Biodiversity effects on dune and salt marsh biogeomorphology – a trait-based approach

von

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Summary

Current climate crisis is associated with rising sea level and increasing frequency and strength of storm surges. This raises the concern of losing coastal ecosystems such as dunes and salt marshes to erosion and drowning. This is particularly serious as these ecosystems fulfill multiple ecosystem services including providing habitats for specialized plants and animals, attenuating wave energy, reducing erosion, and protecting areas of major socio-economic interest from flooding.

Coastal dunes and salt marshes are biogeomorphic ecosystems where the form and function depend on the two-way interaction between geomorphic and biological processes. The primary geomorphic processes in coastal dunes are aeolian processes while salt marshes are shaped primarily by fluvial processes. These abiotic processes influence the vegetation and lead to responses on the community and the species level. In return, plants influence matter and energy flow and thus shape landscape formation.

Despite strong research interest and a general understanding of biogeomorphic ecosystems, there is still a lack of knowledge in a number of aspects of vegetation responses and effects in these ecosystems. Morphologic plasticity of plants is known to help species survive in dynamic and changing environments such as biogeomorphic ecosystems. However, specific trait responses of pioneer species to different physical disturbances are not yet fully known. In biodiversity and ecosystem functioning research it is generally believed that diversity increases ecosystem's resistance and resilience by means of the insurance effect. However, biogeomorphic ecosystems are an exception as it is often the resistance and resilience of single keystone species that are the main drivers for ecosystem stability. Controlled experiments on this matter, however, are lacking. The importance of vegetation in biogeomorphic ecosystems is generally accepted. Yet, there is an ongoing debate whether vegetation has an effect on sedimentation processes in salt marshes. To fill these research gabs, this thesis presents three different studies.

To gain a better understanding of the responses of vegetation to abiotic factors, a controlled greenhouse experiment studying the morphological plasticity of two dune

species is presented. *Ammophila arenaria* and *Cakile maritima* individuals were exposed to artificial sediment accretion and erosion events of varied magnitudes and times after germination. Mortality rate was lower for *A. arenaria* than for *C. maritima*. Growth was mostly increased through burial and erosion in *C. maritima* and decreased in *A. arenaria*.

Further, a mesocosm experiment studying the effects of species and trait diversity on dune resistance and resilience is presented. The comparison of artificial dunes vegetated with *A. arenaria* only or with mixed-species communities showed that single-species dunes were more resistant to wind erosion than were mixed-culture dunes. Surviving species showed no responses in their trait expression after the disturbance event, i.e. no difference in resilience.

Lastly, a study looks at the effects of plant functional traits on sedimentation and erosion in salt marshes. Three salt marsh systems in the Wadden Sea were analyzed: natural marshes on a barrier island, moderately anthropogenic influenced mainland marshes, and highly anthropogenic influenced marsh island. Mean surface elevation change was found to be not sufficient to keep up with current sea-level rise. However, there are pronounced local differences in surface elevation change, a part of which can be explained by distance to marsh edge and plant functional traits. Higher vegetation roughness increases sedimentation; stronger anchoring capacity can reduce erosion.

These three studies demonstrate the vegetation capacity to survive in dynamic environments as found in biogeomorphic ecosystems. Morphological adaptions, resulting in intraspecific trait variance, enable pioneer species to survive abiotic changes. Furthermore, it is shown that in biogeomorphic ecosystems it is mainly the resistance of one key species that is crucial for the resistance of the system. Finally, it is shown that not only aeolian but also fluvial processes in salt marshes are affected by plant functional traits, resulting in changed sedimentation and erosion intensities.

In conclusion, this work shows that a trait-based approach is valuable to better understand biogeomorphic ecosystems. The acquired knowledge can have implications for coastal management. Firstly, it is shown that *A. arenaria* is well adapted to survive

surface displacements and is the main driver for dune resistance to physical disturbances which are expected to increase with climate change-induced weather extremes. This confirms the species' importance for coastal protection against high water levels but also evinces the risk of reducing the natural and necessary dynamics in dune ecosystems. Secondly, it is shown that vegetation affects surface elevation change of salt marshes. Including vegetation in models predict salt marsh development under climate change scenarios. could therefore improve the mode.

Zusammenfassung

Zu den Folgen des Klimawandels zählen u.a. ein Anstieg des Meeresspiegels und eine Zunahme in Häufigkeit und Stärke von Sturmfluten. Dies gibt Anlass zur Sorge, dass Küstenökosysteme wie Dünen und Salzwiesen durch Erosion und Überflutung verloren gehen könnten. Diese Ökosysteme erbringen wichtige Ökosystemdienstleistungen: sie bieten Lebensraum für spezialisierte Tier- und Pflanzenarten, schwächen die Wellenenergie, reduzieren Erosion und schützen wichtige sozioökonomische Gebiete vor Überflutung. Deshalb hätte ihr Verschwinden große negative Auswirkungen.

Küstendünen und Salzwiesen sind biogeomorphologische Ökosysteme, deren Formen und Funktionen von bidirektionalen Interaktionen zwischen geologischen und biologischen Prozessen bestimmt werden. Während die primären geologischen Prozesse in Dünen äolisch sind, spielen in Salzwiesen fluviale Prozesse eine wichtige Rolle. In beiden Ökosystemen bewirken diese abiotischen Prozesse eine Reaktion der Vegetation auf Art- und Individuen-Ebene. Gleichzeitig beeinflusst die Vegetation aber auch die geologischen Prozesse und somit die eigene Umwelt.

Trotz zahlreicher Arbeiten zu biogeomorphologischen Ökosystemen, gibt es Forschungslücken bei der Reaktion und den Effekten von Vegetation auf geologische Prozesse in biogeomorphologischen Systemen. (1) Morphologische Plastizität hilft Pflanzen unter dynamischen und sich ändernden abiotischen Bedingungen, wie sie in biogeomorphologischen Systemen zu finden sind, zu überleben. Spezifische Reaktionen der funktionellen Merkmale von Pionierarten auf unterschiedliche physikalische Störungen sind allerdings nicht bekannt. (2) Untersuchungen zu Biodiversität und Ökosystemfunktionen zeigten, dass die Resistenz und Resilienz von Ökosystemen häufig mit zunehmender Diversität steigt, entsprechend der ökologischen Versicherungshypothese. In biogeomorphologischen Ökosystemen sind es allerdings häufig einzelne Schlüsselarten, deren Resistent und Resilienz entscheidend sind. Alle weiteren Arten tragen nur wenig zur Resistenz des Ökosystems bei. Kontrollierte Experimente hierzu sind allerdings selten. (3) Die wichtige Rolle der Vegetation in biogeomorphologischen Ökosystemen ist unumstritten. Allerdings gibt es eine

andauernde Debatte über den Effekt von Vegetation auf Sedimentationsprozesse in Salzwiesen. Diese Dissertation soll dazu beitragen, mit drei Studien diese Forschungslücken zu schließen.

(1) Um die Reaktion und die morphologische Plastizität von Vegetation auf physikalische Störung besser zu verstehen, wurden Individuen der Dünenarten *Ammophila arenaria* und *Cakile maritima* kontrollierten Versandungs- und Erosionsereignissen unterschiedlicher Intensität und Zeitpunkten nach der Keimung ausgesetzt. *A. arenaria* zeigte eine geringere Mortalität als *C. maritima*. Die Biomasseproduktion wurde durch die physikalische Störung in *C. maritima* größtenteils verstärkt, in *A. arenaria* reduziert.

(2) Um die Effekte von Vegetation bzw. Arten- und Traitdiversität auf die Resistenz und Resilienz von biogeomorphologischen Ökosystemen besser zu verstehen, wurde ein Mesokosmosexperiment durchgeführt. Der Vergleich von künstlichen Dünen, die entweder ausschließlich mit *A. arenaria* bepflanzt wurden oder mit einer Mischkultur aus heimischen Pionierarten zeigte, dass die Monokultur resistenter gegen Winderosion war als die Mix-Kultur. Außerdem zeigte keine der gepflanzten Arten eine Reaktion der funktionellen Merkmale auf die Störung, d.h. die Resilienz unterschied sich nicht zwischen den Bepflanzungstypen.

(3) Die letzte Studie dieser Arbeit untersucht den Effekt von funktionellen Merkmalen auf Sedimentation und Erosion in Salzwiesen. Drei Salzwiesentypen des Wattenmeers wurden dafür ausgewählt: vom Menschen weitestgehend unbeeinflusste Salzwiesen der Barriereinseln, moderate anthropogen beeinflusste Salzwiesen entlang der Festlandküste und hoch artifizielle Marschen auf Halligen. Der mittlere Aufwuchs lag unter dem beobachteten Meeresspiegelanstieg, was das langfristige Fortbestehen der Marschen in Frage stellt. Es gab jedoch gravierende regionale Unterschiede in der Höhenveränderung der Salzwiesen. Ein Teil dieser Varianz ließ sich durch die Distanz zur Marschkante aber auch durch funktionelle Merkmale erklären. Eine höhere Rauheit der Vegetation führte zu verstärkter Sedimentation, eine stärkere Verankerungskapazität bewirkte teilweise eine Reduktion der Erosion.

Zusammenfassung
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Die drei Studien dieser Dissertation zeigen die Fähigkeit der Vegetation durch morphologische Adaptionen, die zu intraspezifischer Varianz in funktionellen Merkmalen führen, auch in dynamischen Ökosystemen zu überleben. Außerdem konnte diese Dissertation experimentell zeigen, dass *A. arenaria* eine Schlüsselart für Küstenökosysteme und hauptauschlaggebend für die Resistenz ist. Des Weiteren konnte gezeigt werden, dass Vegetation nicht nur in Dünen die geologischen Prozesse beeinflusst, sondern auch in Salzwiesen die funktionellen Merkmale der Salzwiesenarten einen Einfluss auf die Sedimentation und die Erosion haben können.

Diese Arbeit zeigt, dass ein trait-basierter Ansatz dabei helfen kann, biogeomorphologische Systeme besser zu verstehen. Die Ergebnisse könnten Implikationen für das Küstenmanagement haben. Die Studien zeigen die gute Anpassung von *A. arenaria* an dynamischen Ökosystemen und bestätigen die wichtige Rolle dieser Art im biogeomorphologischen Dünensystem. Dies macht die Art resistent gegen Klimawandel-Folgen, wie verstärkte Stürme, und bestätigt ihre Nutzung als Dünenbefestigung. Gleichzeitig wird durch die Studien die Gefahr, die natürliche Dynamik des Systems zu ersticken, deutlich. Darüber hinaus wurde gezeigt, dass Vegetation den Aufwuchs von Salzwiesen unterstützten kann, der erforderlich ist, um Salzwiesen langfristig vor dem Untergehen zu schützen. Deshalb sollten Vegetationsparameter in mathematischen Modellen zur Entwicklung der Salzwiesen integriert werden.

Chapter 1

Introduction

1 Introduction

1.1 The concept of biogeomorphology

The essential concept

One of today's major ecological challenges is to assess the matter and energy flow on Earth's surface in order to understand the development of landforms and predict their future state, especially with regard to climate change. As with many key questions in science, this complex topic cannot be dealt with by constraining the view to a single subject. Elton (1927) stated nearly a century ago that we need to enlarge the view to neighboring subjects to understand complex systems. This suggestion led to the emergence of the multidisciplinary approach of biogeomorphology in the late 1980s. Scientists in this interdisciplinary field combine biology and geomorphology to study landform developments. The focus is on the two-way interplay between ecological and geomorphological processes (Viles, 1988). It examines (1) the influence of landforms/geomorphology on the distribution and development of plants, animals and microorganisms and (2) the influence of plants, animals and microorganisms on Earth's surface processes and the development of landforms (Viles, 1988).

The species influencing their environment have been referred to as ecosystem engineers/bioengineers (Jones et al., 1994). Species can influence their environments in two ways. They either passively modify the abiotic environment by means of their physical structures or they actively modify their environment. According to their mode of engineering, they are referred to as autogenic or allogenic ecosystem engineers (Jones et al., 1994). In keeping with this definition, plants that passively change their environment through their physical structure are referred to as "autogenic engineers". On the other hand, beavers for instance, which actively modify their environment by building dams, are referred to as "allogenic engineers" (Jones et al., 1994).

Biogeomorphology covers a variety of processes that link biotic and geomorphological systems, such as bioerosion, bioconstruction, biostabilisation, bioweathering and bioprotection (Corenblit et al., 2015; Naylor et al., 2002). Most of these processes are

biologically mediated Earth system processes. Bioerosion has been referred to as the weathering and/or removal of material by an organic agency (Spencer, 1992). It is the active or passive mechanical and/or chemical erosion of the land surface by species ranging from mollusks to large ungulates. Bioprotection is the active or passive, direct or indirect role of organisms in preventing or reducing the effect of other Earth surface processes such as water and wind erosion while encouraging accretion and sedimentation. Bioprotectors can be microscopic biofilms, algae or larger vegetation (Coombes et al., 2013). Bioconstructors build films, crusts, mounds or reefs of material which is produced internally, bind from other sources, or developed from a combination of the two. Bioconstructions are formed through organisms such as Novastoa, which produce minerogenic material themselves; Sabellariidae which actively accrete material by chemically fixing particulate matter; or through inorganic cementation of organic debris which results in the formation of fluvial tufa barrages (Naylor, 2005). All these bioprocesses are not mutually exclusive and their interrelationships are varied, complex and dynamic (Naylor, 2005).

Ecosystem engineering activity changes the morphology and geomorphological processes of its surroundings. This may feed back to the engineering organisms. A good example are vegetated riverbanks. During low flow conditions, pioneer plants can colonize riverbanks and protect them from erosion (Baptist, 2001). The stabilization of the physical environment will further increase plant growth and subsequently further decrease erosion. This paves the way for new species that depend on less dynamic conditions. Around the world, gradients between high and low sediment dynamics exist. Since plants are adapted to specific conditions they will be abundant in specific locations and become extinct in others.

Biogeomorphic succession

Ecosystems that are shaped in their form and function by the two-way interaction of biologic and geomorphic processes were named "biogeomorphic ecosystems" (BE) by Balke et al. (2014). These ecosystems follow a clear succession and change in their form and function along the successional stages. This succession has been restudied many times since the pioneering study of (Cowles, 1899). Recently, Corenblit et al. (2015) established a general concept of biogeomorphic succession. They defined four phases of BEs: the geomorphic phase, the pioneer phase, the biogeomorphic phase, and the ecological phase. The form and function of each phase are driven by the geomorphological processes, the biological processes, and their interaction. The strength of geomorphological processes decreases while the strength of biological processes increases along the successional stages. The strength of biogeomorphic feedbacks follows a humpback curve and is highest in the intermediate phases. As a result of biogeomorphic feedbacks, a sudden transition can occur between phases (Balke et al., 2014; Corenblit et al., 2015).

In the initial phase, the geomorphic phase, after a flood, storm or any other disturbance, no vegetation develops. Functions and stability of the landforms are driven only by hydrodynamic and aerodynamic forces and the intrinsic cohesiveness of the sediment. The geomorphic environment restricts seed germination. Thus, the geomorphic environment remains mostly within its physical state associated with a landscape dominated by bare substrate (Corenblit et al., 2015).

In the second phase, the pioneer phase, physical disturbance decreases but the geomorphic environment still controls seed germination and seedling survival and growth. When seedlings experience a disturbance-free time (i.e. a "Window of Opportunity") they establish successfully (Balke et al., 2014). The required disturbance-free time varies among species and causes specific species assemblages in disturbed environments. Species initiating the biogeomorphic succession are usually short-lived annual ones. They are adapted to thrive with repeated burial and often even require burial for optimal growth (Corenblit et al., 2011). Successfully established plants

feedback on the geomorphic processes and induce locally and temporally stabilized patches.

In the third phase, the biogeomorphic phase, the geomorphic environment is controlled by feedbacks between plants and geomorphic dynamics. Vegetation becomes increasingly dense, stabilizes larger areas and captures increasing amounts of sediment (Maun, 2009). In the final phase, the ecological phase, vegetation density further increases and biotic interactions become increasingly important while the importance of geomorphic dynamics decreases with greater distance to the source of distrubance and increasing vegetation cover (Corenblit et al., 2015).

Biogeomorphic ecosystems worldwide

The biogeomorphic concept can be applied to a variety of ecosystems along the water-terrestrial interface in fluvial and coastal zones such as riparian zones, seagrass beds, coastal dunes, salt marshes, and mangrove forests (Corenblit et al., 2015). These ecosystems are among the most dynamic and productive ecosystems worldwide. Depending on the regional and local geological, geomorphological and bioclimatic settings, a variety of physical configurations and species life-forms and assemblages have developed. However, they also share common features regarding the relationship between plant dynamics and the geomorphic environment.

These ecosystems cover large parts of the Earth's surface and provide many provisioning, regulating, supporting and cultural ecosystem services, including riparian zones (Nava-López et al., 2016), seagrass beds (Orth et al., 2006), coastal dunes (You et al., 2018), salt marshes (McKinley et al., 2018), mangroves (Thompson et al., 2017). One of the main services of BEs at the terrestrial-aquatic interface is coastal and bank protection through wave attenuation and bed stabilization. They protect the hinterland from flooding and erosion from high water levels and storm surges (Barbier, 2015). Climate change and associated accelerated sea-level rise (SLR) and stronger storm surges make these ecosystem services increasingly important. However, BE's adaptation capacity to SLR is still under discussion and data is still incomplete

(see Table 1.1). Generally, BEs can accumulate mineral particles which may result in surface elevation. The highest elevation rates were found in salt marshes. However, data vary considerably and studies found that sediment accretion also can respond to climate change through feedbacks that involve increased plant growth and production, which lead to faster accretion rates with increasing CO_2 and sea-level rise (Kirwan & Mudd, 2012; Langley et al., 2009).

Table 1.1: Coastal protection and adaptation capacity to SLR of biogeomorphic ecosystems at the terrestrial-aquatic interface.

BEs	Wave attenuation	Bed stabilization	Elevation rates
riparian zones	10 % lower wave height [1]	25 – 65 % less erosion [1]	unknown
seagrass beds	20 % per 9 m (low energy) [2]	14 – 98 % less erosion [3]	-0.08 mm/yr [4]
coastal dunes	yes [5]	~ 50 % less erosion [5]	unknown
salt marshes	80 % per 160 m (low energy) [6] 20 % per 40 m (high energy) [7]	yes [8]	19-22 mm/yr [9]
mangroves	64 % per 260 m/ 95 % per 40 m [10]	yes [11]	4.1 mm/yr [12]

[1] Coops et al. (1996), [2] Paul and Amos (2011), [3] Carr et al. (2010), [4] Gattuso et al. (1998), [5] Feagin et al. (2019), [6] Möller and Spencer (2002), [7] Möller et al. (2014), [8] Spencer et al. (2016), [9] Schürch et al. (2013), [10] Brinkman (2006), 11 Thampanya et al. (2006), [12] McKee et al. (2007).

1.2   The trait-based perspective in ecology

History of vegetation classification

Classifying vegetation according to specific features helps to generalize findings and generate conceptual models. The earliest functional classification was implemented by the Greek philosopher Theophrastus who separated plants into "trees", "shrubs", and "herbs" (Morton, 1981). In modern times, Raunkiær (1934) developed a classification using "life-form" categories. Since then his system has been revised and modified by various authors, but the model's main structure remained unchanged (Ellenberg & Mueller-Dombois, 1967). It subdivides plants based on the place of the plant's growth-point during seasons with adverse conditions. Later, Grime (1974, 1977) presented the "plant strategy scheme" (or CSR Triangle) in which species are classified according to their abilities to cope with competition (C), abiotic stress (S), and disturbance (R). Stresses include factors such as the availability of water, nutrients, and light, along with growth-inhibiting influences like temperature and toxins. Conversely, disturbance encompasses herbivory, pathogens, anthropogenic interactions, fire, and sediment dynamics.

The CSR system has been applied successfully in studies of the distribution and dynamics of many communities (Pierce et al., 2017). However, it turned out that predetermined classes of plant attributes may be meaningful only in vegetation for which they were developed (Grubb, 1985). For example, the competitive ability relates to seed weight in sand dune annuals, while in perennial herbaceous communities, competitive ability relates to root and shoot traits (Lavorel et al., 1997; Rees, 1995). Thus, the research on adaptive strategies also should incorporate methods for identifying the contribution of individual traits.

Therefore, Díaz and Cabido (1997) implemented a functional approach which classifies species according to their "functional traits". The term "trait", however, is not new. Originally, the term was introduced by Charles Darwin (1859) as a predictor of organismal performance. Since then, the term has been used widely despite the lack of an ubiquitously accepted clear definition. It has been used, inter alia, to describe plant

chemical features and soil features (Eviner, 2004). Violle et al. (2007) addressed the resulting confusion regarding the term and the concept and suggested a new definition. This definition, which was further developed by Shipley (2010) and later modified by Garnier et al. (2016), reads as follows: "A trait is any morphological, physiological or phenological heritable feature measurable at the individual level from cell to whole-organism, without reference to the environment or any other level of organization".

From the trait combinations, plant strategies can be derived and plants can be grouped into "functional types". This is a non-phylogenetic grouping of species sharing similar traits in response to abiotic and biotic conditions since the same levels of stress and disturbance should evoke the same plant strategy even on taxonomically different species. Species can be from one ecosystem or from different biogeographic and ecological zones but possess a common life strategy through convergent trait adaption that enables them to thrive in a given environment. Species can be grouped according to common responses (response traits) to the environment and/or common effects (effect traits) on ecosystem processes (Duckworth et al., 2000; Wilson, 1999). This implies that the knowledge of the values of particular abiotic variables resulting in stress and disturbance allows us to predict the typical values of the functional traits found in the local community. The knowledge of the typical functional trait values found in the community and the knowledge of the actual trait values of the species in a regional species pool allows us to predict which of the species will be dominant, which will be subordinated, and which will be rare or absent. Therefore, the analysis of functional types not only help to understand community functioning on a local scale but also facilitates the comparison between communities exposed to similar environmental constraints on a regional scale.

Advantages of traits-based ecology

Some of the core questions asked in ecology are: (1) Why and how do different species perform differently along ecological gradients? (2) Why and how do species interact within a community? (3) Why and how do species affect the functioning of ecosystems? (Garnier & Navas, 2012). To answer these questions a trait-based approach has advantages over to the traditional taxonomic approach, as it is necessary to classify and compare different species. A description of organisms that emphasizes the values of their phenotypic traits over their taxonomic phylogenetic affiliations allows (1) a comparison of these trait values along environmental gradients to understand both how different trait combinations affect the environment ("effect" traits) and how different environments select different trait combinations ("response" traits), (2) a comparison of trait values among many species and environments in order to elucidate general trends that are not limited to narrow taxonomic groups or geographical locations, and (3) to scale up from plant modules to entire ecosystems by assuming that the structure and function at higher organizational levels are largely a result of the composite traits of the individuals present (Garnier & Navas, 2012).

Thus, the functional trait approach helps answering questions on species distribution, community assembly and ecosystem functioning (Garnier & Navas, 2012). Therefore, trait-based models have become highly relevant in ecology (Keddy, 1992), especially because ecologists have tried to predict the effects of different components of global changes (e.g., land use, climate, and modification of biogeochemical cycles) on biodiversity. A trait-based approach makes it possible to generalize findings over similar but spatial distinct areas (Adler et al., 2013). It helps to find general patterns along environmental gradients, gradual changes in biotic and abiotic environmental factors through space or time (Austin, 1986). These gradients can be direct, such as resources or disturbance, or indirect, such as altitude and latitude. In response to a particular environmental factor, different traits vary in different direction and with different amplitudes (Fonseca et al., 2000) and a specific trait response in different directions and amplitudes depending on the environmental factors (Cornwell &

Ackerly, 2009). This means that trait variation is specific to each trait-environmental gradient and should be considered individually (Kleyer & Minden, 2015).

Inter- and intraspecific trait variation

The most widespread approaches in trait-based ecology focus on trait differences among species (McGill et al., 2006). In a description of the functional characteristics of local communities, the mean trait values for the constituent species, weighted by species proportions, are calculated and used as indices (i.e., Community Weighted Mean). However, the variation of traits along environmental gradients is caused not only by species turnover. Given the stochastic (Fox & Kendall, 2002), environmental (West-Eberhard, 2003), or genetic (Doebeli, 1996) factors, traits expressions can vary within one species (Intraspecific Trait Variability, ITV). ITV influences species response to abiotic filters and biotic interaction (Fridley & Grime, 2010; Fridley et al., 2007) and its effect on ecosystems processes (Hughes et al., 2008) and generally adds to the variability of the community (Albert et al., 2011). Still, the fast-growing literature on the ecology of trait variation lacks a profound understanding of the mechanisms by which ITV influences ecological dynamics in comparison to interspecific trait variation (Bolnick et al., 2011).

A recent review by Siefert et al. (2015) showed that about one-quarter of total trait variation within communities and even more when looking at total trait variation among communities was driven by ITV. The relative extent of ITV was greater for whole plant traits (e.g. plant height) than for traits on the organ level (e.g., leaf mass). Furthermore, leaf chemicals (leaf N and P content) had smaller ITV than leaf morphological traits (thickness or area). The relative amount of ITV decreased with increasing species richness and spatial extent, but did not vary with plant growth form or climate.

Generally, ITV leads to a functional continuum rather than a clear-cut species classification (Albert et al., 2010). Therefore, Lepš et al. (2011) pointed out that neglecting intraspecific trait variability across habitats can result in underestimating the response of communities to environmental changes. ITV also influences the interaction

among organisms and between organisms and their environment that ultimately drive the assembly and functioning of communities (Bolnick et al., 2003; Vellend & Geber, 2005). This means that ecological research should include ITV to make models more correct and strengthen the understanding of processes operating at the community level and ecosystem level. Recent studies have shown that adding ITV to the models improves the ability of trait-based analysis, which makes inferences about local community assembly processes (Paine et al., 2011; Siefert, 2012), predicts species interactions (Kraft et al., 2008), elucidates community responses to spatial and temporal environmental gradients (Lepš et al., 2011), researches ecosystem processes such as productivity and nutrient cycling (Breza et al., 2012), and predicts patterns of species diversity and assembly within communities, especially with dominant species (Crutsinger et al., 2010).

In practical use, however, it is difficult to account for ITV. It is difficult to measure trait values on a large number of individuals per species, particularly in species-rich communities. Therefore, the CWM is still a much used, less time and money consuming alternative.

1.3 Combining the biogeomorphic succession model and the functional trait approach

Response and effect traits in a dynamic environment

The effect-response framework introduced by Lavorel and Garnier (2002) classifies species according to their response to the environment and their effect on ecosystem properties. Combining the functional framework with the biogeomorphic succession model can help to better understand processes in BEs because it is the specific trait and not the taxonomic species that affects and is affected by biogeomorphic processes. (see Figure 1.1 for a summary of the interacting processes).

The community organization is determined by three main filters (Belyea & Lancaster, 1999; Lortie et al., 2004): (1) a dispersal filter, which determines the potential colonists available at a particular time and place depending on stochastic events, storage effects and landscape structure; (2) an abiotic filter, which describes the impact of resource availability, disturbance and prevailing environmental conditions (humidity, temperature, etc.); (3) a biotic filter, which refers to the positive and negative interactions among organisms in the community. Species from the regional species pool which establish in a community can be seen as the result of abiotic (climate, resource availability, disturbance) and biotic (competition, predation, mutualisms) filtering that affects which species, based on their traits, can successfully establish at a site (Díaz et al., 1999; Keddy, 1992).

In the first succession phases of BEs, the environmental filters represent the most important selection pressure for coastal and fluvial plants. The filters act on the response traits and different species have evolved adapted response traits to the occurring physical disturbance. Although BEs around the world are highly diverse in geology, geomorphology and climate, as well as species assemblages, species with similar function occur in different sites.

In the first succession phase, the geomorphic phase, with strong dynamics of high frequency, species are favored which exhibit a short life span, high net productivity and production of numerous buoyant seeds and propagules. This combination allows the

plants to germinate and complete their life cycles in the brief undisturbed time (García-Mora et al., 1999). In the second phase, the pioneer phase, where physical disturbance is still high, species are favored which have extensive and rapid investments in roots and which can grow from drifting debris and propagules. Tolerance to submersion, burial and erosion through high plasticity of architecture and biochemical properties is also favored. The strengthening of tissues, stiff stems, small leaves and canopies helps to resist and avoid mechanical disturbance (García-Mora et al., 1999).

In the third phase, the biogeomorphic phase, when biotic interaction becomes more important and physical disturbances are infrequent, high growth rate, rapid underwater shoot extension, tolerance to sediment burial and erosion, control of above- and belowground allocation and adaption of shoot and root morphology to physical disturbance are favored. Other beneficial traits include adaptation to hydrodynamic forces by means of high bending stability, narrow leaf shape, multi-stemmed resprouting from roots and aerenchym tissue for transferring oxygen from the atmosphere to submerged roots. In the final stage, the ecological phase, competitive traits such as large canopy height and deep roots to exploit resources more efficiently are of importance (García-Mora et al., 1999).

However, the range of traits in communities is not always reduced, resulting in convergent response trait development. Trait expression also can be broadened by the process of limiting similarity, leading to divergent response trait development. This implies that these species have different effects on the geomorphic processes because the established engineering species modulate the geomorphic environment depending on their species-specific traits (Corenblit et al., 2015).

The effect trait-driven landscape formation can be well illustrated with the example of coastal dunes. Depending on aboveground architecture and rooting strategies of the plant species (i.e. formation of deep roots or shallow roots), dunes of very different morphologies and sizes are formed (Durán & Moore, 2013). In Western Europe, two widely distributed foredune species are *Cakile maritima* (Scop.) and *Ammophila arenaria* (L.). *C. maritima*, an annual plant with a low canopy height, reduces the airflow and sand transport slowly so that gradual downwind reduction in

sediment transport forms asymmetric dunes with the short slope on the lee side (Hesp, 2002). In contrast, high-density clumps of *A. arenaria* with a higher canopy reduce air flow velocity very rapidly and produce high, hummocky-peaked dune forms with the short slope to the seaward side (Hesp, 2002).
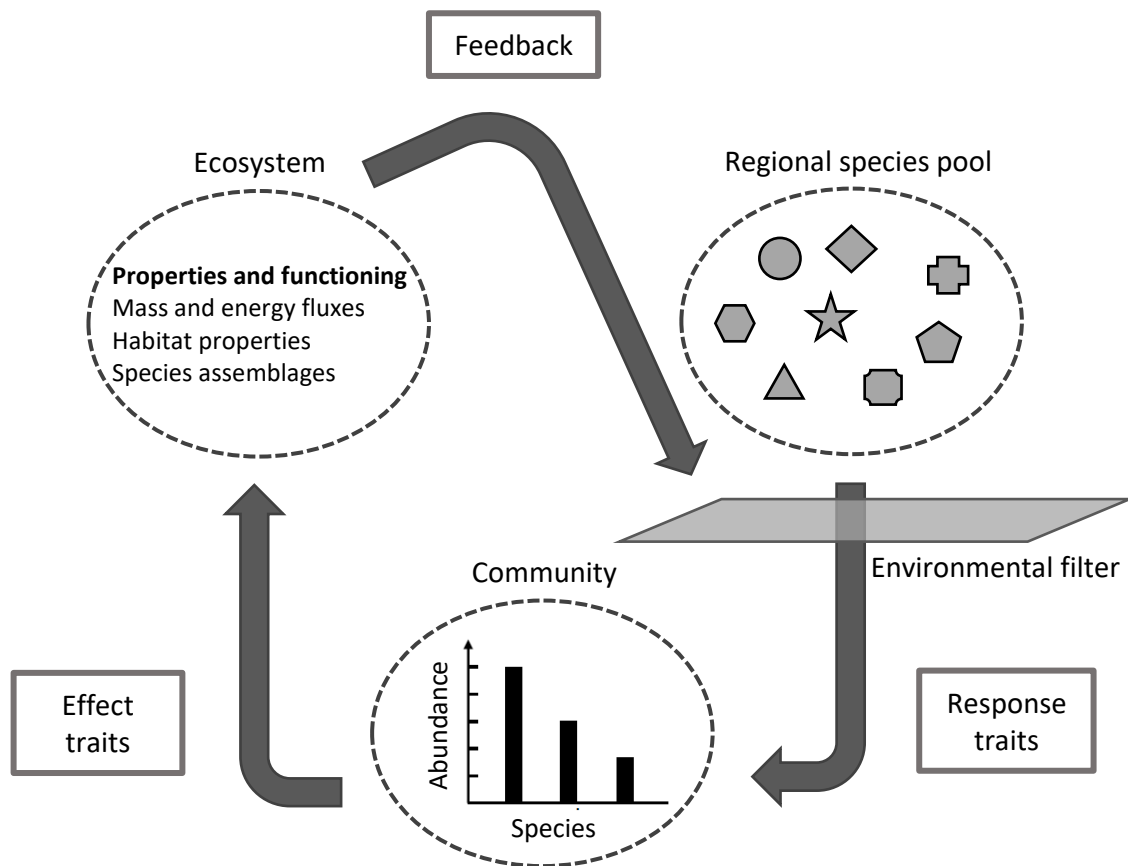

Fig. 1.1: The response and effect framework in a dynamic BE. Species from a regional species pool have to be equipped with the right set of response traits to establish successfully in the local community with the occurring selective filters, the environmental filter being the most important one in BEs. The species assemblage and the plants' specific effect traits shape the form and function of the ecosystem. This altered geomorphic conditions feed back to the response traits (adapted from Corenblit et al., 2015; Garnier et al., 2016; Keddy, 1992; Minden & Kleyer, 2011).

Traits along environmental gradients

Biogeomorphic ecosystems have multiple natural stress/disturbance gradients. Stress refers to external abiotic constraints (e.g., soil moisture or fertility), not caused by the vegetation itself, which limit biomass production (Grime, 2001). Disturbance refers to events external to the vegetation causing partial or total live biomass destruction (e.g. burial by sand) (Grime, 2001). The stress and disturbance gradients have effects on plant traits at the community and at the species level. As mentioned before, the harsh abiotic conditions in BEs are strong selective filters that influence the community assemblage (Sambatti & Rice, 2006). The gradients also lead to local adaptation of plant species. Individuals can adjust to local conditions through phenotypic plasticity of response traits resulting in ITV, which has already been mentioned previously (Crispo, 2008). This manifests itself in locally adapted populations (Kawecki & Ebert, 2004). A plant's physiological status and morphology, in turn, first mediates plant-plant interactions by altering microhabitat conditions for the nursing and associated species. Crutsinger et al. (2010) found, for example, in a Californian coastal dune system that two different phenotypes of *Baccharis pilularis* shrubs differed significantly in their facilitation intensity. Secondly, ITV affects plant-geomorphology interactions.

In fluvial BEs the gradients stretch from the channel to the floodplain and follow the hydrogeomorphic connectivity and topography. In salt marshes and mangroves, gradients stretch from the seashore to inland and are driven by wave energy, the tide, micro-topography and salinity. In coastal dunes they reach from shore to inland and follow hydrodynamic forces, topography and salinity (Corenblit et al., 2015). Environmental gradients are not restricted to BEs but exist in ecosystems around the world, such as pastures (Kleyer, 1999), mountain ranges (Körner, 2007; Schellenberger Costa et al., 2018), forests (Hammill et al., 2016), mires (Wheeler & Proctor, 2000), and savannahs (Kirkman et al., 2001). The environmental gradients can be manifold and include management, temperature, precipitation, nutrients, fire, partial pressure of CO_2, and UV radiation gradients.

Specific response traits vary along specific environmental gradients. Leaf traits such as SLA are related to resource economy and vary with nutrient availability (Lavorel &

Garnier, 2002; Ordoñez et al., 2009). Traits related to plant phenology such as leaf/root morphology vary with water availability (Ackerly, 2004; Mitchell et al., 2008; Niinemets, 2001). Plant morphology, re-growth ability and life cycle traits vary with grazing or fire intensity (Diaz et al., 2007; Hammill et al., 2016). Life form, leaf size, plant height and root architecture respond to changes in temperature or moisture availablity (Moles et al., 2014; Thuiller et al., 2004). Traits related to resource economy such as plant phenology and life form also vary along gradients of secondary succession (Garnier et al., 2004; Navas et al., 2010) and land use (Kleyer, 1999; Lienin & Kleyer, 2011). Management also affects total biomass production (Minden et al., 2016).

The zonation of coastal dune plant communities and salt marsh plants from the shore to their inland margin is recognized worldwide; however, the cause of this pattern remains controversial because of the covariance of several environmental factors, such as sand burial/flooding, salt spray, and microclimate, along a gradient perpendicular to the shoreline (Barbour et al., 1985; Hesp, 1991; Rozema et al., 1985). In coastal dunes, the sediment dynamics resulting in the burial by sand and erosion is thought to be the main factor causing vegetation zonation (Dech & Maun, 2005). Sediment dynamics imposes various stresses on plants. Burial reduces the availability of light, CO_2 and other atmospheric gases to the aboveground organs. Erosion leads to the drying out of roots and reduced ability of water and nutrient uptake. In salt marshes, flooding and soil moisture place the greatest amount of stress on wetland plant communities and are the main drivers of community assembly in wetlands (Blom & Voesenek, 1996; Weiher & Keddy, 1995). Flooding imposes two main stresses on plants. Saturation of the soil causes a depletion of the oxygen available to roots in the soil, leading to soil anoxia and hypoxia (Blom & Voesenek, 1996). Submergence also causes reductions in the availability of light, CO_2, oxygen and other atmospheric gases to the aboveground organs (Mommer & Visser, 2005).

Plants have evolved successful strategies either to avoid or tolerate the stresses associated with sediment dynamics and flooding. Avoidance can be spatial or temporal. Spatial avoidance is achieved with traits that remove the plant from the associated stresses and temporal avoidance is achieved by growing only during times when sediment dynamics or flooding is unlikely. Of the various traits that are known to be associated with flooding

stresses/burial stress, few have been measured at multiple points along an inundation/burial gradient. The traits expressions of salt marsh and dune species along these gradients are summarized in Table 1.2. These traits do not stand alone but traits are coordinated at the whole-plant level and that some traits are correlated with most other traits ("hub" traits) while others are of minor importance (Kleyer et al., 2019).

The trait expressions do not always follow well known physiological concepts. In salt marshes the "physiological-ecological-amplitude" concept was not confirmed on a trait perspective. Canopy height and stem mass fraction, indicating high competitive ability, were found to be higher in the lower marsh than in the upper marsh. Specific leaf area and leaf dry matter content were constrained by a salt-waterlogging gradient rather than by a nutrient gradient. This contrasts the leaf economics spectrum, which describes a trade-off between fast growing species with the potential of quick return of investments of nutrients and species with long lifetime and low rates of photosynthesis (Minden et al., 2012).

Table 1.2: Functional traits along inundation and burial gradients stretching from low inundation/burial intensity to strong inundation/burial intensity. ▲ = trait increases along gradient; ▼ = trait decreases along gradient; ▬ = trait exhibits no relationship to the environmental gradient. Abbreviations: ADM: aboveground dry matter; BDM: belowground dry matter; CH: canopy height; SLA: specific leaf area; LDMC: leaf dry matter content.

Environmental gradient	Functional trait	Response	
Inundation	ADM	▼	(Minden & Kleyer, 2015)
	BDM	▲	(Minden & Kleyer, 2015)
	CH	▼ ▲	(Baastrup-Spohr et al., 2015; Howison et al., 2015; Jung et al., 2010; Violle et al., 2011)
	SLA	▲	(Baastrup-Spohr et al., 2015; Howison et al., 2015; Jung et al., 2010; Violle et al., 2011)
	LDMC	▲▬	(Baastrup-Spohr et al., 2015; Jung et al., 2010)
	Root porosity	▲	(Cheng et al., 2015; Colmer, 2002)
	Adventitious roots	▲	(Colmer, 2002; Kramer, 1951)
	Specific root length	▲	(Ryser et al., 2011; Shi et al., 2015)
	Seed mass	▲▬	(Jung et al., 2010; Stromberg & Boudell, 2013)
Burial	CH	▲	(García-Mora et al., 1999)
	SLA	▼	(Ciccarelli, 2015)
	LDMC	▼	(Ciccarelli, 2015)
	Rooting depth	▲	(García-Mora et al., 1999)
	Succulent	▬	(Ciccarelli, 2015)
	Sea-water dispersion	▲	(García-Mora et al., 1999)
	Seed mass	▲	(Cordazzo, 2002)

1.4 Barrier islands and Halligen in the Wadden Sea

Geological origin of barrier islands and Halligen

The Wadden Sea is the most dynamic landscape in Western Europe. Important structures in the Wadden Sea are the barrier islands and the Halligen. They are found in a long chain parallel to the mainland coastline and stretch from The Netherlands along the German coast to Denmark (Figure 1.2). Given their offshore position, barrier islands and Halligen absorb energy and protect the mainland coastlines from storm events. Simultaneously, they create a unique environment of low-energy, brackish water in the back of the island. The very different appearance of the dune and marsh islands is attributed to their differing genesis.

Fig. 1.2: Overview of the Wadden Sea; mainland of Lower Saxony and Schleswig Holstein (light gray), Wadden Sea islands (dark gray), and Halligen (medium gray).

The genesis of the Wadden Sea barrier islands has been strongly contested in scientific literature. Several hypotheses have been formulated to describe their existence such as the sand spit hypothesis (Penck, 1894), the beach ridge hypothesis (Lüders, 1953), and the offshore sand shoal hypothesis (Barckhausen, 1969). Today, the last one is generally accepted. According to Barckhausen (1969), all barrier islands are built from offshore sand shoals deposited on Pleistocene ridges or heights during storm events. Under moderate wave and wind conditions, sediment deposition continued and built shoals that grew in elevation and were subjected to only episodic inundation during extreme high tides. The sheltered sides of the shoals provided low-energy conditions and allowed tidal flats to develop. Sediment transported from the backshore eventually built primary dunes. Preconditions for the establishment of dune islands are wave-dominated coasts with a small tidal range and wave energy. Optimal conditions are found in microtidal environments (0-2 meter tidal range) while in mesotidal environments (2-4 meter tidal range) barrier islands are less frequent and in macrotidal environments (> 4 meter tidal range) barrier islands are very rare (Boggs, 2011). This explains the chain of barrier islands from Borkum to Wangerooge in the western part of the Wadden Sea between the Ems delta and the Jade River. Between the Jade River and the Elbe River tidal range is higher; therefore, only sandbanks occur. A further precondition is a low gradient of shelf since otherwise the sand would not accumulate into a sandbar but would disperse throughout the shore. Ample sediment supply and a stable sea level also are necessary for barrier island formation and growth. If the sea level change is too large, time will not be sufficient for wave action to accumulate sand into a dune that will eventually grow to a barrier island through aggradation.

The time of origin for the Frisian barrier island chain was between 4000 to 3000 BCE (Hoselmann & Streif, 2004). After most of the modern North Sea basin had changed to dry land during the last Ice Age, the sea level rose again during the Weichselian postglacial transgression (Behre, 2002; Streif, 1989). The sea-level rise was accompanied by a progressive increase in tidal range (Hanisch, 1980). At first, sediment rates were insufficient to keep up with the rapidly rising sea (1 m/century). Thus, large parts of the inundated backbarrier area evolved into subtidal environments with only narrow zones of intertidal sand and mud flats and salt marshes on the landward side. At

about 3000 BCE rates of sea-level rise were exceeded by sediment accumulation rates so that intertidal sand flats developed. As a result of the sediment transport into the backbarrier area, the barrier islands' coast eroded. Subjected to slow flooding, the islands slowly retreated. Until today, barrier islands have been retreating landward at an average migration rate on the order of one to two meters per year. The sandy barrier system protected the hinterland and around 2500 years ago, extensive marshes formed, consisting of thick sequences of clayey and peat sediment (Meier, 2006).

The Halligen in the North Frisian Wadden Sea and off the coast of Denmark have a different origin. With the end of the glacial period and the onset of melting, the sea-level rose and large parts of what is today's North Frisian area were flooded again (Reise, 2005). From about 5000 BCE there was a highly transgressive period and a sea-level high stand period with short intercalated regression until 3000 BCE (Behre, 2007). During the regression periods brackish sediments and peat bogs accumulated, forming reclaimable marshlands, which were protected from the sea by large sandy barrier spits westward of the islands of Sylt, Amrum, and Eiderstedt (Reise, 2005). Around the beginning of the last millennium, land reclamation and drainage were increased. Dikes were built to keep the hinterland dry and to protect settlements from the tides (Riecken, 1982). However, pre-industrial peat digging lowered the elevation within the new polder landscape and allowed the water to flood the area regularly. During a number of catastrophic storm surges during the late Middle Ages, the contemporary appearance of the North Frisian Wadden Sea was formed. Two surge events in particular, known as the First and Second "Grote Mandränke", in 1362 and in 1634, had a strong impact on the landscape. During these events, large parts of arable marshlands were reclaimed by the sea. The Halligen are the last insular remnants of the former continuous marshland (Behre, 2008). In response to these strong floods, people started building artificial mounds (Warften) to protect their lives and belongings. Until today, the Halligen have no dikes or only small overflow dikes, making these mounds the only protection from extreme storm surges.

Abiotic conditions in coastal ecosystems on barrier islands and Halligen

Two types of coastal ecosystems – coastal dunes and salt marshes – are found on barrier islands in the Wadden Sea. Coastal dunes are situated on the windward side and salt marshes on the lee side. As a result of their evolution and location, the Halligen are composed completely of salt marshes. Salt marshes and dunes differ largely in their vegetation. Only a few species (e.g. *Festuca rubra*, *Atriplex hastata*, *Elytrigia pungens*) occur in both coastal environments, and to some extent bridge the differences that exist between salt marshes and coastal sand dunes (Rozema et al., 1985). Dune and salt marsh plant communities are characterized by striking zonation patterns parallel to the shore. Coastal dunes are classified as embryo dunes, foredunes, white dunes, grey dunes, and brown dunes. Salt marshes are classified as pioneer zone, lower and upper salt marshes. Salt marshes on the Halligen mostly resemble the upper salt marsh. The dune and salt marsh ecosystem on barrier islands experiences severe stress in the form of inundation, salinity, sediment dynamic, wind exposure, low water availability, and nutrient deficiency. These factors mediate zonation patters, proportions of the factors are still debated (Crain et al., 2004; Fariña et al., 2018; Lee et al., 2016; Pennings et al., 2005; Rajaniemi & Barrett, 2018; Torca et al., 2019) (Table 1.3).

As a result of tidal movement, coastal salt marshes are subject to periodic flooding by seawater. Inundation frequency and duration is partly driven by elevation (Chapman, 1960). However, in salt marshes local morphology and wind exposure also influence incoming water, making elevation a less suitable predictor for inundation frequency (Bockelmann et al., 2002). Generally, the pioneer zone is regularly submerged during high tide, the lower salt marsh is submerged during spring tides, and the upper salt marsh is flooded only during extreme storm events. In contrast, seawater inundation of the sand-dune coast is rare and restricted to the foredunes and the primary dune ridge, extreme high spring tides included. Only during very-high-energy events, water can break through the white dune crest and penetrate further inland (Rozema et al., 1985).

Table 1.3: Abiotic stressors along a transect of a barrier island from the open coast (left) to the back barrier end of the island (right) representing coastal dunes on the left and salt marshes on the right side. The intensity of stressors along the transect is illustrated by grey triangles. Morphological and physiological adaptations to the respective stressor are shown (adapted from Rozema et al. (1985)).

Inundation exerts a mechanical disturbance and also influences groundwater level and salinity, soil waterlogging, spoil temperature and light availability (Adam, 1990). Yet, especially species growing in the pioneer zone and the lower salt marsh, such as *Spartina anglica*, *Puccinellia maritima*, *Aster tripolium*, are well adapted to inundation (Bouma et al., 2001; Lenssen et al., 1995). Species from the upper salt marsh, such as *Elymus athericus*, *Festuca rubra* and *Juncus gerardii*, have been shown, however, to be negatively affected by inundation (Rozema et al., 1985).

Owing to the periodical inundation with seawater, salt marsh soils are both waterlogged and salty. Both flooding and salinity increase in severity from the marsh upland border to the water's edge (Pennings & Bertness, 2001). Overall soil salinity is lower during wet seasons, yet the decrease is not uniform for all ions and all plant communities (Rogel et al., 2000). Contrary to the salt marsh habitat, the soil salinity in coastal sand dunes is low. In dunes, it is airborne salinity (salt spray) that limits plant growth. It is highest in the beach-foredune environment and generally decreases with distance from the coast (Rozema et al., 1985).

Salts in the soil water may inhibit plant growth for two reasons. Firstly, salty soil water reduces the ability of the plant to take up water and leads to a reduction of growth rate. This is referred to as the osmotic or water-deficit effect of salinity. Secondly, if large amounts of salt enter the plant in the transpiration stream, cells in the transpiring leaves will be injured which causes further reduction in growth. This is referred to as the salt-specific or ion-excess effect of salinity (Greenway & Munns, 1980). However, some species, the halophytes, can tolerate soil salinity or even increase their productivity through salty soil water (Flowers & Colmer, 2008). Salinity tolerance changes through ontogenesis. Seedlings are most sensitive to salt stress as their roots are still in the upper soil centimeters that have the highest salinity (Ungar, 1991). Airborne salt in coastal dunes may have an adverse effect on fitness related traits such as life span and seed mass in species from fixed and inner dunes (Cheplick & White, 2002; Rozema et al., 1985). However, species from the embryo and fore dunes, such as *Cakile* spp., *Ammophila* spp., and *Honckenya* spp., can resist or even increase their productivity to salt spray (Rozema et al., 1985).

Strong onshore winds take up dry sand from the beach, transport it inland and lead to burial of dune plants. The aeolian sediment transport process is controlled by several key factors such as the magnitude and frequency of transporting winds (Wal & McManus, 1993), the influence of incident wind direction (Arens, 1996), beach fetch and sediment supply effects (Bauer et al., 2009), vegetation type and density (Hesp, 2002), as well as moisture content (Jackson & Nordstrom, 1997). Generally, wind and sediment dynamic are strongest in the embryo and foredune community (Maun, 2008). While aeolian processes play a significant role in the morphodynamics and sediment budget of most sandy coastal systems, fluvial dynamic is important in salt marshes. Here, sedimentation and burial depth is, in comparison to dune systems, very small (Schürch et al., 2012).

Burial by sand is thought to be the most important physical stress in coastal dunes that alters species diversity by eliminating disturbance-prone species (Maun, 1998, 2008). Especially species in the embryo and fore dune community are well adapted to burial by sand and show morphological and ecophysiological responses to burial by sand (Harris et al., 2017; Perumal & Maun, 2005). Also, salt marsh species show responses to burial by shoot elongation or even increased productivity. However, they generally survive only smaller amounts of burial depth than some dune species (Deng et al., 2008; Langlois et al., 2001).

Another constraint to plant development in coastal dunes is water scarcity since dunes soils have low water-holding capacity. Especially in the embryo dune and fore dunes, where no humus has been generated, high winds and radiation lead to desiccation and heating of the soil. This leads to drought stress associated with increased leaf temperature due to reduced transpiration rate (Smirnoff & Stewart, 1985). Fore dune species such as *C. maritima* are well adapted to drought and have an efficient water economy by regulating transpiration (Rozema et al., 1985). Other adaptation strategies are leaf roll and elongation of roots into deeper soil profiles (Park, 1990). Adaptations to drought are less well developed in salt marsh species, with the exception of species from hypersaline sites (Rozema et al., 1985).

Another important environmental constraint in coastal habitats is the deficiency in nutrients such as potassium, phosphorous, and carbonate. In salt marshes, nutrient scarcity is especially limiting in the upper salt marsh. In coastal dunes, nutrient deficiency is an important limiting factor throughout the system but is increasingly important in fixed dunes, dune grasslands and inner dunes. The nitrogen availability is one of the main limiting factors for plant biomass production in saline habitats (Ungar, 1991). Thus, the short supply of major nutrient elements such as nitrogen and phosphorus also can explain the sparse vegetation in coastal dunes (Pemadasa & Lovell, 1974). Species in the upper salt marsh and the dunes are adapted to nutrient deficiency by highly efficient uptake, translocation and retranslation of nutrients. The large rhizome growth providing a large surface area for nutrient absorption at the expenses of aboveground biomass is one of these strategies (Hawke & Maun, 1988).

Barrier islands and Halligen in a changing climate

A rise in the global mean sea level was observed at a rate of 2.0 mm/a between 1971 and 2010 (Church, Clark, Cazenave, Gregory, Jevrejeva, Levermann, Merrifield, Milne, Nerem, Nunn, et al., 2013) and projections assume that the sea level will continue rising as global temperature further increases. However, exact projections are difficult if based solely on modern observations. The Fifth IPCC Assessment Report suggests an increase range of 0.26 to 0.82 m by the end of the century, depending on the model and scenario (IPCC, 2014). This wide range of projections illustrates the difficulties in understanding and projecting all relevant processes contributing to sea-level rise (SLR) (Dangendorf et al., 2014). Over the past century global SLR was largely driven by thermal expansion of the oceans and melting glaciers but new processes are assumed to add to future SLR. With future warming Antarctic and Greenland ice melting will continue to contribute substantially to global SLR (Chen et al., 2017; Levermann et al., 2013).

The IPCC (2014) further states that many areas are already experiencing an increase in the frequency of extreme climate events such as windstorms, floods and rainfall. Very probably attributable to anthropogenic climate change, these events are likely to continue in the future. Increasing storminess is expected in many parts of the world but

with strong regional differences (Emanuel, 2005). For the Wadden Sea, long-term models project for the coming century increased occurrence of extreme storms (von Storch & Weisse, 2008). This implies stronger waves and storm surges hitting the islands and mainland coasts.

Coastal dunes and salt marshes are at the interface between land and sea and are undergoing permanent morphodynamic changes at different temporal and spatial scales in response to geomorphological, oceanographic, and anthropogenic factors (Cowell et al., 2003). They are in an equilibrium state and return to their pre-disturbance morphology even when affected by short-term perturbations (i.e. storm surges). This state is achieved when inputs and outputs of energy and matter balance and a system remains in a steady state for long periods of time. However, accelerating SLR and/or extreme disturbance events such as storm surges can lead to sudden changes in coastal ecosystems (van de Koppel et al., 2001). When a salt marsh ecosystem on a barrier island reaches a tipping point, it undergoes a drastic transformation. Its stable vegetated state is altered and the salt marshes are turned into intertidal mudflats or unvegetated subtidal platforms (Marani et al., 2010; van de Koppel et al., 2001).

The tidal flats in the Wadden Sea survive SLR only if sedimentation keeps up with SLR. Island beaches, dunes and an offshore band down to 10 m depth represent sources of the sediment that is transported through tidal inlets into the Wadden Sea, mainly during storm surges. Also, the migration of the barrier islands can support the sediment budget in the tidal flats. Barrier islands naturally move landward over their own tidal sediments (i.e. back-barrier tidal basin) under SLR. The East Frisian Islands were originally formed several kilometers offshore from their present position and gradually shifted south-southeast during the late Holocene SLR (Chang et al., 2006). During the last 2 000 years, islands shifted more than 100 m per century (Steif, 1973). Today, however, fixed boundaries such as dikes and stabilized dunes hinder barrier islands from migrating (Kirwan et al., 2016; Miselis & Lorenzo-Trueba, 2017).

The salt marshes in the Wadden Sea can survive SLR either through high sediment accumulation so that vertical accretion keeps up with SLR or, in the case of mainland salt marshes, via horizontal retreat. However, upland migration is often hindered by

static barriers, such as dikes. Combined with wave-induced marsh boundary erosion, such movement leads to a reduction of suitable habitat, a process known as coastal squeeze (Doody, 2004; Pontee, 2013). However, it is still under discussion how vulnerable our salt marshes are with respect to SLR (Davidson-Arnott, 2005; Feagin et al., 2005; Nicholls et al., 2007; Ranasinghe et al., 2012; Rosati et al., 2013; Schürch et al., 2013).

The dune systems on the barrier islands depend on sediment budget and naturally occurring disturbances. Over the long run, the net sediment balance determines the response of the beach-dune system. A negative budget leads to inland displacement, an equilibrium budget leads to stability/balance, a positive budged leads to seaward displacement of the beach-dune system (Hesp, 2002). A higher intensity or frequency of disturbances, as expected with climate change, may alter community dynamics. The mobility of sand may increase and stabilized dunes (such as forest areas) may be lost to erosion and sand deposition (Martínez et al., 2008). With further SLR, beaches will narrow, leading to increased dune erosion since less energy will be dissipated by the beach (Ranasinghe et al., 2012). This initiates an inland displacement of the entire beach-dune profile (Pethick, 2001), an activation of the face of the foredune (Feagin et al., 2005), and increased inland transport along the entire continuum (Davidson-Arnott et al., 2005).

The low-lying Halligen represent a very special situation in the Wadden Sea. During the long history of settlement, inhabitants have transformed the marshland into a cultural landscape. To enhance drainage, the tidal channel system was straightened and tidal gates were installed. Shallow summer dikes often prevent inundation during moderate high tide events during summer months. They can influence marsh development and accretion (Reise, 2005; Schindler et al., 2014). The small current accretion rate on the Halligen (Schindler et al., 2014; Stock, 2011) in combination with the lack of lateral migration possibility, make these marsh islands especially prone to climate change-induced SLR.

1.5   Research objectives

Climate change-induced accelerated sea-level rise and stronger extreme weather events put coastal ecosystems around the world at risk. Coastal areas are at risk of erosion and drowning if the sediment input and resulting vertical accretion cannot keep up with accelerated SLR. Also in the Wadden Sea area, the salt marshes on the mainland, on the lee side of the barrier islands, and on the Halligen as well as the coastal dunes on the windward side of the barrier islands, are under severe threat. Coastal ecosystems have a high intrinsic value as well as high ecological and socioeconomic values. Amongst other things, they provide habitat for specialized flora and fauna and serve as coastal protection and recreation areas. Therefore, efforts are being undertaken to conserve these ecosystems.

However, fragmented knowledge about the functioning of the ecosystems hinders a well-informed discussion about their resistance and resilience to climate change and suitable adaptation strategies. Coastal ecosystems are biogeomorphic systems and their form and function are shaped through the two-way interaction of biology and geomorphology. The role of vegetation in the ecosystem is mediated by the effect traits. On the other hand, the geomorphology of the ecosystem influences the response traits on the community and species levels. The goal of this dissertation is to add to the knowledge of the functioning of coastal dune and salt marsh ecosystems (Figure 1.3).

The thesis pursued two major objectives:

(1) Explore the specific functional trait responses of pioneer species to geomorphic processes.

(2) Explore the effect of functional traits of coastal species on geomorphic processes.

More specifically, the aim of the thesis was to elucidate the following three topics:

(1) Intraspecific trait variance – What are the trait responses of pioneer dune species to geomorphic processes, i.e. burial and erosion, of different intensities and timings?

(2) Biodiversity vs. key species as main drivers for ecosystem resistance and resilience – What are the effects of mono- and mixed-plant community traits on the resistance and resilience of coastal dunes against wind erosion?

(3) Biogeomorphic processes in salt marshes – What are the effects of marsh vegetation traits on surface elevation change of salt marshes?
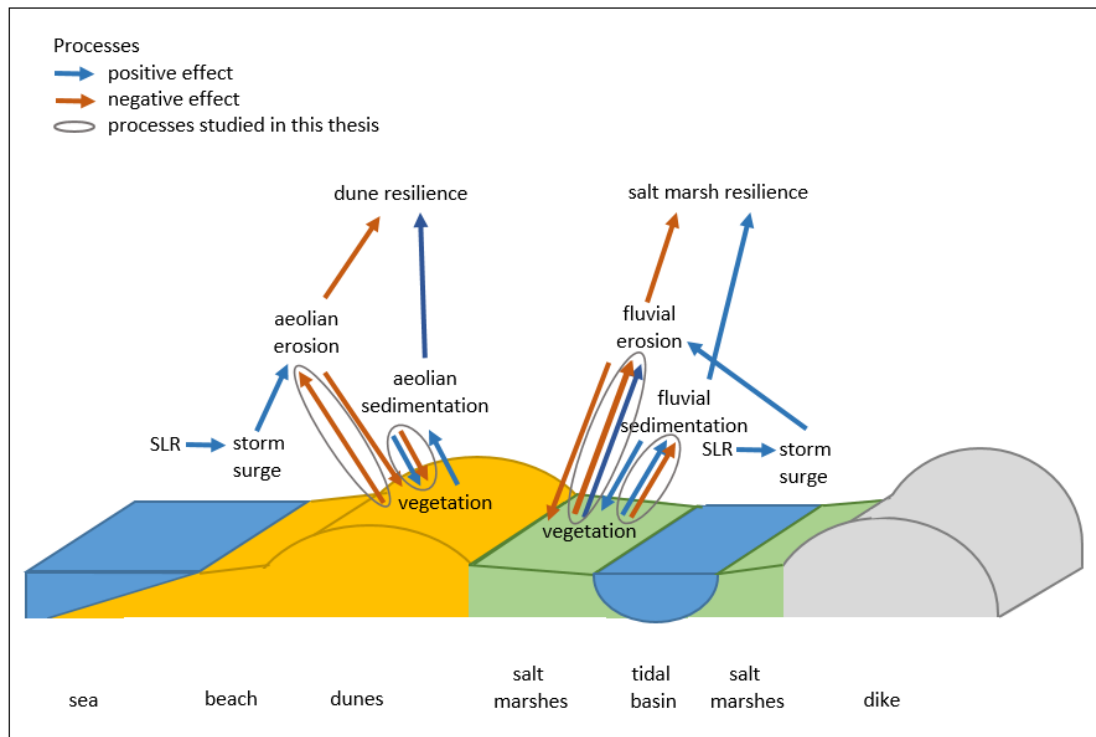

Fig. 1.3: Cross section of a barrier islands in the Wadden Sea. Key processes of vegetated coastal habitats (coastal dunes and salt marshes) are indicated by errors. Circles indicate processes studied in this thesis.

Chapter 2

Morphological plasticity of dune pioneer plants in response to timing and magnitude of sediment disturbance

Julia Bass, Thorsten Balke, Vanessa Minden

2   Morphological plasticity of dune pioneer plants in response to timing and magnitude of sediment disturbance

2.1   Abstract

Dunes are the first line of defense against the impact of rising sea level and more frequently occurring extreme weather events. The building processes of coastal dunes rely on bidirectional interactions between ecosystem-engineering plants and geomorphic processes. As extreme weather events increase, both sand accretion and erosion events in foredunes will intensify. This affects dune plant survival and triggers physiological and morphological adaptations which in turn could have implications for geomorphic processes. In a greenhouse experiment we artificially manipulated sediment levels for *Cakile maritima* and *Ammophila arenaria*, two common European foredune species. Sediment accretion and erosion events of varied magnitudes were applied at different times after germination. We measured mortality rates, biomass allocation, orientation in space (i.e. canopy height), and the turnover rate of disturbed and undisturbed individuals. Both species showed higher mortality after burial than after erosion events. Growth rates increased after burial and erosion in *C. maritima* and decreased in *A. arenaria*. This shows that increased sediment dynamics in coastal dunes caused by climate change may alter vegetation structure. Our findings have implications for coastal management as they underline the ability of dune plant species, especially of *A. arenaria*, to survive and adapt to sediment dynamics. We conclude that *A. arenaria* is highly suitable for management projects, but should be planted with care as it can strongly reduce open space and thus reduce ecosystem dynamics.

Keywords: *Ammophila arenaria, Cakile maritima*, biogeomorphology, dunes, functional traits, ecosystem engineers

2.2 Introduction

Coastal dunes are important aeolian sand formations that protect inland ecosystems and human settlements from marine flooding and wave-induced erosion (Renaud et al., 2016). Current predictions for coastal population growth (Neumann et al., 2015) and rising sea level (Nerem et al., 2018) combined with increasing strengths of storm waves and storm surges (Coumou & Rahmstorf, 2012) will intensify the need for ecosystem and socioeconomic services of coastal dunes (Biel et al., 2017; Everard et al., 2010). Foredunes, i.e. the first dune ridge landward of and parallel to the shoreline, initiate dune succession and represent the first barrier against high water levels. As such, they are particularly important for coastal protection (Hanley et al., 2014; Maun, 2009). Moreover, foredunes are subject to abiotic changes (e.g. wind-induced erosion and sedimentation) and to human-induced development projects, such as man-made barriers and management/restoration projects (Ruggiero et al., 2018).

The process of dune formation depends on the bidirectional interaction between geomorphic processes – wind, water and sediment motion – and ecosystem-engineering plants (Corenblit et al., 2015). Successfully established plants affect sediment deposition and substrate stabilization via their aboveground and belowground plant organs, respectively (Packham & Willis, 1997; Polvi et al., 2014). In this process, shifting sand subjects dune plants to physiological stress and mechanical disturbance. Burial results in reduced light, O_2 and temperature and in increased moisture, nutrients and bulk density (Baldwin & Maun, 1983). Erosion accelerates soil desiccation and reduces nutrient availability (Jiao et al., 2009). This results in a strong zonation of species occurrences along coastal dunes (Maun & Perumal, 1999). The foredunes in particular are characterized by early successional stages with only sparse vegetation and few pioneer species (de Groot et al., 2016; Ellenberg & Leuschner, 2010). This transition zone from bare state towards vegetated state in the costal foredunes is the most critical stage in all biogeomorphic ecosystems (Balke et al., 2014). Due to the lack of positive feedbacks through already established individuals and sediment movement, seedlings are exposed to the full force of physical disturbance and are dependent on stochastically occurring disturbance-free periods (window of opportunity) for

successful germination (Balke et al., 2014). Once established, pioneer species respond differently to sand relocation and employ contrasting strategies to survive under the influence of burial and erosion.

Some species show decreased productivity when buried (e.g. *Zonstera noltiei* (Cabaço & Santos, 2007)) and complete burial is often fatal (e.g. *Agropyro sammophilum*, *Panicum virgatum*, and *Cirsium pitcherii* (Maun, 2009)). Other species respond positively to burial with increased biomass production, for example *Agropyron psammophilum* (Zhang & Maun, 1990a) and *Spinifex serceus* (Maze & Whalley, 1992). Erosion has generally been found to have negative effects on plant survivorship, growth and reproduction in many dune species (Li et al., 2010; Liu et al., 2014; Marbà & Duarte, 1994; Petrů & Menges, 2004).

Burial and erosion-events prevail in three forms: gradually in time, one-time seasonal and in fluctuating episodes throughout the year. One sudden disturbance event has been found to affect plants differently than a gradual burial (Deng et al., 2008; Maun et al., 1996). For example, non-lethal burial exhibits a significantly greater stimulation of growth in *Cirsium pitcheri* when applied repeatedly than when applied in one sudden event (Maun et al., 1996). Burial and erosion have been found to differently affect on mortality rate and plant characteristics of seagrasses (Cabaço et al., 2008). With further climate change, higher probability of storm surge events and predicted changes in precipitation will put dunes at a higher risk of transformation through effects on aeolian sand transportation rates (Pye, 2001). Engineering dune plants relocating sediment shifts and promoting resistant and resilient dunes might be a key to meeting the future environmental challenges of coastal regions.

Here we study the responses of two widely distributed dune pioneer plant species, *Cakile maritima* (Scop.) and *Ammophila arenaria* (L.), to different magnitudes of burial and erosion at varying times after germination. In a greenhouse experiment, plant individuals of the two species were subjected to either sudden disturbance events or gradual disturbance events reflecting in-vivo situations of natural dune ecosystems. Individuals of each group were exposed to different magnitudes of sand burial and sand erosion (± 2, 4, and 8 cm), respectively. Mortality rates and responses of eight plant traits

(e.g. canopy height, specific leaf area, and biomass allocation traits) were analyzed for their responses towards timing and magnitude of burial and erosion. Specifically, regarding mortality rate, we tested the following hypothesis: (1) mortality rate of both species is affected by both timing and magnitude of burial and erosion, with burial exerting a stronger effect than erosion, (2) the lethal effects of burial and erosion are less pronounced when individuals are disturbed gradually, giving them time to adapt, as compared to a situation when they are disturbed only once, (3) within the group of sudden disturbance, lethal effects are more pronounced at an early disturbance. Regarding biomass allocation, the following hypothesis were tested: (4) gradual disturbance provokes stronger effects on fitness related plant traits than sudden disturbance, (5) within the group of sudden disturbed individuals greater magnitude of disturbance leads to stronger effects than lower magnitude, and (6) earlier disturbance leads to stronger effects (e.g. reduced biomass) than late disturbance.

2.3   Methods

Selected species and seed germination

The selected European coastal foredune species differ in their growth forms. *Cakile maritima* (Brassicaceae) is an abundant summer annual plant on the German Wadden Sea islands. This low growing annual plant reduces the airflow and sand transport slowly and thus forms asymmetric dunes with the short slope on the lee side (Hesp, 2002). *Ammophila arenaria* (Poaceae) is a perennial rhizomatous grass which is widely spread in the foredunes (Ellenberg & Leuschner, 2010). Contrary to *C. maritima*, the tall growing *A. arenaria* forms dense clumps which reduce air flow velocity very rapidly and produce high, hummocky-peaked dune forms with the short slope to the seaward side (Hesp, 2002).

C. maritima seeds were collected from randomly chosen foredune plants on the Wadden Sea island Spiekeroog, Germany (53°46' N, 7°44 E) in late summer 2015 and air-dried for three weeks. *A. arenaria* seeds were ordered in February 2015 from Jelitto Staudensamen GmbH, Germany. Seeds of both species were stored in paper bags in

darkness at 4 °C for stratification for approximately 4 month (Walmsley & Davy, 1997). When ready for use, the *C. maritima* fruits were peeled and soaked in water for 3 hours to facilitate germination, whereas *A. ammophila* seeds received no further processing. Non-viable seeds were excluded by pre-germinating all seeds in a climate chamber. For that purpose, seeds were placed in covered plastic Petri dishes on several layers of paper towels saturated with distilled water and rewetted regularly. After approximately three days at 24 °C in darkness, the seedlings displayed a strong radicle, but no roots. They were transplanted individually into sand-filled planting pots (12 cm in diameter). We used a homogeneous sand substrate (0-2 mm grain size) to prevent non-treatment-driven variation across individuals. Pots were watered with tap water into the saucer as needed. Plants were fertilized with Hoagland solution, with 5 ml added per plant individual per week (Hoagland & Arnon, 1950). Pots were randomly arranged in an unheated greenhouse from 25th April to 5th July 2016 for *C. maritima* and 26th June to 11th August 2015 for *A. arenaria*, with an average daily temperature of 22°C and 23°C, respectively.

Experimental design

We designed a full factorial experiment to identify the effects of burial and erosion, as well as the effects of their timing on plant mortality and plant traits. Burial and erosion events of varied magnitude were applied at different times after germination. One subgroup of plant individuals was disturbed only once during the course of the experiment (sudden disturbance events), individuals of the other subgroup were disturbed multiple times (gradual disturbance events). Plants of the sudden disturbance events were disturbed either 5, 20 or 35 days after germination with magnitudes of 2, 4, 8 cm of either burial or erosion, respectively. Plants of the gradual disturbance events were disturbed multiple times, i.e. 5, 15, 25 and 35 days after germination. On each of those days, either 0.5 cm, 1 cm or 2 cm of sand were added or removed, which added up to the same magnitude of burial or erosion as applied in the sudden disturbance treatments (see Table 2.1). Undisturbed plants grown under the same greenhouse conditions were used as a control. Treatments were replicated 10 times, resulting in 250

individuals per species (sudden disturbance events with 18 treatments + gradual disturbance events with 6 treatments + control). Due to mortality unrelated to the experiment, some treatments ended up with fewer replicates.

Table 2.1: Overview of the experimental design: subgroups of plants were exposed either to sudden disturbance events or to gradual disturbance events. In the sudden disturbance events plants were treated either after 5, 20 or 35 days after germination, with burial (or erosion) of either 2, 4 or 8 cm of sand each. In the gradual disturbance event each plant individual was disturbed in total four times, i.e. 5, 15, 25 and 35 days after germination. At each of these days the treatments were either 0.5, 1 or 2 cm of sand addition (burial) or removal (erosion). In the control treatment, plants were not disturbed.

Disturbance mode	Control	Sudden			Gradual
Disturbance timing (d)	-	5	20	35	5+15+25+35
Burial magnitude (cm)	-	+2 +4 +8	+2 +4 +8	+2 +4 +8	+0.5*4 +1*4 +2*4
Erosion magnitude (cm)	-	-2 -4 -8	-2 -4 -8	-2 -4 -8	-0.5*4 -1*4 -2*4

To mimic burial and erosion by adding and removing sand, we customized the planting pots to hold more sand and to release sand. At the start of the experiment and before the seedlings were planted in the pots, each planting pot was encased with an additional plastic collar fixed onto the pot by Velcro strips. The collar was lifted for the burial treatments and lowered for the erosion treatments. Burial of plant individuals was then done by carefully filling the additional space with dry sand using a folding ruler, whereas erosion events were mimicked by removing sediment from around the plant individuals (see Figure 2.1).
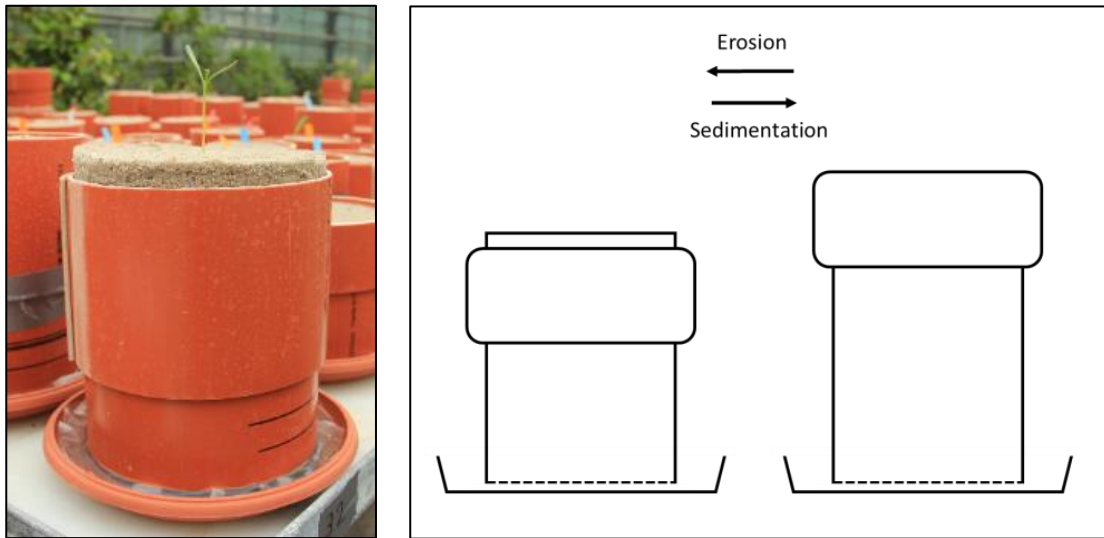
Fig. 2.1: Left: customized planting pot with a young *C. maritima* individual being exposed to erosion treatment by lowering the collar and removing the sand. Right: Schematic overview of the experimental pot with movable collar.

Trait measurements

All plant individuals were harvested after 45 days, which, corresponding to the treatment, allowed for different recovery times of plant individuals in the specific treatments. For example, if an individual was disturbed once at 5 (20, 35) days after germination it received a recovery time of 40 (25, 10) days before harvest. All individuals of the gradual disturbance events recovered 10 days before harvest, as the last disturbance event was applied 35 days after germination.

Before harvesting, canopy height was measured as the distance between the initial substrate surface and the highest fully developed leaf of each plant individual (Pérez-Harguindeguy et al., 2013). Mortality rate was determined by counting all dead plant individuals, i.e. individuals which showed no living organs. From this, we expressed mortality rate as percentage share of dead individuals to living individuals. Plant functional traits representing growth, biomass allocation, orientation of biomass in space, and biomass turnover rate were collected from all surviving individuals. Plants were harvested, cleaned of sand and separated into leaves, stems and roots. After drying

at 70 °C for 72 hours, the dry weight of different organs was measured to the nearest 0.01 g.

Specific leaf area (SLA, mm² mg^{-1}) was calculated for three most recently produced fully developed leaves by dividing the mean leaf area by their mean dry weight. Leaf area was measured with a flatbed scanner using the computer software ImageJ (Abràmoff et al., 2004). Living and dead leaves were counted for each individual. Dead leaves occurring in the course of the experiment were collected and added to the number of leaves of the respective individual. Biomass allocation was determined for total dry weight, dry weights of stems, root and leaves (live and dead). Lastly, Root:Shoot ratio was calculated as the ratio of aboveground to below-ground biomass.

Statistical analysis

Treatment effects on mortality rates were tested with logistic regression, with a binomial response variable (dead (1) and alive (0), model < -glm (response ~., family=binomial (link='logit'))). Predictors were disturbance-timing after germination (four levels: 5, 20, 35 and 5+15+25+35 days), type of sand-relocation (two factors: burial and erosion) and magnitude of disturbance (four levels: 0, 2, 4 and 8 cm) as main factors.

Second, to further elucidate factor-effects on the two subgroups of the experiment (sudden disturbance events/ gradual disturbance events) the analyses were rerun for plant individuals of the specific subgroup. For the sudden disturbance events predictors were disturbance-time (three levels: 5, 20 and 35 days), type of sand-relocation (two factors: burial and erosion) and magnitude of disturbance (four levels: 0, 2, 4 and 8 cm). For the gradual disturbance events, predictors were type of sand-relocation (two factors: burial and erosion) and magnitude of disturbance (four levels: 0, 2, 4 and 8 cm).

To evaluate trait responses towards the different factors of the experiment we first conducted an ANOVA with the effects of disturbance timing, type of sand relocation and disturbance magnitude as factors (see above in mortality section for factor levels) and their interactions on response traits. To elucidate factor-effects on the two subgroups of the experiment (sudden disturbance events/ gradual disturbance events)

the analyses were rerun for plant individuals of the specific subgroup (see above in mortality section for factors and levels).

Prior to statistical analyses, data were inspected for normality and homoscedasticity of errors. When necessary, square root/log/box-cox transformation was applied. When ANOVA was significant ($p < 0.05$), differences between each treatment and the control were analyzed using a paired t-test with Welch correction ($\alpha = 0.05$). Statistical analyses were performed using the computer software R (R Development Core Team, 2016), with the packages car (Fox & Weisberg, 2011), MASS (Venables & Ripley, 2013), rcompanion (Mangiafico, 2016), and ggplot2 (Wickham, 2016).

2.4 Results

Mortality in response to disturbance timing and magnitude

All individuals survived in the control treatment, both for *C. maritima* and for *A. arenaria* (Figure 2.2). Overall, mortality rate was higher in *C. maritima* than in *A. arenaria* with an average of 26 % and 11 % across treatments, respectively. Early disturbance (i.e. after 5 days) resulted in significantly higher mortality rates in both *C. maritima* and *A. arenaria* plants. In *A. arenaria* later disturbance (after 20 and 35 days) decreased mortality rates (see negative estimates in Table 2.2). For both species burial events increased mortality rates (negative estimates of erosion in Table 2.2 and higher mortality numbers for burial in Figure 2.2).

The results of the logistic regression for sudden disturbed individuals indicated that there was a significant association between type of sand relocation and mortality and for disturbance magnitude in *C. maritima*. In *A. arenaria*, the effect of time and magnitude was even more pronounced. Gradual disturbed individuals did not show an increased mortality rate, in response to burial or erosion or to events of different magnitudes (see Table 2.3 and Table 2.4).
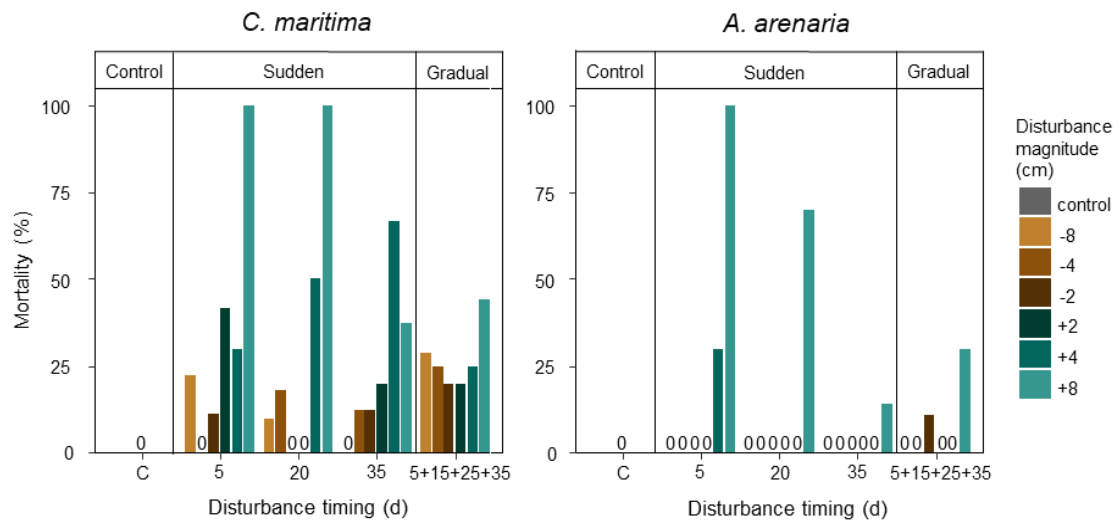
Fig. 2.2: Mortality rate for different types of disturbance events, timing and magnitudes for *C. maritima* and *A. arenaria*. Control (no disturbance), sudden disturbance events and gradual disturbance events are given on the x-axis, color code indicates total magnitude of disturbance, with -2, -4 and -8 cm in the erosion treatments and +2, +4, and +8 cm in the burial treatments.

Table 2.2: Estimates and *p*-values for logistic regression on the effects disturbance "timing", "type of sand relocation" and "disturbance magnitude" on mortality rates of *C. maritima* and *A. arenaria* determined by logistic regression. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	C. maritima ALL			*A. arenaria* ALL		
	Estimate	*p*-value		Estimate	*p*-value	
Time of dist. 5 days	0.93	**0.03**	*	2.31	**<0.01**	**
Time of dist. 20 days	-0.44	0.37		-1.80	**0.04**	*
Time of dist. 35 days	-0.88	0.10		-4.16	**<0.01**	**
Gradual dist.	-0.41	0.38		-2.83	**<0.01**	**
Burial erosion	-1.81	**<0.001**	***	-4.80	**<0.001**	***
Magnitude 0 cm	-19.43	0.99		-20.62	0.99	
Magnitude 2 cm	-1.53	**<0.001**	***	-4.76	**<0.001**	***
Magnitude 4 cm	-1.07	**0.02**	*	-3.52	**<0.001**	***

Table 2.3: Estimates and *p*-values for logistic regression on the effects disturbance "timing", "type of sand relocation" and "disturbance magnitude" on mortality rates of sudden disturbed *C. maritima* and *A. arenaria* determined by logistic regression. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	C. maritima SUDDEN DIST. EVENTS			*A. arenaria* SUDDEN DIST. EVENTS		
	Estimate	*p*-value		Estimate	*p*-value	
Time of dist. 5 days	1.44	**<0.01**	**	3.58	**<0.001**	***
Time of dist. 20 days	-0.43	0.42		-2.81	**<0.001**	***
Time of dist. 35 days	-0.98	0.10		-5.04	**<0.001**	***
Burial erosion	-2.60	**<0.001**	***	-6.63	**<0.001**	***
Magnitude 0 cm	-19.76	0.99		-6.63	**<0.001**	***
Magnitude 2 cm	-2.03	**<0.001**	***	-6.63	**<0.001**	***
Magnitude 4 cm	-1.39	**0.01**	*	-4.37	**<0.001**	***

Table 2.4: Estimates and *p*-values for logistic regression on the effects disturbance "type of sand relocation" and "disturbance magnitude" on mortality rates of gradual disturbed *C. maritima* and *A. arenaria* determined by logistic regression. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	C. maritima GRADUAL DIST EVENTS		*A. arenaria* GRADUAL DIST EVENTS	
	Estimate	*p*-value	Estimate	*p*-value
Burial erosion	-0.25	0.69	-1.21	0.32
Magnitude 0 cm	-18.04	0.99	-18.83	0.99
Magnitude 2 cm	-0.86	0.26	-1.21	0.32
Magnitude 4 cm	-0.57	0.46	-18.89	0.99

Morphological responses to disturbance

The type of sand relocating, i.e. whether the plant individuals were buried or experienced erosion, together with the magnitude of the events showed the strongest effects on almost all plant traits (*F*-values in Table 2.5). For *A. arenaria* the effect of burial/erosion was stronger than for *C. maritima*. Disturbance timing played only a minor role; SLA alone responded strongly to this factor. Furthermore, disturbance timing affected traits strongly in interaction with burial/erosion, whereas the interaction burial/erosion × magnitude hardly affected the plant traits.

In the sudden-disturbance treatments, the type of sand relocation (burial/erosion) and the magnitude of the disturbance events exerted the strongest effects on the plant traits (see *F*-values in Table 2.6). In *C. maritima*, stem biomass and number of leaves were most strongly affected by burial/erosion and were higher under erosion than under burial (Figure 2.3). In the same species, total biomass, root biomass, Shoot:Root Ratio, and SLA were most strongly affected by the disturbance magnitude. The interaction between timing and relocation type was significant only for total biomass, stem and root biomass. As with the whole dataset, the timing of the event, i.e. whether plants were disturbed 5, 20 or 35 days after germination played only a minor role. As a single factor, it affected only canopy height (taller growth at early disturbance) and number of leaves (more leaves at early disturbance). In interaction with relocation type, the timing of disturbance affected total biomass (higher biomass production at early disturbance under burial) and root and leaf biomass (higher leaf mass in early stages under burial, higher biomass in later stages under erosion).

In *A. arenaria* the patterns described for *C. maritima* were even more pronounced. All biomass allocation traits (total, stem, root, leaves) and canopy height were significantly affected by burial/erosion as single factor, with higher biomass allocation under erosion and taller stature under burial (Figure 2.4). This is in contrast to *C. maritima*, which showed higher biomass allocation under burial and higher canopy height only after early disturbance (Figure 2.3). The magnitude of disturbance significantly affected leaf biomass (also in interaction with burial/erosion) and number of leaves, whereas SLA was affected only by disturbance timing, with lower SLA values at early and late stages

of disturbance. To summarize, in the sudden disturbance events, the two species responded strongest to type of sand relocation, magnitude of disturbance and their interactions. Here, trait responses showed opposing patterns: whereas *C. maritima* responded positively to burial, *A. arenaria* responded positively to erosion. Disturbance timing and its interaction with other factors yielded few significant results.

When plant individuals were disturbed multiple times, the strongest factor for plant trait expression was whether plants were buried or eroded, irrespective of species (see *F*-values in Table 2.7). For some traits, magnitude and the interaction between burial/erosion and magnitude were important (total biomass, root biomass, Shoot:Root Ratio), for other plant traits, magnitude was of minor importance (e.g. stem and leaf biomass and number of leaves only in interaction with burial/erosion in *C. maritima* and not significant at all for canopy height (*C. maritima*) and SLA (both species)).

Whereas the response patterns of the two species were similar with respect to the factors, their underlying trait expressions differed strongly. Traits of *C. maritima* responded positively to burial and with significantly higher values compared to the control treatment, traits of *A. arenaria* responded positively to erosion, also with significantly higher values compared to the control treatment (all but Shoot:Root Ratio and canopy height). This indicates a) similar trait responses compared to no disturbance (control) of the two species and b) opposite trait responses of the two species towards the disturbance types, i.e., whether the system experiences burial or erosion. This can also be seen in the sudden disturbance events, but to a lesser degree. This shows that with gradual disturbances the strongest effect on trait expression is driven by disturbance mode, i.e., whether an individual is subjected to burial or erosion. Species differed in their responses: *C. maritima* showed a positive response towards burial while *A. arenaria* responded positively to erosion. The same pattern holds true for sudden disturbance events. However, here trait responses were not as pronounced as in gradual disturbance events. Timing of disturbance had a minor effect only. Magnitude also had a minor effect, indicating that it is more important whether an individual is subjected to burial or erosion than to which disturbance strength it is subjected.

Table 2.5: *F*-values, degrees of freedom (*df*) and significance levels of the effects disturbance timing (t), type of sand relocation (i.e. burial or erosion, be), disturbance magnitude (m) and their interaction on plant traits of *C. maritima* (upper part) and *A. arenaria* (lower part) determined by the three-way ANOVA. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

C. maritima	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
time (t)	3	**4.8** **	1.49	**14.3** ***	1.65	**11.31** ***	**4.27** **	**3.78** *	**6.85** ***
burial erosion (be)	1	**44.72** ***	**265.83** ***	**6.54** *	**25.24** ***	**109.12** ***	**5.92** *	**19.99** ***	2.79
magnitude (m)	3	**85.86** ***	**13.03** ***	**224.59** ***	**10.98** ***	**110.26** ***	1.47	0.62	**5.59** **
t × be	3	**15.89** ***	**6.71** ***	**41.67** ***	**13.91** ***	**24.73** ***	**2.77** *	**4.47** **	0.9
t × m	9	**3.95** ***	**3.35** ***	**3.68** ***	**3.99** ***	**4.31** ***	1.34	**2.6** **	**2.04** *
be × m	3	**17.28** ***	**64.3** ***	1.37	**7.14** ***	**10.51** ***	1.51	**4.24** **	0.26
t × be × m	9	**5.22** ***	1.59	**10.98** ***	**8.38** ***	**5.71** ***	1.15	**2.94** **	0.27
A. arenaria	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
time (t)	3	**10.47** ***	**24.32** ***	**16.13** ***	**4.02** **	**6.54** ***	**8.52** ***	1.33	**2.68** *
burial erosion (be)	1	**264.77** ***	**482.32** ***	**257.15** ***	**23.88** ***	**31.17** ***	**50.12** ***	**55.94** ***	1.04
magnitude (m)	3	**36.65** ***	**54.36** ***	**10.87** ***	**48.3** ***	**16.28** ***	**11.53** ***	**55.82** ***	2.11
t × be	3	**17.84** ***	**15.93** ***	**28.2** ***	1.95	**10.27** ***	0.53	**3.74** *	0.89
t × m	9	**2.52** **	**6.53** ***	**4.27** ***	**2.01** *	**5.85** ***	**2.53** **	**2.63** **	0.56
be × m	3	**45.18** ***	**84.67** ***	**41.48** ***	**6.31** ***	**7.9** ***	**21.01** ***	**11.47** ***	1.08
t × be × m	9	**3.05** **	**3.73** ***	**5.62** ***	1.46	**2.22** *	0.68	**2.69** **	0.89

Table 2.6: *F*-values, degrees of freedom (*df*) and significance levels of the effects disturbance timing (t), type of sand relocation (i.e. burial or erosion, be), disturbance magnitude (m) and their interaction in the sudden disturbance events-treatments on plant traits of *C. maritima* (upper part) and *A. arenaria* (lower part) determined by the three-way ANOVA. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

C. maritima	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
time (t)	2	2.64	**3.59** *	**3.38** *	1.42	0.97	**6.07** **	**4.94** **	1.68
burial erosion (be)	1	**23.22** ***	**106.36** ***	1.05	**7.67** **	**37.38** ***	1.82	**7.65** **	1.38
magnitude (m)	3	**45.31** ***	**8.66** ***	**135.04** ***	**9.99** ***	**63.75** ***	0.67	0.96	**7.02** ***
t × be	2	**17.50** ***	1.63	**32.45** ***	**17.54** ***	**12.91** ***	3.04	**4.4** *	1.39
t × m	6	**2.32** *	**5.48** ***	1.71	**2.76** *	**2.38** *	1.89	**2.42** *	1.16
be × m	3	**11.94** ***	**23.76** ***	**5.41** **	**3.65** *	2.04	2.18	1.5	0.26
t × be × m	6	**3.47** **	0.74	**6.94** ***	**4.28** **	**3.00** *	0.31	1.62	0.46
A. arenaria	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
time (t)	3	**10.47** ***	**24.32** ***	**16.13** ***	**4.02** **	**6.54** ***	**8.52** ***	1.33	**2.68** *
burial erosion (be)	1	**264.77** ***	**482.32** ***	**257.15** ***	**23.88** ***	**31.17** ***	**50.12** ***	**55.94** ***	1.04
magnitude (m)	3	**36.65** ***	**54.36** ***	**10.87** ***	**48.3** ***	**16.28** ***	**11.53** ***	**55.82** ***	2.11
t × be	3	**17.84** ***	**15.93** ***	**28.2** ***	1.95	**10.27** ***	0.53	**3.74** *	0.89
t × m	9	**2.52** **	**6.53** ***	**4.27** ***	**2.01** *	**5.85** ***	**2.53** **	**2.63** **	0.56
be × m	3	**45.18** ***	**84.67** ***	**41.48** ***	**6.31** ***	**7.90** ***	**21.01** ***	**11.47** ***	1.08
t × be × m	7	**3.05** **	**3.73** ***	**5.62** ***	1.46	**2.22** *	0.68	**2.69** **	0.89

Table 2.7: *F*-values, degrees of freedom (*df*) and significance levels of the effects disturbance timing (t), type of sand relocation (i.e. burial or erosion, be), disturbance magnitude (m) and their interaction in the gradual disturbance events-treatments on plant traits of *C. maritima* (upper part) and *A. arenaria* (lower part) determined by the three-way ANOVA. Significance levels are * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| *C. maritima*	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
burial erosion (be)	1	**12.42** ***	**112.39** ***	**20.58** ***	**19.84** ***	**53.67** ***	**7.2** *	**16.18** ***	1.59
magnitude (m)	3	**41.08** ***	1.63	**103.36** ***	1.83	**38.59** ***	1.32	1.35	0.76
be × m	3	**7.66** ***	**23.79** ***	**6.55** ***	**11.57** ***	**9.67** ***	1.71	**6.67** ***	0.33
A. arenaria	*df*	BM.total	BM.stem	BM.root	BM.leaf	SRR	canopy	no.leaf	SLA
burial erosion (be)	1	**244.25** ***	**287.30** ***	**291.16** ***	**18.64** ***	**24.12** ***	**13.44** ***	**31.3** ***	0.7
magnitude (m)	3	**4.01** *	**10.89** ***	**10.66** ***	**15.91** ***	**10.79** ***	**10.53** ***	**11.24** ***	1.68
be × m	3	**32.73** ***	**35.93** ***	**38.19** ***	**4.04** *	**3.77** *	**7.23** ***	**5.07** **	0.47
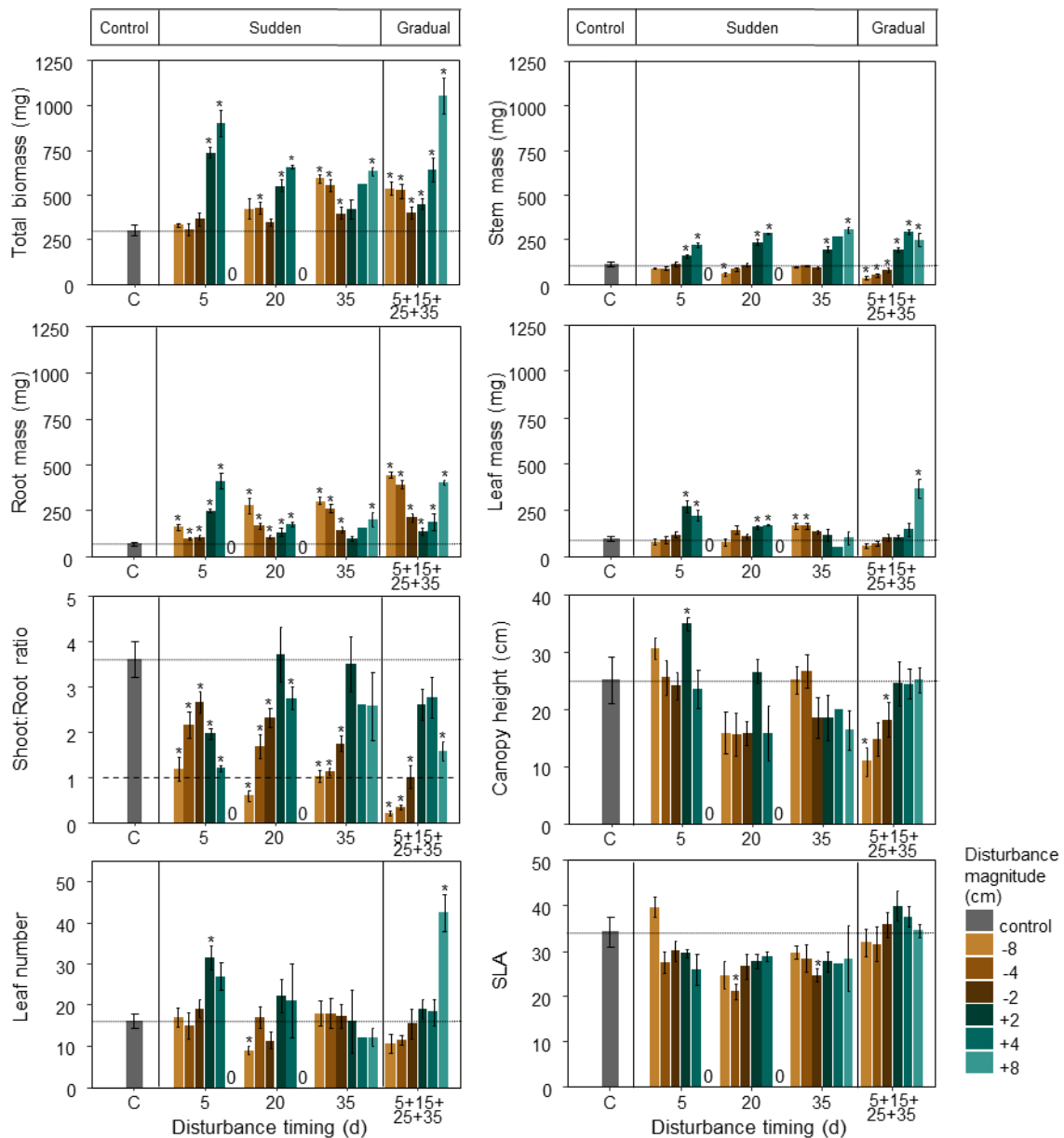
Fig. 2.3: Functional traits of *C. maritima* in the control treatment (no disturbance), in the sudden disturbance events (once after 5, 20 and 35 days) and the gradual disturbance events (a total of four times after 5, 15, 25 and 35 days). Color code indicates total magnitude of disturbance, with -2, -4, and -8 cm in the erosion treatments and +2, +4, and +8 cm in the burial treatments. Bar plots show mean trait values ± SE. Asterisks indicate significant differences between control and respective disturbance treatment according to Welch corrected *t*-test (for precise *t*-values see Appendix Table 2.8).
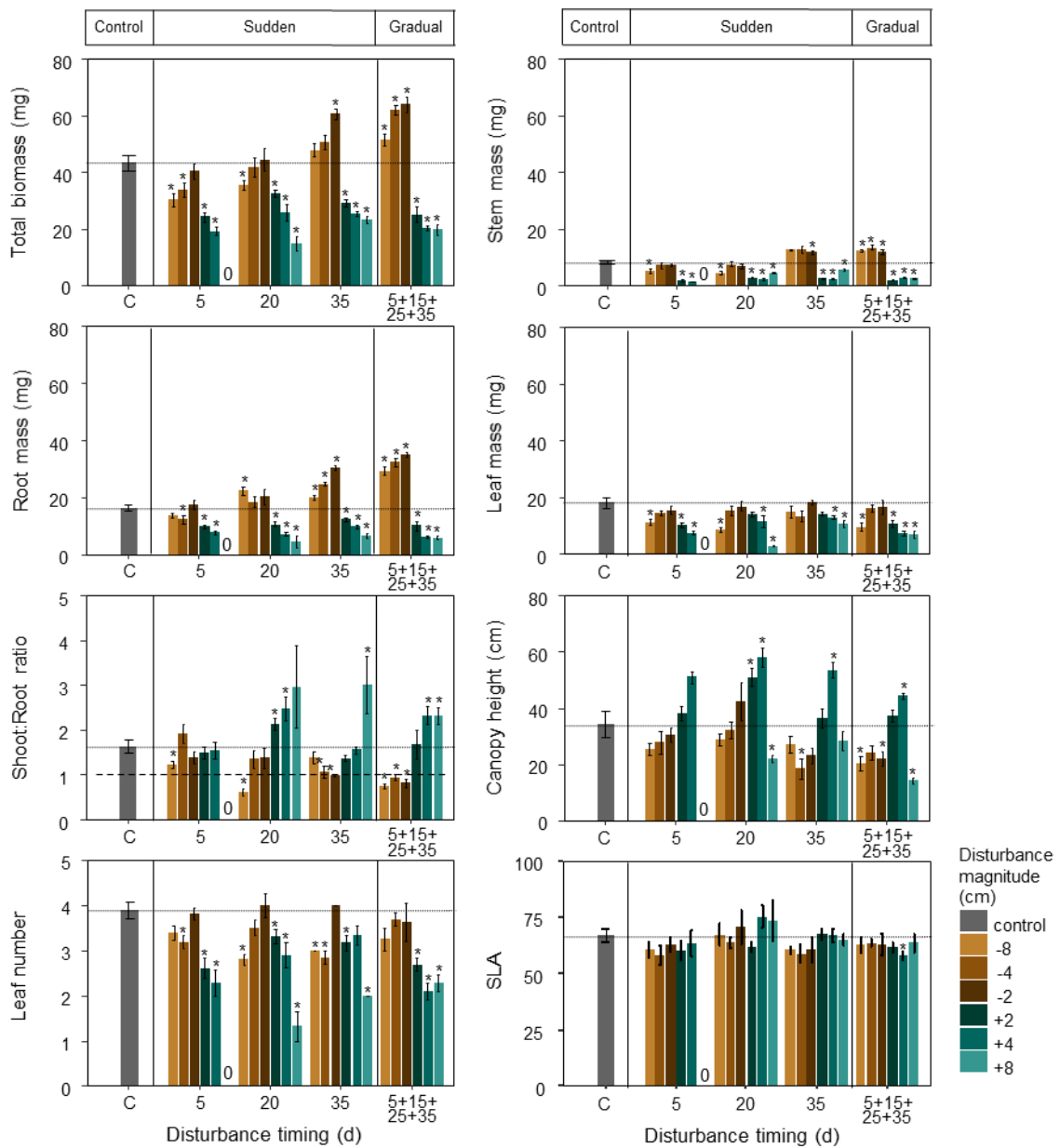
Fig. 2.4: Functional traits of *A. arenaria* in the control treatment (no disturbance), in the sudden disturbance events (once after 5, 20 and 35 days) and the gradual disturbance events (a total of four times after 5, 15, 25 and 35 days). Color code indicates total magnitude of disturbance, with -2, -4, and -8 cm in the erosion treatments and +2, +4, and +8 cm in the burial treatments. Bar plots show mean trait values ± SE. Asterisks indicate significant differences between control and respective disturbance treatment according to Welch corrected *t*-test (for precise *t*-values see Appendix Table 2.9).

2.5   Discussion

Understanding the interaction between vegetation and geomorphic processes in coastal dunes is crucial to predicting dune development, notably with regard to climate change scenarios (Feagin et al., 2015). Predicted climate change scenarios include sea-level rise and increased storm magnitude and frequency, which may alter sediment movement with either stronger burial of plants through sand accretion or stronger uprooting through erosion (De Winter & Ruessink, 2017). Both species considered in this study, *C. maritima* and *A. arenaria*, represent dune-builder species. However, they exhibit important morphological and ecological differences and also show species-specific responses to burial and erosion which might have implications on their abilities as ecosystem engineers.

Disturbance effects on mortality

Both species demonstrated high robustness in response to sediment relocation. However, *A. arenaria* was more robust relative to *C. maritima* as evidenced in lower total mortality. This was expected, given the regrowth ability after burial of *Ammophila* species and is in accordance with previous findings (Kent et al., 2001; Maun & Lapierre, 1984). Based on our results, we distinguish the two disturbance processes of sedimentation and erosion as two very differently perceived processes that evoke different mortality rates. Both species showed higher mortality following burial and lower mortality following erosion events. In the foredunes net dune development is the result of sand accumulation during summer months. Thus, the ability to survive under sedimentation events is especially important for dune species.

The comparison between sudden and gradual disturbance events indicated that both species could better survive a repeated disturbance of the same magnitude than one single event which is in accordance with the literature (Maun et al., 1996). Within the group of sudden disturbance, both species exhibited higher mortality rates at early disturbance. In our experiment, disturbance magnitude was not relative to canopy height but with standardized magnitudes. Therefore, the relative disturbance magnitude was

different each of the three times as canopy heights were increasing with time. The resulting higher relative disturbance intensity in shorter individuals explains the higher mortality at early disturbances. Maun et al. (1996) have shown that individuals buried to more than 75 % of their height are mostly unable to survive as the result of a shift of photosynthetic area from an energy manufacturing state to an energy consuming state.

Disturbance effects on plant traits

Plants are plastic in a variety of ecologically important traits, ranging from various aspects of morphology and physiology to anatomy, developmental and reproductive timing, breeding system, and offspring developmental patterns (Sultan, 2000). For a full understanding of plant responses, these traits should be considered together (Kleyer & Minden, 2015). Considering growth-related traits helps us to understand the overall performance of the individual. Relative to undisturbed individuals, our results indicate an increased performance of *C. maritima* when subjected to burial and, to a lesser extent, to erosion events. Conversely, *A. arenaria* was mostly negatively affected when subjected to burial and erosion. This can be seen in total biomass production which increased in *C. maritima* and mostly decreased in *A. arenaria*. A positive response of growth to burial has been found in a variety of dune species and debilitated populations of foredune plant species were found to be rejuvenated by sand deposition (Harris et al., 2017; Maun, 1998; Zhang & Maun, 1990b, 1992). Even brief periods of burial can have positive effects on plant growth (Zhang & Maun, 1992).

Reasons for increased growth after burial are still debated in literature (Gilbert & Ripley, 2008). Maun (1998) proposed a "multifactor hypothesis", in which the contributing factors were increased activity of mycorrhizal fungi, higher capacity of sink, increased soil volume, increased soil resources, and a physiological hormonal response by the plant (reactive growth). In natural dune systems mycorrhizal activity is enhanced with burial which leads to increased nutrient supply, salinity tolerance, reduced abiotic stresses and formation of wind resistant aggregates (Koske et al., 2008). However, the artificially deposited sand in this study most likely did not increase

mycorrhizal diversity or activity. Upon burial, the normal source-sink relationship is reversed and the stored material is mobilized and transferred to existing photosynthetic tissues (Maun et al., 1996). However, leaf mass did not increase in our study through sediment relocation.

Increased soil volume creates more space which becomes available to the plant for the expansion of its roots. This provides better aeration to the roots and promotes utilization of the nutrients and water contained in the newly deposited sand, which, in turn, enhances biomass production. However, the plant will have to first emerge above the sand surface by utilizing its stored energy reserves and then initiate new roots, which usually takes a few weeks (Langlois et al., 2001). During the course of our experiment no adventive roots were built. Thus, it seems to be unlikely that this was a driving factor in our experiment.

Increased soil volume is usually accompanied by increased soil resources (nutrients and water). In natural dune systems the deposited sand contains, for instance, major nutrient elements such as nitrogen and phosphorous that are assumed to limit growth of several dune species (Kachi & Hirose, 1983). Yet, the added sand in our experiment had almost no nutrients; nutrients were added evenly to all treatments throughout the course of the experiment. Other experiments showed that burial with leached sand containing no nutrients led to improved plant growth (Zhang & Maun, 1992). Nevertheless, the stimulation of growth might be attributed to better water availability as added sand might reduce transpiration. Last, physiological hormonal responses could lead to increased growth. Upon sand accretion a plant must emerge from burial or face local extinction.

Erosion usually leads to water and nutrient stress as roots are partly unable to take up water. The deep root systems of dune species enable the plants to take up water and nutrients even after relocating the upper sediment layer, which ensures survival even after erosion events (Guerrero-Campo et al., 2008). The increased biomass production could be explained by reactive growth.

Looking at traits representing biomass allocation helps to understand the specific strategies applied to survive sediment relocation. This is important when growing in the very dynamic foredune toe with high rates of sediment relocation. Disturbed *C. maritima* individuals invested more into all organs relative to undisturbed individuals. Especially strong sedimentation led to increased stem and root production. The highest increase in biomass was found in roots. *A. arenaria* reduced investments in all organs in response to burial and erosion, with stem and roots being most negatively affected and with the exception of those individuals that were subjected to erosion at a later point. However, most biomass was found to be allocated to roots upon burial and erosion events. As fresh water and nutrients are limited resources in dune ecosystems this is a useful adaptation to sediment relocation (Frosini et al., 2012).

Implication for coastal protection

The potential impacts of increase in sediment movement brought by climate change and the results of this study documenting *C. maritima* and *A. arenaria* responses emphasize the importance of understanding dune species behavior. The studied ecosystem engineers at the forefront of coastal ecosystems are exposed to strong disturbance regimes (Brantley et al., 2014; Wolner et al., 2013). Through effects on establishment success and thus population dynamics, sediment relocation influences dune development because sediment accretion is dependent on species composition and vegetation cover (Keijsers, de Groot, et al., 2015). The changing traits expressions in response to sediment relocation might also have effects on ecosystem properties. Investment in roots as in *C. maritima* leads to stronger erosion control while decreased root biomass as in young *A. arenaria* means less erosion control. However, if sand deposition continues unabated, especially in the early vegetation period, even the sand-dependent species are eliminated and bare areas are created, which are prone to erosion are created.

Eventually, changed abiotic conditions caused by climate change could lead to restructuring of coastlines (Roelvink et al., 2009). Dune species can survive, to a certain

degree, under these dynamic conditions (Maun, 1994). With abiotic and biotic factors, however, the function of the ecosystem engineers can change (Balke et al., 2012). Through morphological responses to a changing environment, dune plants may have a different impact on the ecosystem (Charbonneau et al., 2016; Stallins & Parker, 2003). Therefore, understanding specific responses of engineering plants to sediment relocation is a prerequisite to predicting vegetation sediment capturing and binding capacity. Findings of this study suggest that especially strong storms at the beginning of the growth period could lead to the loss of vegetation and thus supports the practice of planting older *A. arenaria* individuals for dune management. However, our findings also underline that older individuals of *A. arenaria* and *C. maritima* are well adapted to sediment dynamics and the planting of *A. arenaria* could greatly reduce the dynamic in the dune ecosystem, which is an important feature for the persistence of the ecosystem.

Appendix

Table 2.8: Results of *t*-test for each trait for *C. maritima*. Given are *t*-values and significance levels with Welch correction for the comparison between mean trait values of control treatment and respective disturbance treatment. Colored background indicates significant differences to control treatment, read indicate lower values, green indicate higher values within the treatment comparisons. Means are given for the control treatment. A line indicates no surviving individuals in the respective treatment. Significance levels are: ns non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Time (d)	Mag (cm)	BM.total (g)		BM.stem (g)		BM.root (g)		BM.leaf (g)		SRR		CH (cm)		no.leaf		SLA	
Control		302.16		109.92		68.45		92.49		3.56		25.01		16.11		34.15	
5	-8	1.13	ns	-1.45	ns	5.71	***	-0.96	ns	-5.60	***	1.34	ns	0.23	ns	1.41	ns
	-4	-0.05	ns	-1.55	ns	2.79	*	-1.00	ns	-3.40	**	0.13	ns	-0.80	ns	-1.63	ns
	-2	1.36	ns	0.25	ns	2.60	*	0.73	ns	-2.26	*	-0.11	ns	0.94	ns	-1.01	ns
	+2	9.83	***	2.76	*	11.52	***	6.39	***	-5.01	***	2.39	*	4.47	***	-1.29	ns
	+4	8.62	***	5.55	***	12.12	***	5.10	***	-8.89	***	-0.22	ns	2.96	ns	-1.73	ns
	+8	-		-		-		-		-		-		-		-	
20	-8	1.79	ns	-3.62	**	6.89	***	-1.47	ns	-9.40	***	-1.74	ns	-3.45	**	-2.12	ns
	-4	2.77	*	-1.85	ns	6.26	***	2.02	ns	-4.50	***	-1.78	ns	0.05	ns	-3.49	**
	-2	1.28	ns	-0.18	ns	3.46	**	0.49	ns	-3.06	**	-1.98	ns	-1.91	ns	-1.75	ns
	+2	5.50	***	5.53	***	3.03	*	4.62	***	0.04	ns	0.45	ns	1.29	ns	-1.70	ns
	+4	9.63	***	10.52	***	8.06	***	5.85	***	-1.79	ns	-1.38	ns	0.48	ns	-1.46	ns
	+8	-		-		-		-		-		-		-		-	
35	-8	7.11	***	-0.84	ns	11.97	***	4.22	***	-7.84	***	-0.09	ns	0.16	ns	-1.20	ns
	-4	5.58	***	-0.25	ns	9.93	***	4.03	**	-9.35	***	0.41	ns	0.12	ns	-1.27	ns
	-2	2.16	*	-1.00	ns	5.03	***	2.75	ns	-5.38	***	-1.20	ns	0.18	ns	-2.60	*
	+2	1.98	ns	4.40	**	1.95	ns	0.38	ns	-0.18	ns	-1.09	ns	-0.39	ns	-1.55	ns
	+4	-		-		-		-		-		-		-		-	
	+8	8.16	***	9.11	***	4.26	*	0.27	ns	-1.30	ns	-1.53	ns	-1.44	ns	-0.75	ns
5, 15, 25, 35	-8	4.83	***	-4.31	**	17.72	***	-2.14	ns	-11.51	***	-2.99	*	-1.80	ns	-0.51	ns
	-4	4.41	***	-3.73	**	14.80	***	-1.50	ns	-13.96	***	-2.02	ns	-2.11	ns	-0.50	ns
	-2	4.99	***	-3.62	**	13.16	***	0.01	ns	-4.91	***	-2.19	*	-0.62	ns	0.38	ns
	+2	3.34	**	4.59	***	3.57	**	0.80	ns	-2.07	ns	-0.08	ns	1.09	ns	1.22	ns
	+4	4.94	**	8.97	***	3.67	*	1.21	ns	-1.36	ns	-0.03	ns	0.46	ns	0.87	ns
	+8	8.80	***	3.76	*	17.04	***	7.31	***	-5.00	***	0.12	ns	5.74	***	-0.11	ns

Table 2.9: Results of *t*-test for each trait for *A. arenaria*. Given are *t*-values and significance levels with Welch correction for the comparison between mean trait values of control treatment and respective disturbance treatment Colored background indicated significant differences to control treatment, read indicate lower values, green indicate higher values within the treatment comparisons. Means are given for the control treatment. A line indicates no surviving individuals in the respective treatment. Significance levels are: ns non-significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Time (d)	Mag. (cm)	BM.total (g)		BM.stem (g)		BM.root (g)		BM.leaf (g)		SRR		CH (cm)		no_leaf		SLA	
Control		43.27		8.40		16.53		18.33		1.64		34.28		3.90		66.83	
5	-8	-3.45	**	-3.36	**	-2.09	ns	-3.27	**	-2.41	*	-1.48	ns	-2.06	ns	-1.31	ns
	-4	-2.40	*	-1.25	ns	-2.40	*	-1.86	ns	0.83	ns	-1.05	ns	-3.14	**	-1.61	ns
	-2	-0.74	ns	-1.28	ns	0.34	ns	-1.20	ns	-1.33	ns	-0.35	ns	-0.44	ns	-0.88	ns
	+2	-5.85	***	-8.88	***	-5.56	***	-4.08	***	-0.73	ns	1.16	ns	-4.52	***	-1.36	ns
	+4	-7.75	***	-15.72	***	-7.40	***	-6.07	***	-0.52	ns	3.23	**	-4.73	***	-0.67	ns
	+8	-		-		-		-		-		-		-		-	
20	-8	-2.30	*	-4.56	***	3.35	**	-5.44	***	-6.87	***	-0.65	ns	-4.91	***	-0.10	ns
	-4	-0.41	ns	-0.77	ns	0.83	ns	-1.23	ns	-1.57	ns	-0.08	ns	-1.63	ns	-0.73	ns
	-2	0.14	ns	-1.44	ns	1.01	ns	-0.62	ns	-1.37	ns	0.76	ns	0.31	ns	0.24	ns
	+2	-3.34	**	-7.30	***	-4.69	***	-2.15	ns	2.52	*	2.92	*	-2.55	*	-1.27	ns
	+4	-4.22	***	-9.01	***	-8.73	***	-2.49	*	2.66	*	3.85	**	-3.01	**	1.42	ns
	+8	-7.36	***	-5.86	***	-3.95	*	-11.46	***	1.16	ns	-2.23	*	-6.65	**	0.64	ns
35	-8	1.27	ns	5.11	***	2.68	*	-1.22	ns	-1.17	ns	-0.91	ns	-5.03	***	-1.65	ns
	-4	1.94	ns	3.22	**	6.44	***	-1.86	ns	-2.75	*	-2.91	*	-4.53	***	-1.65	ns
	-2	4.99	***	3.95	**	10.22	***	0.22	ns	-5.32	***	-1.80	ns	0.57	ns	-1.11	ns
	+2	-4.62	***	-9.64	***	-3.39	**	-2.02	ns	-1.56	ns	0.78	ns	-3.00	*	0.27	ns
	+4	-6.32	***	-10.85	***	-5.93	***	-2.75	*	-0.28	ns	3.48	**	-2.05	ns	0.11	ns
	+8	-6.65	***	-3.63	**	-6.15	***	-3.73	**	2.48	*	-0.72	ns	-10.75	***	-0.36	ns
5, 15, 25, 35	-8	2.31	*	4.40	***	7.91	***	-3.57	**	-6.50	***	-2.57	*	-2.11	ns	-0.87	ns
	-4	5.36	***	4.92	***	9.10	***	-0.87	ns	-4.66	***	-1.72	ns	-0.85	ns	-0.77	ns
	-2	4.99	***	3.62	**	13.16	***	-0.64	ns	-4.91	***	-2.16	*	-0.62	ns	-0.79	ns
	+2	-4.52	***	-9.20	***	-3.68	**	-3.51	**	0.48	ns	1.05	ns	-5.08	***	-1.27	ns
	+4	-8.07	***	-7.46	***	-10.10	***	-6.32	***	2.57	*	2.34	*	-7.07	***	-2.36	*
	+8	-6.80	***	-7.75	***	-9.14	***	-5.54	***	2.91	*	-4.85	***	-6.27	***	-0.65	ns

Chapter 3

Storm resistance and resilience of natural and artificial coastal foredune communities

Julia Bass, Vanessa Minden, Thorsten Balke
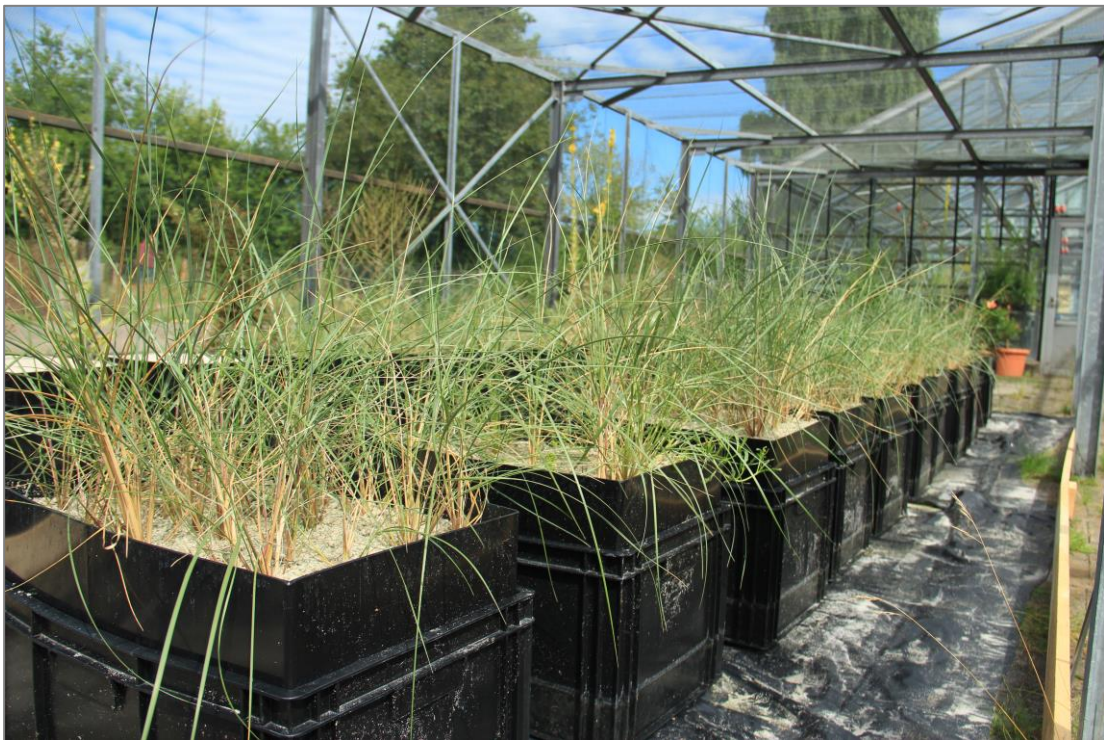
3 Storm resistance and resilience of natural and artificial coastal foredune communities

3.1 Abstract

Coastal dunes represent the first line of defense against storm surges along sandy shores. Accelerated sea-level rise and increased storminess caused by climate change increase the importance of protecting vegetated coastal ecosystems. Thus, dunes often have been restored and stabilized by planting monocultures of marram grass (*Ammophila arenaria*). However, resilience and resistance of *A. arenaria* monocultures versus natural mixed-species composition to storm events have rarely been tested experimentally. To address this gap, we conducted a mesocosm experiment with artificial dunes and a movable wind tunnel. Plastic containers were planted with monoculture (*A. arenaria*), mixed-culture (*A. arenaria, Cakile maritima, Elymus farctus, Honckenya peploides*), or left bare. After an artificial wind erosion event, sediment retention (i.e. dune resistance), survival rate and plant traits of survivors (i.e. dune resilience) were assessed. Monoculture dunes were more resistant than mixed-culture dunes to wind erosion. Differences in resistance between vegetated and non-vegetated dunes were attributed mainly to higher moisture retention in the sediment. Surviving species showed no responses in their trait expression after the disturbance event. Yet, *H. peploides* had lower survival rates than the other species. Our study confirms *A. arenaria* as the main ecosystem engineer in foredune systems and examines the consequences that bio-physical feedbacks in monospecific dune restoration may have on local biodiversity.

Keywords: dune restoration, coastal erosion, biogeomorphology, ecosystem engineers

3.2   Introduction

Accelerated sea-level rise and increased storminess (IPCC, 2014) increasingly threaten coastal areas with flooding and coastal erosion (Hinkel et al., 2014; Neumann et al., 2015). Coastal defence by gray engineering solutions such as dikes and breakwaters, however, have become less desirable because they are expensive and lack adaptive capacities and resilience (Morris et al., 2018). Instead, interest in natural and semi-natural managed structures for coastal defence has increased (Maes et al., 2015; Swann, 2008). Nature-based solutions to coastal protection such as dune creation requires understanding of ecosystem dynamics and biogeomorphological interactions in order to harness their regulating ecosystem services and manage them sustainably (Bouma et al., 2014; Pontee et al., 2016; Spalding et al., 2014). Resistance and resilience of dunes are determined by bio-physical interactions of biota with the abiotic environment and therefore are more difficult to predict than the performance of gray infrastructure. Unlike gray structures, cultivated dune habitats benefit local communities by providing, for example, improved groundwater quality and recreational services (Everard et al., 2010; Gutiérrez et al., 2011; Sigren et al., 2018).

Dune vegetation establishment is limited initially by sediment transport (i.e., burial and erosion), but once vegetation is sufficiently established, biogeomorphic feedbacks (sediment stabilization by roots and wind speed reduction by aboveground biomass) initiate the typical succession sequence/zonation (Bitton & Hesp, 2013; Corenblit et al., 2015). In Europe, zonation occurs from the beach towards the hinterland with mobile foredunes or embryonic dunes (*Cakile maritima* and *Elymus farctus),* white dunes (*Ammophila arenaria*), grey dunes (*Corynephorus canescens*, *Rosa rugosa* and mosses) and brown dunes (*Empetrum nigrum* and *Calluna vulgaris*) (Ellenberg & Leuschner, 2010). The initial colonization by plants will interact eventually with geomorphic processes and determine the shape and position of the dunes and the species distribution (Keijsers, de Groot, et al., 2015; Zarnetske et al., 2012). This succession sequence (in time) and zonation (in space) has been termed "biogeomorphic succession" as similar processes are observed in riparian and salt marsh ecosystems (Corenblit et al., 2015).

The properties of both the established pioneer vegetation and the sediment determine the stability of foredunes subjected to physical disturbance. Aboveground structures modulate the shear stresses at the sediment surface and the sediment entrainment thresholds (Wolfe & Nickling, 1993). Firstly, vegetation directly shelters the soil from the wind by covering the surface (Judd et al., 1996). Secondly, vegetation directly affects wind velocity profiles by increasing surface roughness resulting in the growth of a boundary layer downwind and reduced wind force near the ground (Dupont et al., 2014; Gillies et al., 2002). Finally, vegetation traps windborne particles, thus reducing flux and increasing sediment deposition (Davidson-Arnott et al., 2012; Gillies et al., 2014; Okin et al., 2006). Belowground biomass affects soil properties such as infiltration rate, aggregated stability, moisture content, shear strength and organic matter content, all of which influences soil stability and is referred to as root reinforcement (Gyssels et al., 2005; Sigren et al., 2014). Because dry, sandy soil without organic material lacks cohesion, it is especially prone to aeolian blowout (Jungerius & Van der Meulen, 1988). Ultimately the ecosystem engineering by pioneer dune species on bare sand will reduce disturbance and salinity and positively influence plant growth (i.e., positive biogeomorphic feedback) (Corenblit et al., 2011).

The sediment trapping efficiency of vegetation is affected by sets of functional traits of the occurring plant species (Buckley, 1987; MacGillivray et al., 1995; Mayaud & Webb, 2017). With regard to aboveground traits, plants with high density, high groundcover or projected vegetation cover, and a flexible shoot are most effective in reducing the sand uptake by wind and initiating aeolian sand deposition (Lancaster & Baas, 1998; Mayaud et al., 2016; Udo & Takewaka, 2007). Thus, grass clumps, low in porosity, trap more aeolian sediment than porous shrubs at the patch scale (Mayaud et al., 2016). Belowground traits determine the magnitude of root reinforcement and thus erosion protection of sediment. The finer the roots, the higher their tensile strength (Gray & Barker, 2004; Operstein & Frydman, 2000). Thus, fine roots reduce erosion rates better than a tap root (De Baets et al., 2007). In addition, root tensile strengths, the orientation of roots to the principal direction of strain, root distribution, and root depth influence soil stability (Abernethy & Rutherfurd, 2001; Anderson & Richards, 1987; De Baets et al., 2008).

Soil stability also is increased by species diversity and high variance of aboveground and belowground traits. This effect was found for simulated dykes (Berendse et al., 2015) and alpine ecosystems, where species from different functional groups in particular were highly beneficial for soil stability (Pohl et al., 2009). The positive effects of plant species diversity on erosion resistance could be explained by the compensation or insurance effect, i.e., the capacity of diverse communities to supply species to take over the function of species that became extinct. Furthermore, the combination of roots of different morphologies or trait expressions could increase root reinforcement. High species diversity, therefore, is considered essential for minimizing soil erosion and contributing to greater coastal safety on embankments and other vegetated slopes (Berendse et al., 2015).

To date, little attention has been paid to the effect of diversity on wind-erosion resistance and resilience of coastal dunes. As a matter of fact, coastal dune management along the North Sea recommends planting marram grass (*Ammophila arenaria*) as monocultures (de Groot et al., 2017). Marram grass is known to build extensive root systems that protect the soil against erosion and to survive significant erosion and burial rates (Van der Laan et al., 1997). Although other pioneer dune species growing in the foredunes and white dunes such as *Cakile maritima*, *Elymus farctus*, and *Honckenya peploides* are adapted similarly to burial and erosion, they rarely are considered in restoration and management projects. Knowledge regarding the benefits of artificially planted monocultures and natural mixed-cultures is still insufficient. To address this gap, we used a mesocosm experiment with artificial dunes and a portable wind tunnel. We investigated the effect of mono- and mixed-species cultures on resistance and resilience to wind erosion. Resistance in the context of ecological stability is the property of communities or populations to remain unchanged when subjected to disturbance. Resilience is the ability to return to the reference state after a temporary disturbance (Grimm & Wissel, 1997). Adhering to these definitions, we defined resistance as the ability of vegetation to stabilize the sand against wind relocation and resilience as the ability of the community to bounce back to the undisturbed state after wind disturbance. Specifically, we tested the hypothesis that (1) mixed-culture dunes are both more resistant and resilient than monoculture dunes, (2) resistance and

resilience are driven by specific plant functional traits. This experiment will highlight the role of plant traits in determining the biogeomorphic feedbacks in small dunes. The knowledge gained can be implemented in coastal dune management.

3.3 Methods

Selected species

We selected four common European coastal foredune species which commonly occur together in natural dune systems. The annual *Cakile maritima* is a member of the family Brassicaceae. *Honkenya peploides,* a member of the family Caryophyllaceae, is a patch forming succulent perennial. *Elymus farctus* is a perennial grass from the Poaceae family and *Ammophila arenaria*, a member of the Poaceae family, is a perennial clump-building rhizomatous grass (Ellenberg & Leuschner, 2010). The latter is commonly planted for dune restoration and stabilization (Figure 3.1). *C. maritima* and *H. peploides* seeds were collected from randomly chosen plants on Spiekeroog Island foredunes (53°46' N, 7°44 E), and *E. farctus* seeds from randomly chosen plants on Langeoog Island foredunes (53°44' N, 7°28 E). All seeds were collected in late summer 2015 and air-dried for 3 weeks. *A. arenaria* seeds were ordered from the German Jelitto Staudensamen GmbH seed store in February 2015. Seeds of all species were stored in paper bags in darkness at 4 °C for stratification. Before usage, *C. maritima* seeds were peeled and soaked in water for 3 hours to facilitate germination. *H. peploides* and *E. farctus* seeds were soaked in water only. *A. ammophila* seeds were used without any pre-treatment (Walmsley & Davy, 1997).

Fig. 3.1: Natural foredunes with *A. arenaria* as the dominant species and managed dunes with planted *A. arenaria* stands (Photos: T. Balke).

Mesocosms

All seeds were pre-germinated so that only living seeds were used in the experiment. Seeds were transferred to covered plastic Petri dishes where they were placed on 3 layers of paper towels saturated with 10 ml of distilled water and sprayed with water regularly to prevent drying. After approximately 3 days of darkness in a heating chamber at 24 °C, seedlings displayed a strong radicle but no roots.

Seedlings were then transplanted into plastic containers ($60 \times 40 \times 40$ cm) equipped with an additional movable 10 cm collar. Seedlings were covered by a thin layer of sand. We used a homogeneous sand substrate (0-2 mm grain size) to prevent non-treatment-driven variation across individuals. Containers were watered with tap water from below by maintaining a constant water table. Holes in the bottom, covered with a thin fabric, allowed water to enter but prevented sand from being washed out (see Figure 3.10 in Appendix for a schematic overview of the containers). Plants were fertilized with Hoagland solution by adding 5 ml of solution per week around each plant (Hoagland & Arnon, 1950). Containers were established outside and covered with grating to prevent herbivory. The mean temperature was 19 °C. The experiment ran for 16 weeks in total, from May, 18 2016 to September, 19 2016.

Experimental treatments

We designed a mesocosm experiment to test the effect of mono- and mixed culture communities on wind-erosion resistance and resilience, while controlling for vegetation density. For the monoculture, 12 containers were planted with *A. arenaria* only. For the mixed culture dunes, 12 containers were planted with all four species, *A. arenaria, C. maritima*, *E. farctus*, and *H. peploides*. All containers were subdivided into 24 adjacent 10×10 cm squares with one seedling each, resulting in a total of 24 individuals evenly distributed per container. For the mixed culture dunes, the four species were randomly assigned to a square, resulting in 6 individuals of each species per container. Additionally, 6 containers were left bare as a control. Containers were randomly arranged in watering trays (see Figure 3.2 for an overview of the setup and the planted containers).

Fig. 3.2: Photo of the (A) experimental setup and of a (B) monoculture and a (C) mixed-culture container.

Six of each mono- and mixed-culture dune containers were subjected to a wind disturbance after an establishment period of 3 months. In preparation for the experimental wind treatment, sand was left to dry out for two weeks by removing the water from below and by covering containers with a plastic sheet to keep out rainwater. With the dry-out period standardized, it was possible to analyze the effect of moisture retention by the species, a key factor determining sediment entrainment. Then, the upper 10 cm of sand were exposed by lowering the frame which had been attached to the containers prior to the onset of the experiment. A portable wind tunnel was attached to the containers (see Figure 3.3 and Figure 3.4 for views of the portable wind tunnel). The opening in the front was used to position the wind generator. At the rear end of each container, a 50-cm-long collecting tray captured the dislocated sand. An air-permeable fabric at the rear end of the wind tunnel allowed air to flow through and prevented turbulence, but stopped sand from being blown out of the tunnel. The wind was generated by a leaf blower (Stihl BG 56), which generates a wind flow of max. 180 km/h directly in front of the device. To eliminate any shelter effect of the plants and guarantee equal disturbance intensity throughout the containers, the wind was applied from the front (0 cm), at 20 cm, and at 40 cm into the container. Wind was applied at each position for 1.5 minutes, resulting in a total disturbance of 4.5 minutes to each container. We maintain that this direct application of high-speed wind replicates the maximum instantaneous sediment removal during a storm event. Dislocated sediment from all three wind applications was analyzed together.
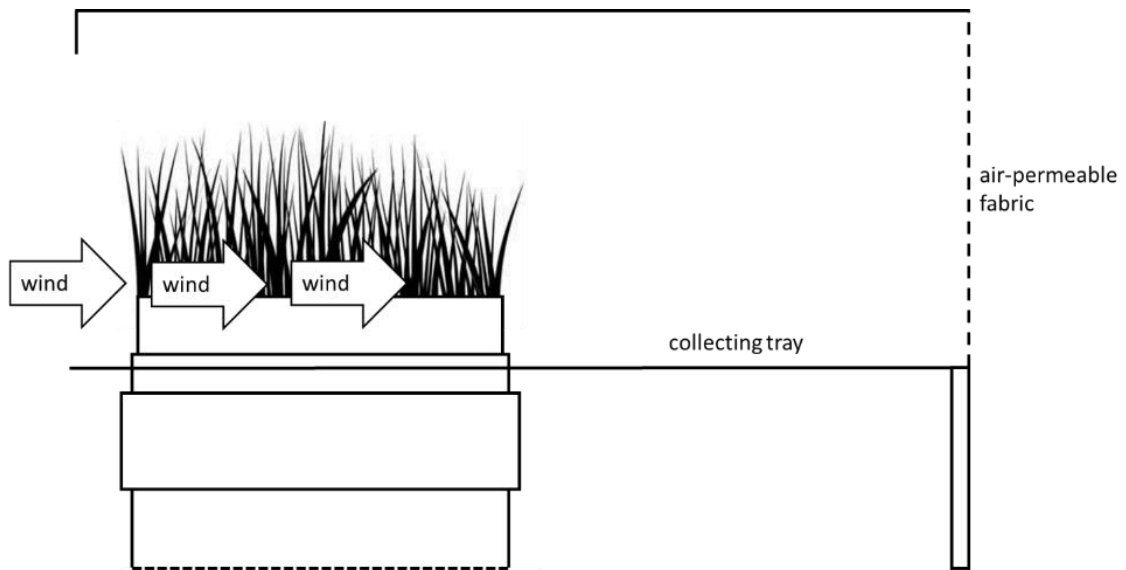
Fig. 3.3: Schematic side view of the portable wind tunnel.

Fig. 3.4: Photo of the wind tunnel installed on an artificial bare dune with the upper 10 cm of soil exposed.

Resistance and resilience measurements

As a measure of resistance against aeolian blowout we quantified dry weight of the dislocated sand from each artificial dune after the mimicked storm event. To elucidate the specific effect of the individuals, we measured the distance from the top of the wind tunnel to the soil surface adjacent to the stems before and after the wind event. To investigate the effect of soil moisture on resistance capacity we measured soil water content of the upper 3 cm of soil before the onset of the disturbance. To do so, we collected 100 cm³ soil in a sampling ring, measured the fresh weight and, after drying for 72 h at 105 °C, the dry weight.

To elucidate the resilience of the mono- and mixed-culture dunes, plants were left to grow an additional 2 months after the disturbance. Then surviving rate and biomass allocation patterns were determined in the disturbed and the undisturbed containers. Survival rate was determined by counting all individuals that were not uprooted and blown away and that showed any sign of living tissue. Biomass allocation patterns were investigated by harvesting all individuals and separating them into organs, stem, leaves, flowering part, and roots. As it was impossible to assign the roots to a specific individual, roots within the 10×10 cm squares were amalgamated. For this, the 10×10 blocks were cut out and roots were washed out.

Statistical analysis

Differences in the amount of dislocated sand between vegetated dunes with mono- and mixed-cultures and bare dunes were analyzed with an ANOVA and a Tukey HSD post-hoc test. A boxcox transformed was applied to meet ANOVA assumption. Differences in elevation change adjacent to the stems of the four species were examined with a Kruskal-Wallis Test and a Pairwise Wilcoxon Test with Bonferroni correction as a post-hoc test. The effect of trait variation on sand moisture variation and on sand stability was analyzed using simple linear regression. The relative importance of the independent variables was compared. Differences of traits from *A. arenaria* growing in mono- and mixed-cultures were analyzed by a Student's *t*-test. To explain the resilience of the two

cultures' differences in traits of species growing in disturbed and undisturbed dunes, results were compared by applying a Student's t-test. If necessary, variables were log transformed prior to the analysis. Statistical analysis was performed using the computer software R (R Development Core Team, 2016) with the packages Rcmdr (Fox, 2016), rcompanion (Mangiafico, 2017), car (Fox & Weisberg, 2011), MASS (Venables & Ripley, 2013), relaimpo (Grömping, 2006), ggplot2 (Wickham, 2016), and lme4 (Bates et al., 2014).

3.4 Results

An analysis of variance showed that the effect of the vegetation type treatment on sand removal was significant, $F(2, 15) = 23.42$, $p < 0.001$. In the monoculture, sediment blowout was around 14 kg/m2, which was 3 times smaller than in the bare dunes (amount of sand blown out 44 kg/m2 ($p < 0.001$)). In the mixed-culture community, sediment loss was 21 kg/m2, approximately 2 times smaller than in the bare dunes ($p < 0.01$). Mixed-culture dunes lost about 1.5 times more sand than monocultures ($p < 0.05$) (Figure 3.5).

Regression analysis showed that all four factors were negatively correlated with the amount of relocated sediment (Figure 3.6). The results of the relative importance analysis of the multiple regression model with dislocated sand (kg/m^2) as target variable indicated that soil moisture explained most of the variance (36 %). Lower relative importance was found for root mass (22 %) and shoot mass (21 %). The lowest relative importance was found for canopy height (19 %).
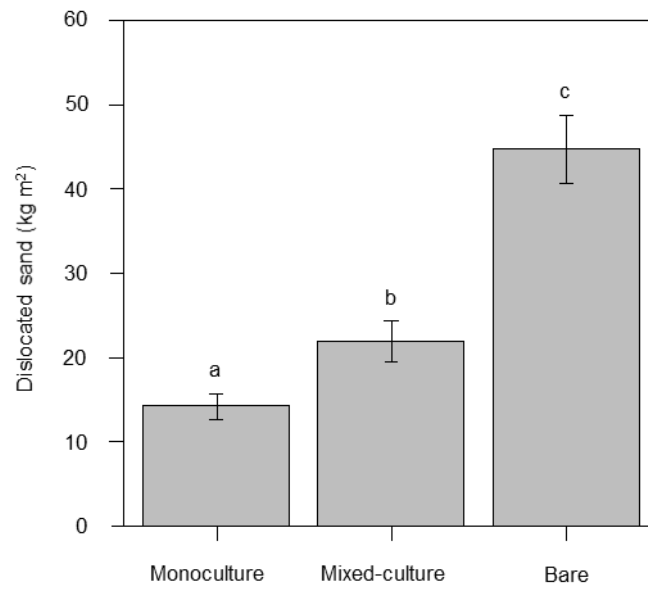
Fig. 3.5: Dislocated sand (mean ± SE) from monoculture dunes, mixed-culture dunes and bare dunes. Letters indicate significant differences among treatments ($p < 0.05$, N = 6 each).
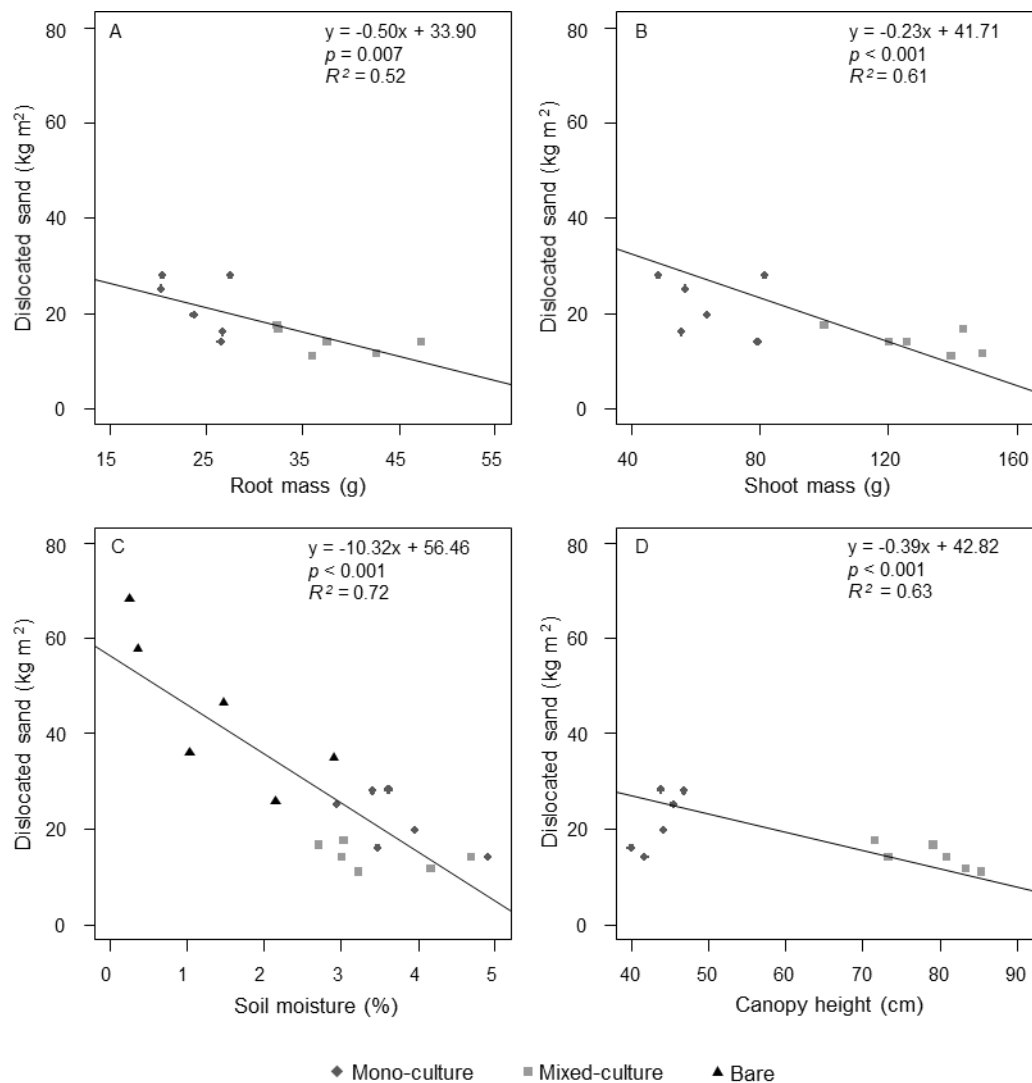
Fig. 3.6: Influence of (A) root mass, (B) shoot mass, (C) soil moisture, and (D) canopy height, on the amount of sand dislocated by wind. Regression lines and R^2 values were derived from simple linear regression.

Elevation change measured adjacent to the species' stems and on bare soil varied significantly ($H(168.88) = 5, p < .001$) (Figure 3.7). Results indicated that negative elevation change was significantly highest on bare soil. A non-significant trend showed that *A. arenaria* and *C. maritima* were most effective in stabilizing the soil surrounding the individual plant. A non-significant trend also showed that *A. arenaria* growing in monoculture more effectively stabilized the soil than when grown in mixed-cultures.

No difference was found between *E. farctus* and *H. peploides* capacity of soil stabilization at the individual plant.

Growth was compared to explain the difference in sand stabilization capacity of *A. arenaria* growing in mono- and in mixed-cultures dunes. Root mass in the 10-cm squares at *A. arenaria* positions did not differ between mono- and mixed-cultures ($t(181) = -1.31$, $p = 0.19$). Shoot mass of *A. arenaria* individuals was significantly higher when grown in mixed-culture ($t(181) = 2.66$, $p < 0.001$) but individuals grew better in mono-culture dunes ($t(181) = -3.52$, $p < 0.001$) (Figure 3.8).
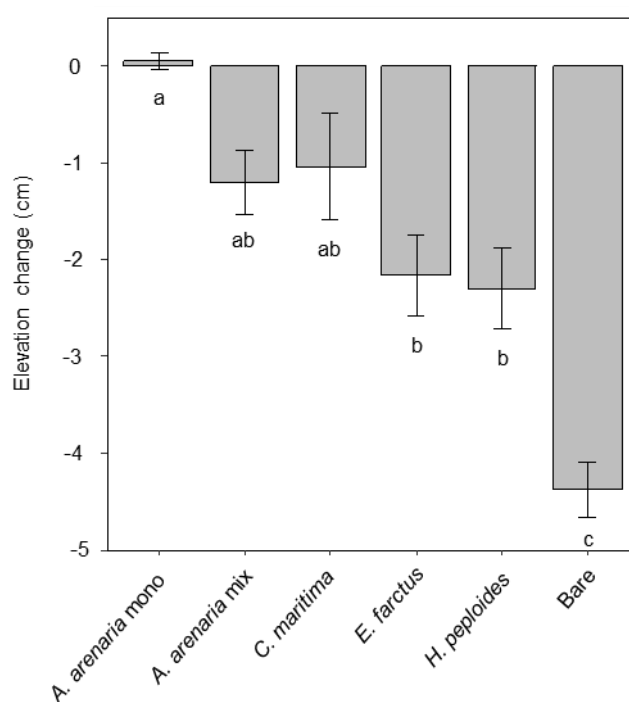
Fig. 3.7: Elevation change (mean ± SE) next to stems of the four investigated species and on bare soil. Groups sharing the same latter are not significantly different (α < 0.05).
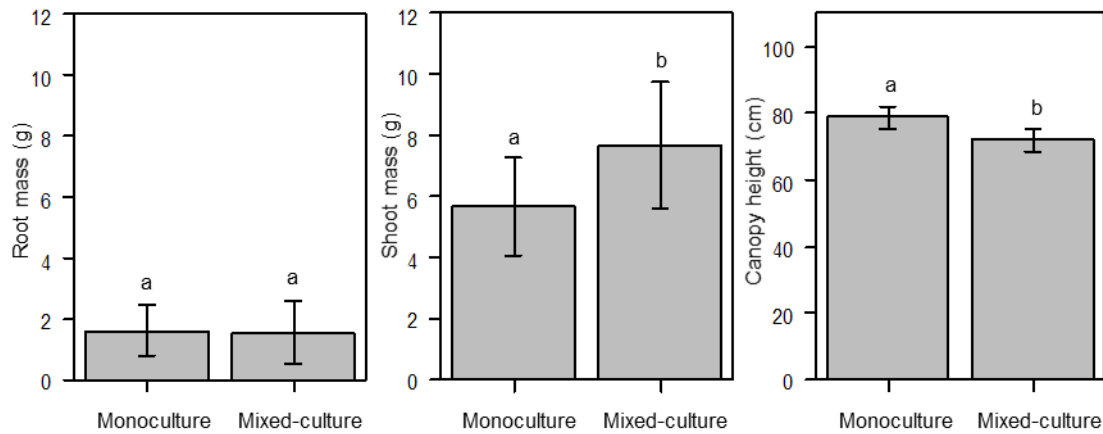
Fig. 3.8: Comparison of root mass (mean ± SE) in 10 cm squares at *A. arenaria* positions and shoot mass and canopy height of *A. arenaria* growing in mono- and mixed-cultures. Groups sharing the same latter are not significantly different (α < 0.05).

Growth performance, assessed by the measurements of functional traits at the end of the experiment, was not affected by the wind disturbance event in any of the species. Only *H. peploides* displayed an increase in height after the storm event and *A. arenaria* growing in monoculture showed slightly reduced root mass in the disturbed treatment (Table 3.1). Survival of species differed with *H. peploides* being most negatively affected (Table 3.2).

Table 3.1: To compare mean trait values of disturbed and undisturbed control a *t*-test for each trait of each species was conducted. Given are *t*-values, degrees of freedom (*df*), *t*-value, and significance level. Significant *p*-values at $\alpha = 0.05$ are shown in bold type.

Community	Species	Traits	df	t	p
Mix	*C. maritima*	root mass	3	0.01	0.99
		shoot mass	3	-0.39	0.72
		canopy height	3	1.45	0.24
	H. peploides	root mass	66	0.14	0.88
		shoot mass	66	-0.10	0.91
		canopy height	66	-3.45	**<0.001**
	E. farctus	root mass	70	1.00	0.32
		shoot mass	70	-0.16	0.87
		canopy height	70	1.59	0.12
	A. arenaria	root mass	87	-1.18	0.24
		shoot mass	87	0.31	0.75
		canopy height	87	1.06	0.31
Mono	*A. arenaria*	root mass	274	2.32	**0.02**
		shoot mass	274	0.76	0.45
		canopy height	274	0.26	0.79

Table 3.2: Survival rate of species under undisturbed control and wind-disturbed condition driven by experimental effects.

	A. arenaria	*C. maritima*	*E. farctus*	*H. peploides*
Undisturbed	100 %	81 %	73 %	100 %
Disturbed	100 %	77 %	58 %	98 %

3.5 Discussion

The comparison of artificial mono- vs. mixed-cultures dunes revealed that monoculture dunes were more resistant to wind erosion than mixed-culture dunes. The lower resistance of mixed-cultures contradicts our expectation that biodiversity enhances stability. Pohl et al. (2009) found a combination of roots of various diameters and morphologies, as present in a diverse plant community, to be most effective in enhancing soil stability. Yet, it can be hypothesized that in our setup reduced wind-erosion resistance in the mixed community was driven by the addition of species expressing disadvantageous trait combinations such as the small species *H. peploides*. Models have shown that for communities of species with very different productivity, high biomass can trump biodiversity (Yachi & Loreau, 1999). In cases where engineering traits are more relevant, single well-equipped species add more to the resistance of the community than a mixed community where density is controlled (Figure 3.9). Furthermore, the comparison of the direct elevation changes adjacent to the individuals revealed that the effect of the individuals on soil stabilization was species-specific. It confirmed that *A. arenaria* was most effective in stabilizing the soil.
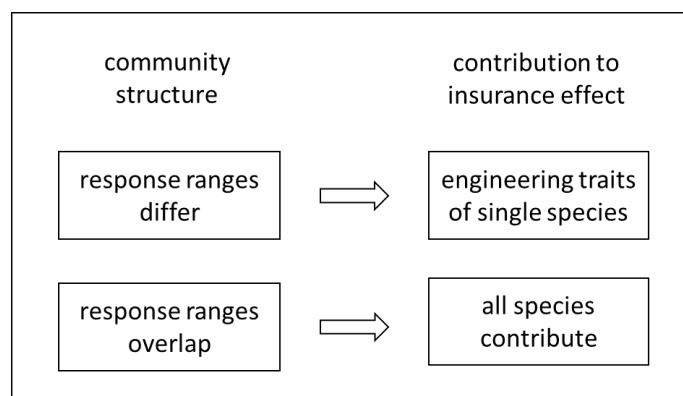
Fig. 3.9: Conceptual diagram of insurance effect in different communities. In biogeomorphic ecosystems where the response range of species in the community differs, the effect of one key species is mainly responsible for the functioning of the ecosystem. In an ecosystem with species that have overlapping response ranges, species contribute more equally to the functioning of the ecosystem.

To further elucidate the effect of specific traits, we used a multiple regression approach for partitioning the individual and shared effects of the four explanatory variables root mass, shoot mass, height, and soil moisture for soil stability. The regression results showed a high importance of soil moisture. At 36 %, soil moisture explained considerably more of the variation than the other variables. The other variables root mass, shoot mass, and height explained around 20% each. A strong effect of the shoot mass also was found by other studies which investigated the effect of shoot mass and habitus on within-canopy velocities and turbulence (Burri et al., 2011; Finnigan, 2000; Hesp, 1983; Poggi et al., 2004). Also height has been found to be important as prostrate growing plants have a low aerodynamic roughness. Thus, reduction of near-surface wind speed is low which implies low deposition and high erosion. In contrast, tall plants exert high surface drag and roughness which implies high deposition and low erosion (Dong et al., 2001). Moreover, densely growing, compact silhouette species were found more effective for soil stabilization than sparsely growing, slim silhouette species. Density increases the extent of downwind flow retardation and thus decreases erosion (Allgaier, 2008; Funk & Engel, 2015). Therefore, the high and dense *A. arenaria* clumps are much more effective in reducing wind erosion.

Contrary to our expectations, diverse belowground growth forms did not enhance soil stability. In developed soils, the root system of the plants increases the stability of soil by transforming loose soil particles into stable aggregates by means of root secretion. Roots cause clay particles to re-orient and bind soil particles, supply the soil with decomposable organic matter, and help to build a microbial community in the rhizosphere (Gyssels & Poesen, 2003; Tisdall, 1994). The roots' effect comes mainly from fine (< 1 mm) and very fine roots (< 0.5 mm) and the extraradical hyphal length (Miller & Jastrow, 1990; Pohl et al., 2009). While in our study root diameter was not explicitly measured, it was obvious that almost all roots were fine and very fine roots. For methodological reasons, we could not assign the roots of our soil cores to specific plant species. However, higher amalgamated root mass in the monoculture containers showed the importance of *A. arenaria* in stabilizing coastal dunes. These results indicate that despite the apparent importance of different species in other studies, *A. arenaria* was largely responsible for the improvement of soil aggregate stability.

These findings demonstrate the key role of single species in ecosystem functioning, at least in sandy substrate.

Our experiments aimed at creating an artificial standardized disturbance event to test the mechanisms of wind disturbance on dune communities. It should be noted that by manually exposing the upper 10 cm of the sediment and by applying the wind generator at the edge and within the vegetation patch, a spatial pattern of wind forces and potential edge effects at the patch scale were avoided. Wind diversion in embryonic dunes creating lee-side deposition of sediments is important in initial dune creation but we were unable to study species-specific effects on deposition rates at this experimental scale.

The strong correlation between soil moisture and soil stability has rarely been studied experimentally. Plants reduce soil desiccation with shading and hydraulic lift (Horton & Hart, 1998). This increases particle cohesion (Pollen et al., 2004), resulting in smaller sediment uptake over a wet surface than over a dry surface (Bauer et al., 2009). Since addition of water by hand or by rain was prevented prior to the disturbance event, soil moisture is a direct function of the ability of the plants to draw up or retain soil moisture in the upper layers. This is not related to species composition.

The comparison between disturbed and undisturbed individuals revealed that none of the surviving species showed a strong response to the wind disturbance event and the associated sediment relocation. This is contrary to our expectations because *A. arenaria* and *C. maritima* showed a significant response to sediment relocation when disturbed at an early life stage (Bass et al. unpublished data). Significant trait responses to sediment relocation also have been found in other species (Guerrero-Campo et al., 2008; Xiong et al., 2001). In this experiment, however, individuals were already three months old upon disturbance and Niinemets (2004) showed that adaptation capacity decreases with age. These results imply that both communities are very resilient and that disturbed dunes would face a new disturbance with the very similar preconditions regarding the plant traits. However, the survival rate after the disturbance event was different, as only *H. peploides* individuals were completely uprooted and blown away while all other species were still anchored after the wind event. This implies lower resilience capacity

in communities with *H. peploides* individuals. It also reflects the annual beachline strategy that species complete one lifecycle between the stormy seasons and start a new cycle when a disturbance-free time allows seedlings to become established (Balke et al., 2014). The reduced biomass production of *A. arenaria* individuals grown in monoculture dunes could be driven by an increased competition for nutrients through higher density of individuals from one species exploiting the same nutrients. Stronger investment in height when grown in monocultures could be driven by increased competition for light.

Our findings have several implications for dune management. It is important for coastal management to understand how vegetation operates within a dynamic system. The complex interaction between vegetation, climate, soil properties and hydrological conditions (Morgan & Rickson, 2003) makes a standardized mesocosm experiment, as presented in this study, very suitable. It is clear from our results that species with high biomass production, above- and belowground, stabilize the soil most effectively. This makes *A. arenaria* a key player in coastal dune stabilization as it builds large root biomass and has extended quick shoot growth (Hong & Lee, 2016). Therefore, the current practice of planting monocultures of *A. arenaria* to reestablish and build coastal dunes as green structures is supported by our results. However, *A. arenaria* also has been introduced as a stabilizing agent to non-native areas and may also displace other early succesional species when planted in monocultures within their native range. Although *A. arenaria* re-engineered formerly low, hummocky dunes into taller, ridge-like dunes and thereby reduced overwash, it also reduced species diversity as it quickly spread through its guerilla strategy and replaced other species (Stallins & Parker, 2003). This type of spread can lead eventually to a monoculture of the invading species (Hertling & Lubke, 2000; Seabloom & Wiedemann, 1994). Thus, careful consideration should be given when planting monocultures, especially where the objective is habitat restoration and rehabilitation.

Appendix
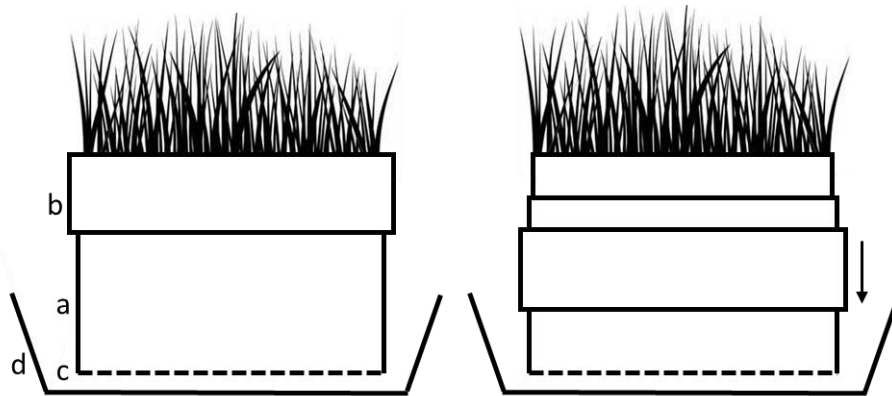
Fig. 3.10: Schematic overview of the planting pots. (a) experimental containers with (b) movable collar to expose upper 10 cm of sand. A (c) permeable mesh kept the sand in the container but allowed watering from below. The water table in the (d) watering tray was kept constant.

Chapter 4

Plant traits affect surface elevation change in salt marshes: an example of biogeomorphic ecosystems

Julia Bass, Dirk Granse, Ingo Hache, Kai Jensen, Volker Karius, Vanessa Minden, Martin Stock, Sigrid Suchrow, Michael Kleyer

4 Plant traits affect surface elevation change in salt marshes: an example of biogeomorphic ecosystems

4.1 Abstract

Current climate crisis is associated with rising sea level, which raises the concern of losing coastal ecosystems such as salt marshes to drowning. Salt marshes fulfill multiple ecosystem services including attenuating wave energy and protecting coastal areas from flooding. Where inland migration is impossible, salt marshes will only persist if their surface elevation gain exceeds sea-level rise. Surface elevation change (SEC) is driven by sedimentation or erosion that can be influenced by abiotic and biotic factors. However, the biotic factors, best described by plant functional traits of the salt marsh vegetation, are not well understood. We assembled a large data set of SEC, plant abundance and trait measurements from the German Wadden Sea, covering natural marshes, unmanaged anthropogenic marshes on reclaimed land, and grazed marshes. By using multiple regression analyses, we studied the effects of functional traits and distance to marsh edge on sedimentation and erosion. Mean SEC in all three marshes was below observed sea level rise (SLR). This questions the ability of marshes to accrete in accordance with recent SLR. However, there were pronounced local differences in SEC, which were jointly explained by distance to marsh edge and by plant traits describing above-ground roughness and below-ground anchoring capacity of the vegetation. Higher roughness increases sedimentation; stronger anchoring capacity can reduce erosion. These findings suggest to include plant functional traits in models on salt marsh surface elevation change to better predict coastal resilience to SLR.

Keywords: Wadden Sea; biogeomorphology; plant functional traits; accretion deficit, surface elevation change

4.2 Introduction

Recent salt marsh loss has induced widespread concern over their ability to withstand sea-level rise (SLR) (Kirwan et al., 2016; Murray et al., 2014; Suchrow et al., 2012). Global mean sea level is estimated to rise 0.26 to 0.82 m during the 21st century (IPCC, 2014), which would result in a 20 to 50 % loss of marsh area in the same time period (Craft et al., 2009; McFadden et al., 2007). These predictions are of great concern because marshes have important ecosystem functions, such as buffering coasts from storm surges, attenuating wave energy, sequestering carbon, improving of water quality, and providing habitat for specialized plants and animals (Barbier et al., 2011; Möller et al., 2014; Shepard et al., 2011; Temmerman et al., 2013).

Historically, tidal marshes have responded to increases in sea level by accreting sediment and/or inland migration (Donnelly & Bertness, 2001; Krone, 1987). Likewise, salt marshes will survive future SLR only if vertical accretion surpasses SLR or if their inland migration is faster than their seaward erosion. However, due to infrastructures such as dykes, roads or housings, this landwards retreat is often not possible, potentially leading to the loss of suitable habitat for salt marsh species and ultimately to the loss of the salt marshes (i.e. coastal squeeze) (Borchert et al., 2018). Thus, in many areas, only vertical accretion ensures the long-term stability and survival of salt marshes (McIvor et al., 2013; Morris et al., 2002).

The term "surface elevation change" (SEC) includes both vertical accretion by sedimentation and marsh loss by erosion. SEC in salt marshes differs worldwide and regionally and is the subject of ongoing debates about possible influencing abiotic and biotic factors. Abiotic factors such as the concentration of suspended sediment and sediment deposition were found to be positively correlated with accretion (Andersen et al., 2011; Chmura et al., 2001). Distance from the intertidal mudflats (Kirwan et al., 2016), distance from main creeks, elevation, as well as tidal currents and waves were found to be negatively correlated with salt marsh accretion (Cadol et al., 2014; Cahoon & Reed, 1995; Esselink et al., 1998; Kolker et al., 2010; Neumeier & Amos, 2006).

Biotic factors are discussed with regard to their influence on salt marsh SEC since salt marshes are a classic example of biogeomorphic ecosystems. In biogeomorphic ecosystems, interactions between plants and geomorphic processes are known to govern the functioning of the system (Baustian et al., 2012; Corenblit et al., 2015). Marsh vegetation is believed to influence SEC in three different ways. First, it is assumed to enhance surface elevation gain directly as it contributes to soil building by organic matter production (Langley et al., 2009; Nyman et al., 2006; Schile et al., 2014). Second, vegetation roughness and plant anchoring in the soil also indirectly affects elevation gain by attenuating wave energy and slowing water flow. This leads to a decline in bed shear stress and mineral sediment trapping is enhanced (Mudd et al., 2010). Lastly, the reduction of bed shear stress and the anchoring effect of the roots also prevent the resuspension of deposited sediments on, and the direct erosion of, saltmarsh surfaces (Fagherazzi et al., 2012; Francalanci et al., 2013; Temmerman et al., 2012).

Considering vegetation roughness has a long tradition in open channel water flow models (Manning, 1891; Strickler, 1923). Surface roughness, including vegetation, is expressed as an empirically derived coefficient in the Gauckler-Manning-Strickler formulas, still widely applied in hydraulics (Bleninger et al., 2006). One drawback of the formula is its use of rather broad vegetation categories (e.g. "short grass", "high grass" for pastures in floodplains), leaving ample room for subjective interpretation (Chow, 1959). Plant functional traits (Lavorel et al., 1997) may allow a more mechanistic understanding of roughness or anchoring, because they are measurable properties of the plants determining the vegetation of a site (Garnier et al., 2007; Kleyer, 1999). However, only a few studies have used a trait-based approach to assess biologically mediated SEC and wave attenuation in salt marshes (Bouma et al., 2005; Mudd et al., 2010). In salt marshes wave attenuation was found to be positively correlated with leaf and stem stiffness (Paul et al., 2012; Rupprecht et al., 2017), vegetation height (Rupprecht et al., 2017), as well as shoot density and shoot biomass (Paul et al., 2012). Increased near-bed turbulences, accompanied by a reduced velocity within the canopy, have been found to decrease sedimentation within vegetated areas (Lefebvre et al., 2010).

Conversely, Reef et al. (2018) found no significant effect of vegetation height and biomass on salt marsh vertical accretion although they did detect deposition of material on the plant/soil surfaces during flood tides. Even negative effects of plants on salt marsh accretion rates have been found. Movements of plants when acted on by waves and currents can scour the surface and can enhance erosion significantly. This holds true for patchy vegetation as found in pioneer zones and along marsh seaward margins (Feagin et al., 2009; Temmerman et al., 2007). Widdows et al. (2008) pointed out that linkages between plant traits and small-scale effects around plants do not necessarily translate to vegetation effects on hydrodynamic conditions measured at the larger scale.

These contrasting results demonstrate a lack of understanding of the interactions between vegetation and salt marsh SEC. The current fragmented knowledge, therefore, prevents many modelers from incorporating biogeomorphic feedbacks in their models on salt marsh resilience to SLR.

Salt marshes occur in different locations along the German North Sea coast. The most natural salt marshes that have remained uninfluenced by direct human activities are found on uninhabited barrier islands, such as the backshore of Mellum, an island off the German coast (see Fig. 1). These salt marshes are protected from the surf by the dunes on the windward side of the island but diurnal tides and storm surges do contribute to SEC. Salt marshes on barrier islands are submerged regularly with accretion rates of 1 to 16 mm/a (Schuerch et al., 2012). Salt marshes along the mainland coastline have experienced more influence from human activities in the course of land reclamation and embankment activities. An average SEC of +6 mm/a was found on the mainland salt marshes (Suchrow et al., 2012). Salt marshes on Halligen, small island-like marsh areas that were disconnected from the German mainland marsh during past storm surge events, are often grazed and become submerged only during storm surges. Here, an SEC of 0.7 to 4 mm/a was found (Schindler et al., 2014). Given the differences between the three salt marsh types in flooding regime and in yearly SEC, it is reasonable to study them separately.

To foster a better understanding of vegetation-SEC interactions, this study aims to elucidate (i) the effects of plant traits on SEC in salt marshes on barrier islands,

mainland coasts and Halligen and (ii) how SEC differ between the three types. Some of these plot data were used for previous analyses (Minden & Kleyer, 2011; Schindler et al., 2014; Suchrow et al., 2012) but not by explaining surface elevation change with plant traits. Specifically, we tested the following hypotheses: (1) SEC decreases with distance from the shore. (2) Sedimentation in salt marshes is facilitated by rough vegetation which is composed of plants with a high canopy height, large stem biomass, stiff stems, and large leaf areas. (3) Erosion of salt marsh ground is reduced through anchoring effects of the belowground parts of the vegetation. In particular, plants with high belowground biomass allocation should stabilize the marsh soil and reduce erosion.

4.3   Methods

Study areas

To elucidate the effect of plant functional traits on sedimentation and erosion of island, mainland and Hallig salt marshes, we analyzed a total of 335 plots located along the German North Sea coast (see Table 4.1 and Figure 4.1). Specifically, 38 plots were established on the island of Mellum on a gradient from the pioneer zone to the upper salt marsh. In addition, 184 plots were located on mainland salt marshes in Lower Saxony at Leybucht, Norderland, and Jade Bight (see Minden and Kleyer (2011)), as well as along the Schleswig-Holstein coastline (see Suchrow et al. (2012)). These plots mainly cover lower and upper saltmarsh communities. Finally, 113 plots were established on Hallig upper salt marsh communities on Langeness, Nordstrandischmoor, and Hooge (see Schindler et al. (2014)).
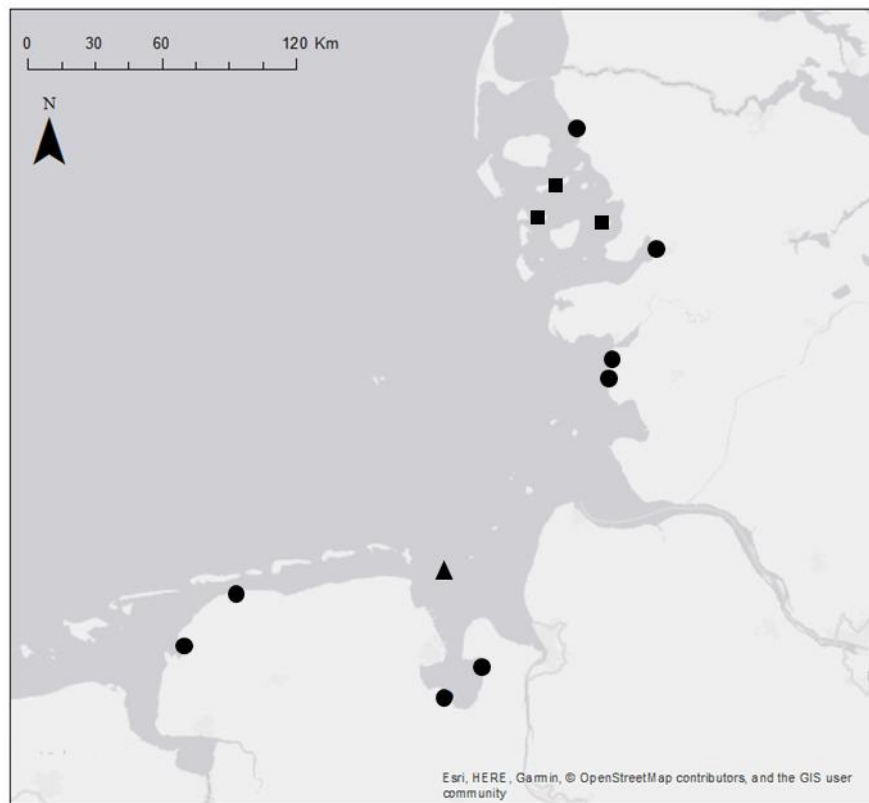
Fig. 4.1: Map of the North Sea coast of Lower Saxony and Schleswig-Holstein as well as the islands and Halligen off the mainland coast. Island study locations are indicated by a triangle (n=38), mainland study locations are indicated by dots (n=184), Hallig study locations are indicated by squares (n=113).

Table 4.1: Plot locations and number of replicates for the three salt marsh types. N_{total} = total number of plots; N_{sedi} = number of plots which experienced sedimentation; N_{ero} = number of plots which experienced erosion.

Salt marsh type	Study site	Coordinates	N_{total}	N_{sedi}	N_{ero}
Island	Mellum	53°43′ N, 8°08′ E	38	23	15
Mainland	Leybucht Norderland Jade Bight Schleswig-Holstein	53°32′ N, 7°07′ E 53°40′ N, 7°19′ E 53°26′ N, 8°09′ E 55-54° N, 8-9 E	184	105	79
Hallig	Langeness Nordstrandischmoor Hooge	54°38' N, 8°36' E 54°33' N, 8°48' E 54°34' N, 8°23' E	113	113	not measured

Data collection

The dependent variables sedimentation and erosion were obtained through different methods in the different study areas, here shortly mentioned: (1) On plots along the mainland coast of Lower Saxony and on the island Mellum, sedimentation and erosion were derived from SEC measurements with sedimentation-erosion bars (Nolte, Koppenaal, et al., 2013). For Lower Saxony data from 3 years (2006 to 2009) and for Mellum data from 6 years (2006 to 2012) were averaged. (2) On plots along the Schleswig-Holstein mainland coast, elevation above sea level was measured in 1987 to 1989 and 2017 to 2018 with an optical (Pentax AL-M5c) or automatic (Spectra Precision Laser Level LL500) levelling instrument, respectively, and yearly surface elevation change was calculated (Suchrow et al. (2012); the data of 2017 to 2018 has not yet been published otherwhere). (3) On the Halligen, sediment accretion data was derived from sediment traps established in 2010 to 2013 on Langeness, Hooge and Nordstrandischmoor (Schindler et al., 2014) and in 2016 to 2017 on Langeness as part of a still running turbidity measurement network (Hache et al., 2019). The later data has not been published before. Data on sedimentation and erosion as well as species composition were taken mostly at the same plots. Only on the Halligen, sedimentation data from 2010 to 2013 were manually extrapolated to the plots where vegetation

analysis was conducted, based on a detailed sedimentation map in Schindler et al. (2014).

The functional trait composition of the vegetation and plot distance to the marsh edge served as predictor variables. For the former, species composition and frequency were recorded at each plot on a $1\,\mathrm{m} \times 1\,\mathrm{m}$ square. Species nomenclature followed Jäger (2016). Canopy height (the distance between the highest fully grown leaf and the soil surface), plant stem biomass, plant leaf biomass, leaf area, and specific stem length (length of a stem divided by its mass) were used to describe the above-ground features of the vegetation that affect surface roughness and therefore sedimentation. Stiff stems require denser, more lignified material than flexible stems and therefore larger mass per unit length. Below-ground biomass, consisting of roots and rhizome biomass, and root specific length were considered because we assumed an anchoring effect reducing erosion. All traits of the salt marsh species were collected in the field following the standards described in Knevel et al. (2005) and Kleyer et al. (2019), albeit not from all plots across the whole coast. Most of the traits were collected on the mainland and island plots in Lower Saxony. We assumed that, due to the regional proximity of all plots and their similar environmental regime, traits collected from populations in Lower Saxony could be assigned to populations in Schleswig-Holstein.

Using a trait-based perspective is impeded by livestock grazing (Rupprecht et al., 2017). Plant traits such as height and aboveground biomass are decreased by grazing (Davidson et al., 2017) which makes trait values a difficult variable to include in statistical models. To account for the local biomass removal through cattle and sheep, trait values were adjusted according to management intensities, available from interviews with farmers and other land users. The "Hallig-Programm", a state program to support Hallig farmers while promoting nature conservation, restricts the number of livestock units per hectare (LSU) to approx. 1 LSU*ha^{-1}, so that grazing intensity mainly varied with grazing days, rather than stocking numbers. Plots were grouped according to recorded grazing intensity into three groups: ungrazed, medium grazing intensity (<300 grazing days*LSU), and high grazing intensity (>300 grazing days*LSU). Canopy height of plants occurring in plots with medium and high grazing

intensity was deliberately adjusted to 14±0.5 cm and 7±0.5 cm, respectively. Subsequently, stem and leaf biomass were reduced in equal proportions. Belowground traits are not strongly altered by grazing, thus local adjustment was not required.

As an abiotic factor, plot distance to marsh edge was also included in the analysis.

Statistical analysis

We assumed that SEC on the near-natural salt marsh on Mellum, the reclaimed salt marsh on the mainland coast and the grazed upper salt marsh on the Halligen responds differently to the combined effect of vegetation properties and distance to shore. We therefore subdivided the dataset according to the three salt marsh types and to plots which on average experienced sedimentation and plots which experienced erosion. On the Halligen only sedimentation was detected. This is in line with the very dense vegetation but is also attributed to the applied method: sediment traps can only detect sedimentation.

We used multiple linear regression to determine the effect of distance to marsh edge as well as vegetation roughness and plant anchoring capacity on sedimentation and erosion. To meet the model's assumption, we chose appropriate transformations using the "bestNormalize" package (Peterson, 2017) within the statistical computing environment R (version 3.5.2) (see Table 2 for applied transformations).

Table 4.2: Roughness and anchoring plant functional traits, abiotic factor, and the dependent variables sedimentation and erosion. Given are respective abbreviations used in this study, minimum and maximum values, units and applied transformation; ORQ, ordered quantile normalization transformation.

Function	Trait	Abbrev	Min	Max	Unit	Transformation
roughness	canopy height	CH	0.6	70.1	cm	ORQ
	plant stem biomass	SBM	22.6	17259.2	mg	boxcox
	plant leaf biomass	LBM	7.1	4172.2	mg	arcsin
	leaf area	LA	16.9	2071.6	mm²	ORQ
	specific stem length	SSL	0.5	9.3	mm/mg	ORQ
anchoring	belowground biomass	BlBM	15	24799	mg	ORQ
	root specific length	RSL	0.4	105.9	mm/mg	ORQ
abiotic	distance to marsh edge	dist	0	779	m	boxcox/ORQ
SEC	sedimentation	sed	0.0	26.7	mm	-
	erosion	ero	-0.1	-41.3	mm	-

Highly correlated plant traits were aggregated with principal component analysis (PCA), to avoid multicollinearity effects on the performance of individual predictors in the regression model. The above-ground traits stem biomass, leaf biomass, stem specific length, and leaf area were aggregated to "shoot mass", using the scores of the first axis of a PCA which explained 66 % of the variation of the four variables. SBM, LBM and LA were positively correlated and SSL negatively correlated with the first PCA axis. Thus, increasing "shoot mass" scores contribute to increasing vegetation roughness (Appendix Figure 4.5). Plants with high "shoot mass" scores were *Limonium vulgare, Aster tripolium, Spartina anglica, Atriplex prostrata,* and *Halimione portulacoides* (Appendix Table 4.5). Anchoring capacity was described by the scores of the first axis

of a PCA using root specific length (RSL) and belowground biomass (BlBM) which explained 67 % of the variation of the correlated variables (Appendix Figure 4.6). Increasing BlBM and decreasing RSL values translate to increasing "anchoring" values. Plants associated with high anchoring capacity are *Plantago maritima*, *Halimione portulacoides, Atriplex littoralis,* and *Limonium vulgare* (Appendix Table 4.6). Traits only marginally correlated satisfied the assumption of independence and entered the statistical analysis directly, i.e., without aggregation.

For each plot the community-weighted mean trait (CWM; i.e., the average trait value or aggregated score of all species co-occurring in a plot weighted by their abundances) were calculated according to the method of Garnier et al. (2007). In order to select the best environmental predictor for sedimentation and erosion, a stepwise variable selection was used to find the best performing model with the lowest AIC (Akaike Information Criterion).

4.4 Results

Mean SECs were not significantly different between regions (ANOVA results: $F(2, 332) = 1.64$, $p = 0.19$) (Figure 4.2). However, there were local differences, especially between island and mainland marshes. On mainland marshes, positive SEC was often found in the Schleswig-Holstein region while many Lower Saxony marshes showed negative SEC. Overall, more than 70 % of the studied plots experienced a positive SEC. On the island salt marsh of, the most natural site in the dataset, SEC varied between -22.4 to 16.5 mm/a, with a mean of 2.0 mm/a. On mainland salt marshes, mean SEC was 0.2 mm/a and values ranged between -41.3 to 26.7 mm/a. Plots on the Halligen salt marsh showed the smallest range of surface gains, 0.4 to 8.9 mm/a with a mean of 2.1 mm/a.
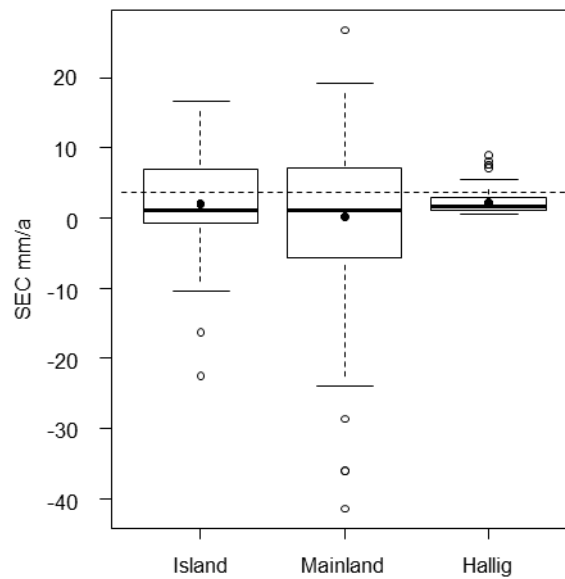
Fig. 4.2: Annual SEC of the three salt marsh types island, mainland and Hallig. The thick line indicates the median, the solid dot the mean. The dashed line shows the annual mean sea-level rise from 1971 to 2008 in the German Bight according to Wahl et al. (2011).

Sedimentation

On the island marshes, sedimentation responded non-linearly to distance to marsh edge, with a peak at intermediate distance and strongly decreasing values near and far from the edge. Plant canopy height showed a slightly bathtub-shaped relationship with highest sedimentation on plots with high canopy heights (Figure 4.3a and Table 4.3). On mainland salt marshes sedimentation showed a bathtub-shaped relationship with distance to marsh edge, with highest values close to the edge. It also showed a hump-shaped relationship with "shoot mass", with highest sedimentation values at higher intermediate "shoot mass" values (Figure 4.3b and Table 4.3). On Hallig salt marshes, we found a linear relationship with distance to marsh edge and a bathtub-shaped relationship with plant canopy height. Sedimentation was highest on plots close to the marsh edge with high vegetation (Figure 4.3c and Table 4.3). Goodness of fit values were all moderate (Table 4.3).
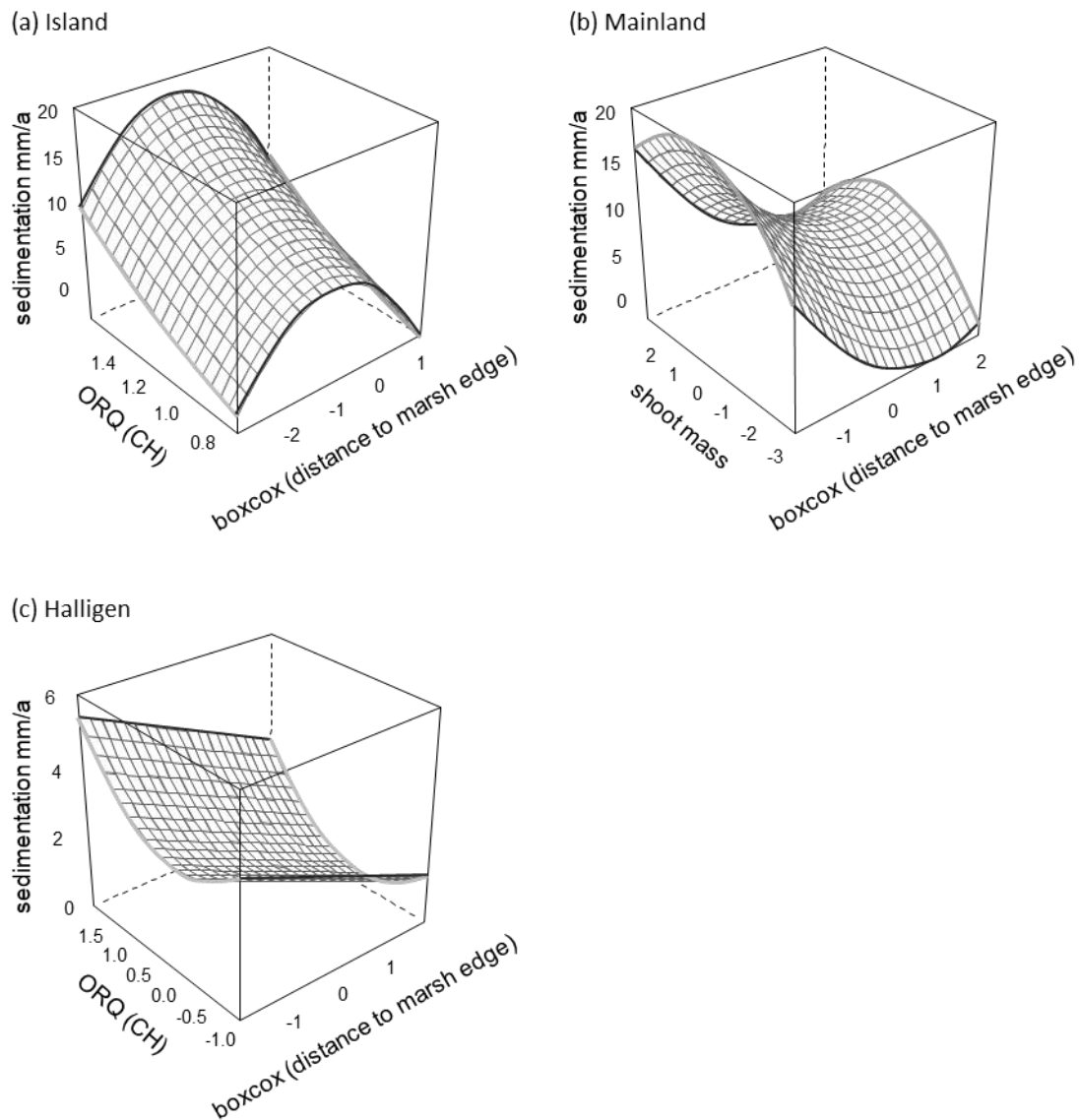
Fig. 4.3: Factors explaining sedimentation on salt marshes of (a) island (N = 23), (b) mainland (N = 105), and (c) Halligen (N = 113). Distance to marsh edge is boxcox transformed where a value of -1 corresponds to 77 m, a value of +1 corresponds to 431 m. Canopy Height (CH) is ORQ transformed where a value of -1 corresponds to 6.8 cm, a value of +1 corresponds to 28.2 cm. "Shoot mass" values are the scores of the first axis from the PCA (see Appendix Figure A1) aggregating SBM, LBM, SSL, and LA.

Table 4.3: Results of the multiple linear regression model for sedimentation on island marshes, mainland marshes and Hallig marshes. Given are estimates, standard error, t-values, and significance levels. Significant p-values at $\alpha = 0.05$ are shown in bold type. In addition, measures of model performance are shown.

	Estimate	SE	t	p	
Island marshes					
intercept	1.87	2.21	0.85	0.408	
distance to marsh edge	-4.64	1.48	-3.14	**0.005**	**
distance to marsh edge^2	-2.37	0.90	-2.64	**0.016**	*
CH^2	5.59	2.21	2.54	**0.020**	*
Adj. $r^2 = 0.27$; variance explained: 37 %; $F(3,19) = 3.72$, $p = 0.03$					
Mainland marshes					
intercept	8.79	0.65	13.52	**<0.001**	***
distance to marsh edge	-3.46	0.66	-5.26	**<0.001**	***
distance to marsh edge^2	1.54	0.43	3.57	**<0.001**	***
shoot mass	0.65	0.39	1.66	0.100	
shoot mass^2	-0.71	0.17	-4.20	**<0.001**	***
CH	-0.71	0.51	-1.39	0.168	
Adj. $r^2 = 0.44$; variance explained: 46 %; $F(5,99) = 17.0$, $p < 0.001$					
Hallig marshes					
intercept	1.70	0.15	11.669	**<0.001**	***
distance to marsh edge	-0.68	0.14	-5.016	**<0.001**	***
CH^2	0.82	0.19	4.195	**<0.001**	***
Adj. $r^2 = 0.29$; variance explained: 30 %; $F(2,110) = 23.7$, $p < 0.001$					

Erosion

On island salt marshes, erosion responded linearly to distance to marsh edge, with high erosion close to the edge. Erosion decreased linearly with increasing anchoring values (Figure 4.4a and Table 4.4). High erosion was found on pioneer zones with abundant *Salicornia spp.*, whereas pioneer zones with *Spartina anglica* were most often characterized by sedimentation (see above). On mainland marshes, erosion showed a hump-shaped relationship with distance to marsh edge, with highest values close to the

edge. It also showed a linear relationship with anchoring with highest values at plots with high anchoring values (Figure 4.4b and Table 4.4). Goodness of fit values were moderate (Table 4.4). Erosion was found on 79 % of all mainland plots in Lower Saxony, but only at 23 % of all mainland plots in Schleswig-Holstein. Almost all mainland plots with erosion were located in upper and lower salt marsh communities.
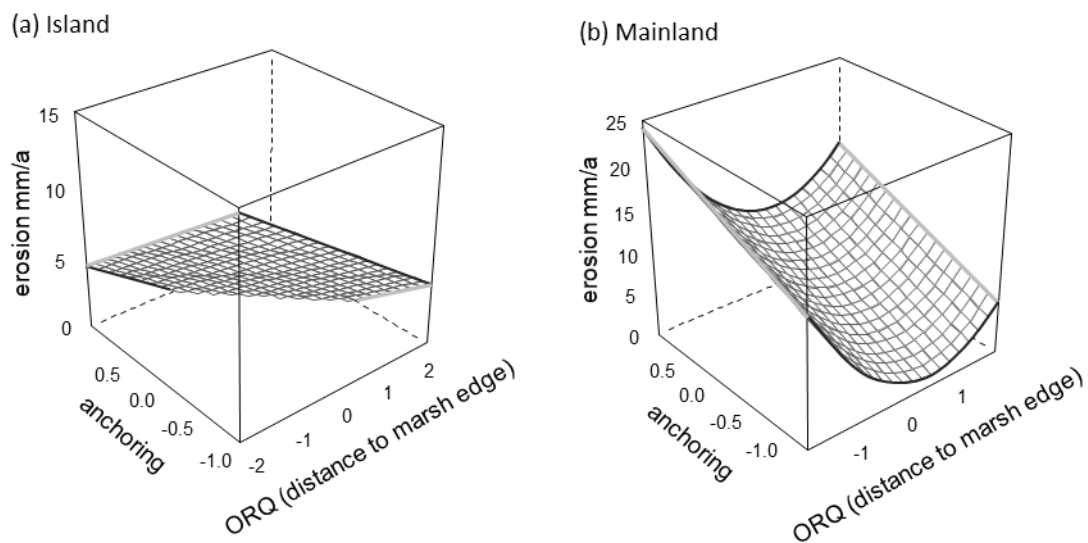
Fig. 4.4: Factors explaining erosion on salt marshes of (a) island (N = 15) and (b) mainland (N = 79). Distance to marsh edge is ORQ transformed where a value of -1 corresponds to 125 m, a value of +1 corresponds to 390 m. "Anchoring" values are the scores of the first axis from the PCA using BlBM and RSL.

Table 4.4: Results of the multiple linear regression model for erosion on island marshes and mainland marshes. Given are estimates, standard error, t-values, and significance levels. Significant p-values at $\alpha = 0.05$ are shown in bold type. In addition, measures of model performance are shown.

	Estimate	SE	t	p	
Island marshes					
intercept	4.16	1.06	3.94	**0.001**	**
distance to marsh edge	-2.41	0.96	-2.50	**0.028**	*
anchoring	-4.83	1.76	-2.75	**0.018**	*
Adj. $r^2 = 0.66$; variance explained: 71 %; $F(2,12) = 14,64$, $p < 0.001$					
Mainland marshes					
intercept	7.66	1.11	6.85	**<0.001**	***
distance to marsh edge	-2.65	0.88	-3.01	**0.004**	**
distance to marsh edge^2	2.62	0.85	3.08	**0.003**	**
anchoring	3.98	1.25	3.18	**0.002**	**
Adj. $r^2 = 0.27$; variance explained: 30 %; $F(3,75) = 10.62$, $p < 0.001$					

4.5   Discussion

The German North Sea coast is particularly sensitive to changes in sea level, as isostatic land subsidence adds to global sea level rise. In addition, it is a meso- to macrotidal region where mean high water determining the marsh tidal-flat border is expected to rise more than mean sea level (Balke et al., 2016). To keep current marsh distribution in place, marsh surface elevation must rise via sedimentation. We found that mean surface elevation change (SEC) on 335 plots distributed along the German North Sea coast is 1.0 mm/a. The interquartile range of all SEC data range from -1.0 to +4.3 mm/a (see also Suchrow et al. (2012) and Schindler et al. (2014)). Assuming similar accretion rates in the future, these observations question the ability of the studied marshes to accrete sufficiently to at least follow recent SLR (Wahl et al., 2011) or predicted future SLR (Bittermann et al., 2017; Church, Clark, Cazenave, Gregory, Jevrejeva,

Levermann, Merrifield, Milne, Nerem, Nunn, et al., 2013; Hay et al., 2015; Schindler et al., 2014).

Our results demonstrate considerable variation in surface elevation change across plots, ranging from -41.3 to +26.7 mm/a. Even at the same plot, surface elevation may change from erosion to sedimentation and vice versa from year to year. This is partly due to the strong stochastic contribution of storm surges. In contrast to the deterministic diurnal tidal regime, a single storm surge can deposit or take away large amounts of sediments (Roman et al., 1997). The spatial distribution of sediment accumulation and in consequence SEC can vary strongly depending on the coincidence of high water, wave energy, water current and wind direction (Hache et al., 2019). Thus, plots with usually rather low sedimentation can suddenly experience high sedimentation. In addition, sedimentation depends on the concentration of suspended matter in the sea water (French, 2006), a parameter we could not include in the models. We therefore expected and found fairly moderate goodness of fit measures of our models, in line with other studies. For instance, Boorman et al. (1998) found a correlation between vegetation height and surface accretion on one salt marsh but none on another marsh. Nevertheless, our results demonstrate that SEC is related to the distance from the shoreline and to the functional properties of the marsh vegetation. Vegetation roughness enhances sedimentation in a non-linear way and therefore supports surface elevation gain. Vegetation anchoring can reduce erosion and therefore lowers elevation loss. To capture the diverse coastal conditions, we picked three different salt marsh types: a natural island that was never inhabited or used, the long mainland coast with considerable variation in wave energy exposure, soil condition and land use, and the Halligen that are small marsh islands with long grazing history. SEC was similar between these saltmarsh types, but SEC relationships with plants traits and distance differed strongly.

Biogeomorphic feedback on sedimentation

Distance to marsh edge was the main explanatory variable for sedimentation in all three salt marsh types, with a strong, (non-) linear decrease in sedimentation further inland.

This is in accordance with previous work showing highest sedimentation in close proximity to marsh edges, creeks and gullies (Cadol et al., 2014; Morris et al., 2002; Moskalski & Sommerfield, 2012; Neubauer et al., 2002; Schindler et al., 2014; Suchrow et al., 2012). The main reason may be a strong decrease in wave energy and current strength at the boundary between mud flats and salt marshes where dense vegetation dissipates energy (Möller & Spencer, 2002). In addition, inundation times are longer and exposure to settling sediment is favored at lower elevations close to the marsh edge (Cahoon and Reed 1995; Leonard 1997; Temmerman et al. 2003). During shallow inundation on high salt marshes, water and sediment are often supplied mainly via the creek system and deposited close to the source and along the creek levees (Temmerman et al., 2005). This would make distance to creeks more important than distance to marsh edge. On the island salt marshes, we found a strong decrease in average sedimentation close to the marsh edge. This can be attributed to a highly dynamic SEC close to the marsh edge, often oscillating between erosion and sedimentation from year to year (Kleyer et al., 2014).

Functional trait related sedimentation pattern

Vegetation roughness significantly increased sedimentation in all three salt marsh types. Roughness is a composite property determined by plant height, leaf size and biomass, shoot biomass and stiffness, all of which may affect wave energy, water current and sediment deposition. Plant height was not correlated to the biomass traits (LBM, SBM) or leaf area (LA) and stem specific length (SSL). Therefore, plant height was used as a separate variable to indicate roughness, while the more strongly correlated traits LBM, SBM, LA, SSL were aggregated to "shoot mass". However, if terrestrial vegetation types such as reeds, mesic meadows and dry grasslands are considered, plant height can be significantly correlated to stem and leaf biomass (Kleyer et al., 2019).

The Hallig vegetation is characterised mainly by upper saltmarsh communities with varying grazing intensity. Strong grazing alters plant height, resulting in a low, homogeneous sward at the end of the vegetation period, when the storm surge season

starts. Ungrazed or less grazed areas may have a similar species composition as the grazed parts (mainly of the Juncus gerardii-Festuca rubra type) but with fully grown, often senescent stems. Thus, the main roughness indicator explaining sedimentation on Hallig salt marshes was plant canopy height. Other studies, however, found a significant impact of grazing on vegetation height on salt marshes, but no subsequent effect on sedimentation (Elschot et al., 2013; Nolte, Müller, et al., 2013). In contrast to the Halligen, sedimentation on the mainland coast was explained by "shoot mass". The mainland coast is characterized by more vegetation types, covering pioneer zone, lower salt marsh, and upper salt marsh; more varied micro-topography (i.e. beds and ditches, levees, dyke foot, hummocks) and different management (from bare soil to grazed and natural conditions, see Suchrow et al. (2012) and Minden et al. (2012)). These diverse conditions are better reflected in the variation of "shoot mass", the first principal component of LBM, SBM, LA, and SSL. They were found to be central organizing traits of herbaceous plant diversity of Northwest Europe (Kleyer et al., 2019). Specifically, the hump-shaped relationship with the peak towards the higher "shoot mass" values (Figure 4.4b) indicates that rigid shoots with high biomass enhance the capacity of the vegetation to trap sediments. Similar results were found by Bouma et al. (2010) in flume experiments for *Puccinellia maritima*, a plant with very flexible shoots, and *Spartina anglica*, characterised by rigid erect stems. Vegetation community structure has been found to affect sedimentation and highest sedimentation coincide with maximum plant population densities and biomass during summer months (Pasternack & Brush, 2002). Other findings showed that grazing induced different vegetation structure which then led to different sedimentation intensities (Andresen et al., 1990; Stock, 2011).

Our findings reflect the concept of ecosystem engineers in salt marshes. Engineering species greatly influence geomorphic processes and modify their own environment by attenuating waves and currents, enhancing sedimentation, and stabilizing sediment. In salt marshes a well-accepted example for an engineering plant species is *Spartina* spp. (Brown et al., 1999; Christiansen et al., 2000; Neumeier & Ciavola, 2004). In our study, stem traits of *Spartina anglica* indicated high stem stiffness (*S. anglica* SSL: 0.51 mm/mg; mean of all salt marsh species: 3.39 mm/mg) and high leaf area

(*S. anglica* LA: 1380.2 mm²; mean of all salt marsh species: 514.19 mm²). The vegetation-directed sedimentation initiates elevation gain, which in turn feeds back on vegetation patterns (Neubauer, 2008; Nyman et al., 2006). Vegetation biomass and community composition are influenced by inundation time and frequency, and thus by relative elevation (Hopfensperger & Engelhardt, 2008; Morris et al., 2002). Hence, there is a continuous two-way interaction between vegetation and landscape forming processes in biogeomorphic ecosystems such as salt marshes (Corenblit et al., 2015).

Functional trait induced erosion patterns

Vegetation also has an effect on erosion. Several studies have purported that wetland vegetation can provide protection from erosion (Barbier et al., 2011; Danielsen et al., 2005; Kathiresan & Rajendran, 2005). van Eerdt (1985) separated the effects of above- and belowground biomass on erosion resistance, showing that it was solely belowground biomass that prevents erosion. On island salt marshes, we found lowest erosion values in plots with high plant root anchoring values. On mainland salt marshes, however, lowest erosion values were found on plots where plant had low anchoring values. These contradictory results are likely due to the different origin of the salt marshes. The island displayed a natural salt marsh zonation, with a pioneer zone close to the salt marsh edge. Here, plots exhibited high erosion that were dominated by the small annual Salicornia spp. with tiny roots. Habitat mapping shows that the pioneer communities are scattered and do not form a coherent zone along the coastline of Lower Saxony where most of the plots with erosion were located (Nationalpark Wattenmeer, 2004). Most marshes originated from land reclamation schemes where rectangular groyne fields were constructed on the mudflats to trap sediment. With establishment of the Wadden Sea National Park in 1986, management shifted from active land reclamation to "let nature take its course" (Common Wadden Sea Secretariat, 2010). In last three decades, some of the reclaimed salt marshes have experienced erosion and the marsh-mudflat boundary has retreated to the lower and upper salt marshes, comprising plants with often low anchoring capability such as *Puccinellia maritima*. In addition, plots were located in sheltered bays and on exposed seaward marshes in Lower Saxony,

leading to high variation in exposure to wave energy and currents. As a caveat, we note that the time series of these plots comprised only three years that have seen particularly strong storm surges as compared to other years (storms "Britta", Nov. 1st, 2006; "Tilo", Nov. 7th, 2007).

Conclusion

Our study comprises an unprecedented dataset of SEC records on German North Sea salt marshes explained by abiotic and biotic factors. On most plots, mean annual accretion was lower than recent annual sea level rise (Wahl et al., 2011). Since inundation frequency defines the lower elevational limit of vascular salt marsh plants on tidal flats (Balke et al., 2016) this may lead to a retreat of the salt marsh edge and the rewetting of the marsh (Schröder et al., 2002). Eventually, it implies the drowning of the low-laying pioneer zones of the island marsh and the mainland marsh. Only sites that have adjacent inland areas and no dyke behind are able to gain new pioneer, lower and upper salt marshes. Site managers and agencies should therefore identify and secure key inland locations near current marshes in order to allow marsh migration to occur backwards. This would allow numerous services of salt marshes to persist (Barbier et al., 2011).

Erosion and sedimentation responded to plant traits and distance to marsh edge. We conclude that salt marsh vegetation is most likely well suited to modify and control sedimentation and erosion dynamics in response to sea-level rise or tidal forces. Using traits instead of species identity increased predictability as studies using species composition as predictor did not find conclusive effects on SEC (Brown, 1998; Silva et al., 2009). The predictive functions we developed allow, in conjunction with the traits of salt marsh plants (Appendix Table 1 and 2) and maps of salt marsh communities available for the Wadden Sea region, to model spatially explicit sedimentation and erosion. Empirically measured plant community mean traits indicate vegetation roughness and anchoring capability in a more mechanistic way than the vegetation roughness classification applied for the widely used Gauckler-Manning-Strickler

formulas in hydraulics (Chow, 1959). The different shape of the response functions from Hallig, mainland and island plots indicate that future studies should take into account differences in salt marsh genesis and land use.

Appendix
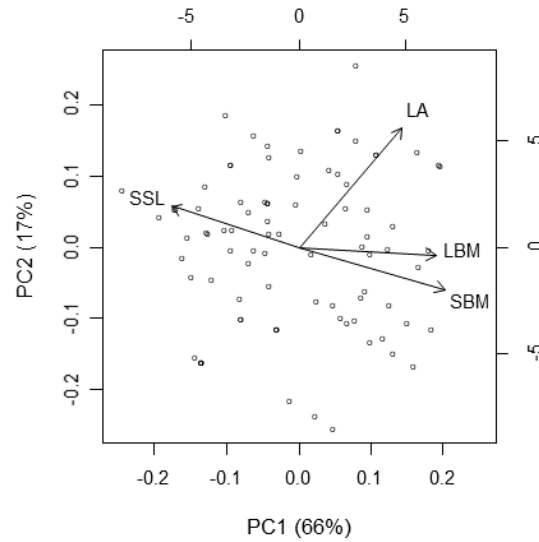
Fig. 4.5: Two-dimensional illustrations of the standard PCA ordination results of plots which experienced sedimentation. Arrows indicate direction of loading for each trait. The scores of the first axis are included in the model as "shoot mass". LBM, leaf biomass; SBM stem biomass; LA, leaf area; SSL, specific stem length.

Table 4.5: Functional traits and the aggregated variable "shoot mass" of species growing on plots which experienced sedimentation. CH, canopy height (cm); SBM, stem biomass (mg), LBM, leaf biomass (mg), SSL, stem specific length (mm/mg); LA, leaf area (mm^2).

Species	shoot mass	CH	SBM	LBM	SSL	LA
Agrostis stolonifera	-0,64	31,08	233,36	50,17	3,57	207,70
Armeria maritima	-0,38	5,88	197,30	353,11	3,94	68,30
Artemisia maritima	1,87	33,25	1765,65	675,61	0,66	208,50
Aster tripolium	2,89	60,84	10074,12	1174,96	0,60	663,90
Atriplex littoralis	2,37	70,13	17259,26	509,12	0,69	494,60
Atriplex prostrata	2,64	42,07	9519,62	2354,47	1,51	815,80
Cochlearia danica	-0,52	7,40	374,18	145,27	4,71	127,70
Elytrigia atherica	1,41	38,90	1036,67	314,35	0,98	773,60
Elytrigia repens	1,05	51,25	720,52	241,33	1,88	904,60
Festuca rubra	-0,96	37,42	144,79	228,60	6,86	126,10
Festuca rubra litoralis	-2,27	26,83	91,32	28,74	7,21	94,00
Glaux maritima	-1,97	8,10	72,94	67,14	4,48	17,00
Halimione portulacoides	2,51	28,71	9183,15	2869,74	0,95	186,20
Juncus gerardii	-1,36	24,72	129,48	54,96	5,04	139,40
Limonium vulgare	3,06	14,51	1193,61	4172,17	0,75	1681,30
Lolium perenne	0,35	34,18	620,65	99,19	2,16	461,60
Lotus corniculatus	-0,56	27,80	135,99	116,48	4,29	374,60
Plantago maritima	1,73	13,15	688,29	1239,13	3,08	1401,70
Poa pratensis	-0,52	31,09	213,71	86,00	4,42	285,70
Potentilla anserina	-0,54	19,94	209,64	386,61	9,28	773,30
Puccinellia maritima	-1,17	28,82	209,93	62,52	4,63	76,20
Salicornia europaea	1,11	17,24	719,96	799,62	1,49	162,40
Spartina anglica	2,83	44,27	1425,34	764,80	0,51	1380,20
Spergularia maritima	-1,15	26,75	548,28	126,09	1,93	46,55
Spergularia media	-0,58	7,72	261,52	173,81	7,08	446,10
Suaeda maritima	0,80	25,02	1602,82	494,34	1,27	32,00
Trifolium repens	-1,34	10,96	75,27	56,77	5,82	474,60
Triglochin maritimum	1,11	22,57	380,47	574,31	2,25	931,50
Vicia cracca	-0,87	27,50	112,19	162,58	4,51	142,10
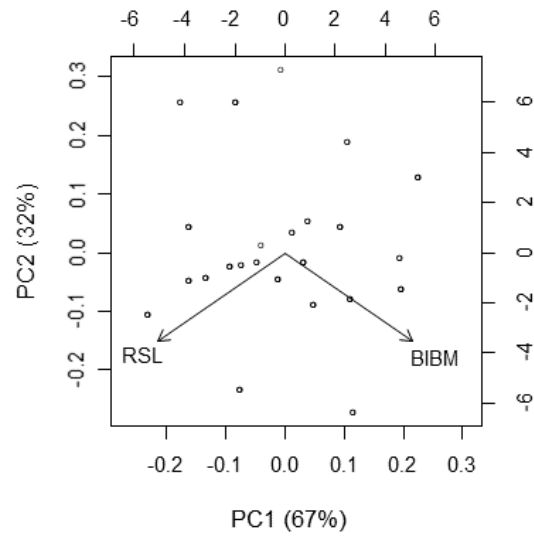
Fig. 4.6: Two-dimensional illustration of the standard PCA ordination results of plots which experienced erosion. Arrows indicate direction of loading for each trait. The scores of the first axis are included in the model as "anchoring". RSL, root specific length; BlBM, belowground biomass.

Table 4.6: Functional traits and the aggregated variable "anchoring" of species growing on plots which experienced erosion. BlBM, belowground biomass (mg); RSL, root specific length (mm/mg).

Species	anchoring	BlBM	RSL
Agrostris stolifera	-2,01	79,44	105,87
Armeria maritima	-0,37	279,73	27,41
Artemesia maritima	0,50	1528,13	17,75
Aster tripolium	1,07	3168,29	15,21
Atriplex littoralis	1,80	3377,80	10,63
Atriplex prostrata	-0,03	498,57	26,54
Cochlearia danica	0,01	48,32	7,09
Elymus pycnanthus	0,16	282,59	15,42
Elymus repens	0,42	316,63	15,10
Festuca rubra litoralis	-1,40	78,50	45,65
Glaux maritima	-0,68	40,44	13,39
Halimione portulacoides	1,84	3908,03	11,03
Juncus geradii	1,03	282,28	6,07
Leontodon autumnalis	-0,28	194,44	25,12
Limonium vulgare	1,11	15173,65	28,53
Lolium perenne	-0,60	186,78	30,07
Plantago maritima	2,09	2063,55	0,98
Puccinellia maritima	-1,39	153,43	56,98
Salicornia europaea	-1,12	165,33	53,24
Spartina anglica	0,34	758,58	16,58
Spergularia media	-0,62	1477,38	69,23
Stellaria media	-1,52	14,96	17,40
Suaeda maritima	-0,77	183,22	34,84
Trifolium maritimum	0,90	967,68	12,97

Chapter 5

Synthesis

5 Synthesis

5.1 Summary of findings

This thesis focuses on the interaction of vegetation and landscape-forming processes in biogeomorphic coastal ecosystems. The loss of these ecosystems and the reduction in related services of coastal marshes and dunes have been observed in several places around the world. It is apparent that we need to better understand the functioning of these ecosystems in order to restore and manage them successfully.

The general aim of determining plants' trait-based responses to and effects on sediment relocation was pursued throughout this thesis. The trait responses of dune plants to disturbance through burial showed strong differences between species. Growth was mostly increased through burial and erosion in *C. maritima* and decreased in *A. arenaria* (Chapter 2). Further, trait-based effects of single vs. multiple species communities on resistance and resilience of artificial coastal dune systems were studied. Mixed-communities were more resistant (Chapter 3). While these first two studies focused on biogeomorphic processes of coastal dune systems, the third study investigated biogeomorphic processes in salt marshes. It examined trait-based effects on sedimentation and erosion processes in salt marsh communities. Effects of roughness and anchoring capacity on sedimentation and erosion were found (Chapter 4).

This thesis used a trait-based approach to understand biogeomorphic ecosystems and examined coastal dunes and salt marshes. Both of which are shaped by similar biogeomorphic processes involving the two-way interactions of landscape forming processes and the functional traits of plants. The following sections will combine the insights from the preceding chapters to highlight the importance and challenges of a trait-based perspective in biogeomorphic research, to point out possible implementations of the results and to suggest topics for future research.

5.2   The "window of adaption" in dune pioneer species

The analysis of trait response to burial and erosion (Chapter 2 and Chapter 3) demonstrated that dune pioneer species may respond to physical disturbance by changes in trait expression, underlining their strong intraspecific variability. In both studies *C. maritima* and *A. arenaria* were subjected at different times after germination to an erosion event of around 2 cm. While in Chapter 2 individuals were exposed to the disturbance at a very early life stage, i.e. when individuals were still small, in Chapter 3 individuals were disturbed at a later life stage when they had most likely reached their maximum biomass and were about to flower.

Combining the data from the two experiments together makes clear that trait responses are different in the two species. In *C. maritima* the relative difference of canopy height to the control did not differ between any of the disturbance timings. In *A. arenaria* relative difference to control was smallest in the late disturbance treatment. Relative shoot mass difference to the control was not different between disturbance timing in *C. maritima* nor in *A. arenaria*. Unfortunately, it is not possible to compare other traits from the two experiments due to experimental related differences in trait collection (Figure 5.1).

These findings are contradicting our assumptions of a "window of adaption". We use this term to describe the period of time during which an individual has successfully germinated but is still prone to sediment relocation and can survive only through fast trait adaptation. This means that an erosion event of a specific intensity during an early life stage evokes stronger trait-responses than an erosion event at a later life stage. Small individuals are more affected by the erosion and need to invest more into their roots to survive than larger, well-settled individuals. However, this effect was not seen when individuals were subjected to a rather small erosion event of around 2 cm as in these experiments.

Nevertheless, these results provide us with a better understanding of the adaptation strategies of the species to sediment relocation and their role in the functioning of the dune ecosystem. Even during early life stages individuals are not strongly affected by a

small erosion event in their canopy height and their shoot mass. They continue to grow unaffectedly, indicating that they have left the "window of adaption". This might be of course different for other traits, especially belowground traits.

The "window of adaption" has implications for the functioning of the natural dune systems. Storms in early spring, when newly germinated individuals are still small, can be especially devastating. During this time, small sediment changes can also lead to the death of the individual when the plant cannot react to the new surface location with fast trait reactions. A storm later in the year, causing the same intensity of sediment relocation, is less critical for the well-established vegetation. Along the German coastline, *C. maritima* germinates around May. Within a couple of weeks, the plants grow to their final habitus. A storm leading to a moderate erosion event in June will not result in the death of individuals. The same holds true for *A. arenaria* individuals that germinate from April to May. However, generative distribution plays only a minor role in this species and the distribution is mainly vegetative. No experimental data exist on the difference between generative and vegetative distributed individuals, but it may be assumed that the individuals grown from rhizomes are more tolerant to sediment relocation. They are connected to the mother individual, which has more height, has deeper roots and more photosynthetically active material. Thus, in the case of a burial/erosion event the new individual can benefit from the mother individual. This narrows the "window of adaption" of *A. arenaria* and makes this species especially important for early dune stabilization.
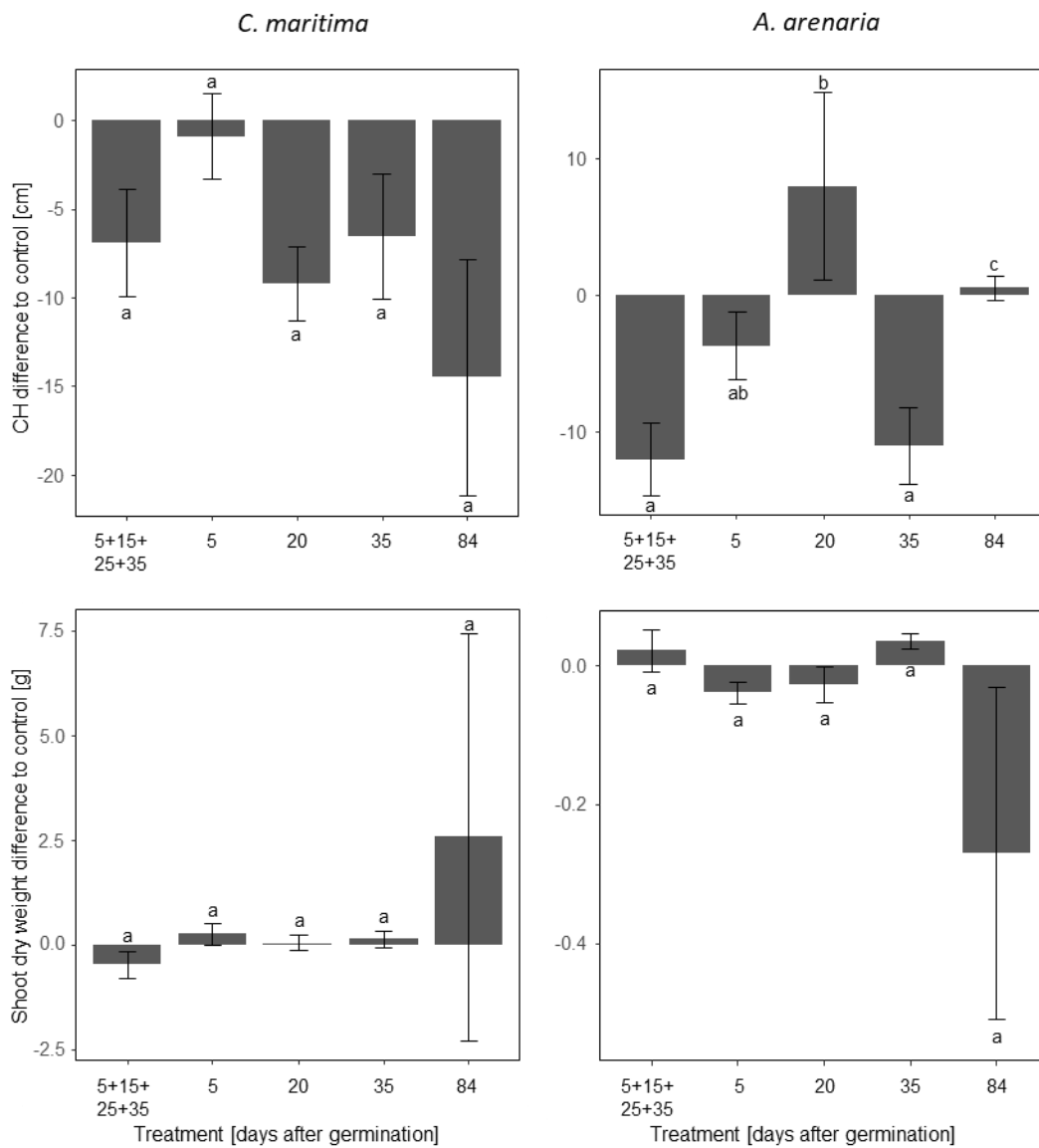
Fig. 5.1: Effect of a gradual and sudden erosion event of about 2 cm at different times after germination on canopy height (CH) and shoot dry weight of *C. maritima* and *A. arenaria*. Shown are the relative changes in comparison to the control treatment (mean ± SD). Treatments sharing the same latter are not significantly different (α = 0.05).

5.3 Is the community weighted mean a suitable index for biogeomorphic ecosystems?

Trait-based studies are very common in modern ecological research. Traits allow the quantification of the comprehensive functional response of plant communities to environmental changes, accounting for both abiotic and biotic drivers (Enquist et al., 2015). However, measuring traits can be cost- and time-consuming. Data on traits have been amassed in large quantities during recent decades and have given ecologists the opportunity to use large vegetation databases instead of measuring trait data anew on each plot. It is standard practice to use Community Weighted Means (CWM) to describe traits of whole communities. For this purpose, researchers use an average trait value per species, obtained by averaging measured trait values of individuals from the same species in different spatial and temporal situations. Then the species' weighted average is used to describe the community structures. CWM permits a generalization of the findings and an examination of the functional response of communities along environmental gradients without measuring each trait again (Shipley et al., 2006; Violle et al., 2007). This approach was used in the third study of the present work.

The first study in this work showed, however, that environmental conditions can lead to significant intraspecific variation. Multiple environmental gradients exist in biogeomorphic ecosystems. We showed that erosion and sedimentation magnitude and timing significantly affect trait expression of dune pioneer species and yield great intraspecific variation. This phenotypic plasticity is also observed in the natural dune systems. A striking phenotypic plasticity is found in *C. maritima* (personal observation) with individuals growing in places further away from the source of disturbance, germinating and flowering earlier in the year and growing much taller with more branches and leaves than their conspecifics closer to the beach.

Combining trait values measures of all these individuals to calculate an average trait value to use in the CWM on plot level can pose problems. Individuals' aboveground biomass in the highly dynamic embryonic dunes would be overestimated while individuals in the back parts of the white dunes would be underestimated. This raises

the issue of whether trait values retrieved from a database are a suitable surrogate for traits measured on site.

Lately, mounting evidence suggests that intraspecific variation, arising from phenotypic plasticity or genetic diversity, plays a crucial role in driving CWM–environment relationships (Albert et al., 2010; Lepš et al., 2011) and determining species' niche breadth (Violle & Jiang, 2009). There is evidence that the CWM does not always represent the community structure accurately (Cordlandwehr et al., 2013; Kattge et al., 2011). However, it is still common practice to average species data from different populations and from habitats at varying altitudes and longitudes. Consideration is not given to the fact that species traits show intraspecific variability from site to site in plastic reactions to changing environmental conditions (Garnier et al., 2001; Mokany & Ash, 2008), genotypic diversity (Whitlock et al., 2010) or a combination of both (Scheepens et al., 2010).

Research has shown that the accuracy of traits retrieved from a database as a surrogate for on-site measurements depends on multiple factors. In a study by Cordlandwehr et al. (2013) the accuracy of database predictions was examined for three widely used plant traits, Canopy Height (CH), Leaf Dry Matter Content (LDMC) and Specific Leaf Area (SLA), in a wet meadow and a salt marsh. For the local species pool, the database values more accurately predicted traits aggregated at the habitat level than for plant communities on plots aggregated at the community level. Traits with lower plasticity (e.g., LDMC) were more accurately predicted by database values. The study found that the accuracy of the database values depends on the scale or level of aggregation (lower at community level), the trait itself (lower in plastic traits) and the type of habitat (lower in extreme habitats, i.e., the salt marsh). Therefore, Cordlandwehr et al. (2013) concluded that for studies at the site scale (e.g., trait-environment relationships) traits retrieved from a regional database and filtered according to habitats will yield good results.

Yet, different traits show different amounts of intraspecific trait variance and are therefore differently suited for export from a database. The study by Cordlandwehr et al. (2013) urged caution with the use of database predictions for those traits linked to

the usage of resources (e.g., CH, LDMC and SLA for light capture) because they are highly variable on a small spatial scale. If the phenotypic plasticity follows a normal distribution, however, trait data from a database are representative of the individuals on the studied plot. Figure 5.2 shows the distribution of trait in the database from the Landscape Ecology Group at the University of Oldenburg. Values from three salt marsh species are shown. It illustrates that many salt marsh species have a substantial phenotypic plasticity. As the distribution represents a rather normal distribution, it is a reasonable basis for calculating a species average. Yet, caution should be taken as some species and some traits might not follow a normal distribution (see Figure 5.2 *Aster tripolium*).
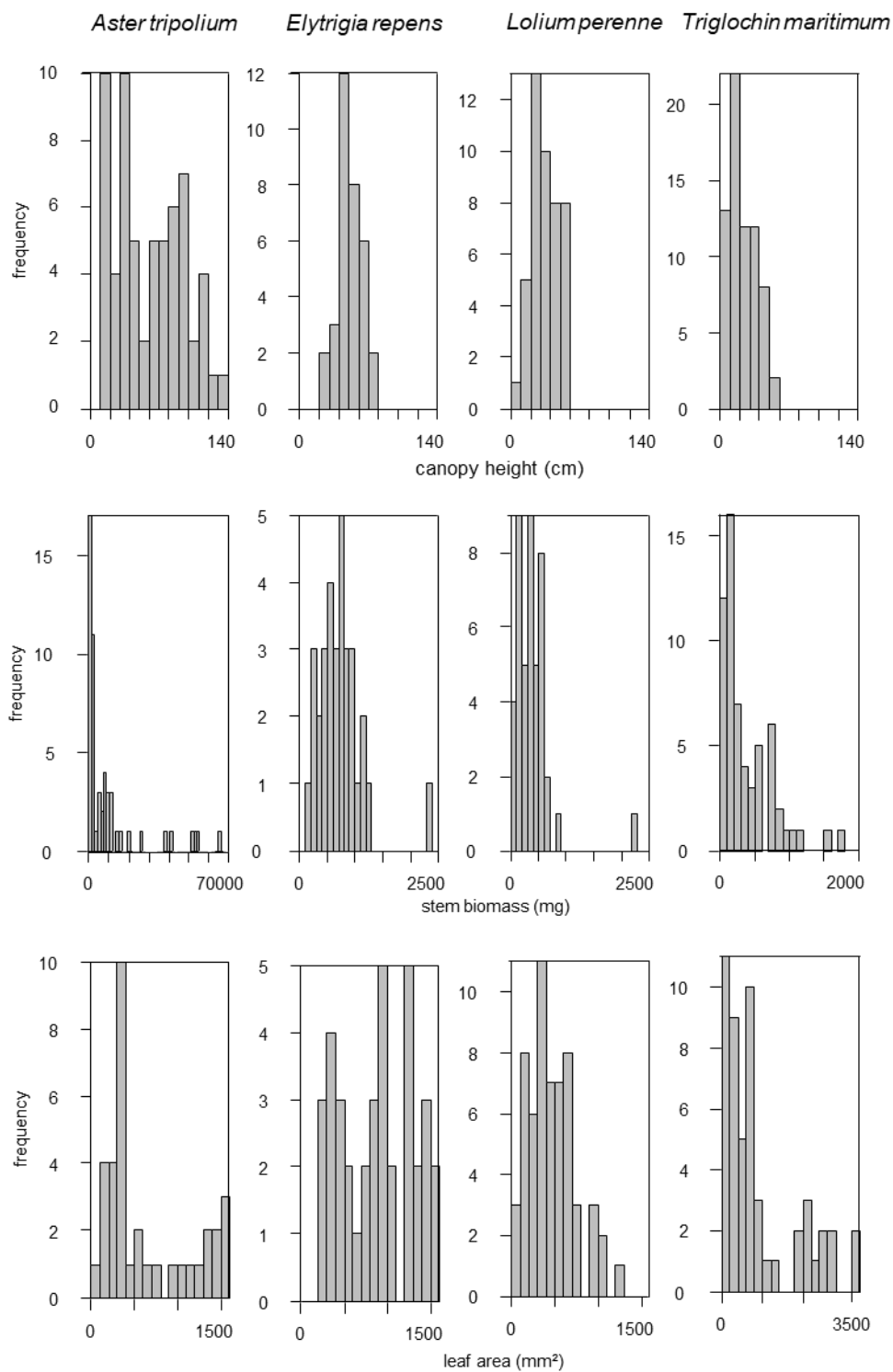
Fig. 5.2: Histograms of intraspecific trait variance for four exemplary salt marsh species (Data from the database of the Landscape Ecology Group, University of Oldenburg).

5.4   Insurance effect vs. keystone species

Combining the results from the three studies in the present work gives us a better understanding of the functioning of dynamic coastal ecosystems. The role of biodiversity of trait diversity is extensively discussed in the context of climate change and habitat loss. In Biodiversity and Ecosystem Functioning (BEF) literature, it is generally assumed that biodiversity increases the resilience and resistance of ecosystems (Yachi & Loreau, 1999). If some species die off as a result of changed biotic and abiotic factors, others can take over their function. This insurance hypothesis proposes that species or phenotypes that are functionally redundant for an ecosystem process at a given time may show an increase in temporal mean productivity, given the asynchronous response to environmental fluctuations. In this case, biodiversity acts as insurance for ecosystem functioning in the event of temporal environmental changes. The potential consequences of biodiversity loss for ecosystem functioning and services have received considerable attention during recent decades (Kinzig et al., 2001; Loreau et al., 2002; Loreau et al., 2001). Much theoretical work and several controlled experiments have shown that species diversity influences the functioning of ecosystems (Ives & Hughes, 2002; Lehman & Tilman, 2000; Tilman et al., 2001; Yachi & Loreau, 1999). It was shown that the long-term sustainability of ecosystems and the services they generate both depend on the conservation of biodiversity on local and landscape levels (Bengtsson et al., 2003; Loreau et al., 2003). The reason is that after disturbance a high diversity of functional groups makes reorganization possible (Bengtsson et al., 2003).

However, not all ecosystems are likely to follow the insurance hypothesis. In BEs such as coastal dunes and salt marshes, the insurance effect is replaced by the effect of keystone species. Here, it is mostly one "keystone species" or "ecosystem engineer" that affects the stability of the ecosystem, especially when faced with physical disturbance (Gutiérrez & Jones, 2008). Originally, the term "keystone species" was used to describe a species that has a disproportionately large impact on its environment relative to its abundance (Mills et al., 1993; Paine, 1969). The classic example is that of a large predator which controls prey populations. The term "ecosystem engineer",

which overlaps in part with this concept, is defined as "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic material. In so doing they modify, maintain, and/or create habitats" (Jones et al., 1994).

In salt marshes the keystone species are *Spartina* spp., and in coastal dunes *Ammophila* spp. (Emery & Rudgers, 2014; Proffitt et al., 2005). These species have a disproportionally high impact on the function of the ecosystems. All other species have only minor additional effects on biogeomorphic processes and mainly benefit from the effect of the keystone species on the ecosystem. The experiments in this work (Chapter 3) very well show this effect in coastal dunes under controlled experimental conditions.

5.5 Implications for management and restoration – lessons learned for trait-based management of coastal dunes

Adaption to climate change and disaster risk reduction have become a priority worldwide, exemplified by global frameworks such as the Paris Agreement (United Nations Framework Convention on Climate Change, 2015) and European actions like the EU Climate Change Adaption Strategy (European Commission, 2013) and the Floods Directive (European Commission, 2007). As coastal ecosystems in particular are at risk of the adverse effects of climate change, adaptation strategies have become a topic of discussion.

At present, no ecosystem exists around the world, which is free from alteration caused by human activities (Vitousek et al., 1997). The degradation of ecosystems' function and the loss of ecological services have accelerated at a constantly. Coastal ecosystems, such as coastal dunes, are in an advanced stage of degradation and are at risk of loss. The causes include climate change-induced SLR, increased storms, decreased precipitation and higher local temperatures and intensive farming in sandy, well-drained habitats, the expansion of ports, growing urbanization and infrastructure, increased pressure from tourism, the promotion of forests and grasses to stabilize moving sands and the introduction of alien species (Millennium Ecosystem Assessment, 2005).

Changes in dune building processes are expected to be manifested through an increase in erosive forces at the expense of accretive forces. This would lead to a negative sand balance and inland migration of the beach-dune system. Bird (1985) reported that 70% of the world's sandy shorelines were eroding or had a negative sediment budget, resulting in erosion and inland displacement of the shoreline (Psuty & Silveira, 2010).

Coastal dunes have become more important as worldwide human population growth increases within 10 kilometers of the coastline (Neumann et al., 2015). Concurrently, SLR and climatological wind speed changes occur as part of ongoing anthropogenic climate change (Hieronymus et al., 2018). The future projections of these variables are still highly uncertain and do not rise in a globally uniform manner, but have been observed to vary in a complex spatial pattern (Church, Clark, Cazenave, Gregory,

Jevrejeva, Levermann, Merrifield, Milne, Nerem, & Nunn, 2013). For the North Sea, an increase in wind speed and subsequently an increase in significant wave height as well as extreme wave heights are predicted (Grabemann & Weisse, 2008). Sea level of the North Sea is predicted to rise (Pethick, 2001) as is extreme sea level (Vousdoukas et al., 2017). These projections increase the importance of coastal dunes which can serve like dikes as flooding protection (Borsje et al., 2011).

Likewise, the importance of managing and restoring coastal dunes is growing. If left unmanaged, coastal dunes would naturally migrate inland (Keijsers, Giardino, et al., 2015). In unsettled areas, coastal ecosystems may be allowed to migrate. In most cases, however, including the barrier islands of the Wadden Sea, migration is restricted by the presence of settlements or farmland. There is great socio-economic interest in managing the coast in a way to fix the sand dunes at their current position (Dronkers & Stojanovic, 2016). Since dunes play an important role in coastal safety, dunes have been managed not only to keep them from migrating land inwards but also to strengthen their ability to protect the hinterland from flooding.

Efforts at coastal protection and improved management have become priorities government authorities (Dronkers & Stojanovic, 2016). During the last decades, management practices have changed as we have learned more about the functioning of the ecosystem. The primary aim has long been surface stabilization to counter deflation and inland engulfment. Practices like boardwalk establishment, sand fences and vegetation planting have become common all over the world (Pizzey, 1975). Because of its effectiveness in stabilizing active dunes, *A. arenaria* has been introduced on almost every temperate coast of the world to stabilize bare sand surfaces (Hilton, 2006; Masterman & Ellison, 2018; Ruggiero et al., 2018). Over time, the grass became highly invasive in temperate, southern hemisphere dune systems (Hilton et al., 2005). It won the competition against native dune-forming species and the extensive grass cover stabilized the foredune, cutting off sand supply from the beaches to the back dunes. Early successional stages and blowouts, a way to rejuvenate the biogeomorphic system, disappeared and indigenous taxa which depend on a dynamic environment were lost. This resulted in a reduction in biodiversity and major changes in dune shape. On New

Zealand's coasts, *A. arenaria* created very high, steep, and concave foredunes that were increasingly susceptible to the local strong storms (Hart et al., 2012). The dunes grown with native vegetation have convex incipient foredunes that can better resist the strong storms (Masterman & Ellison, 2018). Grass encroachment has also become an important environmental problem on European coasts. At present, dynamic pioneer stages are rare in most western European dunes, except for the Wadden Sea islands (Provoost et al., 2011).

It is now evident that in most cases dune stabilization alone is not sufficient for a resistant and resilient coast. because it may create many new problems. First, artificial stabilization alters the aeolian processes and may have a major impact farther inland or downwind. Second, stabilization can be very costly; and third, mobile dunes may be part of the natural successional landscape and should be allowed to function normally. Currently, numerous control programs exist in several countries that aim at eliminating *A. arenaria* and restoring the natural dune processes without sacrificing stability. Several mechanical (excavators and bulldozers) and manual (hand-pulling) removal methods are used and have been proven to be efficient (Pickart, 1997).

Today we know that conservation and coastal management are not irreconcilable, and a balance between them should be aimed at. It became desirable not only to stabilize and protect the area, but also support ecological development. In fact, recent management trends are directed towards acceptance of these systems as valuable wilderness areas. That is, management is best done in accordance with the natural processes and local conditions. That said, when trying to protect coastal areas it should be considered whether stabilization is necessary and, if it is, under what circumstances and which species (preferably native) should be used.

Consequently, there is a growing need to predict specific species performance to find the most suitable ones for ecological management and restoration projects and to evaluate land vulnerability to erosion. Here, plant traits represent a promising tool. A trait-based approach enables fast prediction of species performance for erosion control in coastal dunes. Identifying relationships between plant functional traits and environmental factors has always been an important task in plant ecology (Lavorel et

al., 2007). In the next step, the functional approach is now used to answer applied questions and to help design and evaluate management and restoration projects to prevent shoreline retreat, maintain the shoreline positon or even extend it seaward (Burylo et al., 2014; Gondard et al., 2003).

To generate a long-term impact on erosion processes in a dynamic ecosystem subjected to erosion and sedimentation, plant species must be able to survive mass movement. The ecological performance of a plant species depends on its response to dynamic processes, i.e., resistance to mechanical forces, which is described by the response traits, and on its effect on dynamic processes, i.e., soil stabilization, as described by the effect traits (Figure 5.3).

So far, only very few studies exist, which use a trait-based approach to answer applied questions concerning ecosystem stability under erosive forces and draw conclusions on suitable plant traits for erosion control. Some studies elucidate the interaction between one single species and erosive forces (Mickovski et al., 2005; Shi et al., 2004) and a handful of studies compared several species' performance (Bochet et al., 2000; De Baets et al., 2007; Isselin-Nondedeu & Bédécarrats, 2007). Very few studies examined the performance of several species for erosion control by considering different plant functions and species response and effect traits (Burylo et al., 2014; De Baets et al., 2009).

Thus, the results of this thesis have important implications for coastal management. By combining the results of the first two studies of the present dissertation, we can evaluate species response to sediment dynamic and species effect on sediment dynamic on a trait-based level. It becomes clear that dune pioneer species are affected by a sudden and also a gradual physical disturbance in their early life stages. The strength of the response to the disturbance is species-specific, which shows that species are adapted differently for growth in the dynamic early stages of coastal dunes. It was shown that *A. arenaria* is able to survive theses disturbances better than *C. maritima*. It was also shown that *A. arenaria* stands were more resistant to a wind disturbance than a mixed-species stand.

The high resistance and resilience of *A. arenaria* was driven by their high biomass production. High aboveground biomass production enables individuals to outgrow sedimentation and catch moving sand; high belowground biomass increases resistance to uprooting and promotes soil stability. Following this trait perspective, other species with similar trait expressions could serve the stability of coastal dunes in the same way as *A. arenaria*. This means alternative species can easily be used in parts of the world where *A. arenaria* is not native.

A management strategy based on the scientific knowledge gathered on plant traits can improve coastal defence mechanisms by incorporating natural processes. This makes the projects less costly and more effective. Strategies should be promoted which secure the shoreline from erosion but do not simply cultivate a continuous dune grass sward. This solution exerts stress on any costal environment and, in some instances, may trigger ecological catastrophes. A dune system with diverse vegetation, morphology, and relief could be more resilient to changing condition.

Dunes are naturally in a developmental stage of instability and migration as part of the system. Allowing some degree of mobility should be part of an integrated management strategy. This concept is based on three main considerations: restore and conserve natural processes, create conditions for future natural processes, and develop types of land use that are in accordance with the above (Van der Meulen & Salman, 1996). The concept seeks to incorporate natural processes and human activities within coastal dune systems. The implementation of "soft" techniques includes the cessation of any activity that adversely effects the sediment supply of the dunes, planting vegetation, fencing-off sensitive areas, creating dune walkways, and providing the public with relevant information (Gómez-Pina et al., 2002). This is in contrast to "hard" techniques that protect the coast through the construction of concrete sea walls, revetments, gabions, groynes, and offshore break waters. These measures provide only temporary protection from ocean hazards and each hard method induces changes in currents and might promote erosion problems to adjacent coastal areas. Soft techniques should be used more often in coastal protection as they provide natural, long term protection with no adverse effect to adjacent coastal areas.
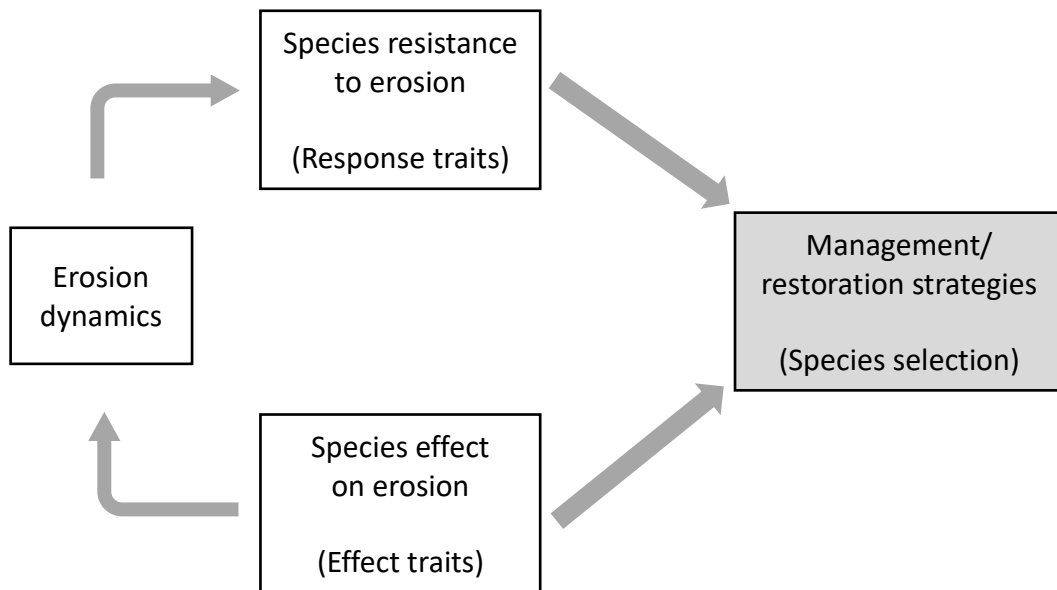
Fig. 5.3: Trait-based conceptual framework for ecological restoration of eroding ecosystems. Species response to erosion and species effect on erosion are studied using a functional approach that analyses response and effect traits. The results can be used to improve existing restoration and management strategies and develop new ones.

5.6   Towards a new research horizon

Based on the present study, future research should further research on plant trait responses to and their effects on landscape forming processes in coastal ecosystems. Further developing well-established concepts concerning principles driving ecosystem functioning and combining them with newly developed ones was a main success of the present dissertation. Even though the concept of phenotypic plasticity in response to environmental changes was established a while ago, there was still a lack of experimental studies. Also the relatively new concept of biogeomorphology and the importance of key species rather than biodiversity for ecosystem functioning lacked experimental evidence and a trait-based perspective. This lack of knowledge implies that the processes of dune and salt marsh establishment and resilience against climate change are still not fully understood. This is despite the fact that these coastal ecosystems are crucial structures for coastal protection.

The studies in this dissertation added significant knowledge to the field of trait-based biogeomorphology. This can chart a course for future research. Our experiment showed that it is difficult to cultivate dune species because some species have seed dormancy, which prevents intact viable from germination even under favorable conditions (see Appendix). Therefore, future research should investigate on germination and cultivation requirements of species of interest. Due to poor germination rates and unsuccessful cultivation of *E. farctus* and *H. peploides,* those species were not included in the burial and erosion experiment (Chapter 2). Adding them to the experiment will added substantial knowledge on species-specific differences in phenotypic responses to physical disturbance.

The experiments on dune species were conducted in a greenhouse under controlled conditions. The advantage of such experiments is that the greenhouse serves as a shield between nature and the cultivated individual. Fluctuating external factors such as variation in precipitation, ground water level, or nutrients can be well controlled while factor of interest can be treated according to the respective research question. The measured specific plant response is therefore due to a change in the factor of interest and is not superimposed by other influences. However, the controlled conditions in the

greenhouse also can influence the growth form of the individuals. There are multiple studies that compare the results of greenhouse and field experiments. A meta-analysis showed that that lab-grown plants had faster growth rates, higher nitrogen concentrations and different morphology (Poorter et al., 2016). For the recovery of mosses from sand burial, it was shown that the general species responses were the same in the field and in greenhouses but the recovery speed was much slower in the field than in the greenhouse (Martínez & Maun, 1999). Perumal and Maun (2005) compared the ecophysiological responses of dune species to burial under field, greenhouse and growth chamber conditions. They found that the lack of inter- and intraspecific competition of plants grown in single pots leads to smaller canopy height and altered SLA as a response to slower growth and better nutrient availability.

The dune plants in our experiments were not subjected to factors such as wind and salt spray as they would be if growing in their natural environment. From personal observations of the author, pioneer species growing under normal conditions in the dunes of Spiekeroog, have a different habitus than individuals growing in the greenhouse, e.g. they seem to invest more in stem stability.

This implies that greenhouse experiments are a very good way to analyze specific responses and effects, but cannot provide fully satisfying answers on responses and effect in a natural environment where multiple varying biotic and abiotic factors exist. For this reason, it would be an interesting addition to the presented experiments to conduct similar experiments in the natural dunes environment to examine the question: How do dune pioneer species growing in different parts of the dune fields respond to sediment dynamic? Analyzing different species could help to better understand their specific strategies for survival in a dynamic environment and to detect general patterns.

This thesis also studied the effect of trait variation on resistance and resilience of coastal dunes to a sudden wind event in a controlled mesocosm experiment. This experiment gave good insight into the effect of *A. arenaria* communities in comparison to natural mixed communities. A highly desirable development would be to use our findings as a starting point for an experiment in the natural dune system with a greater variety of

communities, to address the question of how different types of vegetation communities and resulting trait variance affect the resistance of the dune to a sudden wind event.

This thesis also studied the effect of functional traits on salt marsh elevation change by analyzing field data. However, we still do not fully understand the complex effects of vegetation on surface elevation change in salt marshes. To better understand this complex process and answer the question how plant functional traits affect sedimentation and erosion over salt marshes an experiment in the greenhouse should be conducted.

In conclusion, this thesis has helped, through a trait-based approach in biogeomorphology, to better understand the interaction between plants and landscape forming processes in coastal dunes and salt marshes. The three following questions and studies as suggested above would further add to our understanding of processes in coastal ecosystems.

Appendix

Dune species germination experiment

Introduction

The germination of seeds of many higher plant species in all major climatic regions depends on a range of environmental factors. Through adaptation, germination is timed to avoid unfavorable weather conditions for plant establishment and reproductive growth (Finch-Savage & Leubner-Metzger, 2006). The most important factors for successful germination are water, temperature and light conditions (Bewley et al., 2013). However, some species have seed dormancy, which prevents intact viable from germination even under favorable conditions. In those species a surrounding structure prevents the embryo from germinating (coat-enhanced dormancy) or the embryo itself is dormant (embryo dormancy) (Bewley, 1997). The dormancy can be broken by different types of stratifications such as cold or moist stratification (Urbanova & Leubner-Metzger, 2016). When seeds are germinating for greenhouse experiments, storage conditions such as moisture content, temperature, and relative humidity are factors influencing and germination subsequent survival (Huang et al., 2003; Kauth & Biber, 2015).

For crop species, optimal storage conditions, favorable germination conditions and respective stratification requirements are mostly well known (Geneve, 1998). However, requirements of non-commercial species are generally poorly understood. For dune species, fragmented knowledge on germination requirements exist but no protocol is available. Fluctuating temperatures support the germination of *Ammophila arenaria* (Van der Putten, 1990). Salinity was shown to have an adverse effect on *Elymus farctus* (El-Katony et al., 2015) but no effect was shown for *Cakile maritima* (Debez et al., 2004). Light was found to have an adverse effect on *C. maritima* (Barbour, 1970) but a positive effect on *A. arenaria* (Van der Putten, 1990) and *Honckenya peploides* (Walmsley & Davy, 1997).

Incomplete knowledge on innate dormancy among dune species and high viability, coupled with stringent germination requirements, is likely to result in poor and erratic germination. To close the knowledge gap, we conducted a germination experiment with four dune species widely distributed in Germany: *A. arenaria*, *C. maritima*, *E. farctus*, and *H. peploides*.

Methods

A. arenaria seeds were ordered from Jeletto seed store (Germany), while all other seeds were collected on the barrier islands Spiekeroog and Langeoog. Only seeds which had fallen off the plant were collected to ensure they were fully ripe. All collected seeds were left to dry for 2 weeks. Storage was at 4°C for 4 months for cold stratification. Half of the seeds were stored in dark, dry conditions in paper bags. The other half were stored in wet sand, imitating the natural conditions during winter months. Half of the seeds from the wet and the dry storage were then soaked in water for 20 minutes This can help the seeds soak up water and potentially initiate germination. The other half of the seeds was left untreated. *C. maritima* seeds received an additional pre-treatment in that they were peeled from the pod. All seeds were placed on paper towels saturated with distilled water and transferred into Petri dishes. A lid prevented the seeds from drying out. Petri dishes were regularly checked and more distilled water was added if necessary. Petri dishes were kept in a heating chamber under a 12 h day/12 h night regime at 25/15 °C (=diurnal) or in dark conditions with constant 25°C (=constant). Overall, this resulted in 8 treatments per species (Figure A.1).

For each treatment 30 seeds were used, resulting in 240 seeds per species. The experiment ran for 40 days. It was stopped then since no new germination had occurred after day 30. Germination was defined as visible extension of the radicle.
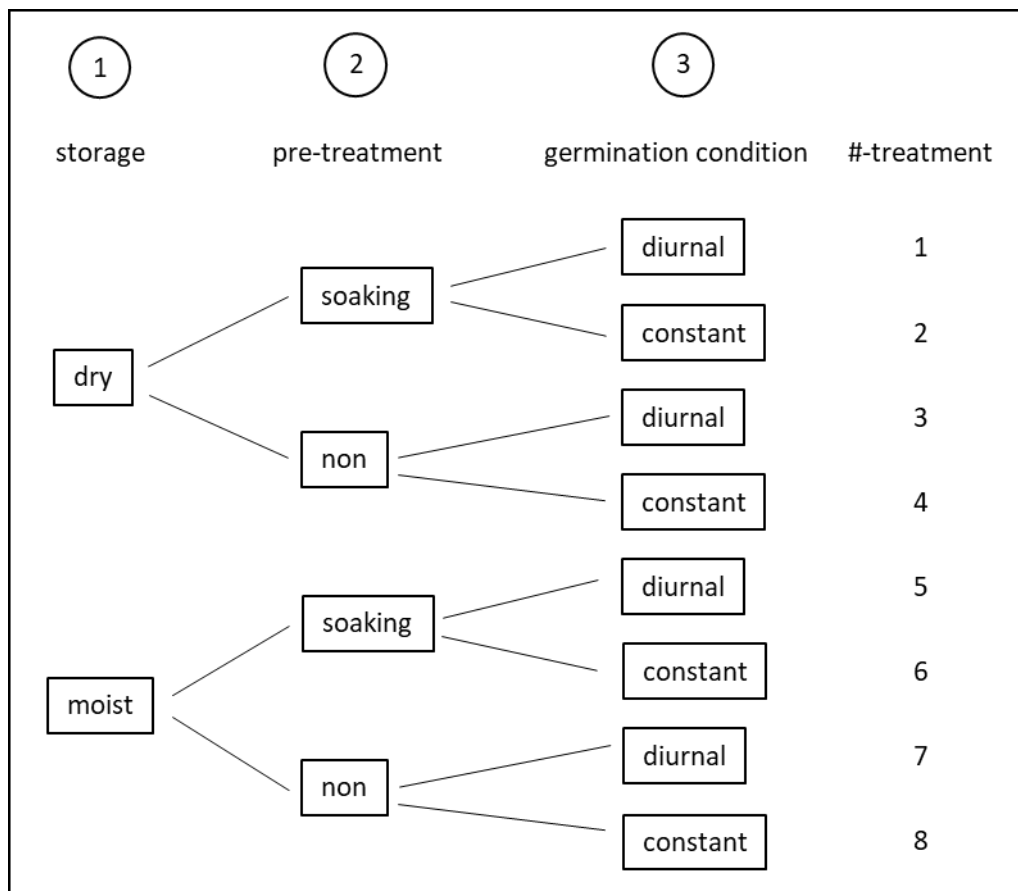
Fig. A.1: Overview of the germination procedure. (1) storage condition; (2) pre-treatment; (3) germination condition. C. maritima seeds were peeled between step (1) and (2).

Results

The germination rate differed among species. *A. arenaria* seeds had a very high germination rate, as did *C. maritima*. The other species, *E. farctus* and *H. peploides,* had rather poor germination rates (Table A.1). In *A. arenaria* the different storage and treatment had no effect on germination rate. In *C. maritima* seeds showed highest germination rates when stored in wet sand, soaked and then kept in diurnal conditions. *E. farctus* had generally low germination rates which slightly improved through wet storage, soaking, and dark conditions. *H. peploides* also had poor germination rates which increased only slightly as a result of dry storage, no pre-treatment and dark germination conditions (Figure A.2).

Table A.1: Overall germination rate of the four tested species.

A. arenaria	C. maritima	E. farctus	H. peploides
97 %	83 %	16 %	5 %
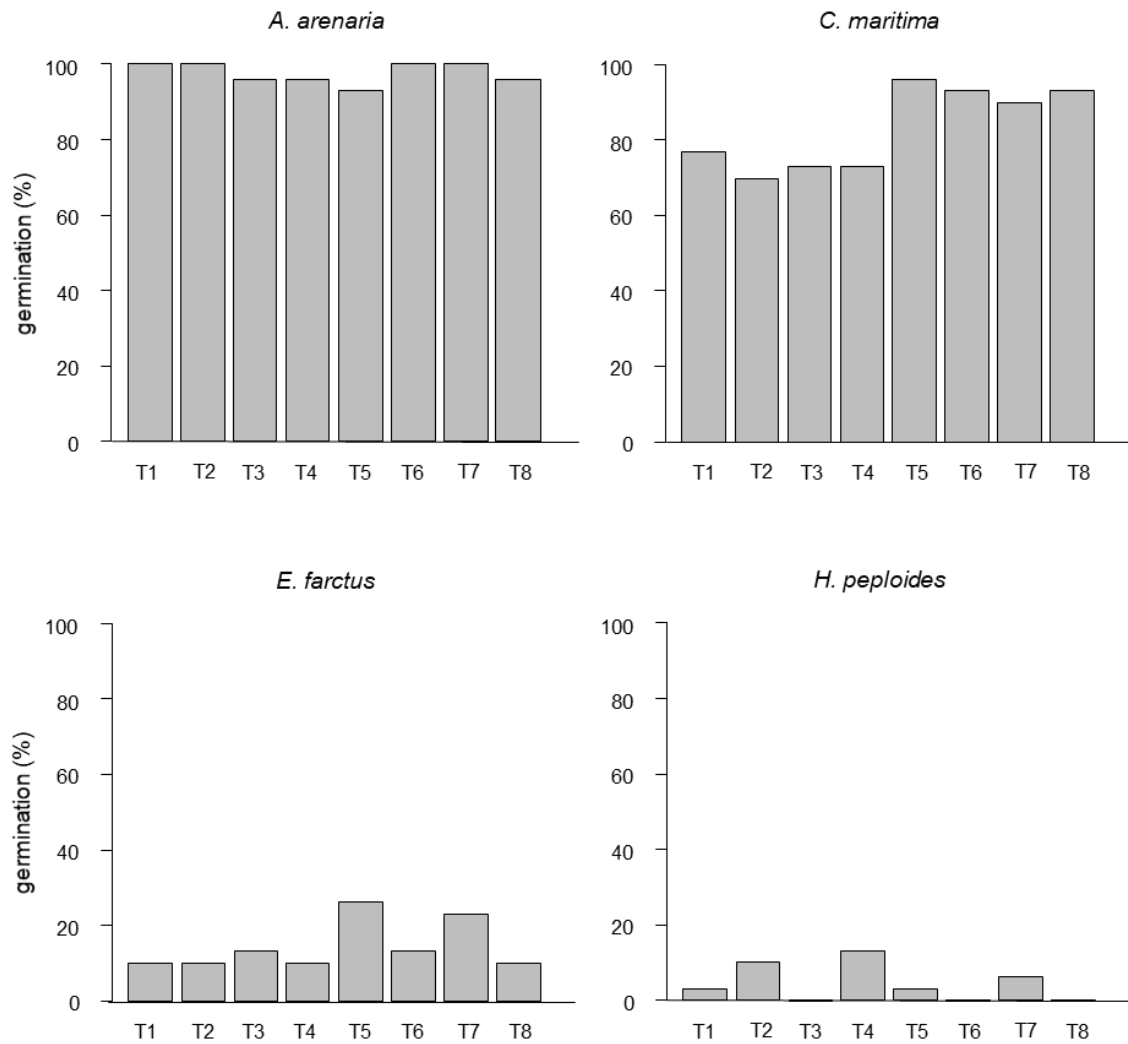
Fig. A.2: Germination rate of A. arenaria, C. maritima, E. farctus, and H. peploides under different treatments T1 to T8. For treatment explanations refer to Figure A.1.

Discussion

The results of this experiment show clear interspecific differences in germination rate. This could show that germination rate is higher in *A. arenaria* and *C. maritima* than in *E. farctus* and *H. peploides*. Species face a trade-off between (a) producing many small seeds each with low rates of seedling survival and (b) producing a few large seeds, each with high rates of seedling survival (Moles & Leishman, 2008). This trade-off also relates to germination success, and is supported by our findings. The large *C. maritima* seeds had a higher germination rate than the small *E. farctus* and *H. peploides* seeds. The very high germination success of *A. arenaria* cannot be compared with the other species since *A. arenaria* seeds were ordered from a seed store where species are cultivated according to high germination rates, while the other seeds were collected from the natural dunes. The results could also indicate that we did not use the optimal conditions for *E. farctus* and *H. peploides* seeds to germinate.

Understanding these interspecific germination requirements is of high value for both the theoretical perspective, which includes the identification of traits associated with germination, and for an applied-science perspective, which includes identifying suitable plant species that can easily be cultivated for restoration projects.

References

Abernethy, B., & Rutherfurd, I. D. (2001). The distribution and strength of riparian tree roots in relation to riverbank reinforcement. *Hydrological Processes, 15*(1), 63-79.

Abràmoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International, 11*(7), 36-42.

Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs, 74*(1), 25-44.

Adam, P. (1990). *Saltmarsh ecology*. Cambridge, UK: Cambridge University Press.

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters, 16*(10), 1294-1306.

Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics, 13*(3), 217-225.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Douzet, R., Aubert, S., & Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Functional Ecology, 24*(6), 1192-1201.

Allgaier, A. (2008). Aeolian sand transport and vegetation cover. In S.-W. Breckler, A. Yair & M. Vest (Eds.), *Arid dune ecosystems* (pp. 211-224). Heidelberg, Germany: Springer.

Andersen, T. J., Svinth, S., & Pejrup, M. (2011). Temporal variation of accumulation rates on a natural salt marsh in the 20th century — the impact of sea level rise and increased inundation frequency. *Marine Geology, 279*(1-4), 178-187.

Anderson, M. G., & Richards, K. S. (1987). *Slope stability: geotechnical engineering and geomorphology*. Chichester, USA: John Wiley & Sons.

Andresen, H., Bakker, J. P., Brongers, M., Heydemann, B., & Irmler, U. (1990). Long-term changes of salt marsh communities by cattle grazing. *Vegetatio, 89*(2), 137-148.

Arens, S. M. (1996). Patterns of sand transport on vegetated foredunes. *Geomorphology, 17*(4), 339-350.

Austin, M. P. (1986). The theoretical basis of vegetation science. *Trends in Ecology & Evolution, 1*(6), 161-164.

Baastrup-Spohr, L., Sand-Jensen, K., Nicolajsen, S. V., & Bruun, H. H. (2015). From soaking wet to bone dry: predicting plant community composition along a steep hydrological gradient. *Journal of Vegetation Science, 26*(4), 619-630.

Baldwin, K. A., & Maun, M. A. (1983). Microenvironment of Lake Huron sand dunes. *Canadian Journal of Botany, 61*(1), 241-255.

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. *Journal of Ecology, 102*(3), 700-708.

Balke, T., Klaassen, P. C., Garbutt, A., van der Wal, D., Herman, P. M. J., & Bouma, T. J. (2012). Conditional outcome of ecosystem engineering: a case study on

tussocks of the salt marsh pioneer Spartina anglica. *Geomorphology, 153-154*, 232-238.

Balke, T., Stock, M., Jensen, K., Bouma, T. J., & Kleyer, M. (2016). A global analysis of the seaward salt marsh extent: the importance of tidal range. *Water Resources Research*.

Baptist, M. J. (2001). *Review on biogeomorphology in rivers: processes and scales*. Delft, Netherlands: Delft University of Technology.

Barbier, E. B. (2015). Valuing the storm protection service of estuarine and coastal ecosystems. *Ecosystem Services, 11*, 32-38.

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.

Barbour, M. G. (1970). Germination and early growth of the strand plant Cakile maritima. *Bulletin of the Torrey Botanical Club, 97*, 13-22.

Barbour, M. G., De Jong, T. M., & Pavlik, B. M. (1985). Marine beach and dune plant communities *Physiological ecology of North American plant communities* (pp. 296-322): Springer.

Barckhausen, J. (1969). Entstehung und Entwicklung der Insel Langeoog. Beitrag zur Quartärgeologie und -paläogeographie eines ostfriesischen Küstenabschnittes. *Oldenburger Jahrbuch, 68*, 239-281.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1-48.

Bauer, B. O., Davidson-Arnott, R. G. D., Hesp, P. A., Namikas, S. L., Ollerhead, J., & Walker, I. J. (2009). Aeolian sediment transport on a beach: Surface moisture, wind fetch, and mean transport. *Geomorphology, 105*(1-2), 106-116.

Baustian, J. J., Mendelssohn, I. A., & Hester, M. W. (2012). Vegetation's importance in regulating surface elevation in a coastal salt marsh facing elevated rates of sea level rise. *Global Change Biology, 18*(11), 3377-3382.

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

Behre, K.-E. (2007). A new Holocene sea-level curve for the southern North Sea. *Boreas, 36*(1), 82-102.

Behre, K.-E. (2008). *Landschaftsgeschichte Norddeutschlands: Umwelt und Siedlung von der Steinzeit bis zur Gegenwart*. Kiel, Germany: Wachholtz Verlag.

Belyea, L. R., & Lancaster, J. (1999). Assembly rules within a contingent ecology. *Oikos, 86*(3), 402-416.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., et al. (2003). Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment, 32*(6), 389-396.

Berendse, F., van Ruijven, J., Jongejans, E., & Keesstra, S. (2015). Loss of plant species diversity reduces soil erosion resistance. *Ecosystems, 18*(5), 881-888.

Bewley, J. D. (1997). Seed germination and dormancy. *The Plant Cell, 9*(7), 1055-1066.

Bewley, J. D., Bradford, K. J., Hilhorst, H. W., & Nonogaki, H. (2013). Environmental regulation of dormancy and germination *Seeds* (pp. 299-339). New York, USA: Springer.

Biel, R. G., Hacker, S. D., Ruggiero, P., Cohn, N., & Seabloom, E. W. (2017). Coastal protection and conservation on sandy beaches and dunes: context-dependent tradeoffs in ecosystem service supply. *Ecosphere, 8*(4), e01791.

Bird, E. C. F. (1985). *Coastline changes. A global review*. Chichester, USA: John Wiley and Sons.

Bittermann, K., Rahmstorf, S., Kopp, R. E., & Kemp, A. C. (2017). Global mean sea-level rise in a world agreed upon in Paris. *Environmental Research Letters, 12*(12), 124010.

Bitton, M. C. A., & Hesp, P. A. (2013). Vegetation dynamics on eroding to accreting beach-foredune systems, Florida panhandle. *Earth Surface Processes and Landforms, 38*(12), 1472-1480.

Bleninger, T., Fenton, J. D., & Zentgraf, R. (2006). *One-dimensional flow modelling and a case study of the River Rhine.* Paper presented at the River Flow 2006, Proc. Int. Conf. on Fluvial Hydraulics.

Blom, C. W. P. M., & Voesenek, L. A. C. J. (1996). Flooding: the survival strategies of plants. *Trends in Ecology & Evolution, 11*(7), 290-295.

Bochet, E., Poesen, J., & Rubio, J. L. (2000). Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes. *Earth Surface Processes and Landforms, 25*(8), 847-867.

Bockelmann, A.-C., Bakker, J. P., Neuhaus, R., & Lage, J. (2002). The relation between vegetation zonation, elevation and inundation frequency in a Wadden Sea salt marsh. *Aquatic Botany, 73*(3), 211-221.

Boggs, S. (2011). *Principles of sedimentology and stratigraphy* (5th ed.). New Jersey, USA: Pearson Prentice Hall.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., et al. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution, 26*(4), 183-192.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., et al. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist, 161*(1), 1-28.

Boorman, L. A., Garbutt, A., & Barratt, D. (1998). The role of vegetation in determining patterns of the accretion of salt marsh sediment. *Geological Society, London, Special Publications, 139*(1), 389-399.

Borchert, S. M., Osland, M. J., Enwright, N. M., & Griffith, K. T. (2018). Coastal wetland adaptation to sea level rise: quantifying potential for landward migration and coastal squeeze. *Journal of Applied Ecology, 55*, 2876-2887.

Borsje, B. W., van Wesenbeeck, B. K., Dekker, F., Paalvast, P., Bouma, T. J., van Katwijk, M. M., et al. (2011). How ecological engineering can serve in coastal protection. *Ecological Engineering, 37*(2), 113-122.

Bouma, T., De Vries, M., Low, E., Peralta, G., Tánczos, I. v., van de Koppel, J., et al. (2005). Trade-offs related to ecosystem engineering: A case study on stiffness of emerging macrophytes. *Ecology, 86*(8), 2187-2199.

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

Bouma, T. J., Koutstaal, B. P., Van Dongen, M., & Nielsen, K. L. (2001). Coping with low nutrient availability and inundation: root growth responses of three halophytic grass species from different elevations along a flooding gradient. *Oecologia, 126*(4), 472-481.

Bouma, T. J., Van Belzen, J., Balke, T., Zhu, Z., Airoldi, L., Blight, A. J., et al. (2014). Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. *Coastal Engineering, 87*, 147-157.

Brantley, S. T., Bissett, S. N., Young, D. R., Wolner, C. W., & Moore, L. J. (2014). Barrier island morphology and sediment characteristics affect the recovery of dune building grasses following storm-induced overwash. *Plos One, 9*(8), e104747.

Breza, L. C., Souza, L., Sanders, N. J., & Classen, A. T. (2012). Within and between population variation in plant traits predicts ecosystem functions associated with a dominant plant species. *Ecology and Evolution, 2*(6), 1151-1161.

Brinkman, R. M. (2006). *Wave attenuation in mangrove forests: an investigation through field and theoretical studies. Ph.D. Thesis.* James Cook University, North Queensland, Australia.

Brown, S. L. (1998). Sedimentation on a Humber saltmarsh. *Geological Society, 139*(1), 69-83.

Brown, S. L., Warman, E. A., McGrorty, S., Yates, M., Pakeman, R. J., Boorman, L. A., et al. (1999). Sediment fluxes in intertidal biotopes: BIOTA II. *Marine Pollution Bulletin, 37*(3), 173-181.

Buckley, R. (1987). The effect of sparse vegetation on the transport of dune sand by wind. *Nature, 325*(6103), 426-428.

Burri, K., Gromke, C., Lehning, M., & Graf, F. (2011). Aeolian sediment transport over vegetation canopies: a wind tunnel study with live plants. *Aeolian Research, 3*(2), 205-213.

Burylo, M., Dutoit, T., & Rey, F. (2014). Species traits as practical tools for ecological restoration of marly eroded lands. *Restoration Ecology, 22*(5), 633-640.

Cabaço, S., & Santos, R. (2007). Effects of burial and erosion on the seagrass Zostera noltii. *Journal of Experimental Marine Biology and Ecology, 340*(2), 204-212.

Cabaço, S., Santos, R., & Duarte, C. M. (2008). The impact of sediment burial and erosion on seagrasses: a review. *Estuarine, Coastal and Shelf Science, 79*(3), 354-366.

Cadol, D., Engelhardt, K., Elmore, A., & Sanders, G. (2014). Elevation-dependent surface elevation gain in a tidal freshwater marsh and implications for marsh persistence. *Limnology and Oceanography, 59*(3), 1065-1080.

Cahoon, D. R., & Reed, D. J. (1995). Relationships among marsh surface topography, hydroperiod, and soil accretion in a deteriorating Louisiana salt marsh. *Journal of Coastal Research, 11*(2), 357-369.

Carr, J., D'odorico, P., McGlathery, K., & Wiberg, P. (2010). Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with

sediment resuspension and light attenuation. *Journal of Geophysical Research: Biogeosciences, 115*, G03011.

Chang, T. S., Flemming, B. W., Tilch, E., Bartholomä, A., & Wöstmann, R. (2006). Late Holocene stratigraphic evolution of a back-barrier tidal basin in the East Frisian Wadden Sea, southern North Sea: transgressive deposition and its preservation potential. *Facies, 52*(3), 329-340.

Chapman, V. J. (1960). *Salt marshes and salt deserts of the world*. London, UK: Leonard Hill.

Charbonneau, B. R., Wnek, J. P., Langley, J. A., Lee, G., & Balsamo, R. A. (2016). Above vs. belowground plant biomass along a barrier island: implications for dune stabilization. *Journal of Environmental Management, 182*, 126-133.

Chen, X., Zhang, X., Church, J. A., Watson, C. S., King, M. A., Monselesan, D., et al. (2017). The increasing rate of global mean sea-level rise during 1993–2014. *Nature Climate Change, 7*(7), 492-497.

Cheng, H., Wang, Y.-S., Fei, J., Jiang, Z.-Y., & Ye, Z.-H. (2015). Differences in root aeration, iron plaque formation and waterlogging tolerance in six mangroves along a continues tidal gradient. *Ecotoxicology, 24*(7-8), 1659-1667.

Cheplick, G. P., & White, T. P. (2002). Saltwater spray as an agent of natural selection: no evidence of local adaptation within a coastal population of Triplasis purpurea (Poaceae). *American Journal of Botany, 89*(4), 623-631.

Chmura, G. L., Coffey, A., & Crago, R. (2001). Variation in surface sediment deposition on salt marshes in the Bay of Fundy. *Journal of Coastal Research, 17*(1), 221-227.

Chow, V. T. (1959). *Open-channel hydraulics*. New York, USA: McGraw-Hill New York.

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.

Church, J. A., Clark, P. U., Cazenave, A., Gregory, J. M., Jevrejeva, S., Levermann, A., et al. (2013). Sea level change. In T. F. Stocker, D. Qin, G. K. Plattner & M. Tignor (Eds.), *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Church, J. A., Clark, P. U., Cazenave, A., Gregory, J. M., Jevrejeva, S., Levermann, A., et al. (2013). Sea-level rise by 2100. *Science, 342*(6165), 1445-1447.

Ciccarelli, D. (2015). Mediterranean coastal dune vegetation: are disturbance and stress the key selective forces that drive the psammophilous succession? *Estuarine, Coastal and Shelf Science, 165*, 247-253.

Colmer, T. D. (2002). Aerenchyma and an inducible barrier to radial oxygen loss facilitate root aeration in upland, paddy and deep-water rice (Oryza sativa L.). *Annals of Botany, 91*(2), 301-309.

Common Wadden Sea Secretariat. (2010). *Wadden Sea Plan 2010.* Paper presented at the Eleventh Trilateral Governmental Conference on the Protection of the Wadden Sea. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Coombes, M. A., Naylor, L. A., Viles, H. A., & Thompson, R. C. (2013). Bioprotection and disturbance: seaweed, microclimatic stability and conditions for mechanical weathering in the intertidal zone. *Geomorphology, 202*, 4-14.

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. *Aquatic Botany, 53*(3-4), 187-198.

Cordazzo, C. V. (2002). Effect of seed mass on germination and growth in three dominant species in southern Brazilian coastal dunes. *Brazilian Journal of Biology, 62*(3), 427-435.

Cordlandwehr, V., Meredith, R. L., Ozinga, W. A., Bekker, R. M., Groenendael, J. M., & Bakker, J. P. (2013). Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology, 101*(3), 662-670.

Corenblit, D., Baas, A., Balke, T., Bouma, T. J., Fromard, F., Garófano-Gómez, V., et al. (2015). Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces world-wide. *Global Ecology and Biogeography, 24*(12), 1363-1376.

Corenblit, D., Baas, A. C. W., Bornette, G., Darrozes, J., Delmotte, S., Francis, R. A., et al. (2011). Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews, 106*(3-4), 307-331.

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs, 79*(1), 109-126.

Coumou, D., & Rahmstorf, S. (2012). A decade of weather extremes. *Nature Climate Change, 2*(7), 491-496.

Cowell, P. J., Stive, M. J. F., Niedoroda, A. W., de Vriend, H. J., Swift, D. J. P., Kaminsky, G. M., et al. (2003). The coastal-tract (part 1): a conceptual approach to aggregated modeling of low-order coastal change. *Journal of Coastal Research, 19*, 812-827.

Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. Part I.-Geographical relations of the dune floras. *Botanical Gazette, 27*(2), 95-117.

Craft, C., Clough, J., Ehman, J., Joye, S., Park, R., Pennings, S., et al. (2009). Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. *Frontiers in Ecology and the Environment, 7*(2), 73-78.

Crain, C. M., Silliman, B. R., Bertness, S. L., & Bertness, M. D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology, 85*(9), 2539-2549.

Crispo, E. (2008). Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *Journal of Evolutionary Biology, 21*(6), 1460-1469.

Crutsinger, G. M., Strauss, S. Y., & Rudgers, J. A. (2010). Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. *Ecology, 91*(4), 1237-1243.

Dangendorf, S., Rybski, D., Mudersbach, C., Müller, A., Kaufmann, E., Zorita, E., et al. (2014). Evidence for long-term memory in sea level. *Geophysical Research Letters, 41*(15), 5530-5537.

Danielsen, F., Sørensen, M. K., Olwig, M. F., Selvam, V., Parish, F., Burgess, N. D., et al. (2005). The Asian tsunami: a protective role for coastal vegetation. *Science, 310*(5748), 643-643.

Darwin, C. (1859). *On the origin of species*. London, UK: John Murray.

Davidson-Arnott, R. G. D. (2005). Conceptual model of the effects of sea level rise on sandy coasts. *Journal of Coastal Research, 21*(6), 1166-1172.

Davidson-Arnott, R. G. D., MacQuarrie, K., & Aagaard, T. (2005). The effect of wind gusts, moisture content and fetch length on sand transport on a beach. *Geomorphology, 68*(1-2), 115-129.

Davidson-Arnott, R. G. D., Bauer, B. O., Walker, I. J., Hesp, P. A., Ollerhead, J., & Chapman, C. (2012). High-frequency sediment transport responses on a vegetated foredune. *Earth Surface Processes and Landforms, 37*(11), 1227-1241.

Davidson, K. E., Fowler, M. S., Skov, M. W., Doerr, S. H., Beaumont, N., & Griffin, J. N. (2017). Livestock grazing alters multiple ecosystem properties and services in salt marshes: a meta-analysis. *Journal of Applied Ecology, 54*(5), 1395-1405.

De Baets, S., Poesen, J., Knapen, A., & Galindo, P. (2007). Impact of root architecture on the erosion-reducing potential of roots during concentrated flow. *Earth Surface Processes and Landforms, 32*(9), 1323-1345.

De Baets, S., Poesen, J., Reubens, B., Muys, d. B., De Baerdemaeker, J., & Meersmans, J. (2009). Methodological framework to select plant species for controlling rill and gully erosion: application to a Mediterranean ecosystem. *Earth Surface Processes and Landforms, 34*(10), 1374-1392.

De Baets, S., Poesen, J., Reubens, B., Wemans, K., De Baerdemaeker, J., & Muys, B. (2008). Root tensile strength and root distribution of typical Mediterranean plant species and their contribution to soil shear strength. *Plant and Soil, 305*(1-2), 207-226.

de Groot, A. V., Janssen, G. M., Isermann, M., Stock, M., Glahn, M., Arens, B., et al. (2017). Beaches and dunes. In S. Kloeppr (Ed.), *Wadden Sea Quality Status Report 2017* (pp. 1-38). Wilhelmshaven, Germany Common Wadden Sea Secretariat.

de Groot, A. V., Oost, A. P., Veeneklaas, R. M., Lammerts, E. J., van Duin, W. E., & van Wesenbeeck, B. K. (2016). Tales of island tails: biogeomorphic development and management of barrier islands. *Journal of Coastal Conservation, 21*(3), 409-419.

De Winter, R. C., & Ruessink, B. G. (2017). Sensitivity analysis of climate change impacts on dune erosion: case study for the Dutch Holland coast. *Climatic Change, 141*(4), 685-701.

Debez, A., Hamed, K. B., Grignon, C., & Abdelly, C. (2004). Salinity effects on germination, growth, and seed production of the halophyte Cakile maritima. *Plant and Soil, 262*(1-2), 179-189.

Dech, J. P., & Maun, M. A. (2005). Zonation of vegetation along a burial gradient on the leeward slopes of Lake Huron sand dunes. *Canadian Journal of Botany, 83*(2), 227-236.

Deng, Z., An, S., Zhao, C., Chen, L., Zhou, C., Zhi, Y., et al. (2008). Sediment burial stimulates the growth and propagule production of Spartina alterniflora Loisel. *Estuarine, Coastal and Shelf Science, 76*(4), 818-826.

Díaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science, 8*(4), 463-474.

Díaz, S., Cabido, M., & Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. In E. Weiher & J. P. Keddy (Eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats* (pp. 338-362). Cambridge, UK: Cambridge University Press.

Diaz, S., Lavorel, S., McIntyre, S. U. E., Falczuk, V., Casanoves, F., Milchunas, D. G., et al. (2007). Plant trait responses to grazing – a global synthesis. *Global Change Biology, 13*(2), 313-341.

Doebeli, M. (1996). Quantitative genetics and population dynamics. *Evolution, 50*(2), 532-546.

Dong, Z., Gao, S., & Fryrear, D. W. (2001). Drag coefficients, roughness length and zero-plane displacement height as disturbed by artificial standing vegetation. *Journal of Arid Environments, 49*(3), 485-505.

Donnelly, J. P., & Bertness, M. D. (2001). Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. *Proceedings of the National Academy of Sciences, 98*(25), 14218-14223.

Doody, J. P. (2004). 'Coastal squeeze' – an historical perspective. *Journal of Coastal Conservation, 10*(1), 129-138.

Dronkers, J., & Stojanovic, T. (2016). Socio-economic impacts — coastal management and governance. In M. Quante & F. Colijn (Eds.), *North sea region climate change assessment. Regional climate studies* (pp. 475-488). Cham, Germany: Springer.

Duckworth, J. C., Kent, M., & Ramsay, P. M. (2000). Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography, 24*(4), 515-542.

Dupont, S., Bergametti, G., & Simoëns, S. (2014). Modeling aeolian erosion in presence of vegetation. *Journal of Geophysical Research: Earth Surface, 119*(2), 168-187.

Durán, O., & Moore, L. J. (2013). Vegetation controls on the maximum size of coastal dunes. *Proceedings of the National Academy of Sciences, 110*(43), 17217-17222.

El-Katony, T. M., Khedr, A.-H. A.-F., & Soliman, N. G. (2015). Nutrients alleviate the deleterious effect of salinity on germination and early seedling growth of the psammophytic grass Elymus farctus. *Botany, 93*(9), 559-571.

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

Ellenberg, H., & Mueller-Dombois, D. (1967). A key to Raunkiær plant life forms with revised subdivisions. *Berichte des Geobotanischen Institutes der Eidgenössischen Technischen Hochschule, Stiftung Rübel, 37*, 56-73.

Elschot, K., Bouma, T. J., Temmerman, S., & Bakker, J. P. (2013). Effects of long-term grazing on sediment deposition and salt-marsh accretion rates. *Estuarine, Coastal and Shelf Science, 133*, 109-115.

Elton, C. S. (1927). *Animal ecology*. London, UK: Sidgwick and Jackson.

Emanuel, K. (2005). Increasing destructiveness of tropical cyclones over the past 30 years. *Nature, 436*(4), 686-688.

Emery, S. M., & Rudgers, J. A. (2014). Biotic and abiotic predictors of ecosystem engineering traits of the dune building grass, Ammophila breviligulata. *Ecosphere, 5*(7), 1-18.

Enquist, B. J., Norberg, J., Bonser, S. P., Violle, C., Webb, C. T., Henderson, A., et al. (2015). Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research, 52*, 249-318.

Esselink, P., Dijkema, K. S., Reents, S., & Hageman, G. (1998). Vertical accretion and profile changes in abandoned man-made tidal marshes in the Dollard estuary, the Netherlands. *Journal of Coastal Research, 14*(2), 570-582.

European Commission. (2007). The EU Floods Directive. from http://ec.europa.eu/environment/water/flood_risk/

European Commission. (2013). EU Climate Change Adaptation Strategy. from http://ec.europa.eu/clima/policies/adaptation/what/documentation_en.htm

Everard, M., Jones, L., & Watts, B. (2010). Have we neglected the societal importance of sand dunes? An ecosystem services perspective. *Aquatic Conservation: Marine and Freshwater Ecosystems, 20*(4), 476-487.

Eviner, V. T. (2004). Plant traits that influence ecosystem processes vary independently among species. *Ecology, 85*(8), 2215-2229.

Fagherazzi, S., Kirwan, M. L., Mudd, S. M., Guntenspergen, G. R., Temmerman, S., D'Alpaos, A., et al. (2012). Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. *Reviews of Geophysics, 50*(1), RG1002.

Fariña, J. M., He, Q., Silliman, B. R., & Bertness, M. D. (2018). Biogeography of salt marsh plant zonation on the Pacific coast of South America. *Journal of Biogeography, 45*(1), 238-247.

Feagin, R. A., Figlus, J., Zinnert, J. C., Sigren, J., Martínez, M. L., Silva, R., et al. (2015). Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Frontiers in Ecology and the Environment, 13*(4), 203-210.

Feagin, R. A., Furman, M., Salgado, K., Martinez, M. L., Innocenti, R. A., Eubanks, K., et al. (2019). The role of beach and sand dune vegetation in mediating wave run up erosion. *Estuarine, Coastal and Shelf Science, 219*, 97-106.

Feagin, R. A., Lozada-Bernard, S. M., Ravens, T. M., Möller, I., Yeager, K. M., & Baird, A. H. (2009). Does vegetation prevent wave erosion of salt marsh edges? *Proceedings of the National Academy of Sciences, 106*(25), 10109-10113.

Feagin, R. A., Sherman, D. J., & Grant, W. E. (2005). Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment, 3*(7), 359-364.

Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist, 171*(3), 501-523.

Finnigan, J. (2000). Turbulence in plant canopies. *Annual Review of Fluid Mechanics, 32*(1), 519-571.

Flowers, T. J., & Colmer, T. D. (2008). Salinity tolerance in halophytes. *New Phytologist, 179*(4), 945-963.

Fonseca, C. R., Overton, J. M., Collins, B., & Westoby, M. (2000). Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology, 88*(6), 964-977.

Fox, G. A., & Kendall, B. E. (2002). Demographic stochasticity and the variance reduction effect. *Ecology, 83*(7), 1928-1934.

Fox, J. (2016). *Using the R Commander: A Point-and-click Interface for R*. Boca Raton, USA: Chapman and Hall/CRC.

Fox, J., & Weisberg, S. (2011). An R companion to applied regression (2 ed.). Thousand Oaks, USA: Sage.

Francalanci, S., Bendoni, M., Rinaldi, M., & Solari, L. (2013). Ecomorphodynamic evolution of salt marshes: Experimental observations of bank retreat processes. *Geomorphology, 195*, 53-65.

French, J. (2006). Tidal marsh sedimentation and resilience to environmental change: exploratory modelling of tidal, sea-level and sediment supply forcing in predominantly allochthonous systems. *Marine Geology, 235*(1-4), 119-136.

Fridley, J. D., & Grime, J. P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology, 91*(8), 2272-2283.

Fridley, J. D., Grime, J. P., & Bilton, M. (2007). Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *Journal of Ecology, 95*(5), 908-915.

Frosini, S., Lardicci, C., & Balestri, E. (2012). Global change and response of coastal dune plants to the combined effects of increased sand accretion (burial) and nutrient availability. *Plos One, 7*(10), e47561.

Funk, R., & Engel, W. (2015). Investigations with a field wind tunnel to estimate the wind erosion risk of row crops. *Soil and Tillage Research, 145*, 224-232.

García-Mora, M. R., Gallego-Fernández, J. B., & García-Novo, F. (1999). Plant functional types in coastal foredunes in relation to environmental stress and disturbance. *Journal of Vegetation Science, 10*(1), 27-34.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., et al. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology, 85*(9), 2630-2637.

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., et al. (2001). Consistency of species ranking based on functional leaf traits. *New Phytologist, 152*(1), 69-83.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., et al. (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. *Annals of Botany, 99*(5), 967-985.

Garnier, E., & Navas, M.-L. (2012). A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development, 32*(2), 365-399.

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

Gattuso, J.-P., Frankignoulle, M., & Wollast, R. (1998). Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics, 29*(1), 405-434.

Geneve, R. L. (1998). Seed dormancy in commercial vegetable and flower species. *Seed Technology*, 236-250.

Gilbert, M. E., & Ripley, B. S. (2008). Biomass reallocation and the mobilization of leaf resources support dune plant growth after sand burial. *Physiologia Plantarum, 134*(3), 464-472.

Gillies, J. A., Nickling, W. G., & King, J. (2002). Drag coefficient and plant form response to wind speed in three plant species: Burning Bush (Euonymus alatus), Colorado Blue Spruce (Picea pungens glauca.), and Fountain Grass (Pennisetum setaceum). *Journal of Geophysical Research, 107*(D24), 4760.

Gillies, J. A., Nield, J. M., & Nickling, W. G. (2014). Wind speed and sediment transport recovery in the lee of a vegetated and denuded nebkha within a nebkha dune field. *Aeolian Research, 12*, 135-141.

Gómez-Pina, G., Muñoz-Pérez, J. J., Ramírez, J. L., & Ley, C. (2002). Sand dune management problems and techniques, Spain. *Journal of Coastal Research, 36*(sp1), 325-332.

Gondard, H., Jauffret, S., Aronson, J., & Lavorel, S. (2003). Plant functional types: a promising tool for management and restoration of degraded lands. *Applied Vegetation Science, 6*(2), 223-234.

Grabemann, I., & Weisse, R. (2008). Climate change impact on extreme wave conditions in the North Sea: an ensemble study. *Ocean Dynamics, 58*(3-4), 199-212.

Gray, D. H., & Barker, D. (2004). Root-soil mechanics and interactions. In S. Benett & A. Simon (Eds.), *Riparian vegetation and fluvial geomorphology* (pp. 113-123). New York, USA: American Geophyisical Union.

Greenway, H., & Munns, R. (1980). Mechanisms of salt tolerance in nonhalophytes. *Annual Review of Plant Physiology, 31*(1), 149-190.

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature, 250*, 26-31.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist, 111*(982), 1169-1194.

Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, UK: John Wiley & Sons.

Grimm, V., & Wissel, C. (1997). Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia, 109*(3), 323-334.

Grömping, U. (2006). Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software, 17*(1), 1-27.

Grubb, P. J. (1985). Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. In J. White (Ed.), *The population structure of vegetation* (pp. 595-621). Dordrecht, Netherlands: Springer.

Guerrero-Campo, J., Palacio, S., & Montserrat-Martí, G. (2008). Plant traits enabling survival in Mediterranean badlands in northeastern Spain suffering from soil erosion. *Journal of Vegetation Science, 19*(4), 457-464.

Gutiérrez, J. L., & Jones, C. G. (Eds.). (2008) Encyclopedia of Life Sciences. Chichester, UK: John Wiley and Sons Ltd.

Gutiérrez, J. L., Jones, C. G., Byers, J. E., Arkema, K. K., Berkenbusch, K., Commito, J. A., et al. (2011). Physical ecosystem engineers and the functioning of estuaries and coasts. In E. Wolanski & D. S. McLusky (Eds.), *Treatise on estuarine and coastal science* (pp. 53-81). Waltham, USA: Academic.

Gyssels, G., & Poesen, J. (2003). The importance of plant root characteristics in controlling concentrated flow erosion rates. *Earth Surface Grocesses and Landforms, 28*(4), 371-384.

Gyssels, G., Poesen, J., Bochet, E., & Li, Y. (2005). Impact of plant roots on the resistance of soils to erosion by water: a review. *Progress in Physical Geography, 29*(2), 189-217.

Hache, I., Karius, V., Gutkuhn, J., & von Eynatten, H. (2019). The development and application of an autonomous working turbidity measurement network: Assessing the spatial and temporal distribution of suspended particulate matter on tidal flats in the North Frisian Wadden Sea. *Continental Shelf Research, 176*, 36-50.

Hammill, K., Penman, T., & Bradstock, R. (2016). Responses of resilience traits to gradients of temperature, rainfall and fire frequency in fire-prone, Australian forests: potential consequences of climate change. *Plant Ecology, 217*(6), 725-741.

Hanisch, J. (1980). Neue Meeresspiegeldaten aus dem Raum Wangerooge. *Eiszeitalter und Gegenwart, 30*(22), 221-228.

Hanley, M. E., Hoggart, S. P. G., Simmonds, D. J., Bichot, A., Colangelo, M. A., Bozzeda, F., et al. (2014). Shifting sands? Coastal protection by sand banks, beaches and dunes. *Coastal Engineering, 87*, 136-146.

Harris, A. L., Zinnert, J. C., & Young, D. R. (2017). Differential response of barrier island dune grasses to species interactions and burial. *Plant Ecology, 218*(5), 609-619.

Hart, A. T., Hilton, M. J., Wakes, S. J., & Dickinson, K. J. (2012). The impact of Ammophila arenaria foredune development on downwind aerodynamics and parabolic dune development. *Journal of Coastal Research, 28*(1), 112-122.

Hawke, M. A., & Maun, M. A. (1988). Some aspects of nitrogen, phosphorus, and potassium nutrition of three colonizing beach species. *Canadian Journal of Botany, 66*(8), 1490-1496.

Hay, C. C., Morrow, E., Kopp, R. E., & Mitrovica, J. X. (2015). Probabilistic reanalysis of twentieth-century sea-level rise. *Nature, 517*(7535), 481-484.

Hertling, U. M., & Lubke, R. A. (2000). Assessing the potential for biological invasion - the case of Ammophila arenaria in South Africa. *South African Journal of Science, 96*, 520–526.

Hesp, P. (1983). Morphodynamics of incipient foredunes in New South Wales, Australia. *Developments in Sedimentology, 38*, 325-342.

Hesp, P. (2002). Foredunes and blowouts: initiation, geomorphology and dynamics. *Geomorphology, 48*(1), 245-268.

Hesp, P. A. (1991). Ecological processes and plant adaptations on coastal dunes. *Journal of arid environments, 21*(2), 165-191.

Hieronymus, M., Dieterich, C., Andersson, H., & Hordoir, R. (2018). The effects of mean sea level rise and strengthened winds on extreme sea levels in the Baltic Sea. *Theoretical and Applied Mechanics Letters, 8*(6), 366-371.

Hilton, M., Duncan, M., & Jul, A. (2005). Processes of Ammophila arenaria (marram grass) invasion and indigenous species displacement, Stewart Island, New Zealand. *Journal of Coastal Research, 21*(1), 175-185.

Hilton, M. J. (2006). The loss of New Zealand's active dunes and the spread of marram grass (Ammophila arenaria). *New Zealand Geographer, 62*(2), 105-120.

Hinkel, J., Lincke, D., Vafeidis, A. T., Perrette, M., Nicholls, R. J., Tol, R. S., et al. (2014). Coastal flood damage and adaptation costs under 21st century sea-level rise. *Proceedings of the National Academy of Sciences, 111*(9), 3292-3297.

Hoagland, D. R., & Arnon, D. I. (1950). The water-culture method for growing plants without soil. *California Agricultural Experiment Station Bulletin, 347*, 346-347.

Hong, S. H., & Lee, E. Y. (2016). Restoration of eroded coastal sand dunes using plant and soil-conditioner mixture. *International Biodeterioration & Biodegradation, 113*, 161-168.

Hopfensperger, K. N., & Engelhardt, K. A. (2008). Annual species abundance in a tidal freshwater marsh: germination and survival across an elevational gradient. *Wetlands, 28*(2), 521.

Horton, J. L., & Hart, S. C. (1998). Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology & Evolution, 13*(6), 232-235.

Hoselmann, C., & Streif, H. (2004). Holocene sea-level rise and its effect on the mass balance of coastal deposits. *Quaternary International, 112*(1), 89-103.

Howison, R. A., Olff, H., Steever, R., & Smit, C. (2015). Large herbivores change the direction of interactions within plant communities along a salt marsh stress gradient. *Journal of Vegetation Science, 26*(6), 1159-1170.

Huang, Z., Zhang, X., Zheng, G., & Gutterman, Y. (2003). Influence of light, temperature, salinity and storage on seed germination of Haloxylon ammodendron. *Journal of Arid Environments, 55*(3), 453-464.

Hughes, A. R., Inouye, B. D., Johnson, M. T., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters, 11*(6), 609-623.

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.

Isselin-Nondedeu, F., & Bédécarrats, A. (2007). Influence of alpine plants growing on steep slopes on sediment trapping and transport by runoff. *Catena, 71*(2), 330-339.

Ives, A. R., & Hughes, J. B. (2002). General relationships between species diversity and stability in competitive systems. *The American Naturalist, 159*(4), 388-395.

Jackson, N. L., & Nordstrom, K. F. (1997). Effects of time-dependent moisture content of surface sediments on aeolian transport rates across a beach, Wildwood, New Jersey, USA. *Earth Surface Processes and Landforms: The Journal of the British Geomorphological Group, 22*(7), 611-621.

Jäger, E. J. (2016). *Rothmaler-Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband*. Heidelberg, Germany Springer Spektrum.

Jiao, J., Zou, H., Jia, Y., & Wang, N. (2009). Research progress on the effects of soil erosion on vegetation. *Acta Ecologica Sinica, 29*(2), 85-91.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos 69*, 373-386.

Judd, M. J., Raupach, M. R., & Finnigan, J. J. (1996). A wind tunnel study of turbulent flow around single and multiple windbreaks, part I: velocity fields. *Boundary-Layer Meteorology, 80*(1-2), 127-165.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010). Intraspecific variability and trait-based community assembly. *Journal of Ecology, 98*(5), 1134-1140.

Jungerius, P. D., & Van der Meulen, F. (1988). Erosion processes in a dune landscape along the Dutch coast. *Catena, 15*(3-4), 217-228.

Kachi, N., & Hirose, T. (1983). Limiting nutrients for plant growth in coastal sand dune soils. *The Journal of Ecology, 71*, 937-944.

Kathiresan, K., & Rajendran, N. (2005). Coastal mangrove forests mitigated tsunami. *Estuarine, Coastal and Sshelf Science, 65*(3), 601-606.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., et al. (2011). TRY–a global database of plant traits. *Global Change Biology, 17*(9), 2905-2935.

Kauth, P. J., & Biber, P. D. (2015). Moisture content, temperature, and relative humidity influence seed storage and subsequent survival and germination of Vallisneria americana seeds. *Aquatic Botany, 120*, 297-303.

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters, 7*(12), 1225-1241.

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science, 3*(2), 157-164.

Keijsers, J. G. S., de Groot, A. V., & Riksen, M. J. P. M. (2015). Vegetation and sedimentation on coastal foredunes. *Geomorphology, 228*, 723-734.

Keijsers, J. G. S., Giardino, A., Poortinga, A., Mulder, J. P. M., Riksen, M. J. P. M., & Santinelli, G. (2015). Adaptation strategies to maintain dunes as flexible coastal flood defense in The Netherlands. *Mitigation and Aadaptation Strategies for Global Change, 20*(6), 913-928.

Kent, M., Owen, N. W., Dale, P., Newnham, R. M., & Giles, T. M. (2001). Studies of vegetation burial: a focus for biogeography and biogeomorphology? *Progress in Physical Geography, 25*(4), 455-482.

Kinzig, A. P., Pacala, S. W., & Tilman, D. (2001). *The functional consequences of biodiversity: empirical progress and theoretical extensions* (Vol. 33). Princeton, USA: Princeton University Press.

Kirkman, L. K., Mitchell, R. J., Helton, R. C., & Drew, M. B. (2001). Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany, 88*(11), 2119-2128.

Kirwan, M. L., & Mudd, S. M. (2012). Response of salt-marsh carbon accumulation to climate change. *Nature, 489*, 550-554.

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.

Kleyer, M. (1999). Distribution of plant functional types along gradients of disturbance intensity and resource supply in an agricultural landscape. *Journal of Vegetation science, 10*(5), 697-708.

Kleyer, M., Balke, T., Minden, V., Peppler-Lisbach, C., Schoenmakers, S., Spalke, J., et al. (2014). Mellum: a highly dynamic landscape, though not for plants. In U. Hellwig & M. Stock (Eds.), *Dynamic isalnds in the Wadden Sea, Wadden Sea Ecosystem No. 33* (pp. 29-43). Wilhelmshaven, Germany: Common Wadden Sea Secretariat.

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

Kleyer, M., Trinogga, J., Cebrián-Piqueras, M. A., Trenkamp, A., Fløjgaard, C., Ejrnæs, R., et al. (2019). Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. *Journal of Ecology, 107*(2), 829-842.

Knevel, I. C., Bekker, R. M., Kunzmann, D., Stadler, M., & Thompson, K. (2005). The LEDA traitbase collecting and measuring standards of life-history traits of the Northwest European Flora (pp. 1-173). Groningen, Netherlands: University of Groningen, Community and Conservation Ecology Group.

Kolker, A. S., Kirwan, M. L., Goodbred, S. L., & Cochran, J. K. (2010). Global climate changes recorded in coastal wetland sediments: empirical observations linked to theoretical predictions. *Geophysical Research Letters, 37*(14), L14706.

Körner, C. (2007). The use of 'altitude' in ecological research. *Trends in Ecology & Evolution, 22*(11), 569-574.

Koske, R. E., Gemma, J. N., Corkidi, L., Sigüenza, C., & Rincón, E. (2008). Arbuscular mycorrhizas in coastal dunes. In M. L. Martínez & N. P. Psuty (Eds.), *Coastal Dunes* (pp. 173-187). Heidelberg, Germany: Springer.

Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science, 322*(5901), 580-582.

Kramer, P. J. (1951). Causes of injury to plants resulting from flooding of the soil. *Plant Physiology, 26*(4), 722-736.

Krone, R. B. (1987). A method for simulating historic marsh elevations. In N. C. Kraus (Ed.), *Coastal sediments '87* (pp. 316-323). New York, USA: American Socieety of Civil Engineers.

Lancaster, N., & Baas, A. (1998). Influence of vegetation cover on sand transport by wind: field studies at Owens Lake, California. *Earth Surface Processes and Landforms, 23*(1), 69-82.

Langley, J. A., McKee, K. L., Cahoon, D. R., Cherry, J. A., & Megonigal, J. P. (2009). Elevated CO2 stimulates marsh elevation gain, counterbalancing sea-level rise. *Proceedings of the National Academy of Sciences, 106*(15), 6182-6186.

Langlois, E., Bonis, A., & Bouzillé, J. B. (2001). The response of Puccinellia maritima to burial: a key to understanding its role in salt-marsh dynamics? *Journal of Vegetation Science, 12*(2), 289-297.

Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., et al. (2007). Plant functional types: are we getting any closer to the Holy Grail? In J. G. Canadell, P. D. E & P. L. F (Eds.), *Terrestrial ecosystems in a changing world* (pp. 149-164). Berlin, Germany Springer.

Lavorel, S., & Garnier, É. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology, 16*(5), 545-556.

Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T. D. A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution, 12*(12), 474-478.

Lee, J.-S., Kim, J.-W., Lee, S. H., Myeong, H.-H., Lee, J.-Y., & Cho, J. S. (2016). Zonation and soil factors of salt marsh halophyte communities. *Journal of Ecology and Environment, 40*(1), 1-4.

Lefebvre, A., Thompson, C. E. L., & Amos, C. L. (2010). Influence of Zostera marina canopies on unidirectional flow, hydraulic roughness and sediment movement. *Continental Shelf Research, 30*(16), 1783-1794.

Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist, 156*(5), 534-552.

Lenssen, G. M., Van Duin, W. E., Jak, P., & Rozema, J. (1995). The response of Aster tripolium and Puccinellia maritima to atmospheric carbon dioxide enrichment and their interactions with flooding and salinity. *Aquatic Botany, 50*(2), 181-192.

Lepš, J., de Bello, F., Šmilauer, P., & Doležal, J. (2011). Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography, 34*(5), 856-863.

Levermann, A., Clark, P. U., Marzeion, B., Milne, G. A., Pollard, D., Radic, V., et al. (2013). The multimillennial sea-level commitment of global warming. *Proceedings of the National Academy of Sciences, 110*(34), 13745-13750.

Li, S.-L., Werger, M. J. A., Zuidema, P. A., Yu, F.-H., & Dong, M. (2010). Seedlings of the semi-shrub Artemisia ordosica are resistant to moderate wind denudation and sand burial in Mu Us sandland, China. *Trees, 24*(3), 515-521.

Lienin, P., & Kleyer, M. (2011). Plant leaf economics and reproductive investment are responsive to gradients of land use intensity. *Agriculture, Ecosystems & Environment, 145*(1), 67-76.

Liu, B., Liu, Z., Lü, X., Maestre, F. T., & Wang, L. (2014). Sand burial compensates for the negative effects of erosion on the dune-building shrub Artemisia wudanica. *Plant and Soil, 374*(1-2), 263-273.

Loreau, M., Mouquet, N., & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences, 100*(22), 12765-12770.

Loreau, M., Naeem, S., & Inchausti, P. (2002). *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford, UK: Oxford University Press.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J., Hector, A., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science, 294*(5543), 804-808.

Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., et al. (2004). Rethinking plant community theory. *Oikos, 107*(2), 433-438.

Lüders, K. (1953). Die Entstehung der ostfriesischen Inseln und der Einfluß der Dünenbildung auf den geologischen Aufbau der ostfriesischen Küste. *Probleme der Küstenforschung im Südlichen Nordseegebiet, 5*, 5-15.

MacGillivray, C. W., Grime, J. P., & ISP Team. (1995). Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Functional Ecology, 9*, 640-649.

Maes, J., Barbosa, A., Baranzelli, C., Zulian, G., Silva, F. B., Vandecasteele, I., et al. (2015). More green infrastructure is required to maintain ecosystem services under current trends in land-use change in Europe. *Landscape Ecology, 30*(3), 517-534.

Mangiafico, S. (2016). Summary and analysis of extension program evaluation in R. from http://rcompanion.org/handbook

Mangiafico, S. (2017). Rcompanion: functions to support extension education program evaluation.

Manning, R. (1891). On the flow of water in open channels and pipes. *Transactions of the Institution of Civil Engineers of Ireland 20*, 161-207.

Marani, M., D'Alpaos, A., Lanzoni, S., Carniello, L., & Rinaldo, A. (2010). The importance of being coupled: Stable states and catastrophic shifts in tidal biomorphodynamics. *Journal of Geophysical Research: Earth Surface, 115*, F04004.

Marbà, N., & Duarte, C. M. (1994). Growth response of the seagrass Cymodocea nodosa to experimental burial and erosion. *Marine Ecology Progress Series, 107*, 307-311.

Martínez, M. L., & Maun, M. A. (1999). Responses of dune mosses to experimental burial by sand under natural and greenhouse conditions. *Plant Ecology, 145*(2), 209-219.

Martínez, M. L., Psuty, N. P., & Lubke, R. A. (2008). A perspective on coastal dunes *Coastal dunes* (pp. 3-10). Berlin, Germany: Springer.

Masterman, R., & Ellison, J. C. (2018). Influence of introduced Ammophila arenaria on coastal progradation: assessment by spatial analysis. *Journal of Aquaculture & Marine Biology, 7*(5), 268-273.

Maun, M. A. (1994). Adaptations enhancing survival and establishment of seedlings on coastal dune systems. *Vegetatio, 111*(1), 59-70.

Maun, M. A. (1998). Adaptations of plants to burial in coastal sand dunes. *Canadian Journal of Botany, 76*(5), 713-738.

Maun, M. A. (2008). Burial of plants as a selective force in sand dunes. In M. Martinez & N. Psuty (Eds.), *Coastal dunes: Ecology and conservation* (pp. 119-135). Berlin, Germany: Springer.

Maun, M. A. (2009). *The biology of coastal sand dunes*. Okford, UK: Oxford University Press.

Maun, M. A., Elberling, H., & D'Ulisse, A. (1996). The effects of burial by sand on survival and growth of Pitcher's thistle (Cirsium pitcheri) along Lake Huron. *Journal of Coastal Conservation, 2*(1), 3-12.

Maun, M. A., & Lapierre, J. (1984). The effects of burial by sand on Ammophila breviligulata. *The Journal of Ecology, 72*, 827-839.

Maun, M. A., & Perumal, J. (1999). Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecology Letters, 2*(1), 14-18.

Mayaud, J. R., & Webb, N. P. (2017). Vegetation in drylands: effects on wind flow and aeolian sediment transport. *Land, 6*(3), 64.

Mayaud, J. R., Wiggs, G. F. S., & Bailey, R. M. (2016). Characterizing turbulent wind flow around dryland vegetation. *Earth Surface Processes and Landforms, 41*(10), 1421-1436.

Maze, K. M., & Whalley, R. D. B. (1992). Effects of salt spray and sand burial on Spinifex sericeus R. Br. *Australian Journal of Ecology, 17*(1), 9-19.

McFadden, L., Spencer, T., & Nicholls, R. J. (2007). Broad-scale modelling of coastal wetlands: what is required? *Hydrobiologia, 577*(1), 5-15.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution, 21*(4), 178-185.

McIvor, A. L., Spencer, T., Möller, I., & Spalding, M. (2013). *The response of mangrove soil surface elevation to sea level rise*. Wageningen, Netherlands Cambridge Coastal Research Unit Working Paper 42.

McKee, K. L., Cahoon, D. R., & Feller, I. C. (2007). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography, 16*(5), 545-556.

McKinley, E., Ballinger, R. C., & Beaumont, N. J. (2018). Saltmarshes, ecosystem services, and an evolving policy landscape: A case study of Wales, UK. *Marine Policy, 91*, 1-10.

Meier, D. (2006). *Die Nordseeküste: Geschichte einer Landschaft*. Heide, Germany: Boyens Offset.

Mickovski, S. B., van Beek, L. P. H., & Salin, F. (2005). Uprooting of vetiver uprooting resistance of vetiver grass (Vetiveria zizanioides). *Plant and Soil, 278*(1-2), 33-41.

Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: synthesis*. Washington, USA: Island Press.

Miller, R. M., & Jastrow, J. D. (1990). Hierarchy of root and mycorrhizal fungal interactions with soil aggregation. *Soil Biology and Biochemistry, 22*(5), 579-584.

Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience, 43*(4), 219-224.

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.

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*(3), 387-401.

Minden, V., & Kleyer, M. (2015). Ecosystem multifunctionality of coastal marshes is determined by key plant traits. *Journal of Vegetation Science, 26*(4), 651-662.

Minden, V., Scherber, C., Cebrián Piqueras, M. A., Trinogga, J., Trenkamp, A., Mantilla-Contreras, J., et al. (2016). Consistent drivers of plant biodiversity across managed ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences, 371*(1694), 20150284.

Miselis, J. L., & Lorenzo-Trueba, J. (2017). Natural and human-induced variability in barrier-island response to sea level rise. *Geophysical Research Letters, 44*(23), 11922-11931.

Mitchell, P. J., Veneklaas, E. J., Lambers, H., & Burgess, S. S. O. (2008). Leaf water relations during summer water deficit: differential responses in turgor maintenance and variation in leaf structure among different plant communities in south-western Australia. *Plant, Cell & Environment, 31*(12), 1791-1802.

Mokany, K., & Ash, J. (2008). Are traits measured on pot grown plants representative of those in natural communities? *Journal of Vegetation Science, 19*(1), 119-126.

Moles, A. T., & Leishman, M. R. (2008). The seedling as part of a plant's life history strategy. In M. A. Leck, V. T. Parker & R. L. Simpson (Eds.), *Seedling ecology and evolution* (pp. 217-238). Cambridge, UK: Cambridge University Press.

Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., et al. (2014). Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science, 25*(5), 1167-1180.

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., Van Wesenbeeck, B. K., et al. (2014). Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience, 7*(10), 727-731.

Möller, I., & Spencer, T. (2002). Wave dissipation over macro-tidal saltmarshes: Effects of marsh edge typology and vegetation change. *Journal of Coastal Research, 36*(1), 506-521.

Mommer, L., & Visser, E. J. W. (2005). Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. *Annals of Botany, 96*(4), 581-589.

Morgan, R. P., & Rickson, R. J. (2003). *Slope stabilization and erosion control: a bioengineering approach*. London, UK: Taylor & Francis.

Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., & Cahoon, D. R. (2002). Responses of coastal wetlands to rising sea level. *Ecology, 83*(10), 2869-2877.

Morris, R. L., Konlechner, T. M., Ghisalberti, M., & Swearer, S. E. (2018). From grey to green: efficacy of eco-engineering solutions for nature-based coastal defence. *Global Change Biology, 24*, 1827-1842.

Morton, A. G. (1981). *History of botanical science*. London, UK: Academic Press.

Moskalski, S. M., & Sommerfield, C. K. (2012). Suspended sediment deposition and trapping efficiency in a Delaware salt marsh. *Geomorphology, 139*, 195-204.

Mudd, S. M., D'Alpaos, A., & Morris, J. T. (2010). How does vegetation affect sedimentation on tidal marshes? Investigating particle capture and

hydrodynamic controls on biologically mediated sedimentation. *Journal of Geophysical Research: Earth Surface, 115*, F03029.

Murray, N. J., Clemens, R. S., Phinn, S. R., Possingham, H. P., & Fuller, R. A. (2014). Tracking the rapid loss of tidal wetlands in the Yellow Sea. *Frontiers in Ecology and the Environment, 12*(5), 267-272.

Nationalpark Wattenmeer. (2004). Biotoptypen-Karten In Nationalpark Wattenmeer (Ed.), *2004*.

Nava-López, M. Z., Diemont, S. A., Hall, M., & Ávila-Akerberg, V. (2016). Riparian buffer zone and whole watershed influences on river water quality: implications for ecosystem services near megacities. *Environmental Processes, 3*(2), 277-305.

Navas, M. L., Roumet, C., Bellmann, A., Laurent, G., & Garnier, E. (2010). Suites of plant traits in species from different stages of a Mediterranean secondary succession. *Plant Biology, 12*(1), 183-196.

Naylor, L. A. (2005). The contributions of biogeomorphology to the emerging field of geobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology, 219*(1), 35-51.

Naylor, L. A., Viles, H. A., & Carter, N. E. A. (2002). Biogeomorphology revisited: looking towards the future. *Geomorphology, 47*(1), 3-14.

Nerem, R. S., Beckley, B. D., Fasullo, J. T., Hamlington, B. D., Masters, D., & Mitchum, G. T. (2018). Climate-change–driven accelerated sea-level rise detected in the altimeter era. *Proceedings of the National Academy of Sciences, 115*(9), 2022-2025.

Neubauer, S. C. (2008). Contributions of mineral and organic components to tidal freshwater marsh accretion. *Estuarine, Coastal and Shelf Science, 78*(1), 78-88.

Neubauer, S. C., Anderson, I. C., Constantine, J. A., & Kuehl, S. A. (2002). Sediment deposition and accretion in a mid-Atlantic (USA) tidal freshwater marsh. *Estuarine, Coastal and Shelf Science, 54*(4), 713-727.

Neumann, B., Vafeidis, A. T., Zimmermann, J., & Nicholls, R. J. (2015). Future coastal population growth and exposure to sea-level rise and coastal flooding-a global assessment. *Plos One, 10*(3), e0118571.

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

Neumeier, U. R. S., & Amos, C. L. (2006). The influence of vegetation on turbulence and flow velocities in European salt-marshes. *Sedimentology, 53*(2), 259-277.

Nicholls, R. J., Wong, P. P., Burkett, V., Codignotto, J., Hay, J., McLean, R., et al. (2007). Coastal systems and low-lying areas. In M. Parry, O. Canziani, P. JP, P. van der Linden & C. Hanson (Eds.), *Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change* (pp. 315–356). Cambridge, UK: Cambridge University Press.

Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology, 82*(2), 453-469.

Niinemets, Ü. (2004). Adaptive adjustments to light in foliage and whole-plant characteristics depend on relative age in the perennial herb Leontodon hispidus. *New Phytologist, 162*(3), 683-696.

Nolte, S., Koppenaal, E. C., Esselink, P., Dijkema, K. S., Schuerch, M., De Groot, A. V., et al. (2013). Measuring sedimentation in tidal marshes: a review on methods and their applicability in biogeomorphological studies. *Journal of Coastal Conservation, 17*(3), 301-325.

Nolte, S., Müller, F., Schuerch, M., Wanner, A., Esselink, P., Bakker, J. P., et al. (2013). Does livestock grazing affect sediment deposition and accretion rates in salt marshes? *Estuarine, Coastal and Shelf Science, 135*, 296-305.

Nyman, J. A., Walters, R. J., Delaune, R. D., & Patrick Jr, W. H. (2006). Marsh vertical accretion via vegetative growth. *Estuarine, Coastal and Shelf Science, 69*(3-4), 370-380.

Okin, G. S., Gillette, D. A., & Herrick, J. E. (2006). Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *Journal of Arid Environments, 65*(2), 253-275.

Operstein, V., & Frydman, S. (2000). The influence of vegetation on soil strength. *Ground Improvement, 4*(2), 81-89.

Ordoñez, J. C., van Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography, 18*(2), 137-149.

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., et al. (2006). A global crisis for seagrass ecosystems. *Bioscience, 56*(12), 987-996.

Packham, J. R., & Willis, A. J. (1997). *Ecology of dunes, salt marsh and shingle*. Berlin, Germany: Springer Science & Business Media.

Paine, C. E. T., Baraloto, C., Chave, J., & Hérault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos, 120*(5), 720-727.

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist, 103*(929), 91-93.

Park, Y.-M. (1990). Effects of drought on two grass species with different distribution around coastal sand-dunes. *Functional Ecology, 4*, 735-741.

Pasternack, G. B., & Brush, G. S. (2002). Biogeomorphic controls on sedimentation and substrate on a vegetated tidal freshwater delta in upper Chesapeake Bay. *Geomorphology, 43*(3-4), 293-311.

Paul, M., & Amos, C. L. (2011). Spatial and seasonal variation in wave attenuation over Zostera noltii. *Journal of Geophysical Research: Oceans, 116*, C08019.

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

Pemadasa, M. A., & Lovell, P. H. (1974). The mineral nutrition of some dune annuals. *Journal of Ecology, 62*, 647-657.

Penck, A. (1894). *Morphologie der Erdoberfläche*. Stuttgart, Germany: Engelhorn.

Pennings, S. C., & Bertness, M. D. (2001). Salt marsh communities. In M. D. Bertness, S. D. Gaines & M. Hay (Eds.), *Marine Community Ecology* (pp. 289-316). Sunderland, USA: Sinauer Associates.

Pennings, S. C., Grant, M.-B., & Bertness, M. D. (2005). Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *Journal of Ecology, 93*(1), 159-167.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*(3), 167.

Perumal, V. J., & Maun, M. A. (2005). Ecophysiological response of dune species to experimental burial under field and controlled conditions. *Plant Ecology, 184*(1), 89-104.

Peterson, R. A. (2017). Estimating normalization transformations with bestNormalize.

Pethick, J. (2001). Coastal management and sea-level rise. *Catena, 42*(2-4), 307-322.

Petrů, M., & Menges, E. S. (2004). Shifting sands in Florida scrub gaps and roadsides: dynamic microsites for herbs. *The American Midland Naturalist, 151*(1), 101-113.

Pickart, A. J. (1997). *Control of European beachgrass (Ammophila arenaria) on the west coast of the United States.* Paper presented at the Symposium of the California Exotic Pest Plant Council.

Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Díaz, S., Kleyer, M., et al. (2017). A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology, 31*(2), 444-457.

Pizzey, J. M. (1975). Assessment of dune stabilisation at Camber, Sussex, using air photographs. *Biological Conservation, 7*(4), 275-288.

Poggi, D., Katul, G. G., & Albertson, J. D. (2004). Momentum transfer and turbulent kinetic energy budgets within a dense model canopy. *Boundary-Layer Meteorology, 111*(3), 589-614.

Pohl, M., Alig, D., Körner, C., & Rixen, C. (2009). Higher plant diversity enhances soil stability in disturbed alpine ecosystems. *Plant and Soil, 324*(1-2), 91-102.

Pollen, N., Simon, A., & Collison, A. (2004). Advances in assessing the mechanical and hydrologic effects of riparian vegetation on streambank stability. In S. Benett & A. Simon (Eds.), *Riparian vegetation and fluvial geomorphology* (pp. 125-139). New York, USA: American Geophyisical Union.

Polvi, L. E., Wohl, E., & Merritt, D. M. (2014). Modeling the functional influence of vegetation type on streambank cohesion. *Earth Surface Processes and Landforms, 39*(9), 1245-1258.

Pontee, N. (2013). Defining coastal squeeze: A discussion. *Ocean & Coastal Management, 84*, 204-207.

Pontee, N., Narayan, S., Beck, M. W., & Hosking, A. H. (2016). Nature-based solutions: lessons from around the world. *Proceedings of the Institution of Civil Engineers-Maritime Engineering, 169*(1), 29-36.

Poorter, H., Fiorani, F., Pieruschka, R., Wojciechowski, T., van der Putten, W. H., Kleyer, M., et al. (2016). Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist, 212*(4), 838-855.

Proffitt, C. E., Chiasson, R. L., Owens, A. B., Edwards, K. R., & Travis, S. E. (2005). Spartina alterniflora genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. *Journal of Ecology, 93*(2), 404-416.

Provoost, S., Jones, M. L. M., & Edmondson, S. E. (2011). Changes in landscape and vegetation of coastal dunes in northwest Europe: a review. *Journal of Coastal Conservation, 15*(1), 207-226.

Psuty, N. P., & Silveira, T. M. (2010). Global climate change: an opportunity for coastal dunes?? *Journal of Coastal Conservation, 14*(2), 153-160.

Pye, K. (2001). Long-term geomorphological changes and how they may affect the dune coasts of Europe. In J. Houston, S. Edmondson & P. Rooney (Eds.), *Coastal dune management. Shared experience of European conservation practice.* (pp. 17-23). Liverpool, UK: Liverpool University Press.

R Development Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rajaniemi, T. K., & Barrett, D. T. (2018). Germination responses to abiotic stress shape species distributions on coastal dunes. *Plant Ecology, 219*(11), 1271-1282.

Ranasinghe, R., Callaghan, D., & Stive, M. J. F. (2012). Estimating coastal recession due to sea level rise: beyond the Bruun rule. *Climatic Change, 110*(3-4), 561-574.

Raunkiær, C. (1934). *The life forms of plants and statistical plant geography*. Oxford, UK: Oxford University Press.

Reef, R., Schuerch, M., Christie, E. K., Möller, I., & Spencer, T. (2018). The effect of vegetation height and biomass on the sediment budget of a European saltmarsh. *Estuarine, Coastal and Shelf Science, 202*, 125-133.

Rees, M. (1995). Community structure in sand dune annuals: is seed weight a key quantity? *Journal of Ecology, 83*, 857-863.

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

Renaud, F. G., Nehren, U., Sudmeier-Rieux, K., & Estrella, M. (2016). Developments and opportunities for ecosystem-based disaster risk reduction and climate change adaptation. In F. Renaud, K. Sudmeier-Rieux, M. Estrella & U. Nehren (Eds.), *Ecosystem-based disaster risk reduction and adaptation in practice* (pp. 1-20). Cham, Germany: Springer.

Riecken, G. (1982). *Die Halligen im Wandel*. Husum, Germany: Husum-Verlag.

Roelvink, D., Reniers, A., Van Dongeren, A. P., de Vries, J. V. T., McCall, R., & Lescinski, J. (2009). Modelling storm impacts on beaches, dunes and barrier islands. *Coastal Engineering, 56*(11-12), 1133-1152.

Rogel, J. A., Ariza, F. A., & Silla, R. O. (2000). Soil salinity and moisture gradients and plant zonation in Mediterranean salt marshes of Southeast Spain. *Wetlands, 20*(2), 357-372.

Roman, C. T., Peck, J. A., Allen, J., King, J. W., & Appleby, P. G. (1997). Accretion of a New England (USA) salt marsh in response to inlet migration, storms, and sea-level rise. *Estuarine, Coastal and Shelf Science, 45*(6), 717-727.

Rosati, J. D., Dean, R. G., & Walton, T. L. (2013). The modified Bruun Rule extended for landward transport. *Marine Geology, 340*, 71-81.

Rozema, J., Bijwaard, P., Prast, G., & Broekman, R. (1985). Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio, 62*(1-3), 499-521.

Ruggiero, P., Hacker, S., Seabloom, E., & Zarnetske, P. (2018). The role of vegetation in determining dune morphology, exposure to sea-level rise, and storm-induced coastal hazards: a U.S. Pacific northwest perspective. In L. Moore & A. Murray (Eds.), *Barrier dynamics and response to changing climate* (pp. 337-361). Cham, Germany: Springer.

Rupprecht, F., Möller, I., Paul, M., Kudella, M., Spencer, T., Van Wesenbeeck, B. K., et al. (2017). Vegetation-wave interactions in salt marshes under storm surge conditions. *Ecological Engineering, 100*, 301-315.

Ryser, P., Gill, H. K., & Byrne, C. J. (2011). Constraints of root response to waterlogging in Alisma triviale. *Plant and Soil, 343*(1-2), 247-260.

Sambatti, J. B. M., & Rice, K. J. (2006). Local adaptation, patterns of selection, and gene flow in the Californian serpentine sunflower (Helianthus exilis). *Evolution, 60*(4), 696-710.

Scheepens, J. F., Frei, E. S., & Stöcklin, J. (2010). Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia, 164*(1), 141-150.

Schellenberger Costa, D., Zotz, G., Hemp, A., & Kleyer, M. (2018). Trait patterns of epiphytes compared to other plant life-forms along a tropical elevation gradient. *Functional Ecology, 32*(8), 2073-2084.

Schile, L. M., Callaway, J. C., Morris, J. T., Stralberg, D., Parker, V. T., & Kelly, M. (2014). Modeling tidal marsh distribution with sea-level rise: evaluating the role of vegetation, sediment, and upland habitat in marsh resiliency. *Plos One, 9*(2), e88760.

Schindler, M., Karius, V., Arns, A., Deicke, M., & von Eynatten, H. (2014). Measuring sediment deposition and accretion on anthropogenic marshland – Part II: the adaptation capacity of the North Frisian Halligen to sea level rise. *Estuarine, Coastal and Shelf Science, 151*, 246-255.

Schröder, H. K., Kiehl, K., & Stock, M. (2002). Directional and non-directional vegetation changes in a temperate salt marsh in relation to biotic and abiotic factors. *Applied Vegetation Science, 5*(1), 33-44.

Schuerch, M., Rapaglia, J., Liebetrau, V., Vafeidis, A., & Reise, K. (2012). Salt marsh accretion and storm tide variation: an example from a barrier island in the North Sea. *Estuaries and Coasts, 35*(2), 486-500.

Schürch, M., Rapaglia, J., Liebetrau, V., Vafeidis, A., & Reise, K. (2012). Salt marsh accretion and storm tide variation: an example from a barrier island in the North Sea. *Estuaries and Coasts, 35*(2), 486-500.

Schürch, M., Vafeidis, A., Slawig, T., & Temmerman, S. (2013). Modeling the influence of changing storm patterns on the ability of a salt marsh to keep pace with sea level rise. *Journal of Geophysical Research: Earth Surface, 118*(1), 84-96.

Seabloom, E. W., & Wiedemann, A. M. (1994). Distribution and effects of Ammophila breviligulata Fern. (American beachgrass) on the foredunes of the Washington coast. *Journal of Coastal Research, 10*(1), 178-188.

Shepard, C. C., Crain, C. M., & Beck, M. W. (2011). The protective role of coastal marshes: a systematic review and meta-analysis. *Plos One, 6*(11), e27374.

Shi, F., Song, C., Zhang, X., Mao, R., Guo, Y., & Gao, F. (2015). Plant zonation patterns reflected by the differences in plant growth, biomass partitioning and root traits along a water level gradient among four common vascular plants in freshwater marshes of the Sanjiang Plain, Northeast China. *Ecological Engineering, 81*, 158-164.

Shi, L., Zhang, Z., Zhang, C., & Zhang, J. (2004). Effects of sand burial on survival, growth, gas exchange and biomass allocation of Ulmus pumila seedlings in the Hunshandak Sandland, China. *Annals of Botany, 94*(4), 553-560.

Shipley, B. (2010). *From plant traits to vegetation structure: chance and selection in the assembly of ecological communities*. Cambridge, UK: Cambridge University Press.

Shipley, B., Vile, D., & Garnier, É. (2006). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science, 314*(5800), 812-814.

Siefert, A. (2012). Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia, 170*(3), 767-775.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., et al. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters, 18*(12), 1406-1419.

Sigren, J. M., Figlus, J., & Armitage, A. R. (2014). Coastal sand dunes and dune vegetation: restoration, erosion, and storm protection. *Shore & Beach, 82*(4), 5-12.

Sigren, J. M., Figlus, J., Highfield, W., Feagin, R. A., & Armitage, A. R. (2018). The effects of coastal dune volume and vegetation on storm-induced property damage: analysis from hurricane Ike. *Journal of Coastal Research, 34*(1), 164-173.

Silva, H., Dias, J., & Caçador, I. (2009). Is the salt marsh vegetation a determining factor in the sedimentation processes? *Hydrobiologia, 621*(1), 33-47.

Smirnoff, N., & Stewart, G. R. (1985). Stress metabolites and their role in coastal plants. *Vegetation, 62*, 273-278.

Spalding, M. D., Ruffo, S., Lacambra, C., Meliane, I., Hale, L. Z., Shepard, C. C., et al. (2014). The role of ecosystems in coastal protection: adapting to climate change and coastal hazards. *Ocean & Coastal Management, 90*, 50-57.

Spencer, T. (1992). Bioerosion and biogeomorphology. In D. M. John, S. J. Hawkins & J. H. Price (Eds.), *Plant-animal interactions in the marine benthos* (Vol. 46, pp. 493-509). Oxford, UK: Clarendon Press.

Spencer, T., Möller, I., Rupprecht, F., Bouma, T. J., van Wesenbeeck, B. K., Kudella, M., et al. (2016). Salt marsh surface survives true-to-scale simulated storm surges. *Earth Surface Processes and Landforms, 41*(4), 543-552.

Stallins, J. A., & Parker, A. J. (2003). The influence of complex systems interactions on barrier island dune vegetation pattern and process. *Annals of the Association of American Geographers, 93*(1), 13-29.

Steif, H. J. (1973). *Das ostfriesische Küstengebiet. Inseln, Watten und Marschen* (Vol. 57). Stuttgart, Germany: Borntraeger.

Stock, M. (2011). Patterns in surface elevation change across a temperate salt marsh platform in relation to sea-level rise. *Coastline Reports, 17*(3), 33-48.

Streif, H. (1989). Barrier islands, tidal flats, and coastal marshes resulting from a relative rise of sea level in East Frisia on the German North Sea coast. In W. van der Linden (Ed.), *Coastal lowlands, Proceedings of a Symposium of the Royal Geological and Mining society of the Netherlands (KNGMG)* (pp. 213-223). Dordrecht, Netherlands: Kluwer.

Strickler, A. (1923). *Beiträge zur Frage der Geschwindigkeitsformel und der Rauhigkeitszahlen für Ströme, Kanäle und geschlossene Leitungen.* Bern, Switzerland: Eidg. Amt für Wasserwirtschaft.

Stromberg, J. C., & Boudell, J. A. (2013). Floods, drought, and seed mass of riparian plant species. *Journal of Arid Environments, 97*, 99-107.

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

Sultan, S. E. (2000). Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science, 5*(12), 537-542.

Swann, L. (2008). The use of living shorelines to mitigate the effects of storm events on Dauphin Island, Alabama, USA. *American Fisheries Society, 64*(11), 47–57.

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

Temmerman, S., Bouma, T. J., Van de Koppel, J., Van der Wal, D., De Vries, M. B., & Herman, P. M. J. (2007). Vegetation causes channel erosion in a tidal landscape. *Geology, 35*(7), 631-634.

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.

Temmerman, S., Moonen, P., Schoelynck, J., Govers, G., & Bouma, T. J. (2012). Impact of vegetation die-off on spatial flow patterns over a tidal marsh. *Geophysical Research Letters, 39*(3), L03406.

Thampanya, U., Vermaat, J. E., Sinsakul, S., & Panapitukkul, N. (2006). Coastal erosion and mangrove progradation of Southern Thailand. *Estuarine, Coastal and Shelf Science, 68*(1-2), 75-85.

Thompson, B. S., Primavera, J. H., & Friess, D. A. (2017). Governance and implementation challenges for mangrove forest Payments for Ecosystem Services (PES): empirical evidence from the Philippines. *Ecosystem Services, 23*, 146-155.

Thuiller, W., Lavorel, S., Midgley, G., Lavergne, S., & Rebelo, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 Leucadendron taxa. *Ecology, 85*(6), 1688-1699.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science, 294*(5543), 843-845.

Tisdall, J. M. (1994). Possible role of soil microorganisms in aggregation in soils. *Plant and Soil, 159*(1), 115-121.

Torca, M., Campos, J. A., & Herrera, M. (2019). Changes in plant diversity patterns along dune zonation in south Atlantic European coasts. *Estuarine, Coastal and Shelf Science, 218*, 39-47.

Udo, K., & Takewaka, S. (2007). Experimental study of blown sand in a vegetated area. *Journal of Coastal Research, 23*(5), 1175-1182.

Ungar, I. A. (1991). *Ecophysiology of Vascular Halophytes*. Boca Raton, USA: CRC Press.

United Nations Framework Convention on Climate Change. (2015). COP21 Paris agreement. from http://unfccc.int/2860.php

Urbanova, T., & Leubner-Metzger, G. (2016). Gibberellins and seed germination. *Annual Plant Reviews, 49*, 253-284.

van de Koppel, J., Herman, P. M. J., Thoolen, P., & Heip, C. H. R. (2001). Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology, 82*(12), 3449-3461.

Van der Laan, D., Van Tongeren, O. F. R., Van der Putten, W. H., & Veenbaas, G. (1997). Vegetation development in coastal foredunes in relation to methods of establishing marram grass (Ammophila arenaria). *Journal of Coastal Conservation, 3*(2), 179.

Van der Meulen, F., & Salman, A. (1996). Management of Mediterranean coastal dunes. *Ocean & Coastal Management, 30*(2-3), 177-195.

Van der Putten, W. H. (1990). Establishment of Ammophila arenaria (marram grass) from culms, seeds and rhizomes. *Journal of Applied Ecology, 27*, 188-199.

van Eerdt, M. M. (1985). Salt marsh cliff stability in the Oosterschelde. *Earth Surface Processes and Landforms, 10*(2), 95-106.

Vellend, M., & Geber, M. A. (2005). Connections between species diversity and genetic diversity. *Ecology Letters, 8*(7), 767-781.

Venables, W. N., & Ripley, B. D. (2013). *Modern applied statistics with S-PLUS*. New York, US: Springer.

Viles, H. A. (1988). *Biogeomorphology*. Oxford, UK: Blackwell.

Violle, C., Bonis, A., Plantegenest, M., Cudennec, C., Damgaard, C., Marion, B., et al. (2011). Plant functional traits capture species richness variations along a flooding gradient. *Oikos, 120*(3), 389-398.

Violle, C., & Jiang, L. (2009). Towards a trait-based quantification of species niche. *Journal of Plant Ecology, 2*(2), 87-93.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional! *Oikos, 116*(5), 882-892.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science, 277*(5325), 494-499.

von Storch, H., & Weisse, R. (2008). Regional storm climate and related marine hazards in the Northeast Atlantic. In H. F. Diaz & R. J. Murnane (Eds.), *Climate extremes and society* (pp. 54-73). Cambridge, UK: Cambridge University Press.

Vousdoukas, M. I., Mentaschi, L., Voukouvalas, E., Verlaan, M., & Feyen, L. (2017). Extreme sea levels on the rise along Europe's coasts. *Earth's Future, 5*(3), 304-323.

Wahl, T., Jensen, J., Frank, T., & Haigh, I. D. (2011). Improved estimates of mean sea level changes in the German Bight over the last 166 years. *Ocean Dynamics, 61*(5), 701-715.

Wal, A., & McManus, J. (1993). Wind regime and sand transport on a coastal beach-dune complex, Tentsmuir, eastern Scotland. *Geological Society, 72*, 159-171.

Walmsley, C. A., & Davy, A. J. (1997). Germination characteristics of shingle beach species, effects of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology, 34*(1), 131-142.

Weiher, E., & Keddy, P. A. (1995). The assembly of experimental wetland plant communities. *Oikos, 73*(3), 323-335.

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.

Wheeler, B. D., & Proctor, M. C. F. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology, 88*(2), 187-203.

Whitlock, R., Grime, J. P., & Burke, T. (2010). Genetic variation in plant morphology contributes to the species-level structure of grassland communities. *Ecology, 91*(5), 1344-1354.

Wickham, H. (2016). *ggplot2: elegant graphics for data analysis*. New York, USA: Springer.

Widdows, J., Pope, N. D., & Brinsley, M. D. (2008). Effect of Spartina anglica stems on near-bed hydrodynamics, sediment erodability and morphological changes on an intertidal mudflat. *Marine Ecology Progress Series, 362*, 45-57.

Wilson, J. B. (1999). Guilds, functional types and ecological groups. *Oikos, 86*, 507-522.

Wolfe, S. A., & Nickling, W. G. (1993). The protective role of sparse vegetation in wind erosion. *Progress in Pphysical Geography, 17*(1), 50-68.

Wolner, C. W. V., Moore, L. J., Young, D. R., Brantley, S. T., Bissett, S. N., & McBride, R. A. (2013). Ecomorphodynamic feedbacks and barrier island response to disturbance: insights from the Virginia Barrier Islands, Mid-Atlantic Bight, USA. *Geomorphology, 199*, 115-128.

Xiong, S., Nilsson, C., Johansson, M. E., & Jansson, R. (2001). Responses of riparian plants to accumulation of silt and plant litter: the importance of plant traits. *Journal of Vegetation Science, 12*(4), 481-490.

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences, 96*(4), 1463-1468.

You, S., Kim, M., Lee, J., & Chon, J. (2018). Coastal landscape planning for improving the value of ecosystem services in coastal areas: Using system dynamics model. *Environmental Pollution, 242*, 2040-2050.

Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B., et al. (2012). Biophysical feedback mediates effects of invasive grasses on coastal dune shape. *Ecology, 93*(6), 1439-1450.

Zhang, J., & Maun, M. A. (1990a). Effects of sand burial on seed germination, seedling emergence, survival, and growth of Agropyron psammophilum. *Canadian Journal of Botany, 68*(2), 304-310.

Zhang, J., & Maun, M. A. (1990b). Sand burial effects on seed germination, seedling emergence and establishment of Panicum virgatum. *Ecography, 13*(1), 56-61.

Zhang, J., & Maun, M. A. (1992). Effects of burial in sand on the growth and reproduction of Cakile edentula. *Ecography, 15*(3), 296-302.

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Curriculum vitae

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2015	Summer School Biodiversity Synthesis, German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

Publication

2015	Klaus, F., Bass, J., Marholt, L., Müller, B., Klatt, B., Kormann, U. Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. Journal of Landscape Ecology, 8(1), 22-31
2014	Bass, J., Klaiber, J., Schuster, I., Weber, F., Wiedemann, E. Somnologie und der Nutzen eines Nickerchens. In N. Weidtmann (Ed.) *Kosmologie – Evolution – Geschichte 2. Der Mensch an der Schnittstelle zwischen Natur und Kultur: Darwinistische Kränkung, Religiosität, Gemeinschaft, Schlaf, Zeit* (pp. 163-202). Berlin, Germany, LIT Verlag

Authors' contributions

Chapter 2: Morphological plasticity of dune pioneer plants in response to timing and magnitude of sediment disturbance

Bass, J., Balke, T., Minden, V. *Submission in preparation*.

JB, TB and VM conceived and planned the experiment. JB conducted the experiment. JB conducted the analysis and prepared the graphs and tables and wrote the initial manuscript. TB and VM contributed to the revision of the manuscript.

Chapter 3: Storm resistance and resilience of natural and artificial coastal foredune communities

Bass, J., Minden, V., Balke, T. *Submission in preparation*.

JB, VM and TB conceived and planned the experiment. JB conducted the experiment. JB conducted the analysis and prepared the graphs and tables and wrote the initial manuscript. TB and VM contributed to the revision of the manuscript.

Chapter 4: Plant traits effect surface elevation change in salt marshes: an example of biogeomorphic ecosystems

Bass, J., Granse, D., Hache, I., Jensen, K., Karius, V., Minden, V., Stock, M., Suchrow, S., Kleyer, M. *Submission in preparation*.

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Erklärung

gemäß § 12 Abs. 2b der gemeinsamen Promotionsordnung der Fakultät II – Informatik, Wirtschafts- und Rechtswissenschaften (für ihr Department für Informatik), der Fakultät V – Mathematik und Naturwissenschaften und der Fakultät VI – Medizin und Gesundheitswissenschaften der Carl von Ossietzky Universität Oldenburg vom 05.09.2014.

Hiermit erkläre ich, dass die vorliegende Arbeit in allen Teilen selbstständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt wurde. Einzelne Kapitel sollen in Fachzeitschriften veröffentlicht werden.

Weiterhin erkläre ich, dass diese Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt oder vorgelegen hat.

Zudem erkläre ich, dass die Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg befolgt wurden und dass im Zusammenhang mit dem Promotionsvorhaben keine kommerziellen Vermittlungs- oder Beratungsdienste in Anspruch genommen wurden.

Mit der Vorlage dieser Dissertation strebe ich eine Promotion zum Dr. rer. nat. an, es soll der Grad eines Doktors verliehen werden.

Julia Bass