon, France** Two Erasmus semeters in biology
May 2005	**Native Woodland scheme course, Tullamore, Ireland** Learning the Native Woodland Scheme system
October 2003	**Start of study of Landscape ecology, University of Münster** Ecosystem protection, maintenance, restauration, rehabilitation
September 2002 – August 2003	**Voluntary Ecological Year, Crann, „Releafing Ireland", Co. Leitrim, Ireland** Planting and pruning broadleaf trees
1989 – 2002	**2nd level Education, Steiner School, Kiel, Germany**

VOLUNTARY AND COMMITTEE WORK

2015	Member of the Public Participation Network Secretariat for County Longford
2014-2015	Member of the local “Grow it yourself” group
2013-2015	Manager of the Ounamoun Reserve for the Irish Wildlife Trust
2012-2015	Treasurer of the Wetlands Heritage community group
2014	Participation in the Transition Town initiation course
2013-2014	Member of the national council of the Irish Wildlife Trust
2012-2014	Member of the County Development Board for Co. Longford

CONFERENCES AND WORKSHOPS

2019	Coastal Ecology Workshop (CEW), Antwerp, Belgium Talk: The interplay of abiotic site conditions, plant traits and ecosystem properties in the Elbe estuary.
2018	Coastal Ecology Workshop, Betws-y-Coed, Wales Talk: Environmental filters in the Elbe estuary – a plant trait analysis.
2017	Coastal Ecology Workshop, Yerseke, The Netherlands Talk: Vegetation of the Elbe estuary, environment – trait interactions.
2017	European Geosciences Union (EGU) conference, Vienna, Austria Poster presentation: Plant functional traits and tidal bank protection .

PUBLICATION

Schoutens, K., Heuner, M., Minden, V., Schulte Ostermann, T., Silinski, A., Belliard, J.-P. & Temmerman, S. (2019). *How effective are tidal marshes as nature-based shoreline protection throughout seasons?* Limnology and Oceanography. 9999, 1-13. doi:10.1002/lno.11149

Schoutens, K., Heuner, M., Fuchs, E., Minden, V., Schulte-Ostermann, T., Belliard, J. P., Bouma, T. J. & Temmerman, S. (2020). *Nature-based shoreline protection by tidal marsh plants depends on trade-offs between avoidance and attenuation of hydrodynamic forces*. Estuarine, Coastal and Shelf Science, 236. DOI:Urn:Nbn:Nl:Ui:10-1874-395996

Author´s contributions

Chapter 6. Unraveling plant strategies in tidal marshes by investigating plant traits and environmental conditions

Schulte Ostermann, T., Heuner, M., Fuchs, E., Temmerman, S., Schoutens, K., Bouma, J. T., Minden, V. *Submitted to: Journal of Vegetation Science.*

VM and TSO planned the analysis and sampling set up. KS recorded data on wave activity. TSO conducted the sampling of vegetation, soil and hydrological data and executed the analysis, prepared graphs and tables and the initial manuscript. VM, MH, EF, ST, KS and TJB contributed to the revision of the manuscript.

Chapter 7. Hydrodynamics affect plant traits in estuarine ecotones with impact on organic carbon sequestration potentials

Schulte Ostermann, Kleyer, M., T., Heuner, M., Fuchs, E., Temmerman, S., Schoutens, K., Bouma, J. T., Minden, V*. Submitted to: Estuarine, Coastal and Shelf Science.*

MK, VM and TSO planned the analysis. KS sampled data on wave activity. TSO conducted the sampling of vegetation, soil and hydrological data and prepared the laboratory and statistical analysis. TSO wrote the initial manuscript, including graphs and tables, MK, VM, MH, EF, ST, KS and TJB contributed to the revision of the manuscript.

Chapter 8. Identifying key traits driving wave attenuation and carbon sequestration potential of tidal marsh vegetation

Schulte Ostermann, T., Heuner, M., Fuchs, E., Temmerman, S., Schoutens, K., Bouma, J. T., Minden, V. *Submission in preparation.*

VM and TSO planned the analysis and sampling set up. KS recorded data on wave activity. TSO conducted the sampling of vegetation, soil and hydrological data and performed the analysis, prepared graphs and tables and the initial manuscript. VM, MH, EF, ST, KS and TJB contributed to the revision of the manuscript.

Selected Pictures

Erklärung

Erklärung gemäß § 11 Abs. 2 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg vom 20.03.2013.

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbständig verfasst habe und alle verwendeten Hilfsmittel vollständig angegeben sind.

Diese Dissertation ist weder als Ganzes noch teilweise an einer anderen Hochschule für ein Prüfungsverfahren eingereicht worden.

Ich strebe mit der Abgabe meiner Dissertation den Grad einer Doktorin an.

Die Leitlinien für gute wissenschaftliche Praxis der Carl von Ossietzky Universität Oldenburg sind eingehalten worden und mit der Promotion wurden keine kommerziellen Beratungsdienste o. ä. erfüllt.

Oldenburg,