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A sandy symphony

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A sandy symphony

Unraveling dune grass interactions and their role in landscape formation

Carlijn Lammers

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A sandy symphony

Unraveling dune grass interactions and their role in landscape formation

PhD thesis

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on the authority of the
Rector Magnificus Prof. J.M.A. Scherpen
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the decision by the College of Deans.

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by

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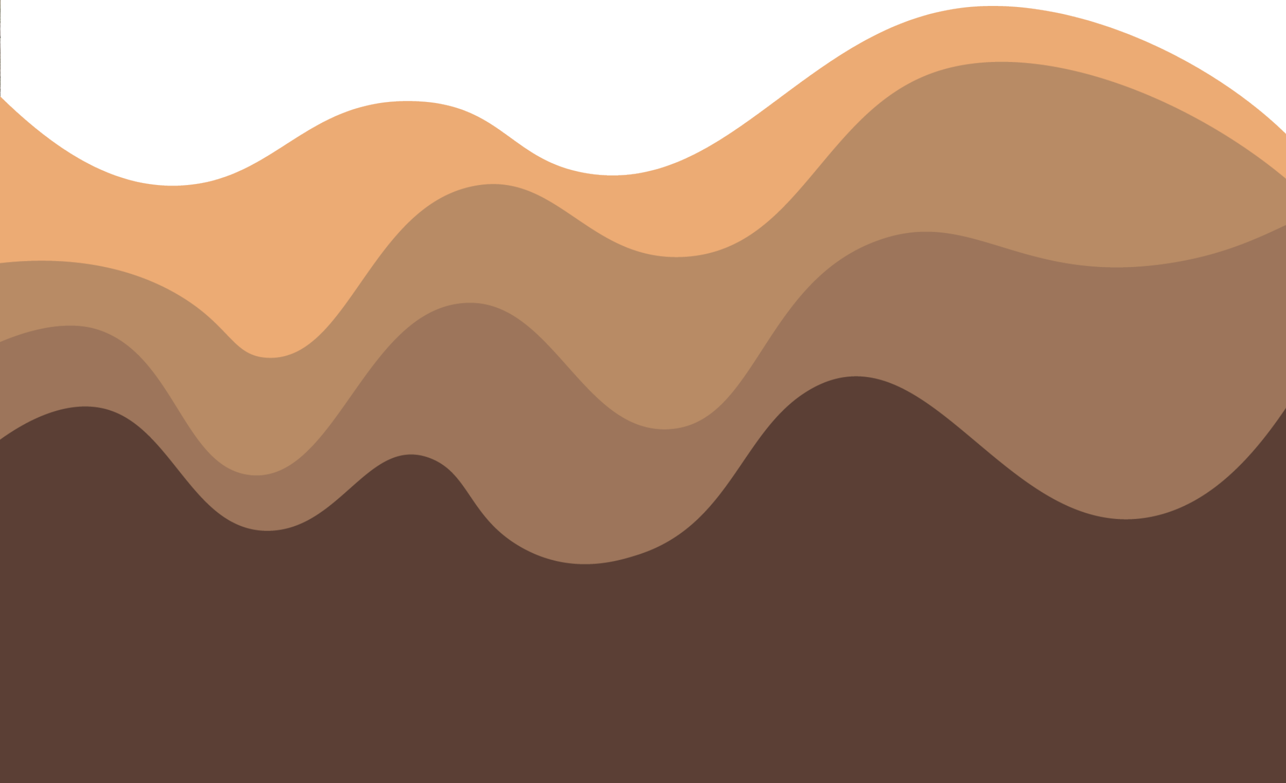
CHAPTER 1

General introduction



1. Coastal ecosystems

Along continental margins, where land and sea meet, unique ecosystems exist. Due to the variety in geomorphological and climatic regimes across the world, a wide array of these coastal ecosystems occur including cliffs, rocky shores, mangroves, salt marshes and sandy shores (Burke et al., 2001; Martínez et al., 2007). These systems are highly dynamic with natural accretion and erosion processes associated with wind, waves, storms and tectonic processes, which occur both at a regular predictable (e.g., tides) and irregular infrequent (e.g., storms) scale (Burke et al., 2001). These ecosystems are among the most productive in the world and provide important goods and services, including, flood protection, carbon sequestration and tourism (Barbier et al., 2011; Martínez et al., 2007). Even though there is a large variation in conditions and vegetation types, systems where land and water meet share common interactions between plants and the geomorphic environment (Corenblit et al., 2015).

1.1.2. Development of vegetated coastal ecosystems - From a bare to a modified habitat

For fluvial and vegetated coastal ecosystems, the transition from a bare to a modified system, such as from a sandy beach to a coastal dune or from a mudflat to a salt marsh, depends on interactions between the geomorphic (e.g., transport of sediment by wind or water) and biological (e.g., vegetation) environment (Corenblit et al., 2007). Therefore, these systems are considered biogeomorphic landscapes (Balke, 2013). Development of biogeomorphic systems can be described as biogeomorphic succession (Figure 1.1). Large disturbances such as storms, tsunamis and floods, can rejuvenate an area after which a bare system is left. In absence of vegetation physical forces dominate and determine the landscape morphology. (Balke, 2013; Corenblit et al., 2007) (Figure 1.1, Physical phase). The establishment of plants depends on the availability of seeds or clonal fragments combined with prevailing environmental conditions (Figure 1.1, Pioneer phase). Species differ in germination requirements and tolerance of their seedlings to disturbances. Therefore, environmental conditions control if, when and which species can establish (Balke, 2013; Corenblit et al., 2011). In periods where conditions are below the species tolerance threshold for long enough to germinate and seedlings to get rooted, vegetation can establish. Such a relatively benign period is known as the 'Window of Opportunity' (Balke, 2013).

After establishment, the physical structures of the plants (i.e., their shoots and roots) reduce wind and/or water flow causing sediment to settle. Dominant species in these water fringing systems share similar response traits to these habitat alterations, such as cord grasses and dune grasses from which growth (e.g., increase in shoot formation and length) is promoted by sediment accretion (Corenblit et al., 2015; Maun, 1998; Van Hulzen et al., 2007). Since the reduction of flows increases with size of plants, sedimentation will increase as the plant grows and expands, resulting in self-reinforcing feedbacks (Van Hulzen et al., 2007; Zarnetske et al., 2012). These positive feedbacks between vegetation and physical conditions (i.e., biophysical feedbacks), make these plant species ecosystem engineers (Gutiérrez et al., 2011; Jones et al., 1994) (Figure 1.1, Biogeomorphic phase). In absence of major disturbances, the physical processes and vegetation can partly become disconnected. For example, with increase in elevation a low marsh can develop into a high marsh, and while the low marsh is frequently inundated by tidal motion, the high marsh is only flooded with more extreme water levels. When the influence of physical forces ameliorates, biological interactions, such as competition between species, become more deterministic for species performance (Corenblit et al., 2007) (Figure 1.1, Ecological phase).

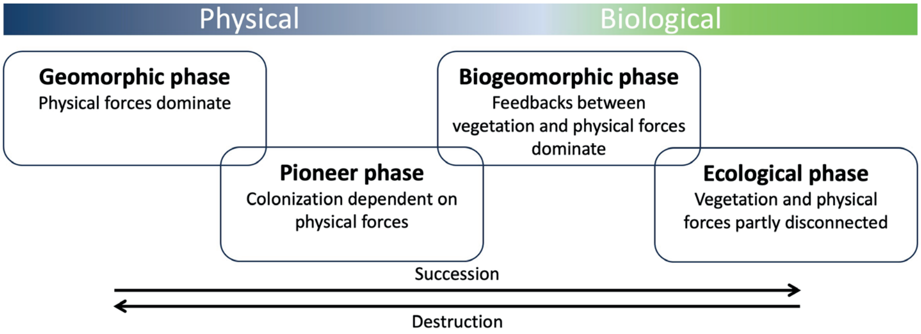


Figure 1.1: Summary of biogeomorphic succession, adapted from Balke 2013 & Corenblit et al. 2007.

2. How ecosystem engineers affect landscape morphology

2.1. Local effects of ecosystem engineers

In these coastal, biogeomorphic landscapes, interactions between vegetation and physical conditions determine landscape emergence and morphology (e.g., Bouma et al. 2005; Zarnetske et al. 2012; Hacker et al. 2019). On a local scale, the plant's morphological characteristics – such as shoot number, density, length, and flexibility – determine flow reduction and subsequently sediment accretion. Generally, higher sedimentation rates are found in dense, tall and inflexible plant species (Bouma et al., 2013; Hacker et al., 2012). For example, dune grasses that have a low shoot density (such as *Elytrigia juncea*), create lower and broader dunes than ones with a high shoot density (such as *Ammophila arenaria*) (Bakker, 1976, Chapter 2, Figure 1.2). Or the stiff shoots of cord grass (*Spartina anglica*) result in more sedimentation than flexible seagrass (*Zostra noltii*) in similar habitats (Bouma et al., 2005, Figure 1.2). The flow velocity combined with the type of medium (i.e., water or wind), and sediment type (e.g., silt or sand) determine how much sediment is transported. Only within a specific range of flow velocities sediment will accumulate, because when flow velocity is too low no sediment will be transported and with a too high flow velocity erosion occurs (Bouma, Friedrichs, Klaassen, et al., 2009; Innocenti et al., 2021). Subsequently, these factors combined – that is, flow velocity, subsequent sediment transport and vegetation characteristics – determine the amount and distribution (e.g., local or down-wind) of accumulated or eroded sediment (e.g., Bouma et al. 2005; Van Hulzen et al. 2007; Zarnetske et al. 2012). Generally, morphological traits of ecosystem engineering vegetation are presented as a species-specific traits (e.g., Bouma et al. 2005; Zarnetske et al. 2012; Hacker et al. 2019). However, environmental conditions can affect plant traits. For example, many clonal plants have been found to specifically place their offspring in beneficial microhabitats in heterogeneous environments (e.g. review by Oborny, 2019). The extent to which morphological traits that determine ecosystem engineering (i.e., their ecosystem engineering traits) are species-specific or context-dependent remains unknown (Chapter 2).

2.2. From individual to landscape

In absence of disturbances, plants can increase in size and thereby the scale of their engineering impact increases. However, also the local changes induced by ecosystem engineers can have large-scale effect on landscape morphology and development. Most noteworthy is that habitat alterations can affect the settlement and performance of other individuals (of their own – i.e., intraspecific – or other species – i.e., interspecific), which can be both positive and negative (e.g., Jones et al., 1994; Davy, 2000; Bruno et al. 2003). The self-reinforcing feedback created by ecosystem engineers is a form of intraspecific facilitation (i.e., facilitative interactions are defined as positive interactions that benefit at least one of the participants while not doing any harm to the other either). In clonal plant patches, these self-reinforcing feedbacks can even happen within a single individual. Through this self-facilitation, ecosystem engineers can expand their niche in hostile conditions (Bruno et al., 2003; Jones et al., 1994). Next to

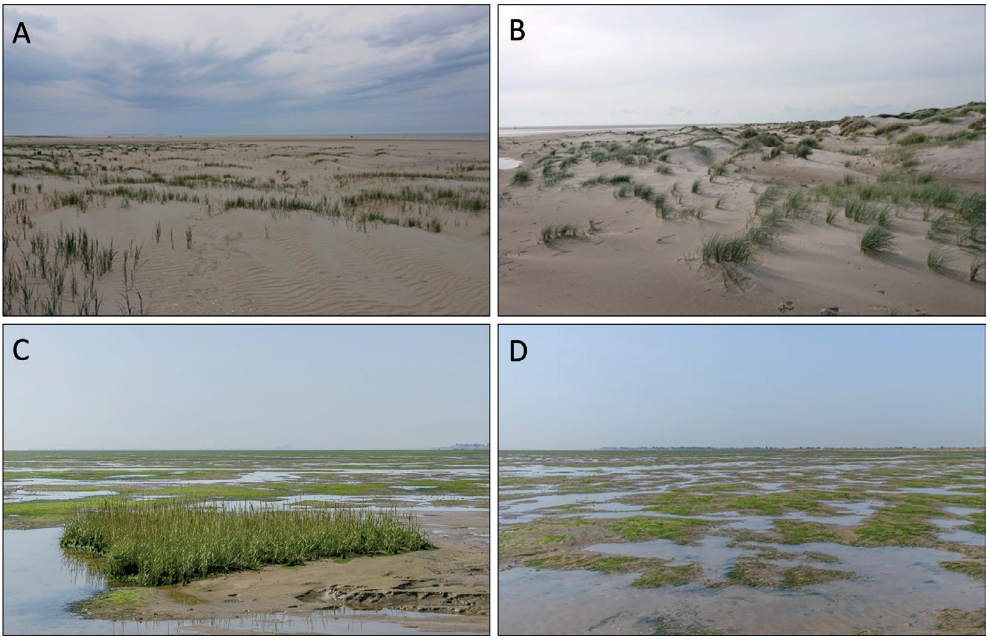


Figure 1.2: Species with different characteristics affect sedimentation in a different way in similar environments. In the coastal dunes (A) sand couch (Elytrigia juncea, at Rømø, Denmark) created low and broad dunes and (B) marram grass (Ammophila arenaria, at Texel, the Netherlands) high and narrow (hummocky) dunes. In salt marshes, (C) cord grass (Spartina anglica, at the Broomway, UK) has a higher sedimentation than (D) dwarf eelgrass (Zostera noltii, at the Broomway, UK). Photos A & B by Carlijn Lammers, C & D by Ian Capper.

facilitating themselves, many ecosystem engineers also facilitate other species. These facilitative interactions can be a direct result of their physical presence – for example, mussels providing hard substrate in a soft-bottom environment for other species to attach to (Altieri et al., 2007) – or through alterations in their habitat – for example, sedimentation by cord grasses facilitates establishment of less flood tolerant species (Davy, 2000). The theory that earlier successional species alter their habitat in a way that benefits the establishment of later successional species, thereby driving ecosystem succession, was already proposed over a century ago (Clements, 1916). In turn, facilitated species can interacts with more species, potentially forming facilitation cascades (Altieri et al., 2007; Thomsen et al., 2010).

However, also negative interactions occur between ecosystem engineers and other species. One way in which negative interactions occur is through scale-dependent feedbacks, which means that there is a local positive and long-distance negative effect of the species (Rietkerk & van de Koppel, 2008). For example, the flow deviation around cord grass (*Spartina sp.*) patches in salt marshes can lead to scouring which reduces plant growth right next to existing vegetation and increases channel formation (Temmerman et al., 2007; van Wesenbeeck et al., 2008). In a broad range of ecosystems, scale-dependent feedbacks are proposed to explain self-organized pattern formation, including salt marshes (Temmerman et al., 2007; van Wesenbeeck et al., 2008), riparian vegetation (Tal & Paola, 2007) and seagrass meadows (van der Heide et al., 2010). Similar to plant-scale feedbacks, interactions between physical forces, such as flow velocity, and plant characteristics determine the strength of these scale-dependent feedbacks (Bouma, Friedrichs, van Wesenbeeck, et al., 2009). Furthermore, negative interactions (e.g., competition for resources) can happen on a local scale but affect the larger landscape. For example, if interacting species are both ecosystem engineers with a differing effect on landscape morphology such as the competing (invasive) congeneric dune grasses, European marram grass (*Ammophila arenaria*) and American beach grass (*Ammophila breviligulata*) (Hacker et al., 2012; Zarnetske et al., 2013). These species build dunes with different morphologies, that is, high and narrow dunes are formed by marram grass and lower and broader dunes by American beach grass. Therefore, invasion by American beach grass in areas dominated by European marram grass can alter landscape morphology (Hacker et al., 2012; Zarnetske et al., 2013). How dune grasses affect establishment of conspecifics or later successional species through habitat modifying activities has yet to be determined (Chapter 3, Chapter 4). Eventually all these interactions, including the biophysical interactions that in turn affect intra- and interspecific interactions, determines ecosystem structure and landscape morphology.

3. Global change, degradation, and restoration of coastal ecosystems

Over the last century coastal ecosystems have been rapidly degrading, mainly due to human-induced changes. These changes occur on a local (e.g., eutrophication or changes in sediment budgets) and global (e.g., sea level rise) scale, with many local pressures being amplified by human induced climate change effects. As a result, amongst others, about 70% of the world's coastal dunes are eroding, while 42% of salt marshes, 35% of mangroves and 29% of seagrass are lost or degraded (Feagin et al., 2005; Gedan et al., 2009; Reid et al., 2005; Waycott et al., 2009). Generally, erosion will lead to landward displacement of vegetated coastal ecosystems. However, barriers restrict such migration, leading to coastal squeeze (i.e., habitat is lost or deteriorated because of structures restricting such migration). This partly happens naturally (for example by cliffs) but is more commonly caused by manmade (infra)structure (Feagin et al., 2005; Martínez et al., 2004). Furthermore, extreme climatic events, such as drought, storms or heat waves, could affect species interactions and subsequently ecosystem structure.

To halt or reverse losses of ecosystems, and their vital functions, there is increasing interest in restoration of these ecosystems (Silliman et al., 2015; Temmink et al., 2020; van der Heide et al., 2021). There are some common restoration practices that happen in many vegetated coastal ecosystems, for example, increasing soil stability and sediment capture by creating structures such as brushwood check dams, and/or planting of ecosystem engineering vegetation (Bakker et al., 2002; Bridges et al., 2018; Ministerie V&W, 2000). While other practices are system specific, such as sand suppletion on sandy shores that are in an erosive state (Ministerie V&W, 2000). Classically, planting of vegetation is done in competition limiting arrays. However, in physically stressful environments neighbors can ameliorate physical stress, increasing survival success (Bertness & Hacker, 1994; Bruno et al., 2003). Over the last decades, inclusion of facilitation in restoration by clumped planting or mimicking larger plant patches gained interest (Silliman et al., 2015; Temmink et al., 2020). However, the success of these novel facilitation-promoting designs is context dependent (Fischman et al., 2019; van der Heide et al., 2021; Woods et al., 2023).

4. The study system - Coastal dunes

Coastal dunes occur along sandy shores, which make up about one-third of the world's coastline (Martínez et al., 2004). They provide many services such as flood protection, drinking water and recreation (Martínez et al., 2007; Martínez & Psuty, 2004). At locations with a positive sand budget and a dominant onshore wind direction, dune areas can expand and develop (Martínez et al., 2004). This thesis focusses on the emergence and early development of the dunes, from beach to embryonic dunes, which depends on establishment and growth of dune grasses.

4.1. Early dune development – Beach to foredunes

Generally, different developmental stages of dunes can be found on a cross-shore gradient from beach to dunes, corresponding to the biogeomorphic succession and primary succession gradient (Figure 1.1 & 1.3). Closest to the shore are bare beach areas that are frequently overwashed (i.e., the physical phase in biogeomorphic succession, Figure 1.1). From the sea, sediment ends up on the beach through currents and waves (Fredsoe & Deigaard, 1992; Swift, 1976). If the sediment dries and wind velocity is high enough, sediment will be transported by wind (i.e., aeolian transport), which is a key component for coastal dunes to form (Martínez & Psuty, 2004; Maun, 2009). The combination of beach width and wind conditions determines the amount of sediment that is transported and subsequently deposited within the dune vegetation (Durán & Moore, 2013; Martínez et al., 2004).

Sand that is transported across the beach can accumulate behind any object (living and non-living) that reduces the wind speed enough for sediment to settle, resulting in small sand dunes. However, the stability of these dunes is depending on the type of object that accumulated the sediment (Hesp, 1989; Maun, 2009). For example, sand accumulated by an annual plant will be redistributed after the plant dies. Only if burial tolerant perennial vegetation traps sediment, more long-lived embryonic dunes can develop (Hesp, 1989; Maun, 2009). While there is a range of burial tolerant species, the most well-known dune building species are

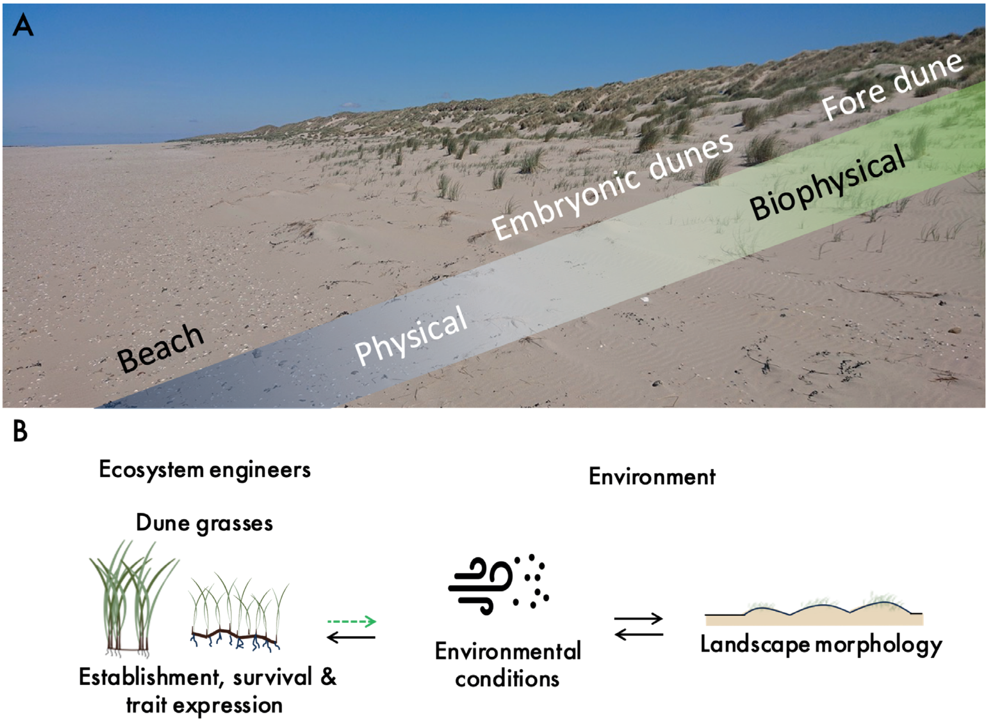


Figure 1.3: A) Along a cross-shore gradient different successive stages of dunes (Beach – Embryonic dunes – Foredunes) are found, that could be described using biogeomorphic succession (Figure 1). B) Graphical representation of biophysical interactions in which dune grasses affect environmental conditions (plant-induced changes indicated with a green arrow), which in turn affect landscape morphology and vice versa.

grass species (Feagin et al., 2015). Generally, at locations with a positive sediment budget embryonic dunes increase in size during the summer, when the plants are in their growing season. However, the fate of embryonic dunes depends largely on the frequency and intensity of erosive events, such as storm surges which mostly happen in winter (Anthony, 2013; van Puijenbroek, Limpens, et al., 2017). In extreme storm conditions, embryonic dunes can completely erode and plants can be dislodged (Anthony, 2013; van Puijenbroek, Limpens, et al., 2017). If the balance in accretion and erosion is favored by accretion, embryonic dunes can develop into more stable foredunes (Hesp, 2002).

4.2. European coastal dunes dominated by marram grass and sand couch

The coastal dunes along the Northwestern European shore are dominated by two often co-occurring native dune grass species: **European marram grass** (*Ammophila arenaria* (L.) Link, hereafter referred to as marram grass) and **sand couch** (*Elytrigia juncea* subsp. *boreoatlantica*) (Figure 1.4). In general, sand couch is found closer to the shoreline than marram grass, where it is the first perennial species colonizing bare beach areas (Bakker, 1976; Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017). It is a more salt tolerant species than marram grass, and has shorter shoots and a lower shoot density (Bakker, 1976; Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017). In response to burial marram grass produces vertical and horizontal rhizomes, while sand couch only creates horizontal rhizomes (Hacker et al., 2019; Harris & Davy, 1986a; Huiskes, 1979). Consequently, sand couch creates low and broad dunes while marram grass creates high and narrow dunes (Bakker, 1976; Figure 1.2). Marram grass is known as a species with a high sediment trapping efficiency (Reijers, Siteur, et al., 2019; Zarnetske et al., 2012). Because of its efficient sediment trapping and stabilizing capacities, it is introduced in a wide range of countries (e.g., South Africa, Australia, New Zealand and USA (Hacker et al., 2012; Hertling & Lubke, 1999; Hilton, 2006)).

5. Objectives and outline of this thesis

This thesis focuses on early dune development in coastal dune ecosystems dominated by sand couch (*Elytrigia juncea*) and marram grass (*Ammophila arenaria*) (Figure 1.2 & 1.4). The objective of this thesis is to elucidate interactions between dune grasses, environmental conditions, and landscape morphology in early dune development to improve our understanding of the natural emergence and functioning of coastal dunes.

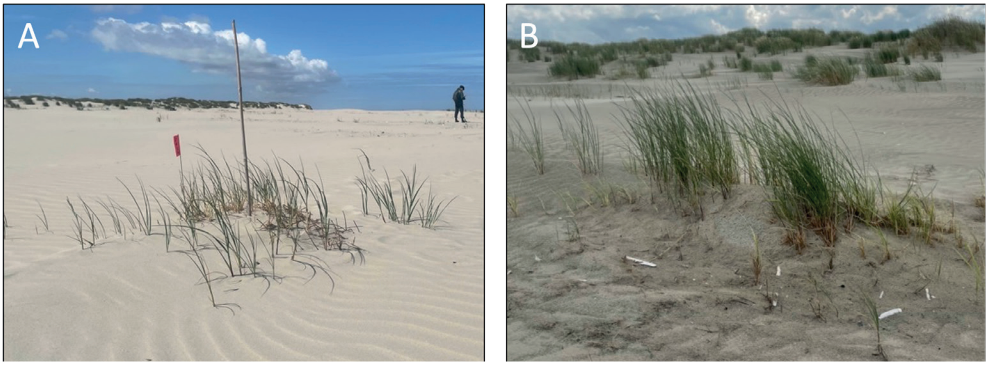


Figure 1.4: A) Sand couch (Elytrigia juncea) and B) European marram grass (Ammophila arenaria)

Morphological characteristics of ecosystem engineers determine the plant-scale feedbacks and therefore emerging landscape morphology, with spatial shoot organization being one of dune grass' dominant morphological traits determining local sediment accretion. In **chapter 2**, we determined how spatial shoot organizations differed between marram grass and sand couch and whether their trait expression was affected by local environmental conditions (Figure 1.5.2). Using a field survey along the Northwestern European shore (Denmark – France), we compared the spatial shoot organization of establishing, clonally expanding individuals of sand couch and marram grass across a range of coastal dune environments.

Subsequently, the interactions between established vegetation, environmental conditions and the establishment potential of vegetation plays a vital role development of the system. In **chapter 3**, we investigated how habitat modification by marram grass through embryonic dune development affects recruitment of conspecifics from seeds and marine dispersed rhizome fragments (Figure 1.5.3). By combining a field survey, field experiment and controlled experiment, we explored how adult marram grass affects the first requirements for successful species establishment, namely: 1) natural availability of seeds or clonal fragments, 2) germination from seeds and clonal fragments and 3) survival of seedlings.

Generally, it is assumed that sand couch primes the landscape for establishment of marram grass. However, it is unknown what the exact role of sand couch and embryonic dunes formed by sand couch is for the establishment of marram grass. In **chapter 4**, we determined the effect of sand couch and its embryonic dune attributes (elevation, distance to sea and sediment dynamics) on establishing marram grass individuals using a field experiment (Figure 1.5.4). Subsequently, we experimentally tested whether the interactions between sand couch and establishing marram grass changed under pressure of extreme heat and drought (**Chapter 5**, Figure 1.5.5).

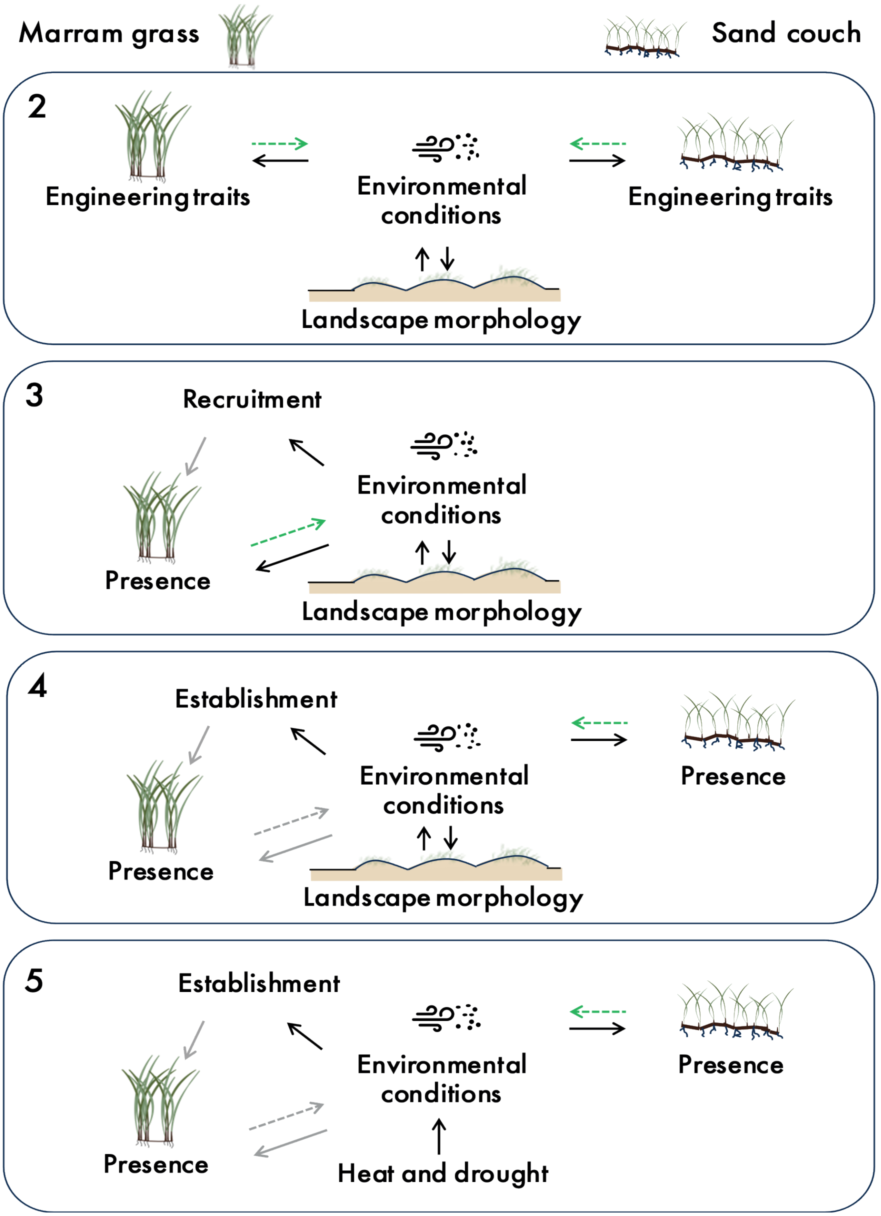


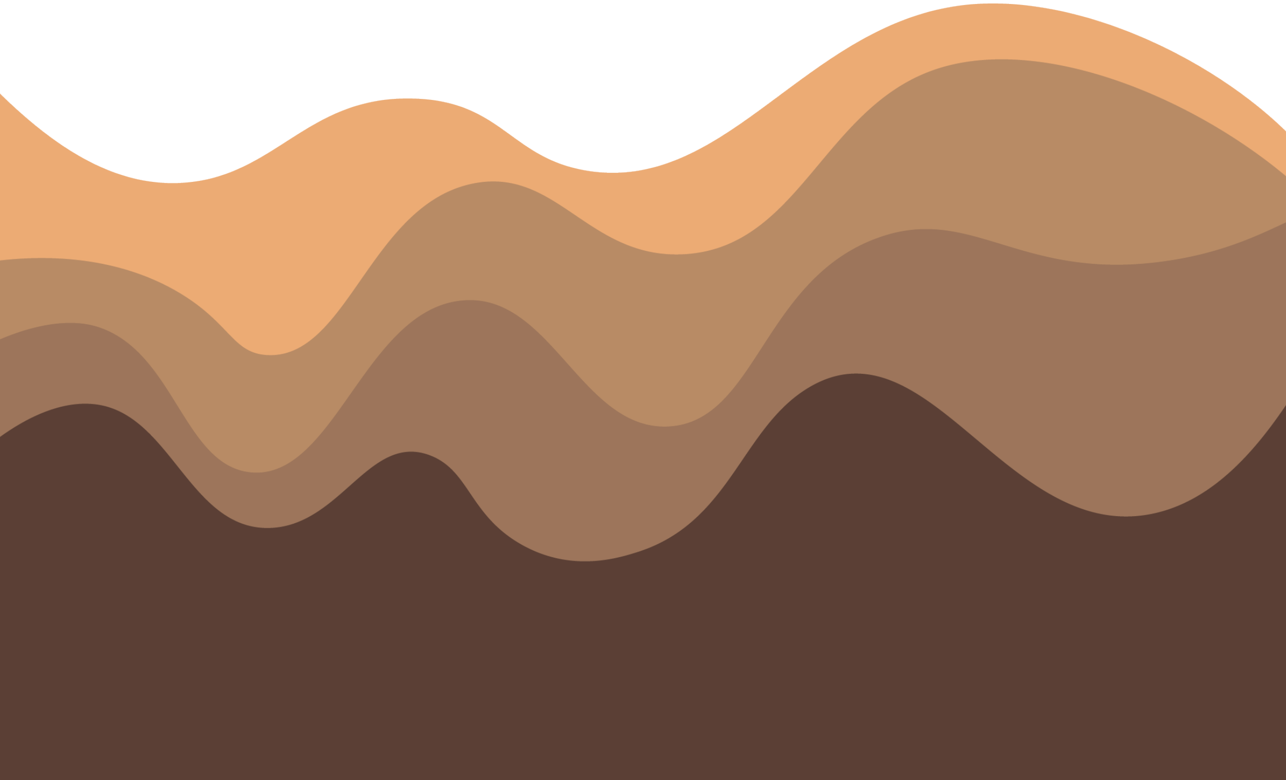
Figure 1.5: An overview of the interactions studied in the chapters of this thesis. The arrows indicate effects, with green arrows being plant-mediated (that is, biotic) effects and grey arrows representing interactions that were not examined.

CHAPTER 2

Are ecosystem engineering traits fixed or flexible: A study on clonal expansion strategies in co-occurring dune grasses

Carlijn Lammers, Clea N. van de Ven, Tjisse van der Heide & Valérie C. Reijers

Ecosystems (2023)



Abstract

Many vegetated coastal ecosystems are formed through ecosystem engineering by clonal vegetation. Recent work highlights that the spatial shoot organization of the vegetation determines local sediment accretion and subsequently emerging landscape morphology. While this key engineering trait has been found to differ between species and prevailing environmental conditions, it remains unknown how the interplay of both factors drive shoot organization and therefore landscape morphology. Here, we compared the spatial shoot organization of young, clonally expanding plants of the two dominant European dune grass species: sand couch (*Elytrigia juncea*) and marram grass (*Ammophila arenaria*) across a range of coastal dune environments (from Denmark to France). Our results reveal that, on average, sand couch deployed a more dispersed shoot organization than marram grass, which has a patchy (Lévy-like) organization. Whereas sand couch exhibited the same expansion strategy independent of environmental conditions, marram grass demonstrated a large intraspecific variation which correlated to soil organic matter, temperature, and grain size. Shoot patterns ranged from a clumped organization correlating to relatively high soil organic matter contents, temperature, and small grain sizes, to a patchy configuration with intermediate conditions, and a dispersed organization with low soil organic matter, temperature, and large grain size. We conclude that marram grass is flexible in adjusting its engineering capacity in response to environmental conditions, while sand couch instead follows a fixed expansion strategy, illustrating that shoot organization results from the interaction of both species-specific and environmental-specific trait expression.

Keywords: biogeomorphology, coastal dunes, clonal expansion, *Ammophila arenaria*, *Elytrigia juncea*, ecosystem engineer, interspecific variation, intraspecific variation

Highlights

- Co-occurring dune grasses have different shoot organizations
- Shoot organization is more flexible in marram grass than in sand couch
- Dune grasses’ engineering traits are both species- and environment-dependent

1. Introduction

Vegetated coastal ecosystems such as coastal dunes, salt marshes and seagrass beds are among the most productive ecosystems in the world and provide important goods and services, including flood protection, carbon sequestration, biodiversity enhancement and tourism (Barbier et al., 2011; Burke et al., 2001; Martínez et al., 2007). The emergence and maintenance of these ecosystems depend on the interaction between sediment stabilization by vegetation and sediment transport by flows of wind or water (Balke, 2013; Corenblit et al., 2011; Jones et al., 1994). With its physical structures the vegetation attenuates wind or water flow, causing airborne or water-suspended sediments to settle. In turn, sedimentation (and other plant induced changes) can feed back to the plant's trait expression, such as shoot elongation or vertical rhizome development, making these systems feedback driven (Hacker et al., 2019; Maun, 1998). The extent to which flows are reduced depends on plant structural traits, such as shoot density, flexibility and length (Bouma et al., 2013; Hacker et al., 2012). Generally, higher sedimentation rates are associated with dense, inflexible and tall vegetation (Bouma et al., 2013; Goldstein et al., 2017; Hacker et al., 2019; Mullins et al., 2019). However, short vegetation can have a higher local sediment trapping compared to a more downwind sediment accumulation of tall vegetation (Hesp et al., 2019). Consequently, variation in structural traits of individual plants can affect large-scale landscape morphology (Baas & Nield, 2007; Corenblit et al., 2015; Hacker et al., 2019; Schwarz et al., 2018).

Coastal dunes occur along wave-dominated sandy shores and protect about one-third of the world's shoreline (Durán & Moore, 2013; Martínez et al., 2007). Dune grasses are the main ecosystem engineering species responsible for building coastal dune landscapes (Feagin et al., 2015). It has long been recognized that shoot density is an important structural trait determining the engineering capacity of dune grasses (e.g., Hesp, 1989; Zarnetske et al., 2012; Hacker et al., 2019). In dense vegetation, local sedimentation rates are high, but area colonization is slow resulting in high and narrow dunes. In contrast, sparse vegetation leads to rapid colonization but low local sedimentation rates, resulting in lower and broader dunes (Hacker et al., 2012, 2019; Hesp, 1989; Zarnetske et al., 2012). Shoot density, and consequently dune shape, is commonly presented as a species-specific trait (Goldstein et al., 2017; Hacker et al., 2019; Zarnetske et al., 2012). Thus far, most field studies have concentrated on comparing differences in shoot densities and their effects in established dune grasses that already formed (embryonic) dunes.

However, differences in structural traits in the initial stages of beach colonization can be at least as important because they potentially have a stronger effect on dune formation by controlling plant survival and sand capture from the start. Recently, it was found that young, establishing dune grass individuals of two species of Ammophila (American beachgrass (*Ammophila breviligulata*) and marram grass (*Ammophila arenaria*)), rather than having a uniform or random shoot organization, deploy a more patchy clonal expansion strategy (Reijers, Siteur, et al., 2019). Strikingly, their shoot organization could be well described by heavy-tailed random walk models in which many smaller steps are alternated by an occasional longer step, that are commonly used to describe optimization in animal search behaviour (Reijers, Siteur, et al., 2019). The two beach grass species were found to employ somewhat different clonal expansion strategies. Supporting experiments revealed that these clonal expansion strategies allowed the plants to balance plant expansion and sediment accretion (Reijers, Siteur, et al., 2019). American beachgrass displayed the most dispersed strategy, which was associated with the highest overall sediment accretion over a large area (i.e., maximized total entrapped sand volume). The more patchy organization of marram grass instead maximized dune building efficiency (i.e., investment in clonal growth versus entrapped sand volume) (Reijers, Siteur, et al., 2019). Follow-up work in two contrasting environments and under experimental conditions highlighted that marram grass shifts its shoot placement strategy depending on sediment availability. When deprived of sediment the plant exhibited a clumped, single-patch organization, whereas the characteristic patchy organization emerged in response to sediment burial (Reijers et al., 2021). While our previous work demonstrates adaptability of shoot organizations in contrasting environments, a continuous gradient in environmental conditions was lacking. Moreover, whether co-occurring dune-building grasses deploy similar expansion strategies in the same environment or adapt comparably to changes in sediment availability remains unknown.

In this study, we investigated 1) how the clonal expansion strategy differs between two co-occurring dune grass species with contrasting dune shapes: sand couch (*Elytrigia juncea*) and marram grass (*Ammophila arenaria*), and 2) how local environmental conditions (that is, soil organic matter, nutrients levels, grain size, distance to sea, temperature, precipitation and wave conditions) affect trait expression of both species by comparing individuals of the same species along the Northwestern European coast (Denmark-France). Sand couch and marram grass are native, often co-occurring European species and are the dominant dune building species along the Northwestern European coast (Figure S2.1). Both species have a rhizomatous clonal growth, with marram grass having the ability to create vertical and horizontal rhizomes while sand couch only creates horizontal rhizomes (Harris & Davy, 1986a; Huiskes, 1979). Generally, marram grass relies on establishment from rhizomal fragments on the beach/foredune interface (Huiskes, 1977), while for sand couch establishment from seeds and from clonal fragments both occur (Harris & Davy, 1986a). Usually, sand couch grows closer to the sea than marram grass, where it initiates dune building by creating low and broad dunes, after which marram grass colonizes and forms higher and more narrow dunes (Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017). Generally, the high, narrow dunes of marram grass are associated with high resistance, while the lower, broader dunes of sand couch potentially build a more resilient landscape, similar to pioneer species on the US east coast (Feagin et al., 2015; Zinnert et al., 2017). The species have some distinct differences in their morphology and physiological tolerance, with sand couch having a higher salt tolerance, shorter shoot length and lower shoot density (Bakker, 1976; Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017).

We hypothesize that in general, sand couch displays a more dispersed shoot pattern than marram grass, corresponding to the observed differences in dune morphologies (Figure S2.1). We expect both species to have context-dependent shoot organizations, but eco-evolutionary mechanisms behind the shoot organizations to be different. Specifically, we expect marram grass to change from a clumped to patchy organization with increase in sediment supply (Reijers et al., 2021), which is generally higher on wide, dissipative beaches (Delgado-Fernandez, 2010; Walker et al., 2017). In contrast, we hypothesize that sand couch's shoot organization is mostly affected by nutrient levels, especially by nitrogen which is generally the most limiting resource in the beach-dune landscape (Kachi & Hirose, 1983; Reijers, Lammers, et al., 2019; Willis, 1965). This hypothesis follows earlier findings on *Elymus mollis*, the pioneer dune grass of the US west coast, that invests more in long rhizomes (dispersed shoot organization) under higher nitrogen levels than marram grass (Pavlik, 1983). Here, we expect a similar response in sand couch with a more dispersed organization at locations with higher nitrogen levels.

2. Methods

2.1. Field survey

We determined the clonal expansion strategies of sand couch (*Elytrigia juncea*) and marram grass (*Ammophila arenaria*) at nine locations along the Northwestern European coast (Figure 2.1). The sampling sites were visited once during the growing season of 2019 (June-October) and were selected for their presence of young, establishing vegetation on the beach/foredune interface where sand is directly supplied from the foreshore. Except for the island of Griend, all selected locations were publicly accessible. However, no beaches with recreational facilities (e.g., restaurants or sports) were selected. Furthermore, all locations are Natura 2000 areas except the dunes near Lemvig (Denmark). These systems have a wide variety in physical conditions such as beach width (ranging from 30 to 800 meters, beach width strongly correlated (r=0.99) with plant-to-sea distance which is used hereafter) and significant wave height (ranging from 0.3 to 1.1 meters) (Table S2.1). Out of these nine sites, young, establishing patches of sand couch and marram grass co-occurred at three sites. At three sites, only isolated patches of establishing sand couch were present, and in the remaining three only isolated patches of marram grass were found. At all locations both species were present in later successional stages.

To determine the plant's clonal expansion strategy, we followed methods as described by Reijers, Siteur et al. (2019). In brief, we selected isolated establishing plants at each location (Table S2.1). From each clonal individual, we cut off and replaced all shoots with a labelled pin. The coordinates of shoots (in cm) were extracted from calibrated still images (between 100*100cm and 150*150cm) using a custom-made MATLAB tool (Reijers & Hoeks, 2019). Subsequently, the step size distribution of each individual plant was determined by connecting all individual shoots of the clonal individual using a nearest neighbour connection algorithm. Each individual was excavated to verify rhizomal connections between the shoots (i.e., confirm that the selected vegetation patch consists of one clonal individual). For characterization of the clonal expansion strategy, we included only those individuals where connections between all shoots were confirmed.

In addition, we determined four other plant traits – shoot length, shoot diameter, tissue nitrogen content and C/N ratio – from each plant. Prior to cutting of the shoots, the length and diameter of five randomly selected shoots were measured. We collected leaf tissue (pooled per clonal individual) to assess leaf nitrogen and carbon levels. After freeze-drying the leaves, they were ground using a ball mill (MM400, Retch Haan, Germany). Using ~1 mg of the homogenized sample, C and N concentrations were determined using an elemental analyser (Carlo Erba NA1500, Thermo Fisher Scientific, Waltham, MA, USA).

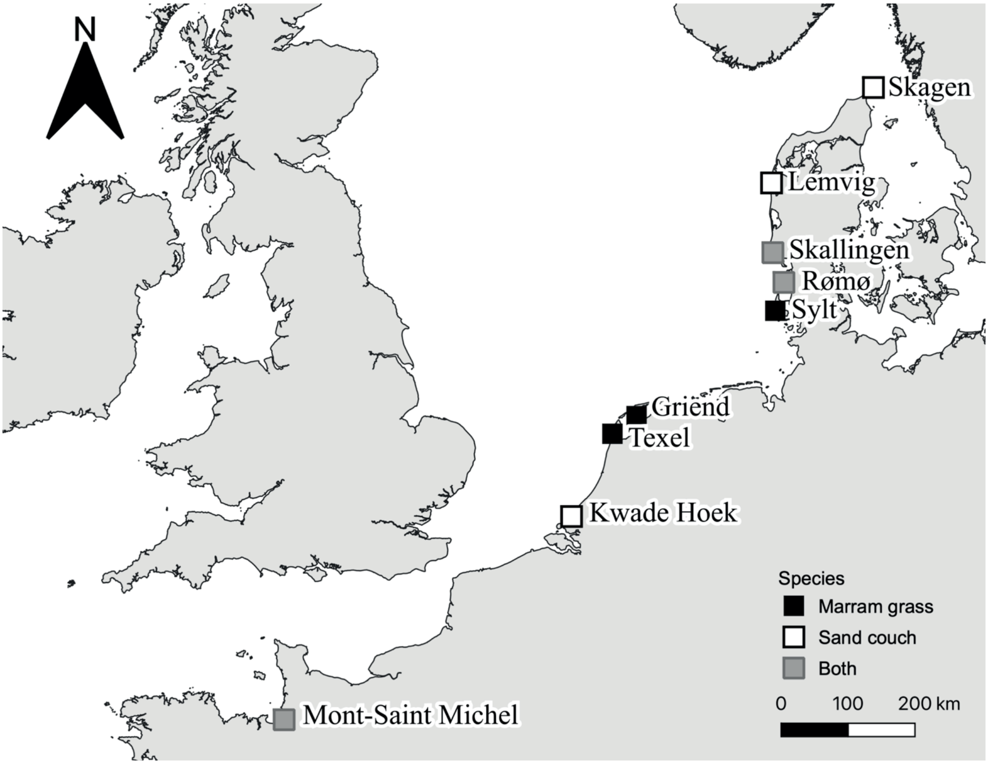


Figure 2.1: Overview of sampling locations along the European coast. Colours indicate if marram grass (black), sand couch (white) or both species (grey) were measured. For an overview of numbers of sampled individuals and environmental characteristics, see Table S2.1.

Finally, we obtained eight environmental variable that characterize each site: organic matter, grain size distribution, sediment total N, orthophosphate, significant wave height, distance to sea (i.e., beach width), average annual temperature and precipitation. Grain size, organic matter, and plant available nitrogen and phosphorus were determined in soil samples taken from between the roots. Grain size was determined in a freeze-dried subsample of the soil using a laser diffraction and polarization intensity differential scattering technology with a particle size analyser (Coulter LS 13 320). Soil organic matter was expressed as loss on ignition (4h, 550 °C). Salt extracts were taken using 17.5 g fresh soil in 50 ml of 0.2 M NaCl. In the extracts, nitrogen and phosphorus levels were determined using an AutoAnalyzer 3 system (Brand and Luebbe, Norederstedt, Germany or Skalar and Seal autoanalyzer). Distance to sea was used as a proxy of beach width, and general sand supply (Delgado-Fernandez, 2010; Walker et al., 2017), and was retrieved for each individual plant. Significant wave height was obtained at the level of each location (sources see Table S2.2), and mean annual temperature and precipitation were retrieved from the closest official weather station for the period 2016-2019 (from local meteorological institutes, sources see Table S2.2).

2.2. Characterizing clonal expansion strategies

To characterize the clonal expansion strategy, the step size distribution was determined for each individual using a nearest neighbour connecting algorithm which was previously validated for marram grass by Reijers, Siteur, et al. (2019). This algorithm consecutively searches the nearest neighbour until all shoots (N) are connected and selects the shortest possible route among N iterations to derive aboveground distances (step-sizes) between shoots. The expansion strategy was determined for the individuals with sufficient step size data (over 30 connections). Smaller plants were discarded from further analyses. Five commonly used random walk models for describing movements were used to describe the observed step size distributions: an exponential (Brownian), a two-mode exponential (Composite Brownian), a log-normal, a power-law (Lévy) and a truncated power-law (truncated Lévy) (see Supplement for a detailed description of different models). We used a Kolmogorov-Smirnov (KS) test to assess whether the observed step sizes were significantly different from the fitted distributions (more info in Supplement). Models were compared with each other using weighted AIC values (Wagenmakers & Farrell, 2004).

Individuals were compared using the scaling exponent (μ) of the truncated Lévy model, as this model was never rejected by the KS-test, and thus fitted acceptably to all individuals (Table S2.3). Thus, for every included individual plant, the observed step size distribution was not significantly different from a truncated Lévy distribution. The probability density function of the truncated Lévy distribution is given by

$$P(s) = \frac{\mu - 1}{s_{min}^{\mu-1} - s_{max}^{\mu-1}} s^{-\mu}$$

For each individual, the minimum step size (s_{min}) was estimated using KS statistics (Clauset et al., 2009). For some of the plants, the estimated s_{min} led to a large loss of steps (>33% loss or <30 steps remaining); in these cases, the measured minimal step size was used as s_{min} with a fixed minimum of 0.68 cm, which is twice the measuring error calculated from translating pixels to cm (~0.34 cm). The scaling component (μ) was determined using maximum-likelihood estimator given that

$$\frac{dLL}{d\mu} = 0$$

And

$$LL = nln\left(\frac{\mu - 1}{{s_{min}}^{\mu - 1} - {s_{max}}^{\mu - 1}}\right) - \mu\sum\nolimits_{i=1}^{n} lns_i$$

with n being the number of shoots and s being the step size. The scaling component of the truncated Lévy is an indication of the shoot organization with lower values indicating a higher proportion of large step sizes (i.e., a more dispersed growth).

2.3. Statistical analysis

Model fitting, validation and verification were done in MATLAB (version 2020b, The Mathworks, Inc.). Further statistical analyses were performed in R (version 3.6.1). First, a general impression of clonal expansion strategies of both species was made using pooled step size data of all individuals. Second, plant traits (i.e., μ exponent of the truncated Lévy, shoot length and diameter, leaf nitrogen and C/N ratio) were compared between locations and species using ANOVA combined with Fisher's least significant difference (LSD) post hoc tests. In addition, the variance in plant traits between both species was tested with a Levene's test. For every test, normality of the residuals was checked and, if needed, the data was transformed using log transformation. P values lower than 0.05 were considered statistically significant.

Principle component analysis of environmental variables (i.e., soil organic matter, median grain size, total soil nitrogen and phosphate, distance to sea, average annual temperature and precipitation and significant wave height) was used to determine which environmental variables were most important in differentiating locations. All variables were averaged per location, centred and standardized to account for different units of the measured variables. Subsequently, it was tested whether the first two principal components correlated with plant traits for both species. Furthermore, the correlation between the individual environmental variables and plant traits was tested. As there were multiple non-normally distributed factors, we based the correlations on Spearman's rank correlation.

3. Results

3.1. Interspecific variation in traits

3.1.1. Clonal expansion strategies

Sand couch had a more dispersed shoot organization (i.e., relatively more large steps) than marram grass as showed by the pooled step size data (Figure 2.2,

Figure S2.2). On average, the expansion strategies of both sand couch and marram grass were best described by heavy-tailed distributions, indicating a patchy strategy that most strongly resembled a Composite Brownian (sand couch) and a truncated Lévy (marram grass) (Figure 2.2). The heavy-tailed distributions (Composite Brownian, Lévy and truncated Lévy) were also the model expansion strategies that best fitted most individual plants (89% of the sand couch individuals and 91% of marram grass individuals) (Figure 2.2, Table S2.3). However, the variation in best fitting models was larger for marram grass than for sand couch, with most marram grass individuals resembling a Lévy distribution (57%), followed by a truncated Lévy (26%) and Composite Brownian (9%). For sand couch, a truncated Lévy distribution was the best fit for 75% of the plants. This indicates a larger variation in shoot organizations within marram grass compared to sand couch. Overall, the truncated Lévy distribution was the model that fitted most individuals (48% in both species combined) and was not rejected for any of the individuals based on KS-statistics (Table S2.3). On average, the μ exponent of the truncated Lévy for sand couch individuals was 1.52±0.038, which reflects a dispersed distribution (Figure 2.3, Figure S2.3). Marram grass had a significantly higher μ exponent reflecting a patchier shoot organization (2.05±0.070, $F_{1,61}=38.49$, $P<0.001$, Figure 2.3, Figure S2.3).

3.1.2. Other traits

On average, sand couch had shorter shoots than marram grass (28.0±1.7 vs 48.1±2.1 cm, respectively, $F_{(1,44)}=33.30$, $P<0.001$, Figure S2.4), with a similar shoot diameter (2.7±0.08 (marram grass) vs 2.5±0.1 (sand couch) mm, $F_{(1,44)}=3.61$, Figure S2.4). Nitrogen levels in the leaf tissue of sand couch were significantly higher than in marram grass (30.5±1.4 mg g^{-1} (sand couch) vs 17.3±0.7 mg g^{-1} (marram grass), $F_{(1,48)}=83.11$, $P<0.001$, Figure S2.4), which also led to a lower C/N ratio in sand couch (16.5±0.9 (sand couch) vs 28.3±1.3 (marram grass), $F_{(1,48)}=73.15$, $P<0.001$, Figure S2.4).

3.2. Intraspecific variation in traits

The variation in shoot organization was much larger for marram grass than for sand couch (Levene's test, $F_{1,61}=10.9$, $P=0.002$, Figure 2.3, Figure S2.5). Sand couch displayed a similar shoot organization across locations, while marram grass ranged from a clumped configuration on Griend (μ = 2.51±0.10) to a dispersed, sand couch-like, organization on Rømø (μ = 1.67±0.11, Figure 2.3, Figure S2.3). Furthermore, the variance in leaf nitrogen levels was larger in sand couch than in marram grass (ranging from 1.9 ± 0.1% at Skagen to 3.9±0.1% at Lemvig for sand

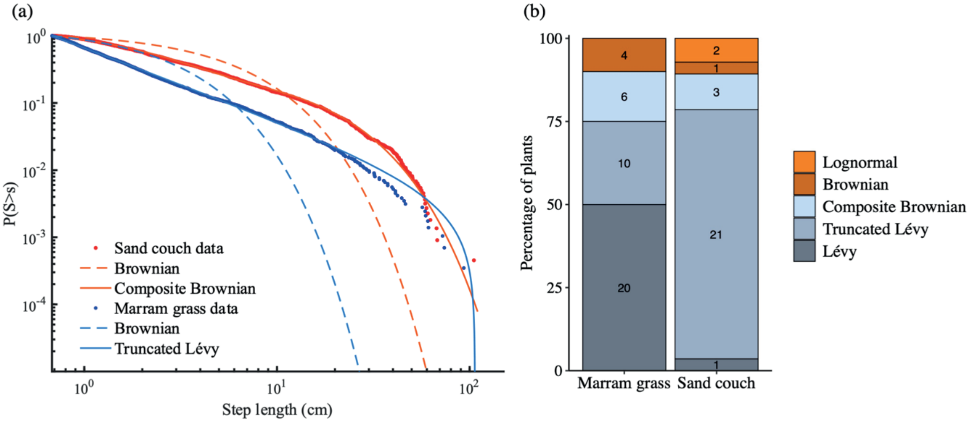


Figure 2.2: ***A)*** *The clonal growth strategy showed as the inverse cumulative frequency distribution of the pooled step sizes of marram grass (Ammophila arenaria, blue point data, 2875 steps) and sand couch (Elytrigia juncea, red point data, 2211 steps). The slope of the sand couch data is less steep than the one of marram grass, representing a larger number of longer steps in sand couch and thus a more dispersed growth.* ***B)*** *Percentage of best fitting random walk models per species based on wAIC values. The numbers within the bars represent the number of individuals with the corresponding best fitting random walk distribution. Most of the plants (of both species) displayed a heavy-tailed distribution (Composite Brownian, Truncated Lévy or Lévy).*

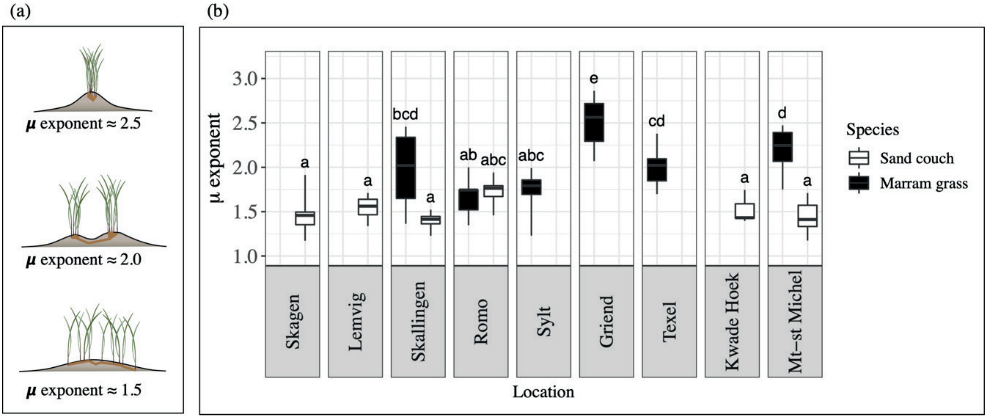


Figure 2.3: The clonal expansion strategies of sand couch (E. juncea) and marram grass (A. arenaria) found along the European coast with; ***A)*** *A conceptual depiction of how shoot organization relates to the μ exponent of the truncated Lévy distribution and* ***B)*** *the found μ exponents of sand couch and marram grass at sampled locations, showing a larger variation in clonal growth strategies of marram grass than sand couch. The horizontal bars depict median value, box height the first and third quartile and whiskers the minimum and maximum values. Locations are ordered from north to south (left to right). Letters depict LSD post hoc grouping ($P < 0.05$).*

couch and 1.5 ± 0.2 % at Sylt to 2.0 ± 0.2 % at Texel in marram grass, Levene's test, $F_{1, 58}$=9.90, *P=0.003*, Figure S2.4). The variance of shoot length and diameter was similar for both species but did differ between locations (Figure S2.4).

3.3. Correlation of intraspecific traits with environmental variables

In the principal component analysis, axis 1 explained 38.8% of the environmental variation between locations with soil organic matter (r=0.94), significant wave height (r=-0.84) and average annual temperature (r=0.74) being the most highly weighted variables (Figure 2.4, Table S2.4). Axis 2 explained 18.1% with grain size (r=0.71), temperature (r=0.62) and precipitation (r=-0.49) begin most influential (Figure 2.4, Table S2.4). No significant correlations between PC1, PC2 or individual environmental variables and shoot organization of sand couch were found. For marram grass, PC1 correlated significantly with the scaling exponent and shoot length (Table 2.1). From the individual environmental variables, soil organic matter and average annual temperature correlated positively to the scaling component of marram grass (r=0.60, *P<0.001* and r=0.36, P=0.04, respectively, Table 2.1), indicating a shift from dispersed to a clumped organization with increase in soil organic matter and temperature. Median grain size correlated negatively (r=-0.43, *P*=0.01), indicating a more dispersed organization with increase in grain size (Table 2.1).

For both species plant traits correlated to multiple environmental variables (Table 2.1). For marram grass, shoot length had the strongest correlation with soil organic matter and grain size (similar to shoot organization; r=0.58, *P<0.001* and r=-0.43 *P=0.01*, respectively). Furthermore, the shoot diameter was most strongly correlated with distance to sea and significant wave height (r=0.47, *P=0.006* and r=-0.46, *P=0.02*, respectively) while no correlations between foliar nitrogen or C/N ratio and environmental variables were found. For sand couch, shoot length correlated significantly with soil phosphate level and grain size (r=-0.57, *P=0.003* and r=0.67, *P<0.001*, respectively), shoot diameter correlated to soil organic matter (r=0.46, *P=0.02*) and foliar N level and C/N ratio correlated to soil nitrogen content (r=0.43, *P=0.03* and r=-0.48, *P=0.01*, respectively).

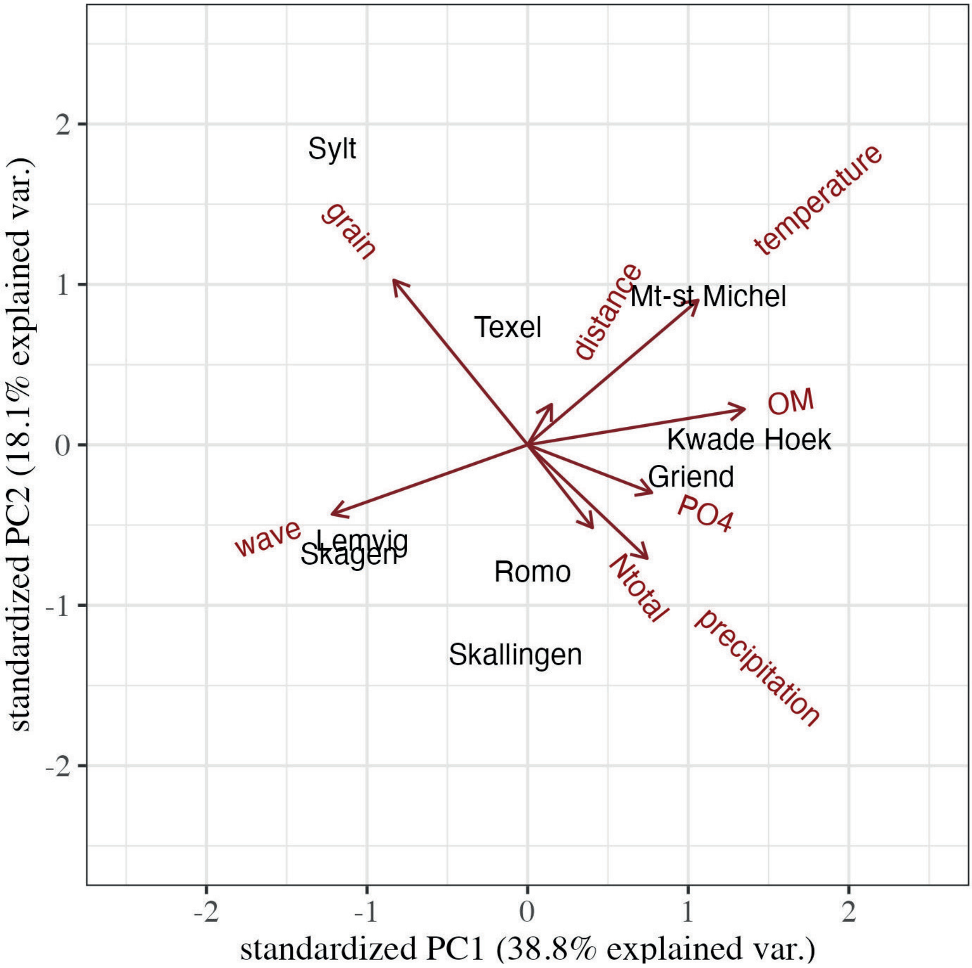


Figure 2.4: Principal component analysis including averaged environmental variables per location. Soil organic matter (OM), significant wave height (wave) and temperature were the most important for PC1, which explained 38.8% of the variation. Grain size (grain) and precipitation were most influential for PC2, which explained 18.1% of the variation.

Table 2.1: Correlation matrix comparing measured plant characteristics (columns) and environmental variables. Including correlations for marram grass (top) and sand couch (bottom). Numbers represent Spearman's rank correlation coefficient. Only significant correlation coefficients (P>0.05) are presented.

Maram grass	**µ exponent**	**Shoot length (cm)**	**Shoot diameter (mm)**	**%N Leaf**	**C/N ratio Leaf**
PC1	0.48	0.59			
PC2					
Soil organic matter (%)	0.60	0.58			
Significant wave height (m)			-0.46		
Average annual temperature (°C)	0.36				
Soil phosphate level (mg g^{-1})		0.35			
Average annual precipitation (mm)					
Median grain size (µm)	-0.43	-0.56			
Soil nitrogen level (mg g^{-1})			0.37		
Distance to sea (m)			0.47		
Sand couch					
PC1			0.43		
PC2			0.46		
Soil organic matter (%)					
Significant wave height (m)					
Average annual temperature (°C)					
Soil phosphate level (mg g^{-1})		-0.57			
Average annual precipitation (mm)					
Median grain size (µm)		0.67			
Soil nitrogen level (mg g^{-1})				0.43	-0.48
Distance to sea (m)					

4. Discussion

In our comparison of clonal expansion strategies of dune grasses across Northwestern Europe, we found that heavy-tailed expansion strategies dominate for both species. Thus, most individuals deploy a strategy that deviates from a simple dense vegetation patch and display a more patchy shoot organization, balancing expansion rate and sediment capturing efficiency (Reijers, Siteur, et al., 2019). However, pattern characteristics differed between both species with sand couch demonstrating a more dispersed shoot organization associated with sand capture over a large area, while the patchier organization of marram grass is associated with high local sand-capturing efficiency (Reijers, Siteur, et al., 2019). Whereas marram grass expressed intraspecific variation in clonal expansion strategy, from dispersed to clumped which correlated with soil organic matter, temperature and grain size, contrary to our expectations, sand couch demonstrated very little variation. These findings demonstrate that shoot organization is not solely a species-specific or environmental-specific trait, but instead depends on the interaction of these two variables. Hence, our study highlights the need to study key traits for ecosystem engineering species and associated engineering strength across a range of environmental conditions and through time to understand the reciprocal interactions between trait expression, environmental conditions and the ecosystem engineering capacity.

4.1. Relation between interspecific variation in structural traits and dune morphologies

The two dominant dune building grasses of Western Europe are associated with different dune morphologies. Whereas dunes formed by sand couch remain relatively low (max ±3 m), they are much broader than the high (max ±20 m) dunes formed by marram grass (Bakker, 1976; van Puijenbroek, Nolet, et al., 2017, Figure S2.1). Similar to previous studies comparing North American beach grasses (Hacker et al., 2019), we found clear differences between the species' structural traits (e.g., shoot length and shoot pattern) that are associated with differences in sand capturing ability (Zarnetske et al., 2012; Reijers, Siteur et al., 2019). The dispersed growth of sand couch promotes sand capture over a large area, consequently building relatively low and broad dunes, while the patchier growth strategy of marram grass is associated with higher local sand trapping efficiency, promoting a taller and narrow dune form (Reijers, Siteur, et al., 2019). Additionally, sand couch had on average a lower shoot length which is associated with less per-shoot flow reduction and thus less sediment accretion (Hesp, 1989; Van Dijk et al., 1999). This suggests that in similar conditions marram grass has locally higher sedimentation rates, leading to the emergence of higher, but steeper dune profiles than sand couch (Figure S2.1).

As a result of the difference in shoot organization and length, it is likely that changes of flooding are higher for sand couch than for marram grass in similar conditions during dune development, from plant establishment to foredune formation. However, as sand couch is more salt tolerant, it is less vulnerable to flooding (Sykes & Wilson, 1989; van Puijenbroek, Teichmann, et al., 2017). Instead, flooding may even be beneficial for sand couch as nutrients are transported to the beach during overwash (Reijers, Lammers, et al., 2019). In contrast, marram grass is known to perform well in nutrient-poor conditions as the species can recycle its own material through litter-decomposition feedbacks and thus requires less allochthonous material transported during overwash events to grow (Kooijman & Besse, 2002). In line with this, we found that foliar nitrogen levels of sand couch correlated with soil nitrogen levels, while no significant correlation was found in marram grass. Overwash events do not only transport material from the sea to the coast (e.g., sediment and nutrients) as wave run-ups during storm surges can cause massive dune erosion (Haerens et al., 2012; van Puijenbroek, Limpens, et al., 2017; Vellinga, 1982). Whereas marram grass can vertically outgrow high burial rates by building a strong underground network of roots and rhizomes that bind sand and resist erosion, the more sparsely growing sand couch outgrows accumulated sand through shoot elongation leaving the dune body more vulnerable to erosion (Feagin et al., 2015; Konlechner et al., 2016; van Puijenbroek, Limpens, et al., 2017). However, the higher nutrient use efficiency causes sand couch to exhibit a faster recovery and higher recolonization potential than marram grass which makes this species less vulnerable to erosion events on a population level (Harris & Davy, 1986b; Reijers, Lammers, et al., 2019; Sykes & Wilson, 1990; van der Putten, 1990).

Based on the observed differences in species' structural traits (e.g., shoot length and organization) and dune morphologies, we hypothesize that sand couch has evolved towards building a dune landscape that balances the risks of flooding and erosion (i.e., dislodgement, osmotic stress) with its potential benefits (i.e., nutrients, low burial), whereas we expect that marram grass has evolved to maximize sand capture to escape flooding completely. In that light, the so-called pioneer species sand couch could have adopted a dispersed clonal expansion strategy associated with rapid expansion and high resilience, whereas the patchy strategy of marram grass promotes high local engineering associated with building resistance, but lower resilience (Reijers, Lammers, et al., 2019). To disentangle such feedback relationships, we suggest that plant trait expression, physical conditions, vegetation-sedimentation feedbacks and coastal morphodynamics need to be monitored in the field over the course of multiple years.

4.2. Intraspecific variation in clonal expansion strategies of different dune grass species

We expected both species to express variation in clonal expansion strategy in response to their environment, with marram grass responding to sediment supply (i.e., with increase in distance to sea) and sand couch to nitrogen levels. However, whereas the clonal expansion strategy of marram grass clearly differed between locations, the strategy of sand couch hardly varied (Figure 2.3, Figure S2.5). Contrary to our expectations, we found no correlation between distance to sea (for example, beach width) and the shoot organization of marram grass and no response of sand couch to differences in soil nitrogen levels. The latter finding seemingly contrasts with earlier experimental studies on an American pioneer dune grass that found that lower nitrogen levels promote biomass allocation to the rhizomes to escape nutrient stress and increase landscape colonization rates (Pavlik, 1983). However, our values are similar or even lower than the low nitrogen levels used in the experimental study, which were described as “nutrient stress”. Although we found more variation in leaf nitrogen levels for sand couch than marram grass (from 1.7% to 4.2% vs 1.0% to 2.7%), we report no variation in shoot organization for sand couch.

In line with previous findings (Reijers et al., 2021) for marram grass, we found a clear variation in the clonal expanding strategy, ranging from clumped (max μ exponent of 2.9) to dispersed (min μ exponent of 1.2) with on average a Lévy-like expansion strategy. Although our previous work showed that a trait shift in expansion strategy could be related to different sediment supply rates – with a clumped strategy being the most efficient at low sedimentation rates and a patchy to dispersed strategy at higher sedimentation rates (Reijers et al., 2021) – in our current study we find no correlation with distance to sea, which was used as a proxy for sediment availability (Delgado-Fernandez, 2010; Walker et al., 2017). Instead, we found that the scaling component was positively correlated with soil organic matter and temperature and negatively correlated with grain size (Table 2.1).

Generally, higher soil organic matter levels and sediment with a smaller grain size are found in more sheltered locations, that experience less disturbance and are associated with lower sedimentation rates (Incera et al., 2003; Nylén et al., 2015). On these locations – with a relatively high soil organic matter content and small grain size – marram grass displayed a more clumped shoot organization (that is, a higher scaling exponent). Another explanation for the positive correlation between soil organic matter and shoot clumping may be that retention of water, which is a scarce resource in these sandy systems, increases with increase in soil organic matter content. As a result the local environment becomes increasingly favourable causing the plant to place new shoots in close proximity (Rawls et al., 2003). Furthermore, higher temperatures were correlated with a more clumped organization. However, previous studies found no correlation between dry mass production or tillering and temperature in marram grass (Biel & Hacker, 2021; Huiskes, 1979). It is possible that the found positive correlation is rather an effect of site selection than of temperature (for example, more sheltered locations were selected at lower latitudes), additional field observations are needed to disentangle these effects.

Other included environmental factors did not correlate with observed differences in clonal expansion strategy. However, some correlations with shoot length and diameter were found. No clear pattern in environmental variables and these plant traits between species was visible (or even contrasting correlations were found). As the age of the individuals and some environmental variables (i.e., elevation or overwash history) were unknown, climatic events such as storms or droughts that might impact plant traits could not be included. Additionally, for some of the included variables the spatiotemporal resolution (Table S2.2) might be too coarse to assess the relation between individual trait expression and local environmental conditions. Next to variation in environmental conditions, the unexplained variation in clonal expansion may be caused by genetic variation between individuals and locations (Rodríguez-Echeverría et al., 2008). Little is known about the genetic variation within and between marram grass populations and the relation between trait expression and genetic variation. Future research that includes genetic diversity could disentangle the effects of environmental variability and genetic variation on trait expression in landscape forming species. Overall, our results demonstrate that the expression of this key ecosystem engineering trait is dependent on species identity and is relatively fixed for sand couch, but flexible for marram grass. Therefore, we emphasize that trait-based approaches and biogeomorphic models that use mean trait values derived from trait databases should be aware of potential intraspecific differences in trait expression (Brückner et al., 2019; De Battisti et al., 2019). Furthermore, we argue that extensive field sampling with repeated measures to link vegetation growth patterns and landscape morphodynamics is essential to understand the complex interactions between multiple factors including species identify, genetic background, environmental conditions and individual age that together steer trait expression.

4.3. Implications for restoration

Marram grass has been introduced around the world to stabilize drifting sand and fortify coastal landscapes (e.g., Hertling & Lubke, 1999; Gadgil, 2002; Rozé & Lemauviel, 2004; Nordstrom, 2021). Within its native range, our survey demonstrated that environmental conditions impact its spatial organization, while planting designs are, irrespective of environmental conditions with 30 to 60 cm spacing between individuals, in dispersed competition-limiting arrays (van der Putten, 1990). Over the last decades, emphasis on including intraspecific facilitation (i.e., changing to a clumped, facilitation maximizing design) in restoration of vegetated coastal ecosystems increased (Fischman et al., 2019; Silliman et al., 2015; Sofawi et al., 2017; Temmink et al., 2020). While many of these studies stress the importance of intraspecific facilitation, our results imply that the optimal planting design is context-dependent (van der Heide et al., 2021) and species-specific (Reijers et al., 2021; Reijers, Siteur, et al., 2019). Our results suggest that for marram grass, restoration efficacy could be increased by understanding more in depth the relation between plant organization and physical conditions. For sand couch, our work predicts that the optimal planting design would be dispersed – but still heavy-tailed patchy – irrespective of the location.

Outside its native range, marram grass plantings have drastically altered coastal dune environments by changing dune morphology, reducing sediment transport to the hinterland and lowering local biodiversity (e.g., in New Zealand, South Africa and USA) (Gadgil, 2002; Hertling & Lubke, 1999; Pickart, 2021). Dunes planted with marram grass generally grow higher, more stable and homogeneous. While these high dune landscapes formed by marram grass are resistant – by withstanding and mitigating storm surges – the lower dunes that are formed by faster growing native grasses might be more resilient as they possibly have higher recovery potential after erosive events (Pickart, 2021). By planting ecosystem engineering species with different structural traits or trait-environment relationships, coastal landscapes might lose their natural resilience (Feagin et al., 2015; Hsu & Stallins, 2020; Pickart, 2021; Schwarz et al., 2016). Therefore, inclusion of other species in restoration projects, such as sand couch for Northwestern Europe, may result in faster dune formation and a more heterogeneous landscape with potentially a higher resilience.

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Supplementary Material

Supplementary Tables

Table S2.1: Information on sampling sites and environmental variables. Locations are ordered from north (top) to south (bottom). The number of plants represents the number of individuals that were included for analyses per location. For sources of distance to sea, temperature, precipitation, and wave height see Table S2.2, all other soil characteristics were measured in collected soil samples. Mean temperature and precipitation between 2016-2019 with the standard error representing variation between years.

Location	GPS (wgs 84)	Sampled species	Collection date	Median grain size (µm) ± se	OM (% loss on ignition) ± se	Total N (mg g-1) ±se	PO4- (mg g-1) ±se	Distance to sea (m)	Mean annual temperature (^{o}C) ±se	Mean annual precipitation (mm) ±se	Significant wave height (m)
Skagen (DK)	57°45’ 6.15 ”N	*E. juncea*	16-07-2019	268.6 ±6.3	0.13 ±0.01	0.003 ±0.00	0.001 ± 0.000	26.0 ±2.4	8.8 ±0.2	772.6 ±83.6	0.9
Lemvig (DK)	56°27’ 32.81 ”N	*E. juncea*	15-07-2019	416.2 ±8.5	0.18 ±0.01	0.01 ±0.00	0.001 ± 0.000	66.0 ±0.6	9.4 ±0.1	841.2 ±82.9	1.1
Skallingen (DK)	55°31’ 30.38 ”N	*E. juncea*	13-07-2019	225.1 ±7.8	0.15 ±0.00	0.005 ±0.00	0.001 ± 0.000	123.8 ±6.1	9.5 ±0.2	889.5 ±92.6	0.7
	55°31’ 30.38 ”N	*A. arenaria*	13-07-2019	227.2 ±8.3	0.26 ±0.01	0.03 ±0.01	0.002 ± 0.001	137.0 ±4.7			
Rømø (DK)	55°7’ 46.88 ”N	*E. juncea*	14-06-2019	220.7 ±7.6	0.15 ±0.01	0.01 ±0.00	0.002 ± 0.000	174.7 ±2.6	9.7 ±0.1	824.7 ±82.8	0.5
	55°4’ 29.61 ”N	*A. arenaria (n=5)*	09-07-2019	282.7 ±18.8	0.22 ±0.01	0.02 ±0.01	0.001 ± 0.000	291.4 ±6.1			
Sylt (DE)	54°44’ 49.06 ”N	*A. arenaria (n=5)*	12-06-2019	785.3 ±18.0	0.10 ±0.01	0.002 ±0.00	0.001 ± 0.000	79.4 ±7.4	10.3 ±0.2	658.6 ±83.2	0.6

Griend (NL)	53°15’ 6.20 ”N	*A. arenaria (n=8)*	15-09-2019	202.0 ±3.6	0.49 ±0.05	0.01 ±0.00	0.005 ± 0.001	95.8 ±10.6	10.5 ±0.1	742.9 ±72.2	0.3
Texel (NL)	52°59’ 40.49 ”N	*A. arenaria (n=8)*	02-10-2019	296.8 ±5.2	0.28 ±0.03	0.004 ±0.00	0.001 ± 0.000	645.3 ±7.4	11.0 ±0.1	771.9 ±70.4	0.8
Kwade Hoek (NL)	51°50’ 37.66 ”N	*E. juncea*	10-09-2019	210.0 ±1.2	0.71 ±0.03	0.003 ±0.00	0.002 ± 0.000	174.7 ±2.2	11.3 ±0.1	1015.4 ±0.4	0.3
Bay Mont-Saint Michel (FR)	48°42 ’11.17” N 1°30’ 55.82 ”W	*E. juncea*	07-08-2019	344.6 ±12.0	0.67 ±0.01	0.01 ±0.01	0.001 ± 0.000	80.2 ±2.6	12.1 ±0.2	814.1 ±119.8	0.2
	48°42’ 11.17” N 1°30’ 55.82 ”W	*A. arenaria (n=5)*	07-08-2019	337.9 ±14.7	0.55 ±0.05	0.02 ±0.00	0.001 ± 0.000	82.0 ±1.7			

Table S2.2: Overview of online retrieved data with the level at which conditions were collected (i.e., plant level or location level) and the data source. Some additional information on the used data is given under 'note'.

Characteristic	Level	Source	Note
Distance to sea (m)	Plant	Google earth	
Significant wave height (m)	Location	https://jhnienhuis.users.earthengine.app/view/changing-shores	Selected closest point to location
Mean annual temperature (°C) & mean annual precipitation (mm)	Location	Germany (Sylt); https://cdc.dwd.de Denmark (Rømø, Skallingen, Lemvig, Skagen); https://www.dmi.dk Netherlands (Griend, Texel, Kwade Hoek); https://www.knmi.nl/ France (Mont-Saint Michel); https://meteofrance.com	Selected closest weather station, average between 2016-2019

Table S2.3: Fit of different random walk models on individual sand couch (E.) and marram grass (A.) plants. The number of steps represents the original number of steps. The fitting of different distributions was done after removal of steps that were smaller than s_{min}. S_{min} *was determined using maximum-likelihood methods and Kolmogorov-Smirnov statistics (Clauset and others 2009) or set to a fixed minimum of 0.68 when either >33% of steps were lost or <30 steps remained. Model selection was based on weighted AIC values (wAIC) and model verification was done based on the two-sample Kolmogrov-Smirnov (KS) test (rejection at the 5% significance level). The truncated Lévy and Composit Brownian were not rejected for any of the plants. For the sake of simplicity, the* μ *exponent of the truncated Lévy was used to compare individuals.*

Location	Plant	Steps	%steps < smin	smin	smax	µ exp TLévy	wAIC Brown	wAIC Lévy	wAIC TLévy	wAIC CBrown	wAIC LogN	KS Brown	KS Lévy	KS TLévy	KS C-Brown	KS LogN
Skagen (DK)	E. 1	32	3.1%	0.68	28.1	1.17	0.12	<0.01	**0.60**	0.14	0.14	0.31	0.19	0.48	0.63	0.01
	E. 2	58	0.0%	0.83	56.3	1.35	0.04	<0.01	**0.57**	0.33	0.05	0.33	0.10	0.45	0.67	<0.01
	E. 3	44	25.0%	1.09	45.0	1.91	<0.01	**0.64**	0.26	0.10	<0.01	0.10	0.70	0.71	0.71	<0.01
	E. 4	37	0.0%	0.74	60.7	1.50	<0.01	0.20	**0.48**	0.32	<0.01	0.01	0.56	0.52	0.74	<0.01
	E. 5	77	6.5%	0.68	16.9	1.46	0.15	<0.01	**0.70**	0.15	<0.01	0.30	0.10	0.42	0.61	<0.01
Lemvig (DK)	E. 1	37	0.0%	0.75	50.5	1.62	<0.01	**0.45**	0.51	0.04	<0.01	0.03	0.52	0.62	0.64	<0.01
	E. 2	50	6.0%	0.68	41.6	1.34	0.02	0.01	**0.49**	0.39	0.09	0.25	0.17	0.53	0.75	<0.01
	E. 3	72	0.0%	0.80	58.7	1.51	<0.01	0.04	**0.75**	0.21	<0.01	0.05	0.20	0.46	0.65	<0.01
	E. 4	49	22.4%	1.29	34.7	1.71	<0.01	0.34	**0.62**	0.05	<0.01	0.18	0.61	0.70	0.69	<0.01
Skallingen (DK)	E. 1	48	0%	0.89	135.2	1.52	<0.01	0.37	**0.61**	0.02	<0.01	0.01	0.60	0.74	0.68	<0.01
	E. 2	47	2.2%	0.68	50.7	1.42	<0.01	0.07	**0.86**	0.06	<0.01	0.12	0.33	0.67	0.66	<0.01
	E. 3	46	4.3%	0.68	23.7	1.23	0.07	0.00	**0.84**	0.06	0.02	0.27	0.13	0.54	0.63	<0.01
	E. 4	35	5.7%	0.68	25.2	1.41	<0.01	0.08	**0.79**	0.13	<0.01	0.09	0.47	0.61	0.66	<0.01
	A. 1	62	0%	0.75	15.6	2.46	<0.01	0.44	0.11	**0.45**	<0.01	<0.01	0.47	0.44	0.65	<0.01
	A. 2	54	11.1%	0.68	32.1	1.36	<0.01	0.01	**0.88**	0.11	<0.01	0.08	0.28	0.64	0.71	<0.01
	A. 3	119	4.2%	0.68	93.3	2.30	<0.01	**0.80**	0.09	0.11	<0.01	<0.01	0.18	0.18	0.29	<0.01
	A. 4	59	0.0%	0.54	28.4	1.74	<0.01	0.43	**0.56**	0.01	<0.01	<0.01	0.61	0.61	0.66	<0.01
Rømø (DK)	E. 1	115	5.2%	1.12	105.3	1.79	<0.01	0.15	0.17	**0.68**	<0.01	<0.01	0.53	0.57	0.71	<0.01

	E. 2	91	5.5%	0.76	42.0	1.46	<0.01	<0.01	**0.96**	0.04	<0.01	<0.01	0.29	0.57	0.67	<0.01
	E. 3	212	1.4%	0.86	62.6	1.94	<0.01	0.38	**0.61**	0.01	<0.01	<0.01	0.55	0.52	0.51	<0.01
	E. 4	119	16.0%	0.99	43.2	1.67	<0.01	0.03	**0.77**	0.20	<0.01	<0.01	0.50	0.52	0.70	<0.01
	E. 5	149	1.3%	0.88	67.9	1.76	<0.01	0.16	**0.84**	<0.01	<0.01	<0.01	0.54	0.67	0.44	<0.01
	A. 1	87	0.0%	0.78	19.5	2.00	<0.01	0.38	**0.60**	0.02	<0.01	0.03	0.44	0.55	0.60	<0.01
	A. 2	88	0.0%	0.83	32.2	1.74	<0.01	0.12	**0.78**	0.11	<0.01	0.01	0.42	0.54	0.62	<0.01
	A. 3	72	0.0%	0.72	13.4	1.74	0.24	0.02	**0.44**	0.30	<0.01	0.33	0.18	0.36	0.56	<0.01
	A. 4	68	0.0%	0.69	20.0	1.35	**0.58**	<0.01	0.32	0.09	0.01	0.52	0.04	0.42	0.59	<0.01
	A. 5	99	2.0%	0.68	39.5	1.52	<0.01	0.01	**0.94**	0.05	<0.01	0.02	0.21	0.51	0.62	<0.01
Sylt (DE)	A. 1	34	0.0%	0.70	26.0	1.23	0.01	0.01	**0.94**	0.04	<0.01	0.23	0.25	0.66	0.64	0.01
	A. 2	61	0.0%	0.79	106.7	1.69	<0.01	**0.61**	0.39	<0.01	<0.01	0.01	0.55	0.67	0.29	<0.01
	A. 3	53	5.7%	0.76	73.9	1.86	<0.01	**0.72**	0.24	0.04	<0.01	<0.01	0.68	0.69	0.70	<0.01
	A. 4	82	30.5%	1.19	45.7	1.79	<0.01	0.39	**0.53**	0.08	<0.01	<0.01	0.62	0.55	0.66	<0.01
	A. 5	107	19.6%	0.89	56.8	1.99	<0.01	**0.48**	0.17	0.35	<0.01	<0.01	0.36	0.35	0.45	<0.01
Griend (NL)	A. 1	127	18.1%	0.52	21.3	2.65	<0.01	**0.88**	0.11	0.01	<0.01	0.01	0.65	0.64	0.69	<0.01
	A. 2	235	17.9%	0.68	20.9	2.33	<0.01	**0.68**	0.29	0.03	<0.01	<0.01	0.50	0.55	0.65	<0.01
	A. 3	242	32.2%	0.68	7.5	2.84	<0.01	0.40	0.18	**0.42**	<0.01	0.01	0.26	0.28	0.35	<0.01
	A. 4	134	29.9%	0.68	6.5	2.86	<0.01	**0.63**	0.22	0.14	<0.01	0.20	0.30	0.33	0.47	<0.01
	A. 5	68	16.2%	0.68	19.2	2.07	<0.01	**0.62**	0.30	0.08	<0.01	0.06	0.58	0.62	0.72	<0.01
	A. 6	112	25.9%	0.68	11.4	2.48	<0.01	**0.69**	0.23	0.08	<0.01	0.17	0.55	0.59	0.73	<0.01
	A. 7	137	35.8%	0.68	17.3	2.18	<0.01	**0.64**	0.34	0.02	<0.01	0.08	0.56	0.64	0.70	<0.01

	A. 8	124	35.5%	0.68	4.0	2.68	**0.58**	0.12	0.29	0.01	<0.01	0.56	0.30	0.48	0.57	<0.01
Texel	A. 1	188	3.2%	0.61	40.1	2.04	<0.01	**0.63**	0.37	<0.01	<0.01	<0.01	0.65	0.72	0.55	<0.01
(NL)	A. 2	71	7.0%	0.68	18.6	1.70	<0.01	0.02	0.18	**0.79**	<0.01	0.13	0.12	0.26	0.50	<0.01
	A. 3	40	22.5%	1.09	8.5	2.38	0.04	**0.53**	0.37	0.05	<0.01	0.40	0.68	0.68	0.73	0.02
	A. 4	40	15.0%	0.68	4.0	1.90	**0.81**	0.01	0.11	0.02	0.04	0.65	0.27	0.55	0.66	0.01
	A. 5	69	13.0%	0.65	18.2	2.13	<0.01	**0.71**	0.29	0.01	<0.01	0.03	0.72	0.72	0.65	<0.01
	A. 6	78	5.1%	0.68	22.7	2.01	<0.01	**0.57**	0.37	0.06	<0.01	0.09	0.51	0.60	0.74	<0.01
	A. 7	102	20.6%	0.68	12.9	1.70	0.03	0.01	**0.85**	0.11	<0.01	0.41	0.19	0.46	0.67	<0.01
	A. 8	100	32.0%	0.90	31.9	2.08	<0.01	**0.64**	0.26	0.11	<0.01	0.01	0.61	0.59	0.65	<0.01
Kwade	E. 1	137	0.0%	0.71	52.7	1.43	<0.01	<0.01	0.15	**0.85**	<0.01	0.01	0.03	0.24	0.53	<0.01
Hoek	E. 2	134	1.5%	0.68	40.0	1.40	<0.01	<0.01	0.05	**0.95**	<0.01	0.07	0.01	0.22	0.67	<0.01
(NL)	E. 3	96	18.8%	1.49	57.5	1.74	<0.01	0.18	**0.81**	0.01	<0.01	0.01	0.55	0.69	0.70	<0.01
	E. 4	128	0.0%	0.69	44.0	1.59	<0.01	0.01	**0.88**	0.11	<0.01	<0.01	0.38	0.56	0.68	<0.01
	E. 5	119	12.6%	1.27	57.9	1.43	<0.01	<0.01	**0.98**	0.02	<0.01	0.03	0.16	0.69	0.72	<0.01
Baye	E. 1	137	0.0%	0.70	11.1	1.57	0.01	0.04	**0.89**	0.06	<0.01	0.28	0.40	0.67	0.68	<0.01
Mont-	E. 2	134	1.5%	2.07	46.7	1.71	<0.01	0.15	**0.79**	0.06	<0.01	0.11	0.51	0.68	0.72	<0.01
Saint	E. 3	96	18.8%	0.77	24.1	1.33	**0.73**	<0.01	<0.01	0.03	0.24	0.64	0.02	0.22	0.63	<0.01
Michel	E. 4	128	0.0%	0.68	45.5	1.17	0.45	<0.01	0.01	0.01	**0.53**	0.49	0.01	0.24	0.48	<0.01
(FR)	E. 5	119	12.6%	0.68	67.4	1.41	0.02	<0.01	<0.01	0.49	**0.50**	0.30	0.04	0.19	0.66	<0.01
	A. 1	182	15.9%	0.68	37.6	2.07	<0.01	**0.41**	0.21	0.38	<0.01	0.01	0.15	0.22	0.43	<0.01
	A. 2	56	0.0%	0.63	35.8	2.39	<0.01	**0.47**	0.08	0.45	<0.01	<0.01	0.51	0.49	0.63	<0.01

	A. 3	72	2.8%	0.63	58.8	2.25	<0.01	**0.68**	0.10	0.22	<0.01	<0.01	0.56	0.56	0.60	<0.01
	A. 4	125	11.2%	0.67	17.6	2.47	<0.01	**0.82**	0.18	<0.01	<0.01	0.02	0.58	0.60	0.59	<0.01
	A. 5	71	4.2%	0.68	61.2	1.75	<0.01	**0.56**	0.43	0.01	<0.01	<0.01	0.71	0.71	0.67	<0.01

Table S2.4: Variable loadings from the first two principal components of the PCA, with the variables with the highest loadings per principal component in bold. Percent variance explained in the environmental data by each principal component are: PC1, 38.8% and PC2 18.1%.

	PC1	**PC2**
Soil organic matter	**0.94**	0.15
Median grain size	-0.57	**0.71**
Soil nitrogen	0.28	-0.36
Soil phosphate	0.54	-0.20
Distance to sea	0.10	-0.17
Average yearly temperature	**0.74**	**0.62**
Average yearly precipitation	0.52	**-0.49**
Significant wave height	**-0.84**	-0.30

Characterizing clonal growth strategies

For the comparison of growth strategies between individuals, we chose to use the scaling exponent of a truncated Lévy distribution (see methods). However, we tested five commonly used models for describing movements on every individual plant: an exponential (Brownian), two-mode exponential (Composite Brownian), log-normal, power-law (Lévy) and truncated power-law (truncated Lévy) (Clauset et al., 2009; Edwards et al., 2012; Reijers, Siteur, et al., 2019). Here, we will shortly summarize probability functions and maximum likelihood estimators for the different models.

Exponential distribution (Brownian)
The first tested model was an exponential (Brownian) model which long has been the default random walk model, corresponding normal diffusion. The probability density function of the exponential distribution is:

Equation 1: $$P(s) = \lambda e^{\lambda(s_{min} - s)}$$

with s being the step size and s_{min} being the minimum step size of the distribution. Parameter λ was derived from the data using the maximum likelihood estimator:

Equation 2: $$\hat{\lambda} = \frac{n}{\sum_{i=1}^{n}(s_i - s_{min})}$$

where n is the number of shoots.

Two-mode exponential distribution (Composite Brownian)
The probability density function of the two-mode exponential distribution (Composite Brownian) is:

Equation 3: $$P(s) = w_1 f_1(s) + (1 - w_1) f_2(s)$$

with f_1 and f_2 being exponential distributions (see equation 1) and w_1 the weighing factor between the two exponential distributions. The parameters were derived by numerically maximizing the log-likelihood function:

Equation 4: $$L\sum_{i=1}^{n} log(P(s))$$

Log-normal distribution
The probability density function of the log-normal distribution is:

Equation 5: $$P(s) = \frac{1}{2\sigma\sqrt{2}}\exp\left[\frac{-(\ln s - \mu s - \mu)^{2}}{2\sigma^{2}}\right]$$

with μ and σ being the mean and standard deviation of the log-transformed data, respectively.

Power-law distribution (Lévy walk)
The Lévy walk model is a model that follows a power-law distribution. The probability density function is given by:

Equation 6: $$P(s) = ((\mu - 1)s_{min}{}^{\mu-1})s^{-\mu}$$

with s being the step size and s_{min} the minimum step size. The μ parameter was derived from the data using the maximum likelihood estimator (Edwards et al., 2012):

Equation 7: $$\hat{\mu} = 1 + \frac{n}{\sum_{i=1}^{n}(\ln(s_i(s_i) - \ln(s_{min}))}$$

The power-law distribution can be considered as a Lévy walk if the parameter ranges between 1 and 3.

Truncated power-law distribution (Truncated Lévy walk)
Finally, there is a bound or truncated version of the power-law distribution (truncated Lévy) that we used to compare clonal growth strategies. While the previously presented power-law distribution is unbound, most natural movements are restricted to a certain physical boundary level. In our case, we included the maximum step size found in the field as our upper boundary (s_{max}), next to the lower boundary (s_{min}) (see methods). As a result, the power-law distribution will at some point give way to an exponential scaling.

Best fitting models
Using weighted Akaike Information Criterion (wAIC) values for all models, we determined which of the candidate models was the best fit for the found step size distribution (Wagenmakers & Farrell, 2004).

Equation 8: $$wAIC_i = \frac{\exp\{-0.5(AIC_i - AIC_{min})\}}{\sum_k^n \exp\{-0.5(AIC_i - AIC_{min})\}}$$

We tested the goodness of fit of the five candidate models with a one-sample Kolmochorov-Smirnov (KS) test, following methods proposed by Clauset and others 2009.

Supplementary figures

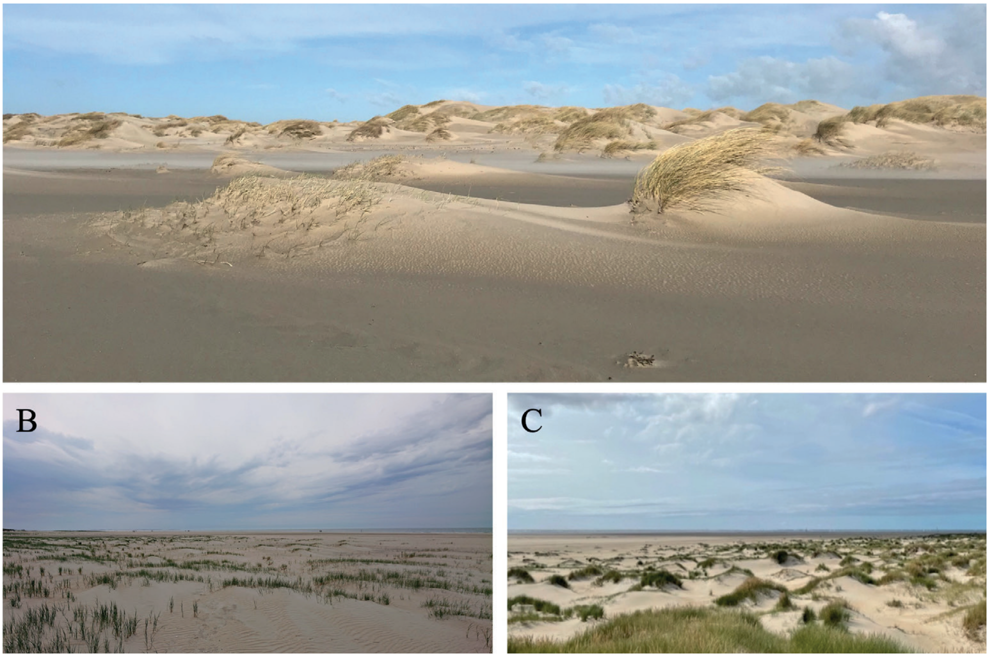

Figure S2.1: Impression of dunes formed by sand couch and marram grass. A) Dunes formed by sand couch (left) and marram grass (right) at Texel, the Netherlands. The photographed individuals are larger than the in this survey included individuals. B) Foredunes dominated by sand couch at Rømø, Denmark and C) foredunes dominated by marram grass at Texel, the Netherlands. A clear difference in dune (and plant) morphology between the species is visible.

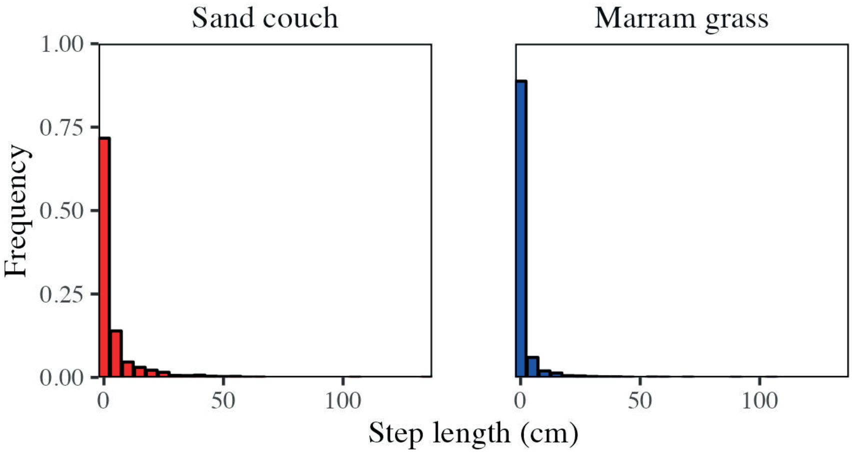

Figure S2.2: Histogram of frequency of step sizes (bins 5 cm) for sand couch (Elytrigia juncea) and marram grass (Ammophila arenaria). Small steps occurred more often in marram grass than in sand couch, indicating more patchy and/or a denser growth for marram grass than sand couch.

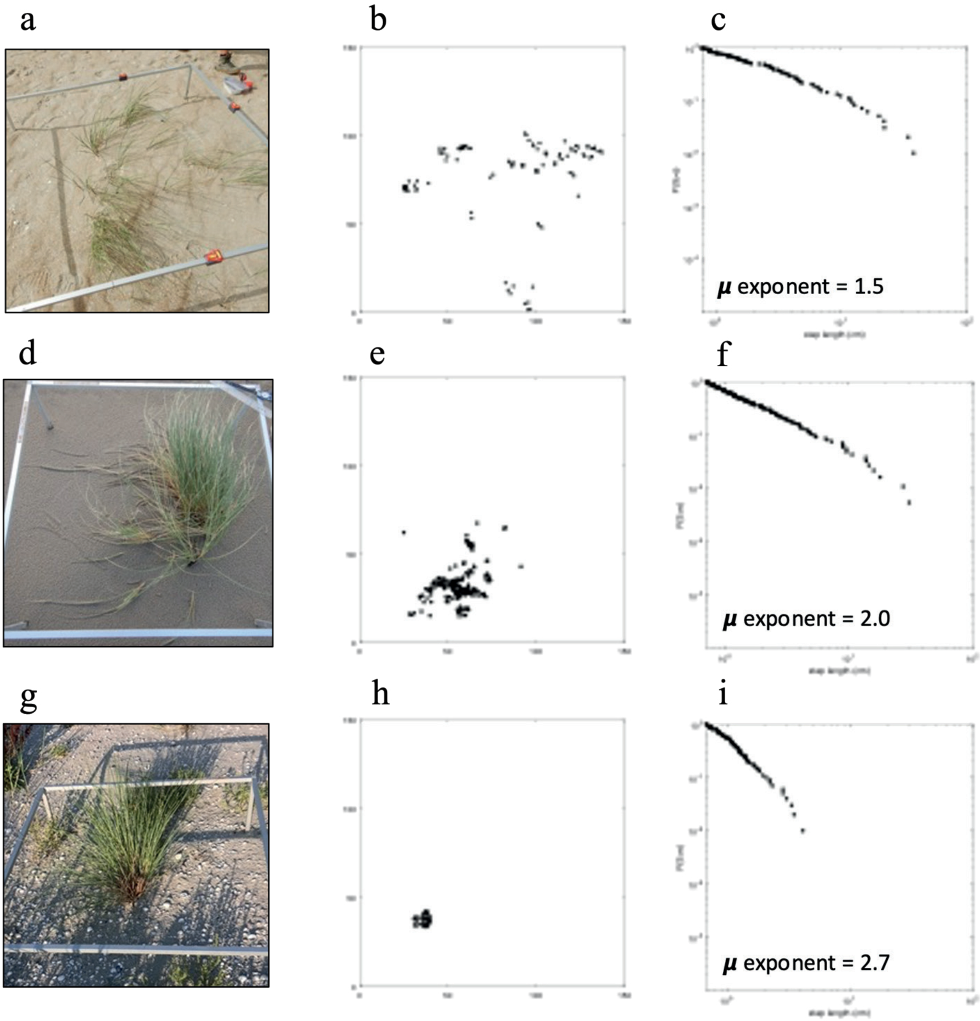

Figure S2.3: Field photos (A, D, G), shoot patterns (B, E, H) and inverse cumulative frequency distributions (C, F, I) from marram grass (Ammophila arenaria) individuals with a range of clonal expansion strategies. On top a dispersed individual (A, B, C) which was located at Rømø, Denmark (plant A.5), in the middle a patchy individual (D, E, F) at Texel, the Netherlands (plant A.1), and below a clumped individual (G, H, I) at Griend, the Netherlands (plant A.8). The scaling component (μ exponent) of the truncated Lévy fitted on the step-size data for the three individuals is included (C, F, I), a lower scaling component (~1.5) corresponds to a more dispersed individual and a higher scaling component (~3) corresponds to a more clumped individual, while a scaling component of ~2 closely resembles a patchy, Lévy like, organization.

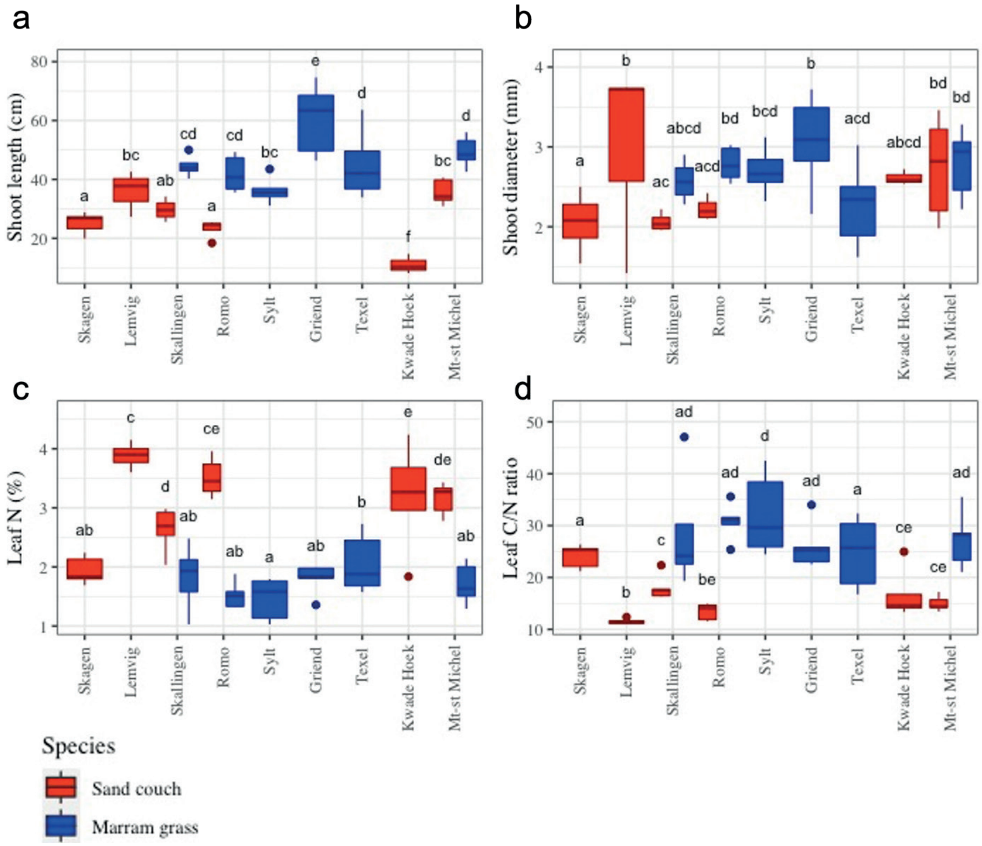

Figure S2.4: Shoot length (a), shoot diameter (b), leaf nitrogen level (c) and leaf C/N ratio (d) per location and species. Locations on the x-axis are ordered from north (left) to south (right). Letters depict LSD post hoc grouping (P<0.05).

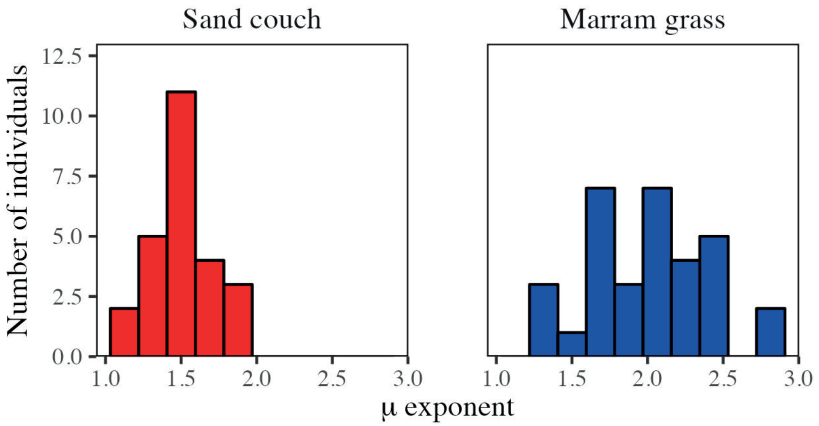

Figure S2.5: Histogram of scaling (μ) exponents from the Truncated Lévy model for marram grass (top panel) and sand couch (bottom panel). Showing a larger variation in shoot organizations for marram grass compared to sand couch.

CHAPTER 3

Habitat modification by marram grass negatively affects recruitment of conspecifics

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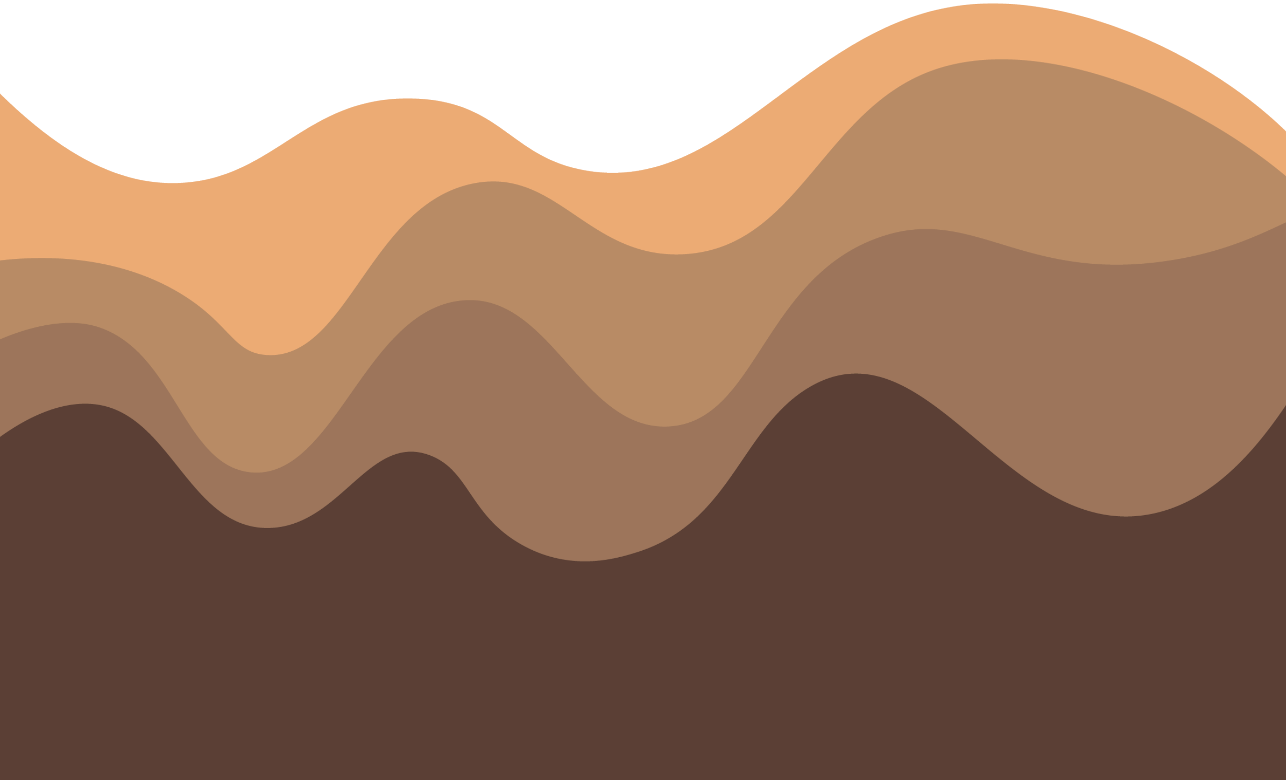
Accepted manuscript



Abstract

Ecosystem engineers alter their environment often benefiting their own survival and growth yielding self-reinforcing feedbacks. Moreover, these habitat modifications have been found to facilitate recruitment of conspecifics for some species, while for others engineering inhibits recruitment. Whether dune grasses facilitate or inhibit recruitment of conspecifics is yet unknown. Here, we investigated how habitat modification by European marram grass (*Ammophila arenaria*) through embryonic dune development affects recruitment from seeds and marine dispersed rhizome fragments. Specifically, we tested at three locations with different dune morphologies how habitat modification affected natural seed and rhizome presence and shoot emergence from plots in which seeds or rhizome fragments were added. In addition, we investigated how sediment burial (i.e., the main effect of habitat modification by dune grasses) affected germination and emergence in a controlled experiment. Results show that regardless of habitat modification or beach width, seeds and rhizomes were absent in natural conditions. Habitat modification negatively affected shoot emergence from seeds (8x less) and rhizomes (4x less) and was negatively related to sediment dynamics. Furthermore, fewer seedlings were found with higher elevations. In controlled laboratory conditions, the highest seedling emergence was found with slight burial (0.5-3cm); both germination and seedling emergence decreased as seeds were buried deeper or shallower. Overall, habitat modification by marram grass negatively affects recruitment of conspecifics through increased sediment dynamics and elevation. Consequently, storm events or eradication programs that include removal of adult vegetation - which leads to an unmodified system - might benefit new recruitment from seeds or clonal fragments.

Keywords: Habitat modification, Coastal dunes, Plant recruitment, *Ammophila arenaria*, Sediment dynamics

1. Introduction

The early stages in the life cycle of plants – from seed and sprout to small plants – are often the bottleneck for successful species long-term establishment thereby affecting population dynamics and distribution (Grubb, 1977). Such bottlenecks arise as the environmental tolerance in early stages often differs from the adult stages that are typically more resistant (Del Vecchio et al., 2020; Grubb, 1977). For example, American beach grass (*Ammophila breviligulata*) is vulnerable to desiccation in its seedling stage but drought tolerant as adult (Laing, 1958; Maun, 1994). Apart from recruitment from seeds, clonal plants have vegetative growth as a second mode of reproduction which can have different establishment requirements compared to seeds (Harris & Davy, 1986a; van der Putten, 1990). In general, populations of clonal plants are maintained and expanding through vegetative growth, rather than through establishment from seeds. However, after disturbance events establishment via seed dispersal allow for (re)colonization of new regions at larger distances (Herben et al., 2015; Silvertown, 2008). Ecosystems that experience frequent and regular physical disturbances, such as fluvial and coastal ecosystems (e.g., rivers, salt marshes and coastal dunes), are often regulated by strong bottlenecks for species establishment. Here, flooding and sediment transport by water and wind inhibits plant establishment and recruitment only occurs during relatively calm periods called 'Windows of Opportunity' (Balke et al., 2014; Corenblit et al., 2007).

In harsh coastal environments, ecosystem engineering plants, such as mangroves, cordgrasses and dune grasses, alter their physical environment invoking feedback loops that improve living conditions for themselves and associated species (Crain & Bertness, 2006; Jones et al., 1994). Throughout an ecosystem engineering plant's life cycle, the effect of environmental conditions changes from influencing germination and establishment potential to influencing their ability to grow, expand and engineer their environment (Balke et al., 2011; Schwarz et al., 2015). For some coastal ecosystem engineers, these habitat modifications also benefit recruitment of conspecifics. For instance, mussels and oysters provide attachment structures and predation shelter for larval recruitment and mangrove roots or seagrass shoots stabilize the soil through water flow reduction which benefits seedling survival (Balke et al., 2011; Rodriguez-Perez et al., 2019; van der Heide et al., 2014; Zipperle et al., 2009). However, habitat modification can also negatively affect new recruitment. For example, ecosystem engineering by smooth cordgrass (*Spartina alterniflora*) can result in increased soil ammonia levels, which in turn can lower seedling establishment (Lambrinos & Bando, 2008). Whether habitat modification by dune grasses facilitates or inhibits recruitment of conspecifics is yet unknown.

Dune grasses are the dominant ecosystem engineering species in temperate coastal dune systems. As these systems occur at the land-sea interface, there is a sharp change in environmental conditions such as salinity levels, wind intensity, sediment transport and soil temperatures from sea inland (Hesp, 1989; Martínez

& Psuty, 2004). Conditions close to the shoreline are generally too harsh for establishment, but above the high-water line dune grasses can establish during periods of low or absent disturbance (Balke et al., 2014). Once seedlings or plant fragments are rooted, they clonally expand and start accumulating sediment by reducing flows of wind with their physical structures, thereby forming embryonic or incipient dunes. Over time, these embryonic dunes can develop into more stable foredunes (Hesp, 2002; van Puijenbroek, Limpens, et al., 2017). These plant-mediated modifications to the environment lead to an increase in bed-level elevation, soil moisture levels and a drop in soil temperatures (Baldwin & Maun, 1983). All these changes can potentially benefit recruitment of conspecifics, due to reduced flood risk and with increased moisture and lower temperatures desiccation is less likely, which are thought to be the main factors determining seedling survival in coastal dunes (Maun, 1994). However, sediment accretion might also negatively affect recruitment as burial poses direct stress for many species (Bonte et al., 2021; Lim, 2011; Maun & Lapierre, 1986).

The aim of this study is to determine how habitat modification by European marram grass (*Ammophila arenaria* hereafter referred to as marram grass) affects recruitment of conspecifics. Marram grass is one of the dominant dune grasses along the Northwestern European coast. It is known for its efficient dune building and therefore has been introduced in coastal regions worldwide (e.g., Bakker, 1976; Hacker et al., 2012; Hertling & Lubke, 1999; Hilton, 2006). In Europe, marram grass flowers between June and August, followed by a peak in seed dispersal in September (Huiskes, 1979). Seeds that disperse in September will only be able to germinate the next spring since the seeds need cold stratification (Huiskes, 1979). Dispersal via rhizome fragments, the second, asexual, mode of recruitment, is dependent on storm events (Hilton & Konlechner, 2011). As seed or rhizome availability is the first requirement for successful establishment, we determined seed and marine dispersed rhizome availability in spring at three locations with different beach-dune morphologies. Second, we experimentally tested shoot emergence from seeds and rhizome fragments in modified and unmodified habitats at these three locations. Lastly, we examined the effect of sediment burial (i.e., the most important effect of habitat modification by marram grass) on seed germination and emergence in controlled conditions.

We hypothesize that most marram grass seeds will be dispersed close to adult vegetation (Pope, 2006), and we therefore expect a higher seed availability close to vegetation. Furthermore, the presence of marine dispersed rhizomes is expected to be dependent on the presence of vegetation (as a source) in combination with beach width, with higher chances of erosion and potential rupture of adult vegetation on short, steep beaches than on wide beaches with a gentle slope (Anthony, 2013; Itzkin et al., 2021). Since we expect that habitat modification can both have negative (e.g., sediment burial) and positive (e.g., increased moisture levels) effects it is hard to predict whether it will facilitate or inhibit recruitment (Baldwin & Maun, 1983; Bonte et al., 2021; Lim, 2011). Furthermore, we expect lower seedling emergence with increased burial in controlled conditions.

2. Methods

2.1. Field sites

We selected three beach – dune locations on the Dutch Wadden Island Texel. The widest system was ±420 m (mean sea level (MSL) – top foredune), the intermediate location ±260 m and the narrow location ±140 m wide (Figure 3.1, Figure S3.1). On the wide and intermediate locations embryonic dunes (i.e., a modified environment) were present, while on the narrow beach they were absent. At the wide location embryonic dunes stretched ±170 m and at the intermediate location ±55 m. As a consequence of beach width, presence of vegetation and other environmental conditions, dune morphologies differed between locations (Figure 3.1, Figure S3.1).

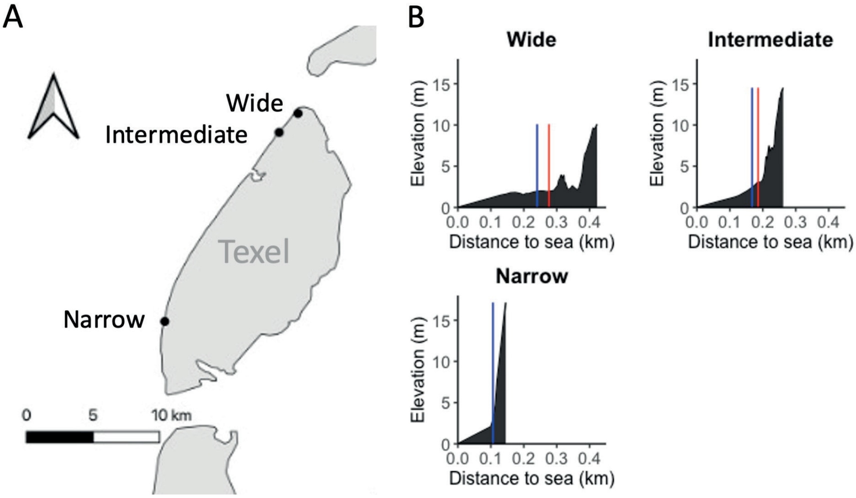


Figure 3.1: A) Location of the field sites on Texel. B) Dune profiles of the locations based on a transect with RTK-GPS. The blue vertical lines indicate plot locations in the unmodified zone (on the beach) and the red vertical lines the plots in the modified zone (in the embryonic dunes). At the narrow location no embryonic dunes were present.

2.2. Natural seed and rhizome availability

The natural presence of seeds and marine dispersed rhizomes in the early successive stages of dunes was determined at the selected locations in March 2021 by sieving sediment cores (ø10 cm, 20 cm depth) over a 1 mm mesh. The cores were placed along a transect with 3m spacing between cores (3 parallel transects interspaced ±4 m per location, Figure S3.2). The transects started where the first marram grass vegetation was present and on the narrow and intermediate locations stretched until the foot of the foredunes (n=21 for narrow, n=54 for intermediate). On the wide location, the transects crossed the embryonic dune field but did not reach the foredune (n=60). From each core the elevation was determined using RTK-GPS and the distance to the closest adult vegetation was measured. All material (shell and organic) that was left after sieving was taken to the lab to separate seeds and rhizomes from other material and count the number of seeds and rhizomes.

2.3. Establishment field experiment

To test the establishment potential of marram grass in relation to habitat modification and beach width, a field experiment was executed from the beginning of May 2020 – March 2021. Two zones per location were selected: 1) the unmodified or beach zone between the high-water line and embryonic dune (hereafter the 'unmodified zone') and 2) the modified or embryonic dune zone where adult vegetation modified its environment (hereafter the 'modified zone'). Since embryonic dunes were absent at the narrow location, here only the unmodified zone was included.

At each zone (5 in total across 3 locations as described above), we established 30 2x2m plots. Each plot was assigned to one of 3 treatments 'seed', 'rhizome' or 'control', resulting in 10 replicates per treatment per zone and a total of 150 plots. To ensure that there was no wrack (i.e., organic material that is washed up on the beach by waves) in the plots at the start of the experiment, the top layer of the soil (±10 cm) was raked in each plot and, if present, wrack was removed prior to sowing. An area of ±0.5 m around the plots was cleared of vegetation. Subsequently, the seed plots were sown with marram grass seeds (1600 per plot, purchased at Jelitto perennial seeds ®). Since we aimed to test how the environmental conditions affected the germination, we decided to use commercially purchased seeds to minimize uncertainty of germination potential that might occur in locally harvested seeds (Del Vecchio et al., 2022). The seeds were mixed in the top 5 cm of the soil and spread across the plot. Prior to sowing, seeds were stored in dark, dry, and cold (8°C) conditions for 4 weeks. We chose to use 1600 seeds per plot based on germination rates described by van der Putten (1990), who found that seedling numbers did not significantly increase with densities over 400 seeds m-2. In the rhizome plots, wrack (1600 g fresh weight per plot) was mixed with the top 5 cm of the soil. The wrack was collected in the field at the intermediate location. On average 78% of the weight of the sampled wrack consisted of rhizome parts, which had a total of approximately 3000 nodes (based on 4 subsamples). The two dominant dune grasses along the North Sea coast of Texel are marram grass and sand couch (Elytrigia juncea), no distinction between rhizomes of both species was made and no separation between rhizome parts and other organic material was made. Control plots were treated in the same way as experimental plots, without the addition of seeds or wrack. We assigned one of the treatments to the plots in a randomized block design. The plots were >1 m apart and on bare soil. Shoot emergence was followed between May and October 2020. Every fortnight, shoot numbers were counted and, when present, shoot length of 10 randomly selected shoots was measured. In March 2021, the survival of individuals over winter was determined. Besides, sediment cores (ø10 cm, 20cm depth, n=1 per seed plot) were taken to determine retention of sown seeds in the experimental plots.

Soil moisture and salinity were determined in sediment samples (n=5 per zone per location) from the top 5 cm of the soil twice a month from June-August. Moisture levels were determined as loss on drying (48h at 60°C). Water extracts were taken from the soil using 17.5 g fresh soil in 50ml milliQ to measure soil salinity (mS/m). Sediment dynamics were measured as bed level change using a bamboo marker at one corner of each plot. Each time, the aboveground length of the bamboo marker was measured to track bed level changes. At the start and end of the experiment elevation (m MSL) was measured at each plot corner using RTK-GPS. At each location light and temperature were logged (Onset HOBO Pendant temperature/light logger) hourly between May-September on ground level, for the wide and intermediate location the logger was placed between the unmodified and modified zone and at the narrow location between the plots at the unmodified zone.

2.4. Burial laboratory experiment

The main effect of habitat modification by marram grass is the accumulation of sand (Reijers, Siteur, et al., 2019; Zarnetske et al., 2012). To identify the effect of sediment accumulation on seed germination, we buried seeds (purchased at Jelitto perennial seeds ®) between 0 and 13 cm. Depths were intended to be

0, 2, 5, 8 or 13 cm, however, examination of the burial depth at the end of the experiment revealed that not all seeds ended up at the intended planting depth. For all analyses, the treatment groups were adapted to the actual burial depth which resulted in unequal group sizes (0-0.5 cm n=400; 0.5-3 cm n=454; 3-6 cm n=419; 6-10 cm n=352; 10-13 cm n=375). Seeds were planted in germination trays (4.8*4.8*15 cm, 60 cells per tray) in untreated beach sand, which was sieved over a 1 mm mesh (collected at paal 9, Texel, the Netherlands, January 2021). Seeds were stored in dark, dry, and cold conditions (April 2020 – January 2021). To maximize germination, the seeds were wetted and kept cold (8°C) 7 days prior to planting (van der Putten, 1990). Five seeds were planted per cell and treatments were randomized per tray. Cultivation followed a day-night rhythm (12h/12h), simulated through changes in light intensity and temperature (day: 25°C, night: 15°C). Seeds were watered every other day, upon need.

The seedlings were grown for 49 days, throughout which emergence (triweekly) and shoot length (weekly) were determined. At the end of the experiment, seedlings were excavated. Subsequently, shoot (above and below sediment level) and root length were determined for a maximum of 100 seedlings per group. For a total of 176 seedlings (0-0.5 cm n=54, 0.5-3 cm n=78, 3-6 cm n=50, 6-10 cm n=13, 10-13 cm n=2), shoots were separated from the roots, dried (70°C, 48h) and weighted.

2.5. Statistical analyses

Statistical analyses were performed using the software programme R (version 4.2.1). For every test, normality of the residuals was checked and, if needed, the data were transformed using log transformation and, when transformation was ineffective, non-parametric tests were used. *P* values lower than 0.05 were considered statistically significant.

2.5.1. Establishment field experiment

First, we determined differences in recruitment success between treatments (control, rhizomes and seeds) and zones. We defined recruitment success as the maximum number of shoots per plot over the growing season (May-October 2020). We first fitted (mixed) models (with poisson (package "lme4" (Bates et al., 2015), negative binomial (package "MASS", (Ripley et al., 2013)), and zero-inflated (package "pscl", (Zeileis et al., 2008)) distributions) to the data. However, neither of these models could produce a fit as the data contained only zeros in controls. Therefore, we opted for a (non-parametric) Kruskall-Wallis signed rank test combined with a pairwise Wilcoxon signed rank test with Holm correction for multiple comparisons, separating analyses between zones to achieve a balanced design (as one location lacks a zone). As a second step, we examined differences in plot success between locations and zones for the rhizome and seed treatment separately. Again, we fitted generalized linear models with poisson, negative binomial and zero-inflated distributions and selected the best fitting models based on Akaike information criterion (AIC). The best models had negative binomial distributions, which we combined with a pairwise comparison of the estimated marginal means (package "emmeans", (Searle et al., 1980)) with a Tukey correction for multiple comparison. Finally, to test which environmental factors acted as drivers of the observed differences in recruitment success, we correlatively explored the relation between plot success and moisture, elevation and sediment dynamics using linear models. First, the change in sediment level (cm) per day per plot between every consecutive measurement was calculated. Sediment dynamics per plot were expressed as the standard deviation of the bed level change per day in cm. Subsequently, it was tested whether moisture, elevation and sediment dynamics correlated to each other using a Pearson correlation test. As (log) moisture and elevation correlated significantly ($r=-0.74$, $P<0.001$, Figure S3.3) and elevation was measured in a higher spatial resolution (plot level instead of every other block level), we only included elevation and sediment dynamics to test the relation between plot success (i.e., max shoot number) and environment using generalized linear models with a Poisson distribution. To compare the length of shoots in September (when they were on average the tallest) and survival over summer (maximum number of shoots compared with number of shoots at the end of September) between treatments (rhizome and seed) and zones we fitted linear mixed-effect models with a Gaussian distribution including location as random factor (package "lme4", (Bates et al., 2015)). P-values were calculated in a type 3 ANOVA via Satterthwaite's degrees of freedom method (package "lmerTest", (Kuznetsova et al., 2017)).

2.5.2. Burial laboratory experiment

Final seedling emergence and germination were compared between burial depths using a generalized linear model with binomial distribution combined with a Tukey post hoc test. To compare emergence over time between burial depths, time-to-event analyses, as described by Onofri et al. (2022), were used. A log-logistic time-to-event model was made for the different burial depths. Next, it was tested whether the model was significantly different from a reduced model using a Likelihood Ratio Test (LRT, compCDF from package drcte). Lengths and weights were compared between burial groups using ANOVA combined with Tukey post hoc tests.

3. Results

3.1. Seed and rhizome availability

Regardless of beach width (i.e., different locations) or position along the successional gradient (i.e., in modified or unmodified conditions) no seeds or rhizome fragments were found in any of the sediment cores (n=135). Overall, cores were taken at elevations ranging from 1.5 to 7.8 m MSL and from within adult marram grass vegetation up to 5.8 m from vegetation (median 1.8 m).

3.2. Establishment field experiment

Both in the modified and the unmodified system, more shoot emerged in the rhizome and seed plots than in the control plots, where no shoots emerged in any of the plots (Figure 3.2). In the modified system, no significant difference in shoot emergence between seeds and rhizomes was found (11.5±5.3 seed vs 0.9±0.3 rhizome, Figure 3.2). However, in the unmodified zone significantly more shoots emerged from seeds than from rhizomes (91.6±15.6 seed vs 3.4±0.5 rhizome, Wilcoxon signed rank, $P<0.001$). Moreover, the difference between both zones was larger for seeds (8 times more shoots in the unmodified system, unmodified vs modified, GLM NB, $z=4.5$, $P<0.001$) than for rhizomes (3.8 times more shoots, unmodified vs modified, GLM NB, $z=2.7$, $P=0.006$). No differences in shoot emergence from rhizomes were found in the same zone between locations (Figure S3.4). On the other hand, the number of seedlings (shoots originating from seed) in the unmodified zone increased by 12.5 times when the beach was wide compared to narrow (wide 190.3±16.6, intermediate 69.4±16.7, narrow 15.1±4.4; wide vs narrow, GLM NB, $z=3.7$, $P=0.003$, Figure S3.4).

Next, we tested how the plot success related to environmental conditions (i.e., elevation, sediment dynamics, soil moisture, soil salinity and temperature). Since temperatures were similar across locations, we decided to omit temperature from the comparison. Moreover, the EC in water extracts was outside the salinity range where an effect on germination could be expected (between 0 and 0.7 mS/cm, average 0.1±0.03 mS/cm, compared to van Puijenbroek et al. (2017) and Del Vecchio et al. (2020), Table S3.1). Therefore, salinity was also excluded from the comparison. Besides, temperature, light and salinity levels indicated that no flooding happened during our experimental period. As elevation correlated with

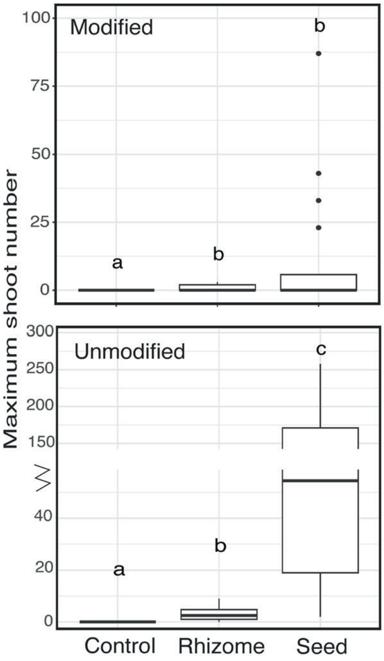


Figure 3.2: Result of the field experiment with the maximum number of shoots found per treatment in the modified zone (top) and the unmodified zone (bottom). Letters depict differences in Kruskal-Wallis combined with pairwise Wilcox signed rank test (P<0.05). Horizontal lines indicate the median, box height depicts the first and third quartiles.

moisture levels (r=-0.74, P<0.001, Figure S3.3) we compared the number of shoots only with elevation and sediment dynamics (which were measured on a plot level, while moisture was measured every other block). Lower sediment dynamics related to a higher maximum number of shoots, both from rhizomes and seeds (GLM, P<0.001, Figure 3.3, Model diagnostics; Figure S3.5, Table S3.2 and S3.3). Furthermore, more seedlings were found at lower elevations (GLM, P<0.001, Table S3.3, Figure 3.3) while there was no significant relation between elevation and shoot emergence from rhizomes (Table S3.2, Figure 3.3). Generally, sediment dynamics was higher in the modified system than in the unmodified system (deviation bed level 0.74±0.05 cm (modified) vs 0.31±0.02 cm (unmodified), $F_{1,147}$= 90.96, P<0.001; averages in accretion 7.5±0.7 cm (modified) vs 3.0±0.2 cm (unmodified) and erosion 8.4±0.7 cm (modified) vs 3.4±0.3 cm (unmodified)). After the growth season, at the end of September 2020, shoots that emerged from rhizomes were on average longer than those from seedlings (15.7±1.5 cm vs 11.0±1.2 cm, respectively, $F_{1,65}$=6.9, P=0.01, Figure S3.6). There were no significant differences in length between locations or zones (Figure S3.6). Summer survival – i.e., the number of shoots present at the end of September compared to the

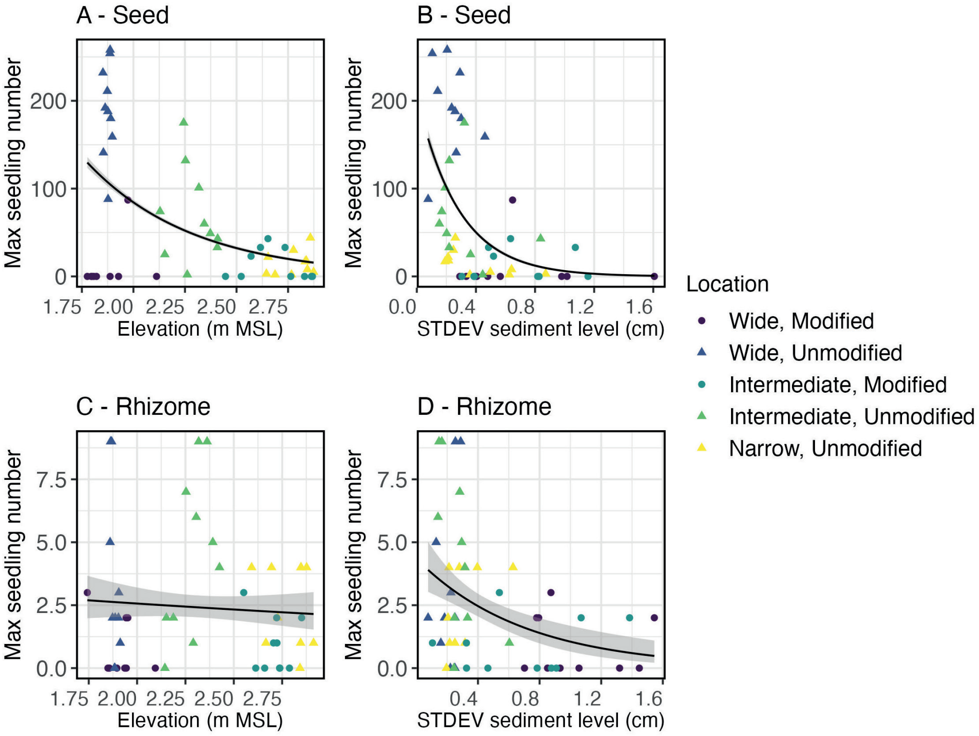


Figure 3.3: Maximum seedling numbers from seeds (A, B) and rhizomes (C, D), compared to elevation (m MSL, A&C) and compared to sediment dynamics (expressed as standard deviation in sediment level (cm), B&D). The lines indicate fitted generalized linear models with Poisson distribution (in A, B & D, P<0.001, and B P=0.26, regression parameters in Table S3.2 and S3.3).

maximum number of shoots per plot – was significantly higher for rhizomes than for seeds (46.1±6.9% vs 12.5±3.6%, respectively, $F_{1,65}$=16.2, P<0.001, Figure S3.6). There were no significant differences in survival between locations and zones (Figure S3.6). Furthermore, there were no significant correlations between sediment dynamics or elevation and survival. Almost all plants died over winter with only 22 seedlings remaining in March 2021. The remaining seedlings were all found in the same plot in the unmodified zone at the wide location.

The number of ungerminated seeds remaining in the experimental plots after winter was highest at the wide location in the unmodified system (29±11%) followed by the intermediate location (19±5%). These were higher numbers than found in the unmodified zone at the narrow location (2±2%, Wilcoxon signed rank, P=0.039) and in the modified system (0% (wide) and 8±8% (intermediate), Wilcoxon signed rank, P=0.032). Since environmental factors were not measured during winter no relation between seed retention or seedling survival and these factors could be made.

3.3. Burial laboratory experiment

At the end of the experiment, seeds buried between 0.5 and 3 cm had the highest emergence rate (80.4%). Seeds on top of the soil were less successful in germinating (34.5%) and more burial lead to a decrease in seedling emergence (3-6 cm 55.9%, 6-10 cm 13.3%, 10+ cm 0.8%, GLM, Tukey, P<0.05, Figure 3.4). Besides, with increase in burial the time to emergence increased except for the unburied seeds, which were slower to germinate (curves were unequal, LR value=1316.21, df=12, P<0.001, Figure 3.4). Similarly, growth after emergence was slower for seedlings from unburied seeds than buried seeds (which had a similar growth after emergence, Figure S3.7). Next to a lower seedling emergence, also a lower germination rate (germinated but not emerged + emerged seedlings) was found with deeper burial (for all groups GLM, Tukey, P<0.05, Figure 3.4).

Seedlings originating from unburied seeds were shorter (i.e., shoot and root length combined) than the shoots buried up to 10 cm, only the emerged seedlings from over 10 cm depth were not significantly longer (ANOVA, Tukey, P<0.05, Figure 3.4). No significant differences in above and below ground length were found between the different burial depths. However, with increasing burial depth roots were relatively shorter and belowground shoot length increased (keeping the total below ground plant parts of similar length, Figure 3.4). Similarly, shoot and root weights were lower for the seedlings from unburied seeds than for seeds buried up to 6 cm, but comparable to seedlings from deeper buried seeds (ANOVA, Tukey, P<0.05, Figure 3.4). Between the different burial depths again no significant differences were found. However, conversion to weight per cm tissue demonstrated that seedlings germinated from unburied seeds had a higher mass which decreased with increasing burial (Figure S3.7).

4. Discussion

In this study, we examined the impact of habitat modification by marram grass on recruitment of conspecifics focusing on the first two requirements for successful establishment: 1) availability of seeds and marine dispersed rhizome fragments and 2) shoot emergence. While in theory more seeds should be deposited close to vegetation (Mclachlan, 2014; Pope, 2006), no seeds or marine dispersed rhizome fragments were found in natural conditions regardless of proximity to vegetation or beach-dune morphology. In sowed plots, seed retention over winter

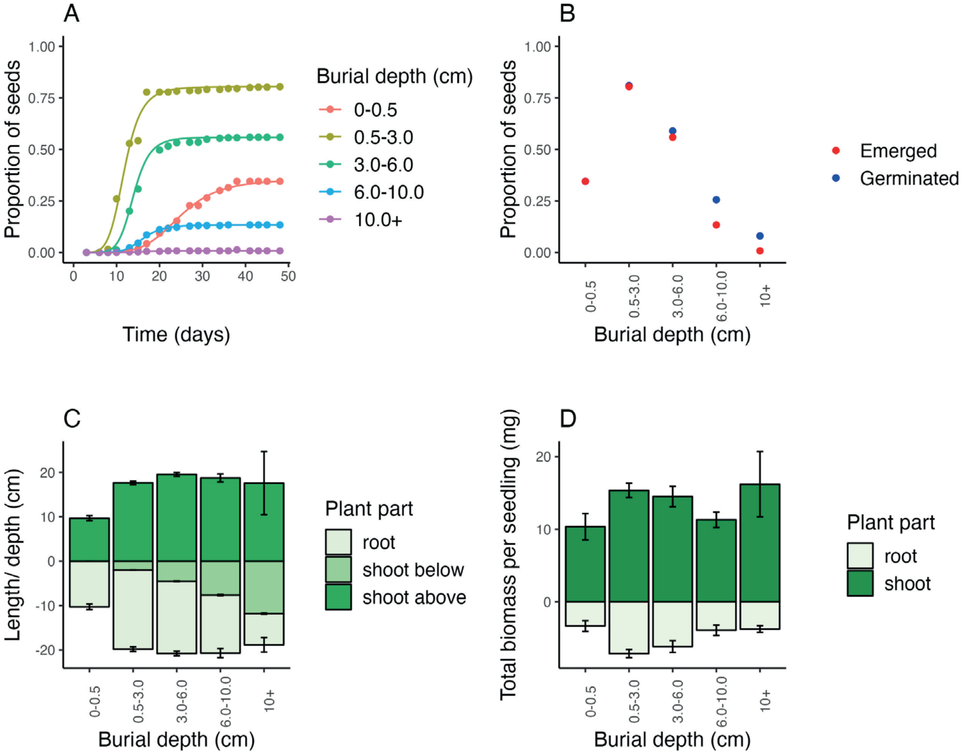


Figure 3.4: A) The proportion of seedling emergence over time from seeds buried at different depth (indicated with different colors). The points represent the seedling counts and the lines are log-logistic time-to-event models. B) The proportion of seeds from which seedlings emerged in red and germinated (including emerged seeds) in blue at the end of the experiment (49 days). C) The final lengths of the shoots and roots of seedlings from different burial depths. From the shoots both above sediment and below sediment level were measured. The zero represents the sediment level and above ground parts are represented as positive values and below ground parts as negative values. D) The total biomass per seedling with roots and shoots separated.

was higher in unmodified than in modified conditions. Moreover, burial over 3 cm significantly lowered seed germination and seedling emergence. Combined with measurements on sediment dynamics, these findings suggest that plant-induced sediment dynamics reduce seed retention as shoot emergence from seeds and rhizome fragments was severely hampered in modified conditions and was negatively related to sediment dynamics. Our findings indicate that vegetation-induced sediment dynamics negatively affect seed availability and shoot emergence from seeds and rhizome fragments, thereby hampering the establishment of conspecifics. These findings highlight the complex interaction between habitat modification and marram grass population dynamics during the early stages of dune development.

Based on the number of marram grass individuals (>5 individuals per 100 m-2) and estimates of seed numbers ranging between 2.000 to 30.000 seeds per individual (Laing, 1958; Lim, 2011; Salisbury, 1952), an input of hundreds of thousands of seeds per year in vegetated dune habitats can be expected. From these seeds, ±78% is expected to be dispersed within a meter from the adult vegetation (Pope, 2006). Yet, we found no seeds in the natural system, irrespective of proximity to adult vegetation. It is likely that plant-induced sediment dynamics reduce seed retention, which can result in seed burial with accumulation or secondary dispersal (i.e., the seeds are moved elsewhere) in erosive events. In other vegetated coastal ecosystems, such as salt marshes and seagrass beds, seed retention increases with burial depth since soil disturbance is lower at greater depth (Marion & Orth, 2012; Z. Zhao et al., 2023; Zhu et al., 2014). In coastal dunes, the same might apply, but it is likely that the dynamic upper layer is considerably larger. In summer, we found an average bed level change of 16 cm in the modified system, with erosion likely increasing in winter (van Puijenbroek, Nolet, et al., 2017). Therefore, the 20 cm layer we tested might have been too shallow to confirm seed presence in more stable soil layers. It is likely that with sediment erosion, which can be caused by wind and flooding, secondary dispersal of seeds occurs. Since the dominant wind direction in the Netherlands is onshore, we expect that secondary dispersal by wind moves the seeds inland to the more stable (fore) dune areas.

While the seeds retention might increase with burial depth, we found a clear negative effect of burial on seed germination and emergence (Figure 3.4). Burial over 3 cm germination rates already clearly decreased and with over 10 cm burial only 0.8% of the seeds were able to emerge. Therefore, the lack of seedlings in control plots likely results from a lack of seeds in the upper soil layer combined with a negligible germination potential from seeds that might have been buried in deeper (20+ cm) soil layers. In field conditions, we found a negative relation between sediment dynamics and shoot emergence (Figure 3.3), with both accretion and erosion likely having negative effects. We did not specifically test the effect of erosion on seedlings. However, similar to other dune plants, cordgrasses and mangroves, we expect erosion to result in uprooting and desiccation of seedlings, increasing mortality (Balke et al., 2013; Cao et al., 2018; Maun, 1994). We expected that higher soil moisture levels in presence of vegetation might benefit seedling establishment (Baldwin &Maun, 1983), but found no significant differences in moisture levels between modified and unmodified conditions

(Figure S3.3). However, we did find a negative correlation between moisture and elevation (Figure S3.3), and a negative relation between elevation and maximum seedling numbers (Figure 3.3). Since adult marram grass vegetation entraps sediment, it increases elevation, which implicates another negative effect of habitat modification on seedling establishment. As the environmental conditions interact with each other and with adult vegetation, additional experiments with higher spatial and/or temporal resolution of measurements would be needed to disentangle specific effects of elevation, moisture, and other small-scale dynamics on seedling germination, emergence and mortality.

Similar to seeds, no marine dispersed rhizome fragments were found in our survey. Contrasting to seed input, the spread of marine dispersed rhizomes is harder to predict. Dispersal of rhizomes is dependent on storm conditions and – as rhizome bud viability is maintained after submersion in seawater up to 13 days – with longshore currents rhizomes could, in theory, be transported hundreds of kilometers (Aptekar & Rejmánek, 2000; Hilton & Konlechner, 2011). In our experiment, we expected a more vigorous growth from rhizomes than from seeds (Harris & Davy, 1986a; van der Putten, 1990). Surprisingly, the number of shoots originating from rhizomes was on average 25 times lower than from seeds, while the rhizome fragments had on average 3000 nodes per plot and 1600 seeds were sown per plot. However, growth and survival of shoots over summer were significantly higher for shoots originating from rhizomes (Figure S3.6). Additionally, the effect of habitat modification was less profound for rhizomes (±4 times less growth in modified conditions) compared to seeds (±8 times less growth in modified conditions).

We hypothesize that the difference in shoot numbers from seed and rhizomes was a result of dry conditions after the experiment started (Table S3.1). Although the effect of drought on marram grass rhizome fragments is unknown, for two reed species it was found that drought lowers viability of rhizome fragments (Mann et al., 2013). Similarly, we expect rhizome fragments of marram grass to be more vulnerable to desiccation than the seeds, as they had not germinated yet. The shoots that emerged from rhizomes likely had a higher resource availability than seedlings, benefiting their growth (van der Putten, 1990). Increased growth enlarges their ability to deal with sediment accretion because of the reduced probability of complete burial, which is almost always fatal (Maun, 1998). Moreover, rhizome fragments are expected to be less prone to erosion because seedlings rely only on their roots for anchoring while the shoots emerging from rhizomes have whole rhizome fragments as anchoring. These factors combined presumably reduced the negative effects of habitat modification on shoot survival for rhizome fragments, also resulting in a higher survival of the few shoots that emerged from rhizomes.

Marram grass is known for its high sand trapping efficiency as an adult, facilitating its own growth and survival through sediment accumulation (Reijers, Siteur, et al., 2019; Zarnetske et al., 2012). However, we found that these biophysical, self-facilitating feedbacks inhibit recruitment of conspecifics in early dune development. Removal of adult vegetation and associated dune forms likely plays an important role in population dynamics of marram grass, especially in embryonic dunes that are most prone to erosion (Itzkin et al., 2021; van Puijenbroek, Limpens, et al., 2017). Storms can remove vegetation leaving an unmodified system where recruitment potential is higher. Additionally, storms can lead to dispersal of clonal fragments on the beach providing a source for establishment (Hesp & Martínez, 2007; Hilton & Konlechner, 2011). While erosion might reduce seed availability in the upper soil layers (van Regteren et al., 2019), it might also expose seeds that were previously buried in the dune body (Hilton et al., 2019). As marram grass seeds can stay viable over 21 years, seeds that were buried for a long period of time can still germinate when they resurface (Hilton et al., 2019). In addition to natural erosive events, manual removal of marram grass vegetation can have similar results. For example, recent attempts to eradicate marram grass in New Zealand (where it is an invasive species), were followed by an unexpected increase in seedlings establishment, prolonging their eradication program (Hilton et al. 2019). Overall, our results show how interactions between adult vegetation and the physical environment can inhibit recruitment of conspecifics in dune grasses and highlight the unpredictability of establishment events as these mainly occur after erosive events.

Acknowledgements

We thank all volunteers that helped in the field, Thomas Meerwijk, Tinder de Waal and Bartel Komin for their help in the field and laboratory and Paula Swinkels for collecting sediment samples. We thank Staatsbosbeheer Texel for permission to conduct this experiment. This study was financially supported by the Netherlands Organization of Scientific Research (NWO-Vidi grant 16588, awarded to TvdH). VR was funded by NWO-Veni grant VI.Veni.212.059.

Supplementary Material

Supplementary Tables

Table S3.1: Environmental data. Max daily temperature measured with HOBO onset temperature loggers. Soil salinity was measured in sediment samples (see Methods) and rain data from the Cocksdorp (closest measuring point) were downloaded from the Royal Netherlands Meteorological Institute (https://www.knmi.nl/nederland-nu/klimatologie/monv/reeksen)

	Wide	**Intermediate**	**Narrow**
Max daily temperature at sediment level (May – August)	29.2±0.5	30.4±0.6	30.8±0.7
Average soil salinity (EC in soil solution, mS/cm)	0.2±0.04	0.02±0.005	0.03±0.005
Rain (mm, May 2020)	12.8		
30-year average rain (mm, May)	44.3±4.1		

Table S3.2: Estimated regression parameters, standard errors, z-values and P-values for the Poisson generalized linear model comparing shoot numbers originating from rhizomes with sediment dynamics (Deviation sediment height) and elevation.

	Estimate	**Std. error**	**Z value**	**P value**
Intercept	2.10	0.57	3.69	<0.001
Deviation sediment height (cm)	-0.27	0.23	-1.13	0.26
Elevation m MWL	-1.42	0.33	-4.26	<0.001

Table S3.3: Estimated regression parameters, standard errors, z-values and P-values for the Poisson generalized linear model comparing seedling numbers (i.e., shoots originated from seeds) with sediment dynamics (Deviation sediment height) and elevation.

	Estimate	**Std. error**	**Z value**	**P value**
Intercept	9.02	0.13	68.76	<0.001
Deviation sediment height (cm)	-2.90	0.11	-26.57	<0.001
Elevation m MWL	-1.80	0.06	-28.58	<0.001

Supplementary figures

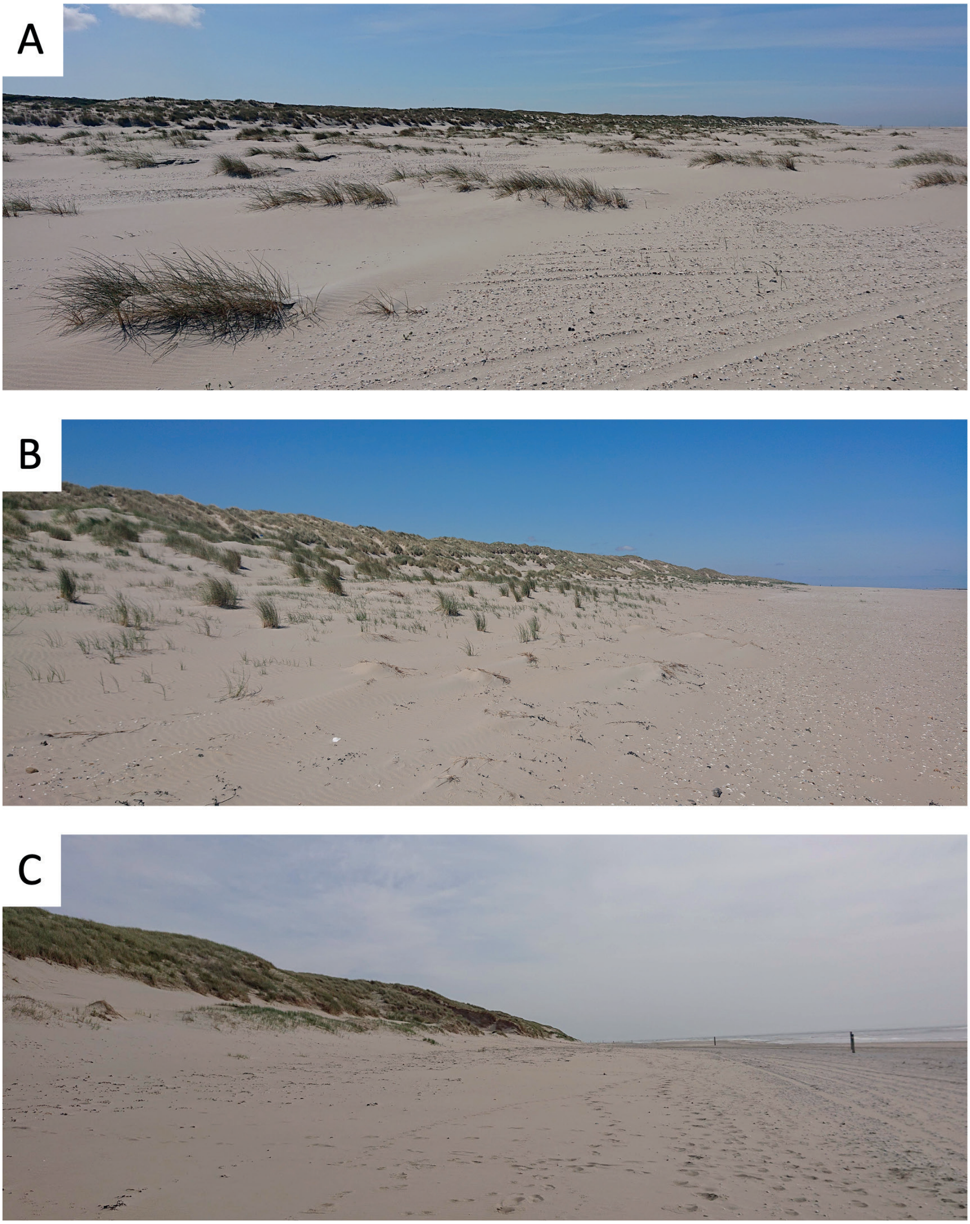


Figure S3.1: Impression of the three selected locations and their vegetation/successive dune stages with A) the wide location (±420m MSL-top foredune), B) the intermediate location (±260 m MSL-top foredune) and C) the narrow location (±140m MSL-top foredune).

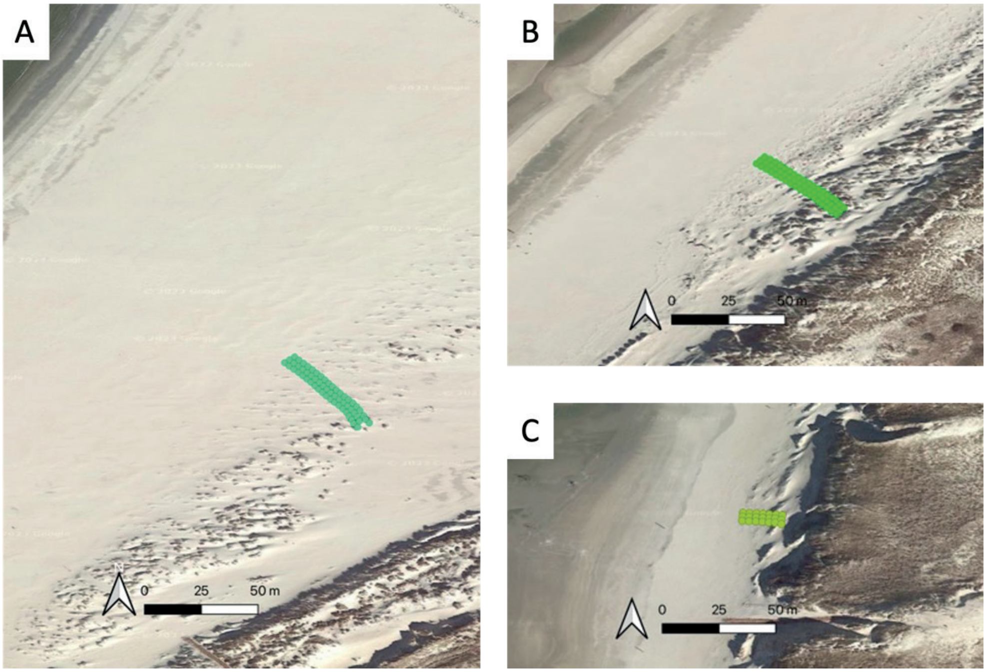


Figure S3.2: Places of sediment cores taken to determine seed availability, with A) the wide location, B) the intermediate location and C) the narrow location.

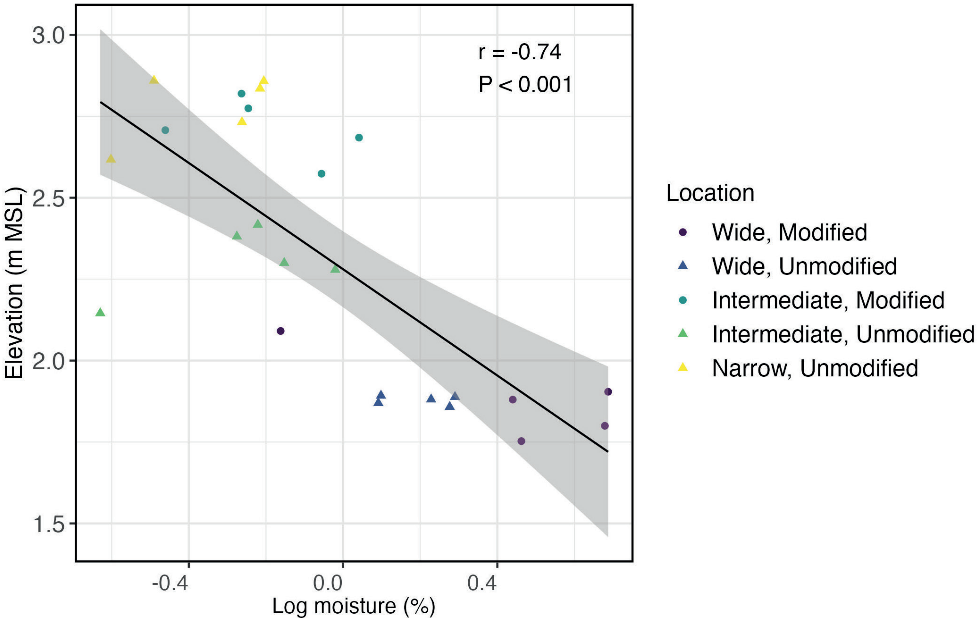


Figure S3.3: Relation between elevation (m MSL) and (log) moisture (%) for the field experiment. Colors indicate locations and shapes represent zones.

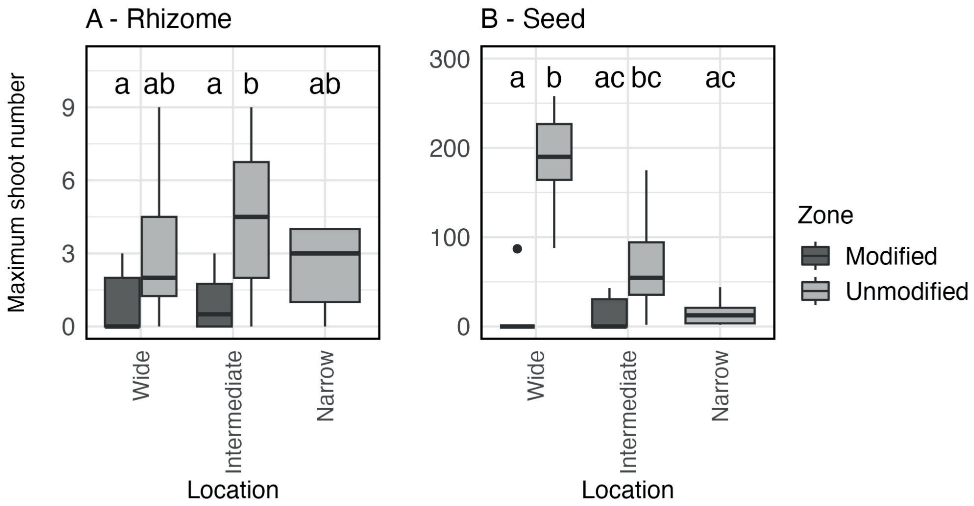


Figure S3.4: The maximum number of shoots per plot for rhizomes (A) and seeds (B) per location and zone (dark boxplots representing the modified zone and light boxplots representing the unmodified zone). Letters depict significant differences based on negative binomial generalized linear models combined with pairwise comparison of estimated marginal means (P<0.05). Horizontal lines indicate the median, box height depicts the first and third quartiles.

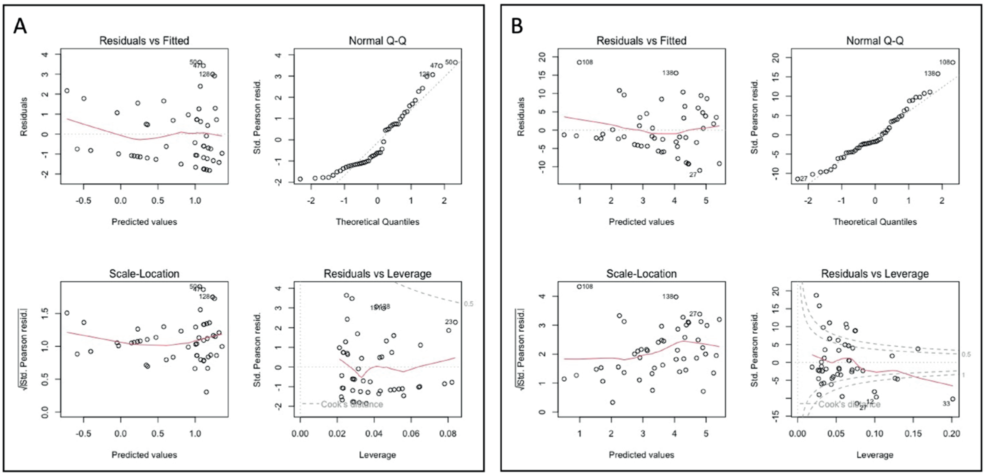


Figure S3.5: Model diagnostics of the GLM comparing plot success with sediment dynamics and elevation (Table S3.2, Table S3.3) for rhizomes (A) and seeds (B). Shapiro test of normality for the residuals had a p-value > 0.05.

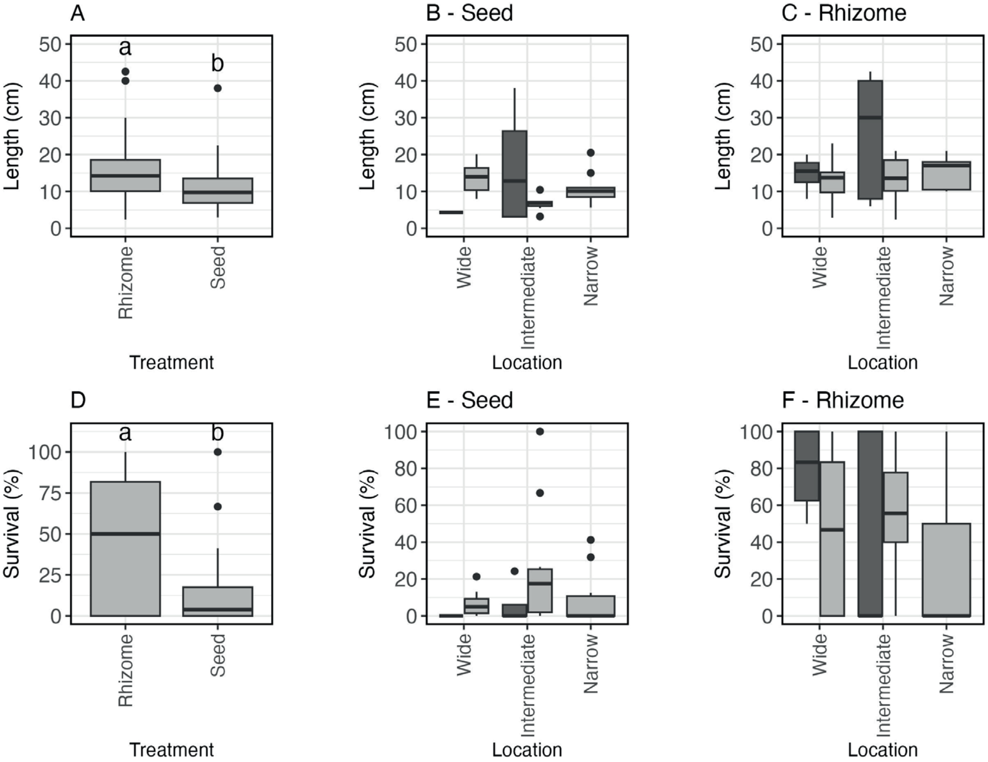


Figure S3.6: A), B) and C) depict shoot lengths at the end of the growth season (September 2020), A) per treatment, B) from seeds, divided per location and zone and C) from rhizome, divided per location and zone. Lengths were averaged per plot (plots with shoots per treatment=35, n=10 shoots per plot). D), E) and F) depict survival of shoots over summer (i.e., maximum number of shoots divided by the number at the end of the growth season), D) per treatment, E) from seed, divided per location and zone and F) from rhizome, divided per location and zone. Letters depict significant differences using Kruskal Wallis test (P<0.05). Horizontal lines indicate the median, box height depicts the first and third quartiles.

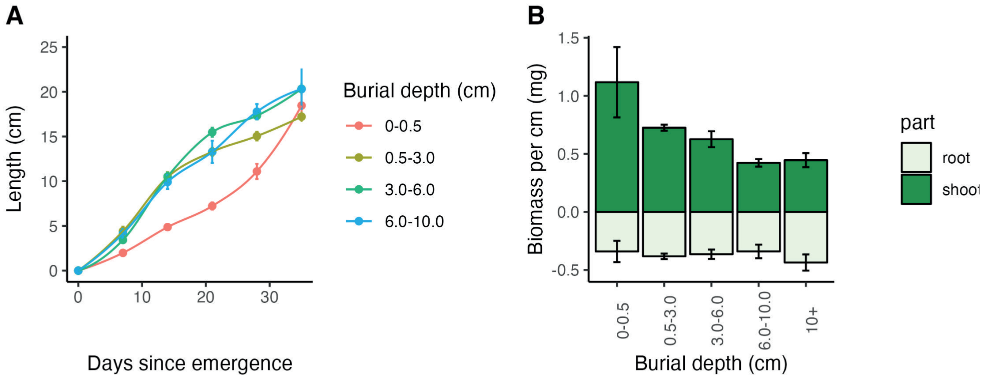


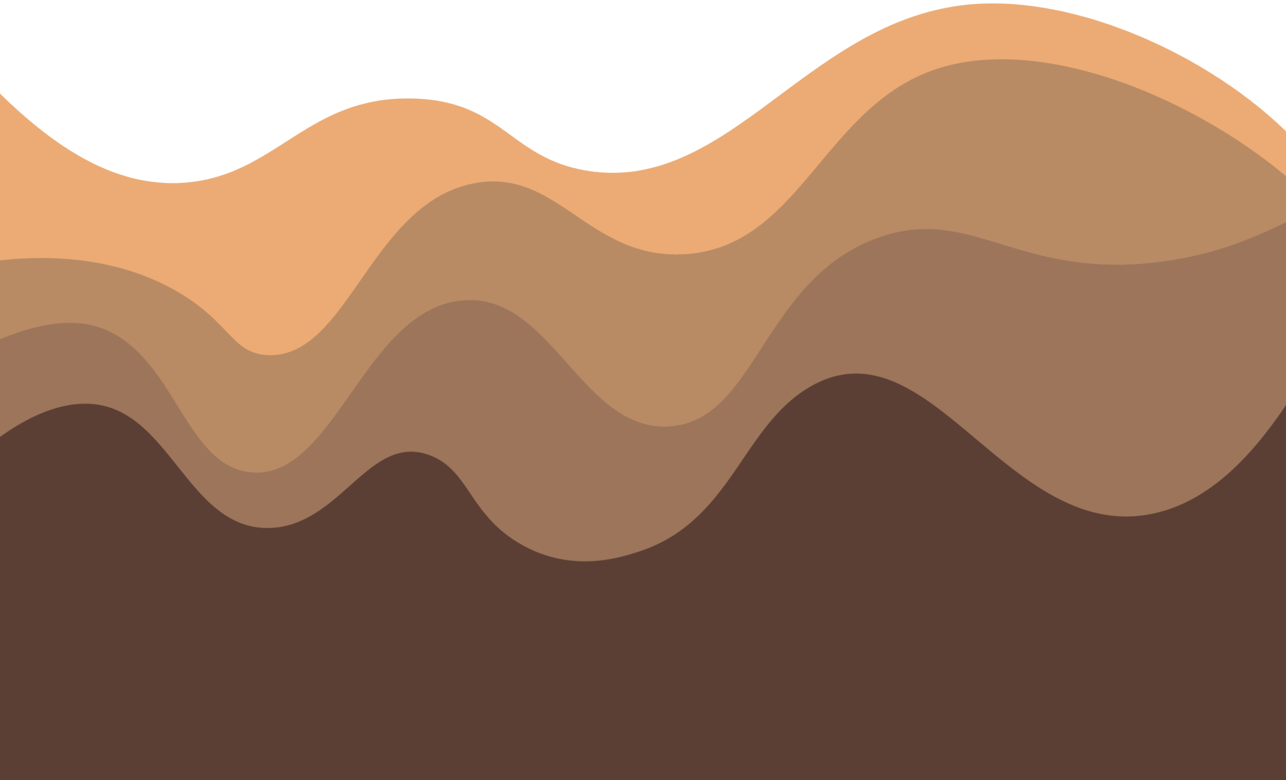
Figure S3.7: A) Seedling growth after emergence for seedlings originating from different burial depths (indicated by different colors). Seedlings that turned out to be buried deeper than 10cm were not individually followed over time, therefore that group is not included. B) Biomass per cm for seedlings from seeds buried at different depths separated between shoot and root biomass.

CHAPTER 4

Interspecific interactions between dune grasses: landscape formation by sand couch negatively affects marram grass' establishment

Carlijn Lammers, Valérie C. Reijers & Tjisse van der Heide

Submitted manuscript



Abstract

Ecosystem engineers are often suggested to drive early vegetation succession by modifying environmental conditions. Along the Northwestern European coast, dune formation is classically believed to start with sand couch (*Elytrigia juncea*), followed by marram grass (*Ammophila arenaria*) once sufficiently large dunes have formed. However, these ideas lack experimental validation, leaving the specific relationship between sand couch, the landscape they form, and marram grass establishment unknown. Here, we experimentally investigated this relationship by planting 975 young marram grass plants in two distinct, sand couch dominated, embryonic dune systems. Using structural equation models, we examined the effect of sand couch and its landscape attributes (elevation, distance to sea and elevation change) on marram grass establishment. Results show an indirect negative effect of sand couch via landscape modifications on survival of establishing marram grass. Specifically, sand couch elevated the environment and elevated areas in turn eroded more in winter, which was the key factor reducing marram grass survival. Moreover, we observed the highest survival in the lower areas surrounded by sand couch dunes. Contrary to the idea that created elevation is a prerequisite, we hypothesize that dune formation by sand couch benefits marram grass establishment by creating relatively low-lying, stable and sheltered microsites.

Keywords: Interspecific facilitation, Dune succession, Structural equation modeling, Sand couch, Marram grass

1. Introduction

Ecological interactions play a critical role in structuring and functioning of ecosystems (Bertness & Callaway, 1994; Bruno et al., 2003; He et al., 2013; Silliman et al., 2015). These interactions occur between species but also within species or even (clonal) individuals. Habitat-modifying species are a prime example of self-facilitation: through modifications to their habitat they improve their living conditions and can extent their own realized niche in hostile conditions (Bruno et al., 2003; Crotty & Bertness, 2015; He & Bertness, 2014). For example, cordgrasses and dune grasses reduce wind and water flow with their physical structures, thereby increasing sedimentation that in turn promotes their own growth and survival (Maun, 1998; Van Hulzen et al., 2007). In vegetated coastal ecosystems, such as salt marshes, mangroves and coastal dunes, habitat-modifying species play a crucial role in the emergence and development of the landscape (Crain & Bertness, 2006). By altering their environment they create a habitat that not only benefits their own growth and survival, but also affect establishment and performance of other species (Castillo et al., 2021; Huxham et al., 2010; Thomsen et al., 2010), laying the groundwork for further development and structuring of the ecological community.

Over a century ago, Clements (1916) already posed the theory that in vegetation succession (i.e., development from a bare to a vegetated system) each dominant species alters its environment in a way that benefits the establishment of the next dominant species (Clements, 1916). In coastal dunes, vegetation succession is classically described as a developmental process from a bare beach to dune grasses to shrubs followed by eventually trees/forest (Clements, 1916; Cowles, 1899; Miyanishi & Johnson, 2007). Here, dune grasses are presented as a single group with the same dune building function. That is, embryonic dunes emerge when sediment is deposited around dune grass (Maun, 2009). Dune grass growth (i.e., increase in shoot formation and length) is promoted by burial and as the plant increases in size more sand is deposited, creating a self-reinforcing feedback (Hacker et al., 2019; Maun, 1998; Zarnetske et al., 2012). In time, these embryonic dunes have the potential to grow into foredunes that form a resistant coastal defense line after which other species such as shrubs are able to establish (Durán & Moore, 2013; Hesp, 1989). However, also within this group of dune grasses, multiple species with different traits interact both on a local (i.e., within patch) and larger (i.e., dune or landscape) scale through habitat modifications, affecting further vegetation establishment and dune development. Overall, species identity, prevailing conditions and interactions between different species and environmental conditions will determine coastal dune development and morphology (Hacker et al., 2019; Reijers et al., 2021; Zarnetske et al., 2012).

In most coastal dune systems, several different dune grass species co-occur and shape the environment, with changing species dominance over a cross-shore gradient. For example, along the Florida coast (USA) bitter panicum (*Panicum amarum*) often dominates younger developing dunes (<5 years) while sea oats (*Uniola paniculata*) dominates the older and more development dune ridges (Johnson, 1997). On the Northwestern European coast sand couch (*Elytrigia juncea*) is generally found closer to the shore than European marram grass (*Ammophila arenaria*, hereafter referred to as marram grass) (Bakker, 1976). The general assumption is that, also in these early dune developmental stages, the earlier successional species (i.e., panicum and sand couch) alter their habitat in a way that benefits the establishment of the later successional species (i.e. sea oats and marram grass) (Bakker, 1976; Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017; Westhoff, 1970). While local interactions between some (USA based) dune grass species have been tested in relation to species invasions, (altered) disturbances, and intraspecific facilitation (Biel & Hacker, 2021; Fischman et al., 2019; Franks & Peterson, 2003; Woods et al., 2023; Zarnetske et al., 2013), the potential role of habitat modification-mediated interspecific facilitation in driving early vegetation succession has not been tested.

In this study, we examine the role of sand couch and the embryonic dune landscape it forms on the establishment of marram grass. Sand couch, with its high salt tolerance and rapid dispersed growth, can colonize bare beach areas where it creates broad and low embryonic dunes (Lammers et al., 2023; van Puijenbroek, Teichmann, et al., 2017). It is generally assumed that marram grass, which is a less salt tolerant species, is only able to establish once sand couch has built sufficiently large embryonic dunes that hold a freshwater lens (Bakker, 1976; Reijers, Lammers, et al., 2019; van Puijenbroek, Teichmann, et al., 2017; Westhoff, 1970). The more dense and patchy growth of marram grass is associated with efficient dune building and results in high, narrow dunes (Lammers et al., 2023; Reijers et al., 2021; Reijers, Siteur, et al., 2019). In time, marram grass outcompetes sand couch by locally entrapping more sediment than sand couch can withstand. Using a field experiment, we determined the role of sand couch and its landscape attributes (i.e., elevation, distance to sea and elevation changes) for survival and growth of establishing marram grass. Following earlier work (Bakker, 1976; van Puijenbroek, Teichmann, et al., 2017; Westhoff, 1970), we hypothesize that the sand couch landscape is beneficial for the survival and growth of marram grass, mainly because of the created height (i.e., reduced risk of flooding). Furthermore, we expect that sand couch directly benefits survival of marram grass through increased soil stability (Davy et al., 1993; van der Putten, 1990). However, marram grass' shoot formation might be hampered by presence of sand couch due to competition for space and resources (Hacker et al., 2012; Zarnetske et al., 2012).

2. Methods

2.1. Field experiment

To determine whether sand couch and the landscape created by sand couch either facilitate or inhibit establishment of marram grass, we conducted a field experiment between April 2021 and October 2022 on the Dutch Wadden island Schiermonnikoog (Figure 4.1, Figure S4.1, S4.2). In this experiment, we planted marram grass plants (n=975) at two embryonic dune locations where sand couch dominates. Over the last decades, beaches at both locations have been accreting (Luijendijk et al., 2018) and there has been a general expansion of dune area (AHN, 2022). The first location was an exposed site at the tail of the island where only sand couch was present and no foredunes were formed yet (max elevation ±4 m to mean sea level (MSL) (AHN, 2022), n=750, Figure S4.1). The second location was a more sheltered site, where both sand couch and marram grass co-occurred. Here, foredunes dominated by marram grass had already developed (max elevation ±10 m to MSL (AHN, 2022), n=225, Figure S4.1). Marram grass transplants were planted on bare soil (±13%, n=130) or in sand couch patches with ranging sizes (±87%, n=845; min – max size: 0.1 – 628 m2), in a range of distances from the North Sea (207 – 870 m, Figure 4.1) and elevations (1.35 – 3.33 m to MSL, Figure 4.1).

Prior to the experiment, the marram grass plants were grown from seed in pot soil at a plant nursery. They were about 8 months old at the start of the experiment and were transplanted with their pot soil, which was buried up to sediment level. At the start of the experiment and subsequently before and after the growth season in 2021 and 2022 (i.e., in April and October), the survival and growth (measured as the number of shoots per transplant) of marram grass plants were determined. In addition, bed level elevation at each plant was determined using an RTK-GPS.

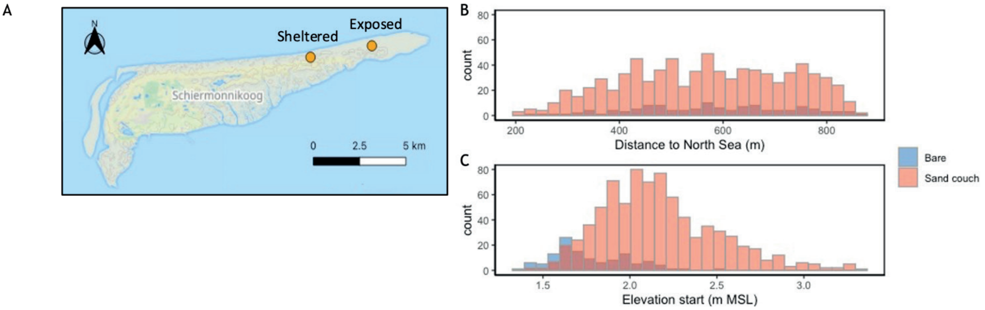


Figure 4.1: A) Locations of the experiment on Schiermonnikoog, The Netherlands, with west the more sheltered location and east the more exposed location. Impression of the variation in B) distance to North Sea (m) and C) elevation (m MSL) for the marram grass transplanted on bare soil (blue) and within patches of sand couch (red).

2.2. Statistical analyses

Since we expected random variation in the initial survival of marram grass transplants irrespective of environmental conditions, we applied an acclimatization period of 6 months until October 2021. After the acclimatization period 752 marram grass plants were alive (exposed n=557, sheltered n=195), which were included in the analyses.

To examine the effects of sand couch and landscape settings on survival and growth of marram grass plants, we first fitted (generalized) linear mixed-effect models exploring direct relations between landscape variables, marram grass survival and growth. Subsequently, we constructed a structural equation model (SEM, Figure 4.2) to combine both direct and indirect effects. Next to survival or growth, the models included the presence of sand couch, distance to North Sea, elevation at which marram grass was planted (hereafter referred to as elevation), elevation change in winter (i.e., difference in elevation between October 2021 and April 2022), and elevation change in summer (i.e., difference in elevation between April 2022 and October 2022).

2.2.1 Hypothesized relations between sand couch, landscape features and marram grass survival and growth

Presence of sand couch

We expected a direct positive effect of sand couch on survival of marram grass transplants because of increased soil stability and anchoring between roots of sand couch (Davy et al., 1993; van der Putten, 1990). On the other hand, growth might be hampered by presence of sand couch due to competition for space and resources (Hacker et al., 2012; Zarnetske et al., 2012).

In theory the presence of sand couch is dependent on distance from the North Sea, with a larger likelihood of sand couch being present with increasing distance from the North Sea (Bakker, 1976; van Puijenbroek, Teichmann, et al., 2017). However, here we expected no significant relation between distance to North Sea and presence of sand couch because of the design of the field experiment, with the deliberate selection of bare and vegetative patches at any distance from the North Sea.

Distance to North Sea

We expected a higher survival of transplants with increasing distance from the

North Sea, because we expect that with distance transplants were more sheltered (e.g., lower wave impact in storm conditions) in a way that is not captured solely by increase in elevation or elevation change (Anthony, 2013). We did not expect a direct effect of distance from the North Sea on the growth of marram grass transplants.

Elevation

We expected elevation to depend on presence of sand couch, which through entrapment of sediment elevates the environment, and to increase with distance from the North Sea (van Puijenbroek, Limpens, et al., 2017; van Puijenbroek, Nolet, et al., 2017). Marram grass survival was expected to increase with elevation because flooding risk decreases and freshwater availability increases with elevation (Röper et al., 2013; van Puijenbroek, Teichmann, et al., 2017; Westhoff, 1970). Similarly, a positive relation between growth and elevation was expected because of these beneficial conditions.

Elevation change

Sediment dynamics were expected to play an important role in transplant survival and growth as both excessive burial and erosion were expected to increase transplant mortality and dislodgement (Maun, 1998). Therefore, survival was expected to decrease with increasing dynamics both in summer and in winter. In summer, on average accretion was expected, while in winter higher erosion rates were expected due to a higher likeliness and frequency of storm conditions in winter (Anthony, 2013; van Puijenbroek, Nolet, et al., 2017). Since partial burial promotes tillering in marram grass, we expect more growth with slight accretion in summer (Huiskes, 1979). Since the growth is very slow in winter, no effect of sediment dynamics in winter on growth was expected (Huiskes, 1979).

Sand couch was expected to capture sediment in summer resulting in a bigger elevation change in sand couch patches, while we expected sand couch to reduce erosion in winter reducing overall sediment dynamics (van Puijenbroek, Nolet, et al., 2017). As wave exposure during storm conditions is higher closer to the North Sea, we expected higher sediment dynamics closer to the North Sea in winter (Anthony, 2013). Lastly, we expected a larger increase in elevation with higher initial elevations in summer, while a less profound effect was expected in winter (van Puijenbroek, Nolet, et al., 2017).

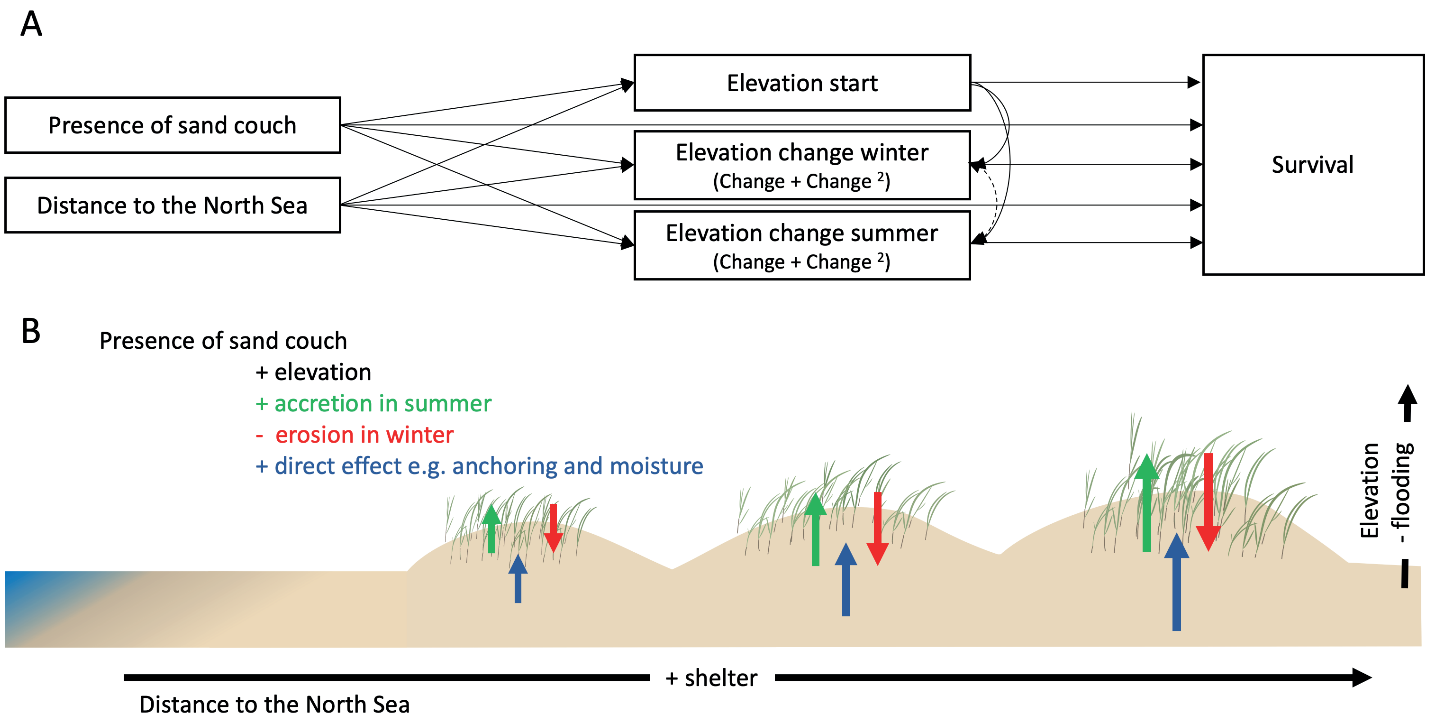


Figure 4.2: A) Diagram of the conceptual structural equation model describing hypothesized relations between presence of sand couch, distance to the North Sea, elevation, elevation change (winter + winter^2 and summer + summer^2) and survival or growth. B) Graphic representation of hypothesized relations.

2.2.2. Mixed effect models

To investigate direct effects between landscape variables, we fitted linear mixed-effect (LME) models exploring the effect of sand couch presence and distance from North Sea on elevation and the effect of these factors (i.e., elevation, distance to North Sea and presence of sand couch) on elevation change in summer and winter, including location as random effect. To obtain a (close to) normal distribution, we log transformed elevation data.

To examine the direct relations between survival and landscape variables (i.e., presence of sand couch, distance to North Sea, elevation and elevation change in summer and winter), we fitted a generalized linear mixed-effect (GLME) model with location as random effect. For elevation change in winter and summer, we expected an optimum in survival with stable to slight burial condition (see hypothesized relations). We first tested whether this held true by comparing Akaike's information criterion (AIC) values of GLME models. The first model testing the relation between survival and elevation change and a second model testing survival against elevation change + elevation change^2. For both seasons, the GLME model including the unimodal function were a better fit (i.e., AIC values were over 2 points lower). Therefore, we included values for elevation change in summer and winter based on their optimum using the regression coefficients of their respective GLME models including survival, elevation change and elevation change^2 (i.e., $y=ax+bx^2$, in which 'y' is the new measure of elevation change, 'a' and 'b' are regression coefficients and 'x' the elevation change in m).

In a similar manner, we tested the direct relation between growth and landscape variables by fitting an LME model including location as random effect. In these analyses only marram grass plants that were alive (exposed n=161, sheltered n=160) were included. Growth was included as fraction of the number of shoots at start (i.e., number of shoots at end divided by the number of shoots at start) and log-transformed to normalize the distribution (i.e., in the log-transformed data zero represents no growth, a positive value growth and a negative value a reduction of shoots). Similar to survival, we expected an optimal growth at slight burial. We used the same methods (with an LME model instead of an GLME model) to determine whether there was an optimum, but for growth the unimodal function of elevation change in summer and in winter was not a better fit.

All described models were fitted in R (version 4.2.1, package "lme4" (Bates et al., 2015)). We used stepwise backward elimination of variables based on significance levels (determined using package “lmerTest” (Kuznetsova et al., 2017)). Variables were considered significant at a significance level of $P=0.05$. In the backward selection procedure, models were compared using AIC values. The model with only significant variables and the lowest AIC value was considered the best fit. For the best fitting models, we obtained conditional R^2 for linear mixed-effect models (package “MuMIn” (Nakagawa et al., 2017)).

2.2.3. Structural equation model

To explore the combined direct and indirect effects of sand couch presence, distance to North Sea, elevation, elevation change in winter and summer on survival of marram grass, we constructed a SEM using the piecewiseSEM package (Lefcheck, 2016; Figure 4.2). Since there was no indication that factors controlled by sand couch presence, elevation or distance to North Sea (i.e., no indirect effects) affected marram grass growth, based on results from the fitted linear mixed-effect models, we did not fit a structural equation model for growth. We used the fitted (generalized) linear mixed-effect models as basis for the SEM and in case regression coefficients had an insignificant regression coefficient stepwise backward selection was applied. Furthermore, directed separation ($P>0.05$) between non-tested relations was checked and overall goodness of fit statistics were determined using Fisher’s C, with a P value greater than 0.05 being considered acceptable.

To explore differences between the exposed and sheltered location, we fitted two more SEMs using the same approach as described above, only with (generalized) linear models instead of (generalized) linear mixed-effect models.

3. Results

3.1. Sand couch landscape variables

Results of the linear mixed effect model showed a significant positive effect of sand couch and distance to the North Sea on elevation ($F_{1,748.0}=186.5$, $P<0.001$ (elevation), $F_{1,747.1}=190.4$, $P<0.001$ (distance), conditional $R^2=0.68$, Figure S4.3). In winter, erosion was more profound than in summer (min – max elevation change: -1.14 – 0.30 m vs -0.61 – 0.58 m, respectively, Figure S4.3). In winter, a significant negative effect of elevation and positive effect of distance to North Sea on elevation change were found ($F_{1,749.0}=334.4$, $P<0.001$ (elevation), $F_{1,743.5}=67.2$, $P<0.001$ (distance), conditional $R^2=0.66$, Figure S4.3). Meaning that higher elevation was related to a bigger elevation change (i.e., relatively more erosion with higher

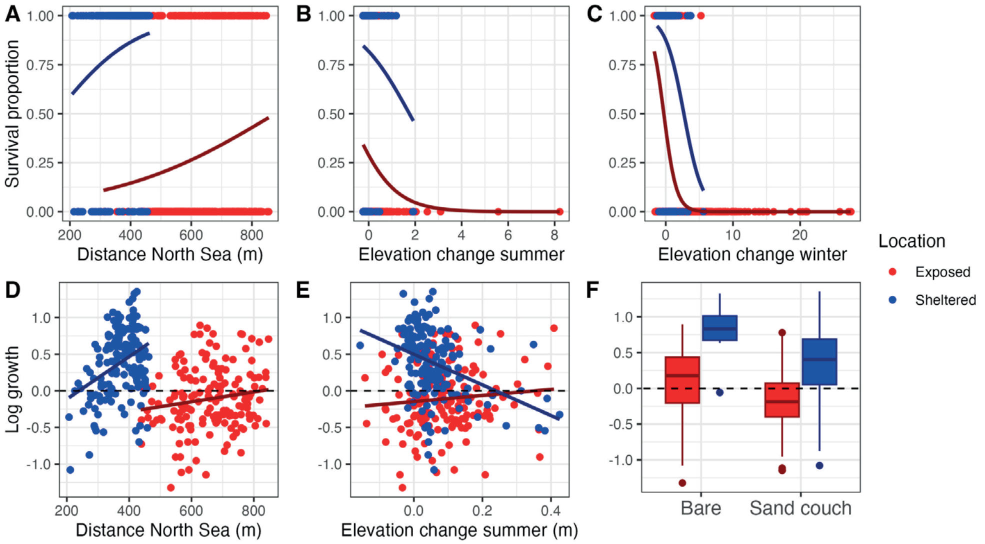


Figure 4.3: Relation between distance to North Sea and survival (A), elevation change in summer (the lower the value the closer to a change of 0.12m) and survival (C), and elevation change in winter (the lower the value the closer to a change of 0.30m) and survival (C). The effect of distance to North Sea (D), elevation change in summer (E) and presence of sand couch (F) on (log) growth. The dashed lines represent no increase, negative values a decrease in shoots and positive values an increase in shoots. In the boxplot (F) horizontal bars represent median values and box height the first and third quartiles.

elevation, Figure S4.3) and with a further distance from the North Sea there was, on average, less erosion/more accretion (Figure S4.3). In contrast, no significant effects of elevation, distance to North Sea or presence of sand couch on elevation change in summer were found (Figure S4.3).

In relation to survival, the optimum elevation change in winter was 0.3 m (corresponding maximum accretion we found in winter) and in summer 0.12 m. The calculated values of 'elevation change' for the structural equation model had a minimum value representing the optimum (converted values representing the optimum were -1.7 winter vs -0.2 in summer), the more deviation from this value (in positive direction) the further from the optimum (in summer this indicated both more and less change than 0.12 m, while in winter the higher the value the lower the elevation change/the more erosion).

3.2. Direct effects on survival and growth of marram grass transplants

Marram grass survival in winter (27.8%) was much lower than survival in summer (91.1%). The survival was best explained by a model including distance to the

North Sea (χ^2=12.1, P<0.001), elevation change in winter (χ^2=95.4, P<0.001) and elevation change in summer (χ^2=7.5, P=0.006, conditional R^2=0.83, Figure 4.3). Presence of sand couch and elevation had no direct significant explanatory value for marram grass survival.

At the start of the experiment the marram grass plants had an average of 14±0 shoots. After two growth seasons, the surviving marram grass individuals (exposed – bare n=29, exposed – sand couch n=132, sheltered – bare n=8, sheltered – sand couch n=152) had on average 36±2 shoots, with a large variation between individuals (min – max shoot number: 1 – 380). Results from the stepwise backward linear mixed effect regression procedure showed that there was a negative effect of presence of sand couch ($F_{1,316.2}$=13.9, P<0.001), a positive effect of distance to the North Sea ($F_{1,312.2}$=16.3, P<0.001) and a negative effect of elevation change in summer ($F_{1,316.2}$=4.0, P=0.047, conditional R^2=0.70, Figure 4.3). There were no significant direct effects of elevation or elevation change in winter on growth. Furthermore, no significant effects of elevation, distance or sand couch on elevation change in summer were found (i.e., no indirect effects on growth).

3.3. Combined direct and indirect effects on the survival of marram grass

The strongest effect on survival was the direct effect of elevation change in winter (path coefficient -0.82, Figure 4.4, Table S4.1). Both sand couch and elevation did not have a direct effect on marram grass survival, but an indirect negative effect on survival through increased elevation change (sand couch created elevation, higher elevation related to more erosion, and more erosion leads to higher mortality/loss. Path coefficients; sand couch -0.16 and elevation -0.41, Table S4.1). Distance to North Sea had a direct positive effect on survival and also a positive effect through

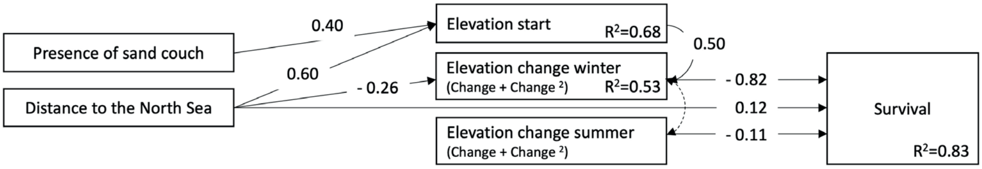


Figure 4.4: The best structural equation model for survival of marram grass. Only significant paths were included in the best fitting model (i.e., all presented arrows are significant). The presence of sand couch and distance to the North Sea positively affect elevation. Higher elevation related to more erosion in winter while a further distance from the North Sea related to less erosion in winter (i.e., more accretion). Furthermore, marram grass survival was higher farther from the North Sea, with less erosion (i.e., a higher value for the optimum in elevation change in winter) and with less deviation from the optimal elevation change in summer (i.e., 0.12 m). Besides, a correlated error between the optimum in elevation change in winter and summer was included.

elevation change in winter (i.e., further from the North Sea change was closer to the optimum). It also had an indirect negative effect through increase in elevation with distance from North Sea, but the overall path coefficient was positive (0.09, Table S4.1).

3.4. Differences between the exposed and sheltered location

Generally, the exposed location was more variable in landscape features with a larger variation in elevations (min – max: 1.45 – 3.29 m to MSL (exposed) vs 1.67 – 2.68 m to MSL (sheltered)), distances from the North Sea (min – max: 310 – 855 m (exposed) vs 207 – 462 m (sheltered)) and elevation changes (winter min – max: -1.14 – 0.30 m (exposed) vs -0.39 – 0.18 m (sheltered); summer min – max: -0.61 – 0.58 m (exposed) vs -0.15 – 0.49 m (sheltered), Figure S4.3).

Overall, the survival rate was three times higher at the sheltered location than at the exposed location (82.1 vs 28.9%, respectively). The results of the structural equation model in exposed conditions were similar to the overall structural equation model, with stronger correlations with all explanatory variables except distance to North Sea (Figure S4.4, path coefficients in Table S4.1). In sheltered conditions, on the other hand, the relation between elevation, elevation change and survival were weaker (path coefficients; elevation -0.27 (sheltered) vs -0.46 (exposed); elevation change winter -0.26 (sheltered) vs -0.91 (exposed); elevation change summer insignificant (sheltered) vs -0.16 (exposed); Table S4.1). Moreover, here the presence of sand couch had a direct positive effect, while elevation had a direct negative effect on survival of marram grass (Figure S4.4, Table S4.1).

At the end of the experiment, the plants had on average more than twice as many shoots at the sheltered location than at the exposed location (53.6±4.2 vs 18.1±1.7 shoots, respectively, $t = -7.7$, $P<0.001$). In the separate linear models, we found opposing effects of landscape variables on growth. In exposed locations, little of the variation in growth could be explained (multiple $R^2=0.09$) with a significant positive effect of elevation ($F=4.96$, $P=0.02$), negative effects of elevation change in winter ($F=5.18$, $P=0.02$) and presence of sand couch ($F=7.00$, $P=0.009$, Figure 4.3, Figure S4.4). In sheltered conditions more variation in growth could be explained (multiple $R^2=0.26$). In contrast to the exposed location, here, a significant negative effect of elevation on growth was found ($F=14.04$, $P<0.001$, Figure S4.5). Furthermore, a positive effect of distance from the North Sea ($F=21.97$, $P<0.001$, Figure 4.3) and a negative effect of elevation change in summer (i.e., less growth with more accretion) were found ($F=15.23$, $P<0.001$, Figure 4.3).

4. Discussion

In this study, we explored the role of sand couch and the embryonic dune landscape they formed on survival and growth of establishing marram grass plants. We expected sand couch to facilitate marram grass establishment, both directly (e.g., through anchoring) and indirectly (e.g., through dune formation). Surprisingly, however, results from our field experiment indicate an indirect negative effect of sand couch on survival of marram grass through habitat formation. Specifically, elevation was higher in presence of sand couch and a higher elevation was related to more erosion in winter, which in turn was the most important factor reducing marram grass survival. While the indirect negative effect of sand couch through elevation was independent of location, the direct effects of sand couch on survival (i.e., neutral in exposed and positive in sheltered conditions) and growth (i.e., negative in exposed and neutral in sheltered conditions) were location and thus context dependent.

Survival of marram grass was most strongly affected by elevation change in winter (Figure 4.4, Table S4.1). Contrary to our expectation, sand couch did not reduce erosion in winter, but indirectly stimulated this process through the created elevation, which increased erosion potential. That is, depending on dune morphology and winter conditions, large dunes can erode more substantially than smaller dunes (van Puijenbroek, Nolet, et al., 2017), which we found in our experiment. While vegetation is generally found to reduce erosion in winter, the extent to which this happens depends on the morphological characteristics of the species and environmental conditions (e.g., wind and wave conditions) (Feagin et al., 2023; Innocenti et al., 2021; Maximiliano-Cordova et al., 2019). Since sand couch has a relatively dispersed shoot organization and short shoots, it is less effective at reducing erosion than, for example, marram grass (van Puijenbroek, Nolet, et al., 2017). Moreover, there were multiple storms during our experiment of which some resulted in (partial) flooding of the dune system (Table S4.2). The largest flooding event occurred on 19 February 2022, with water levels reaching 3.0 m to MSL. Since wave runup causes more erosion than wind (Innocenti et al., 2021), we expect that these flooding events had a major effect on erosion in our experiment. However, since storm erosion is the result of complex interactions between amongst others wind conditions, wave energy, timing of tide versus peak storm conditions, beach and dune morphology and vegetation (Feagin et al., 2015; Innocenti et al., 2021; Itzkin et al., 2021; van Puijenbroek, Nolet, et al., 2017), we cannot conclusively determine the impact of storms compared to other conditions in winter.

Next to elevation change in winter, also elevation change in summer and distance to North Sea had a direct effect on survival of marram grass, but these were not directly related to presence of sand couch. We expect that the positive effect of distance to sea was mainly an effect of shelter, for example, in storm conditions the wave energy dissipates with beach/dune width (Anthony, 2013). In our structural equation model, we included optimal values for sediment change. A more elegant solution would have been to include elevation change as composite variables in our model, however in the currently available R packages a combination of (generalized) linear mixed effect models and composite variables are not available yet (Lefcheck, 2016). As expected, both excessive burial and erosion in summer (optimum +0.12m) caused a higher mortality of marram grass. Contrary to our expectations, elevation change in summer was not explained by presence of sand couch, elevation, or distance from the North Sea. A possible explanation might be that sand couch does not only affect local sedimentation but also affects sediment dynamics of surrounding bare areas (Zhao & Gao, 2021). Overall, these results indicate that marram grass survival is highest in relatively stable and sheltered parts of the landscape.

Overall, shoot formation of marram grass was negatively affected by sand couch presence. Negative species interactions are often a result of competition for limiting space or resources (Hacker et al., 2012; Zarnetske et al., 2012). Which resources or other mechanisms play a role here is unknown, as this was beyond the scope of our current research. However, since the marram grass plants were transplanted within their pot soil, which is relatively high in nutrient levels compared to sand, it seems unlikely that nutrients limited marram grass' growth. Furthermore, marram grass grew more with increasing distance from North Sea, which we hypothesize to be the result of the more sheltered conditions (i.e., smaller impact of waves and flooding). In general marram grass is known as a highly burial tolerant species with growth being stimulated by high sand supply (Huiskes, 1979). However, we found a negative effect of burial on shoot formation, suggesting that places with highest accretion exceeded burial levels at which growth is promoted.

We conducted our experiment at two locations that were relatively close (± 3 km) but different in landscape morphology and dynamics. As supported by, for example, the stress gradient hypothesis, species interactions can differ depending on environmental conditions (Biel & Hacker, 2021; Brown et al., 2018; Fischman et al., 2019; He et al., 2013). In our experiment, the direct (i.e., local) interaction between sand couch and marram grass changed depending on location. At the sheltered location, the direct effect was neutral to positive (i.e., no direct effect on growth and a positive effect on survival) while at the exposed location it was neutral to negative (i.e., a negative effect on growth and no direct effect on survival). Based on the stress gradient hypothesis, facilitation would be expected to be more important in stressful conditions. However, in extreme conditions facilitative effects may decrease or cease (Fischman et al., 2019; Maestre et al., 2009). In our study, the conditions on the exposed location may have exceeded the thresholds at which sand couch can facilitate marram grass survival. Potential direct positive effects on survival could be increased anchoring (i.e., reduced changes of being uprooted or removed by wind/wave motion) or a different microclimate compared to bare soil, such as a lower soil temperature or higher soil moisture levels (Baldwin & Maun, 1983). Additional research testing microclimate differences between bare and sand couch patches and their effect on marram grass development are needed to determine through which mechanisms sand couch promotes or inhibits marram grass.

In several ecosystems it has been found that species interactions can differ depending on spatial scale with scale-dependent or cross-habitat interactions as clear examples (e.g., Donadi et al., 2013; van de Koppel et al., 2006; van Wesenbeeck et al., 2008). For example, on tidal flats mussel beds inhibit cockles on a short distance but facilitate them on a (relatively) long distance by enhancing settlement in the wake of the beds. Similarly, on cobble beaches cordgrass was found to compete with forb species on a small scale while facilitating them on a large scaler by attenuating hydrodynamics (Donadi et al., 2013; van de Koppel et al., 2006). We hypothesize that sand couch negatively affects marram grass through created elevation locally, but that through their dune formation, sand couch creates relatively sheltered and stable microsites benefitting marram grass' establishment. However, additional research will be needed to test this hypothesis and the potential environmental dependency of such interspecific interactions. Our study highlights that observed vegetation patterns can have complex underlying processes and the need to study species interactions across spatial scales. Overall, we expect sand couch to play an important role in priming the landscape for establishment of marram grass, albeit in a more indirect manner than commonly suggested.

Acknowledgements

We thank The Fieldwork Company and many volunteers for their help setting up and monitoring the experiment. We thank Natuurmonumenten for their permission to conduct the experiment at National park Schiermonnikoog. This work was financially supported by the Netherlands Organization of Scientific Research [NWO-Vidi grant 16588, awarded to TvdH]. VR was funded by NWO-Veni grant VI.Veni.212.059.

Supplementary material

Supplementary tables

Table S4.1: Statistics of the structural equation model testing the effects of elevation, elevation change in summer, elevation change in winter, presence of sand couch and distance to the North Sea on survival of marram grass transplants (Figure 3, 4, Figure S2)

Conditional R^2	**All data**	**Exposed**	**Sheltered**
Elevation	0.68	0.35	0.40
Elevation change winter	0.53	0.22	0.09
Survival	0.83	0.52	0.26

Path coefficients			
Distance to North Sea	0.090	0.047	0.261
Elevation	-0.406	-0.466	-0.279
Sand couch	-0.163	-0.195	0.216
Elevation change winter	-0.816	-0.916	-0.263
Elevation change summer	-0.108	-0.163	Insignificant

Correlated errors			
Winter ~~ Summer	0.103	0.083	NA

Goodness of fit			
Fisher's C	11.642 (P=0.17)	4.325 (P=0.83)	0.772 (P=0.68)

Table S4.2: The 5 days with the highest water levels measured during our experiment, with measurement location 'Schiermonnikoog' (EPSG 25831). Data from https://waterinfo.rws.nl/#/nav/bulkdownload.

Date Time (CET)	Water level (cm to MSL)
01-02-2022 22:30:00	246
07-02-2022 02:20:00	255
18-02-2022 23:50:00	260
19-02-2022 01:00:00	296
21-02-2022 12:50:00	254

Supplementary figures

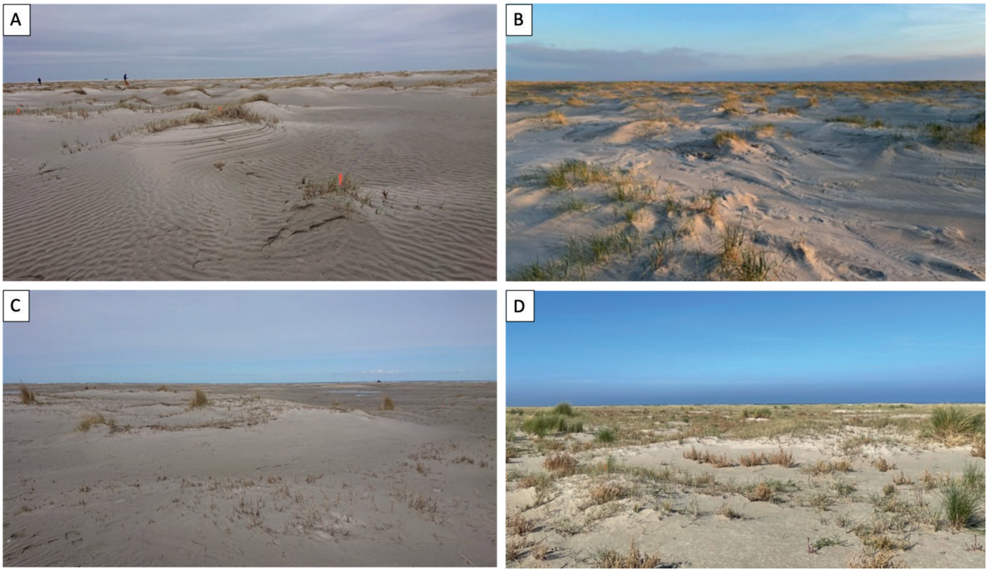


Figure S4.1: Impression of the embryonic dunes on the Dutch Wadden island Schiermonnikoog. From the start of the experiment in April 2021 (A, C) and after the growth season in October 2021 (B, D). On top (A, B) the exposed location, where only sand couch naturally occurred, and on the bottom (C, D) the sheltered location, where embryonic dunes were dominated by sand couch but also marram grass and dune annuals (e.g., Cakile maritima) were present.

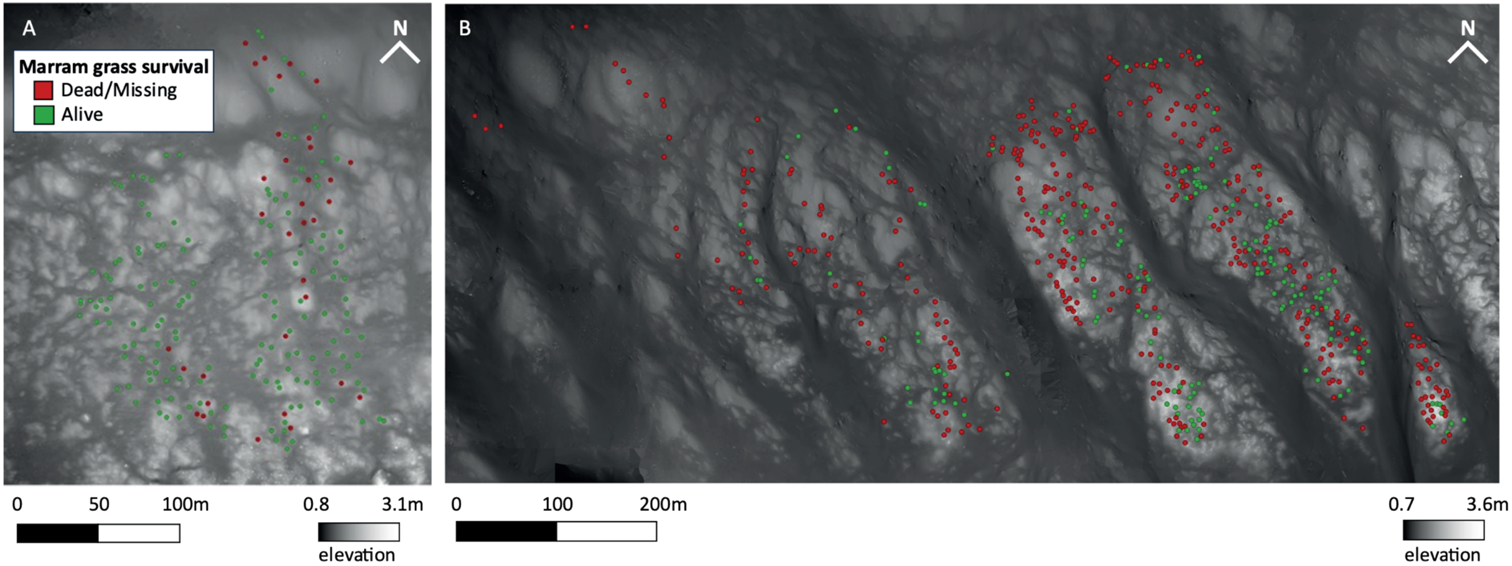


Figure S4.2: Digital surface model (from start of the experiment, April 2021, m to MSL) of the sheltered (A, n=195) and exposed (B, n=557) location with the placement of marram grass transplants with indication if they were alive (green) or dead/missing (red) at the end of the experiment (October 2022). Note, the scales (distance and elevation) are different for the two panels. The North Sea is located north of the depicted areas and the foredunes (sheltered) andr Wadden Sea (exposed) to the south.

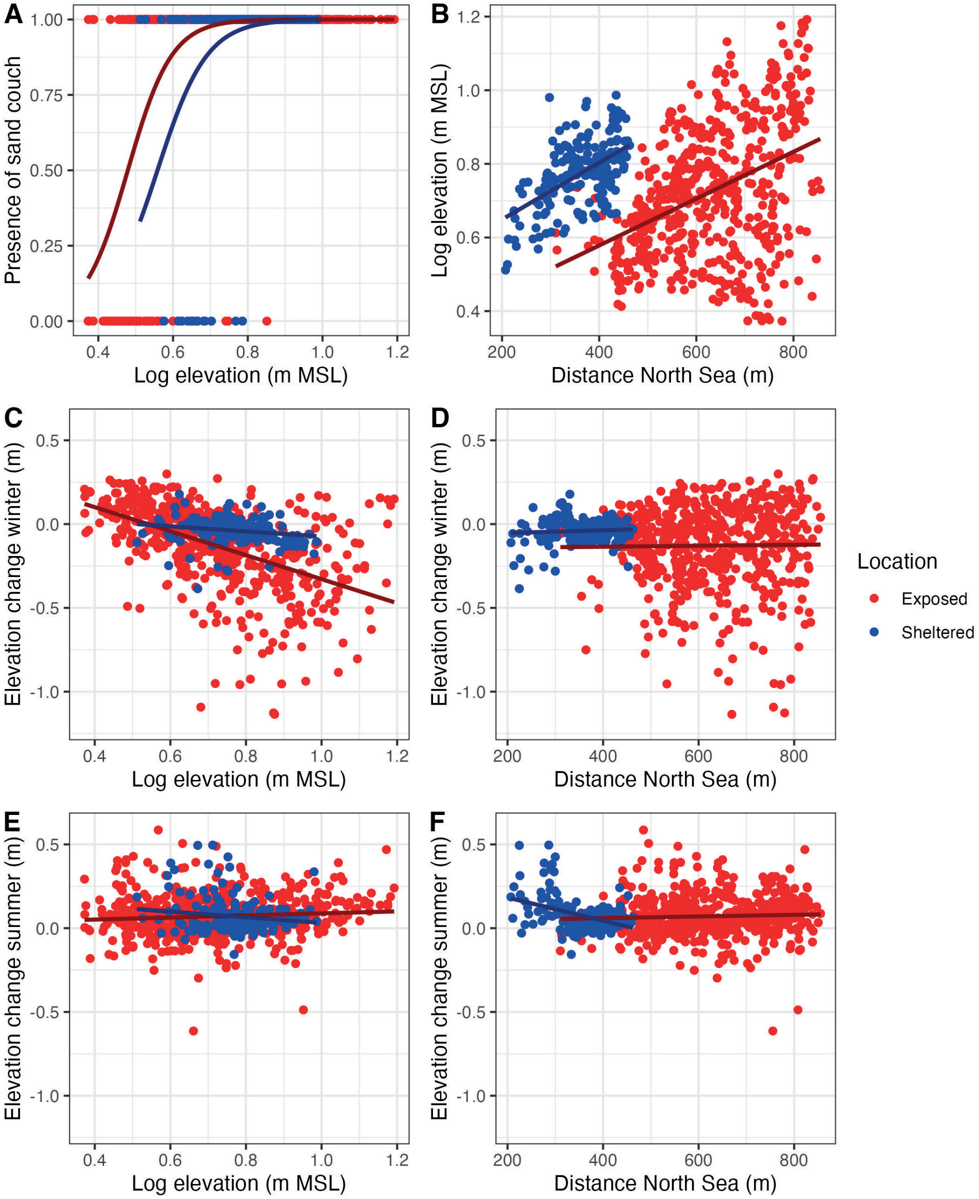


Figure S4.3: Relation between sand couch presence and elevation (A), distance to North Sea and elevation (B), elevation and elevation change in winter (C), distance to the North Sea and elevation change in winter (D), elevation and elevation change in summer (E) and distance to North Sea and elevation change in summer (F). Elevation is always presented in its log-transformed value, while the other values are the non-transformed (original) data. Colors indicate location (red for exposed and blue for sheltered) and lines indicate (generalized) linear models.

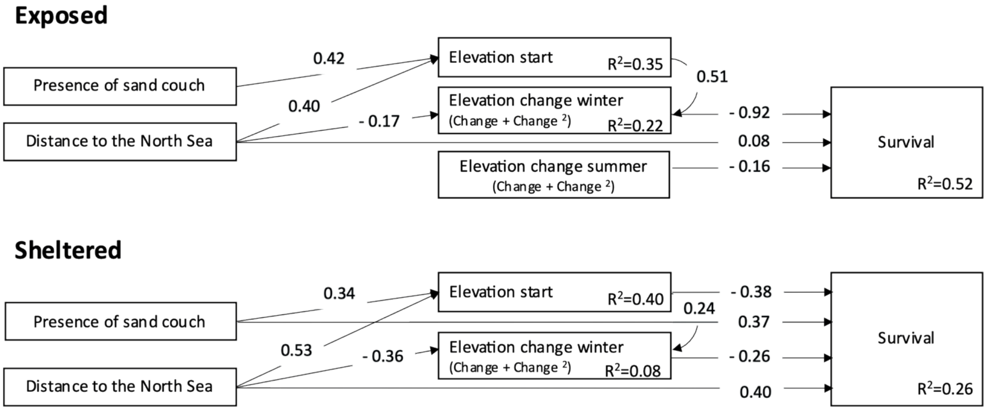


Figure S4.4: The best structural equation models for survival of marram grass per location. Only significant paths were included in the best fitting model (i.e., all presented arrows are significant). In both models, the presence of sand couch and distance to the North Sea positively affect elevation and higher elevation related to more erosion in winter while a further distance from the North Sea related to less erosion in winter (i.e., more accretion). Furthermore, marram grass survival was higher farther from the North Sea and with less erosion (i.e., a higher value for the optimum in elevation change in winter). In exposed conditions, a negative effect of summer elevation change on survival was found (i.e., further from the optimum of 0.30 m less survival).

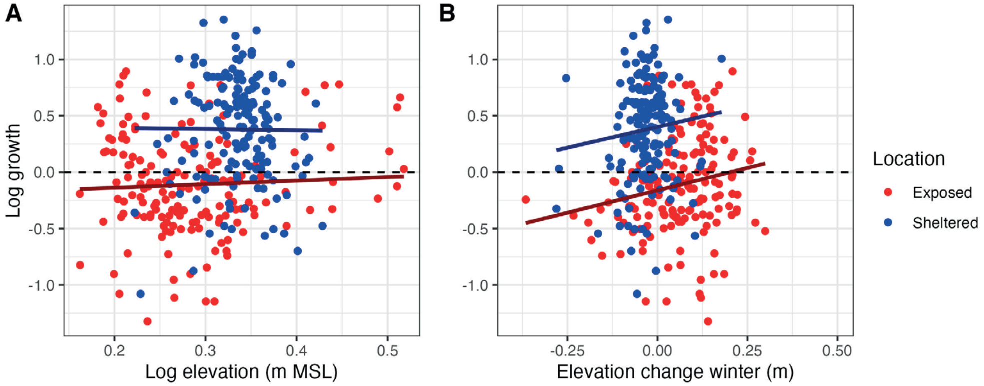


Figure S4.5: Relation between (log) growth of marram grass and (log) elevation (A) and (log) growth of marram grass and elevation change in winter (B).


5KC

CHAPTER 5

Extreme heat and drought did not affect interspecific competition between dune grasses

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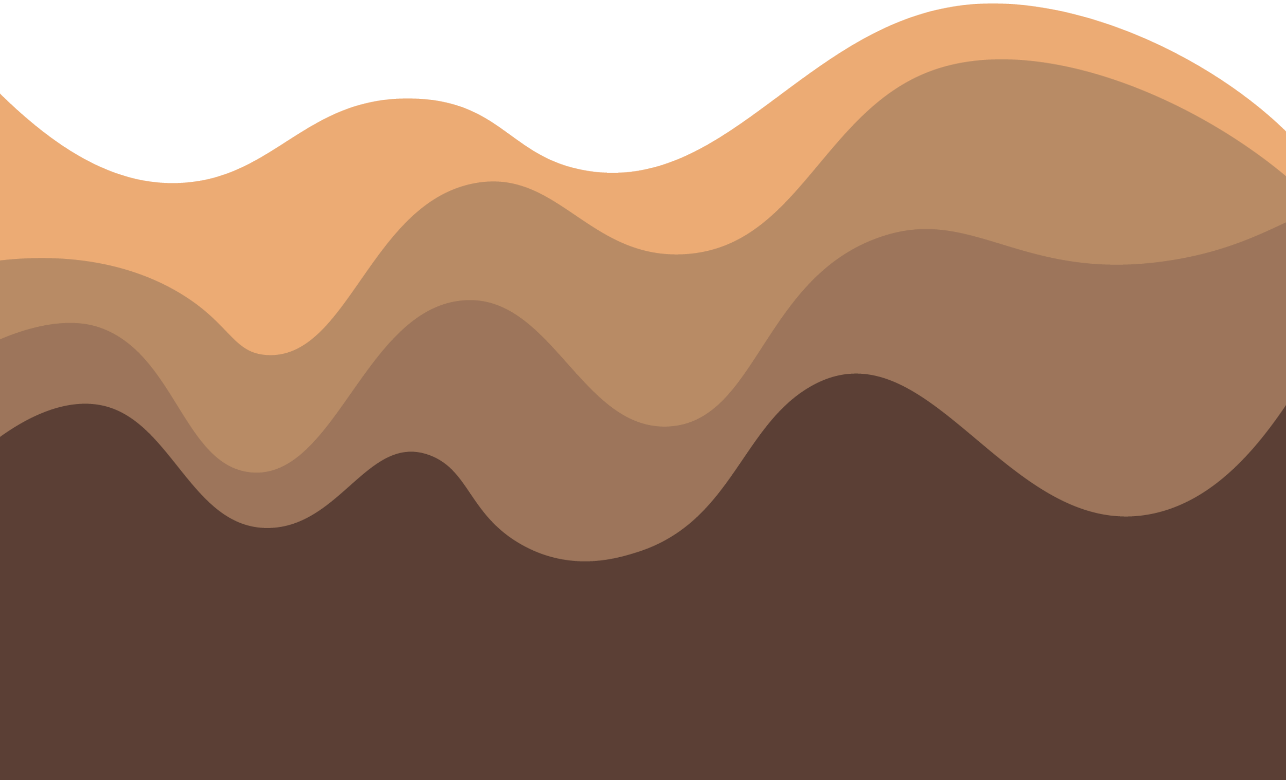
Manuscript in preparation



Abstract

The frequency of extreme climatic events, such as storm and heatwaves, is predicted to increase because of climate change. Understanding interactions between species in environmental extremes plays a vital role in predicting ecosystem resilience. In this study, we examined how heat and drought combined with interspecific interactions between early pioneer sand couch (*Elytrigia juncea*) and marram grass (*Ammophila arenaria*) affected growth and survival of the latter species in an embryonic dune system. In a 4-week field experiment, we transplanted marram grass within sand couch patches or on bare sediment. This plant interaction treatment was combined with a heat and drought treatment that was simulated with greenhouses that inhibited rainfall and increased temperatures (average daily maximum temperature +4°C). Results show that the presence of sand couch significantly reduced growth (i.e., formation of new shoots, shoot and root length and aboveground biomass) of marram grass. By contrast, the heat and drought treatment had no significant effects on growth or survival of marram grass, irrespective of species interactions. The neutral response suggests that even in its early establishment marram grass is highly heat and drought resistant. Our results indicate that the interactions with sand couch play a more important role in marram grass establishment and subsequent dune development than extreme heat and drought.

Keywords: Heat, drought, *Elytrigia juncea*, *Ammophila arenaria*, embryonic dunes, climate change

1. Introduction

Coastal vegetated ecosystems, such as coastal dunes, salt marshes and mangroves, provide important services, for example, flood protection, carbon sequestration, biodiversity enhancement, and tourism (Barbier et al., 2011; Martínez et al., 2007). However, these ecosystems are rapidly declining worldwide due to anthropogenic impacts. Clear examples are local disturbances such as habitat destruction due to the construction of hard coastal defenses, but also global impacts resulting from human-induced climate change (Crain et al., 2009). Predicted effects of climate change include sea level rise and an increase in frequency and intensity of extreme climatic events, such as storms or heatwaves (IPCC, 2022). These changes could affect species interactions and ecosystem structure resulting in extinction, range shifts and ecosystem degradation (Bates et al., 2014; Urban, 2015).

The resilience of ecosystems to extreme climatic events can be significantly influenced by various positive and negative interactions between species and environmental conditions. For example, the mutualism between cordgrass and ribbed mussels enhances desiccation resilience of cordgrass, but this interaction weakens in repetitive drought events (Derksen-Hooijberg et al., 2019). In seagrass ecosystem, the positive relationship between seagrass, lucinid bivalves, and their endosymbiotic bacteria, that prevents the accumulation of the phytotoxin sulphide, can make the system more susceptible to the negative effects of drought-mediated desiccation (de Fouw et al., 2016; van der Heide et al., 2012). On the other hand, competing congeneric dune grass species marram grass (*Ammophila arenaria*) and American beach grass (*Ammophila breviligulata*) show contrasting responses to warming and burial treatments, with marram grass having a neutral to positive response and American beach grass a negative response. Subsequently, competition effects between these species are reduced with burial and warming. Therefore, the likelihood of these species coexisting under predicted climate change effects increases (Biel & Hacker, 2021). Hence, understanding relations between dominant species interactions and extreme climatic events is of vital important to predict ecosystem resilience.

Coastal dune systems are an example of ecosystems that are predicted to be particularly vulnerable to climate change (IPCC, 2022). Coastal dunes develop as burial-tolerant grasses trap sediment by reducing flows of wind with their aboveground structures (Maun, 2009; Zarnetske et al., 2012). First, small embryonic dunes are formed that in time can develop into more stable foredunes (Hesp, 1989). As storm intensity and frequency increases the dune system may become more vulnerable because of an increase in plant mortality, habitat destruction and a reduced recovery time for vegetation (e.g. Charbonneau et al., 2022; Durán Vinent & Moore, 2015; Feagin et al., 2015). However, with increasing temperature, precipitation, nutrient concentrations (which is a non-climate change related anthropogenic driven change), and reduced windiness, which are all beneficial for vegetation development, a global increase in dune vegetation cover was observed over the last three decades (Jackson et al., 2019). This in turn has reduced the dynamic nature of coastal dunes. Generally, dynamic dunes have a higher resilience (e.g., the potential to recover after a storm), while the stable dunes have a higher resistance (e.g., the potential to withstand storm events) (Feagin et al., 2015; Hsu & Stallins, 2020; Pickart, 2021). Overall, the development, resistance and resilience of coastal dunes all depend on the balance between erosion (in winter) and plant recovery and sediment accumulation (in summer).

Along the Northwestern European shoreline coastal dunes are formed by two dominant dune building grasses: sand couch (*Elytrigia juncea*, hereafter referred to as sand couch) and European marram grass (*Ammophila arenaria*, hereafter referred to as marram grass). While it is generally assumed that sand couch is the pioneer species that facilitates marram grass by forming sufficiently large dunes reducing flooding risk and increasing freshwater availability (e.g., Westhoff, 1970), we recently discovered that sand couch negatively affects marram grass establishment through dune formation (Chapter 4). We found that the chance of erosion in winter increased with increasing elevation caused by ecosystem engineering of sand couch. The increased erosion in turn leads to a higher marram grass mortality (Chapter 4). However, locally, the presence of sand couch had opposing effects on establishing marram grass depending on conditions. In more sheltered conditions, the presence of sand couch was neutral to positive for marram grass (i.e., sand couch had no direct effect on growth and a positive effect on survival) while in more exposed conditions it was neutral to negative (i.e., a negative effect on growth and no direct effect on survival) (Chapter 4). Therefore, the interaction between both species might also change in different climatic extremes.

In this study, we examine how interspecific interactions with sand couch combined with effects of heat and drought affect establishing marram grass in a cross-factorial field experiment. We expect that the combination of heat and drought negatively affects the growth and survival of marram grass. Since the experiment is performed in relatively sheltered conditions, we expect a neutral (growth) to positive (survival) relation between sand couch and establishing marram grass in ambient conditions. We hypothesize that sand couch may mitigate heat and drought effects through increased soil moisture levels (Westhoff, 1970). Moreover, based on the stress gradient hypothesis, facilitation is expected to be more important in stressful conditions (He et al., 2013). Therefore, we predict that sand couch improves marram grass performance compared to non-vegetated plots in simulated heatwave conditions (i.e., differences in marram grass performance between sand couch and non-vegetated plots becomes larger in stressful conditions).

2. Methods

2.1. Study area

The study was conducted in an embryonic dune field on the Dutch Wadden island

Schiermonnikoog (latitude: 53.5021938, longitude: 6.2284338, Figure 5.1) between July 7th and August 3rd, 2022. On the selected location the total beach-foredune width was ±450m and an extensive embryonic dune field (±150m) dominated by sand couch was present. Over the last decades, the beach has been accreting accompanied by an expansion of the dune area (AHN, 2022; Luijendijk et al., 2018). The location was considered relatively sheltered because of the wide beach and relatively high, marram grass dominated, foredunes sheltering the embryonic dunes (max elevation foredunes ±10m (AHN, 2022; Chapter 4)).

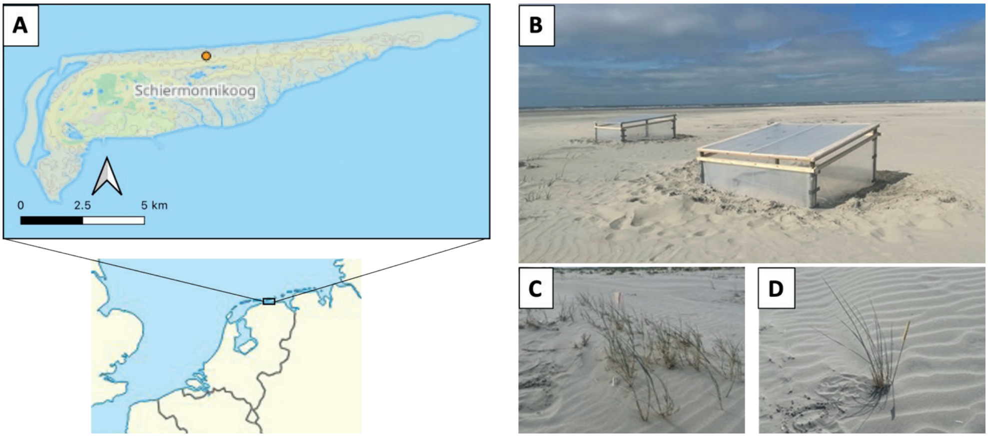


Figure 5.1: A) The location of the field experiment in the embryonic dunes of the Dutch Wadden island Schiermonnikoog. B) The shelters that were used to increase temperatures and drought. C) An example of the selected sand couch patches with a transplanted marram grass individual. D) An example of a transplanted marram grass on bare soil. Pictures were taken at the start of the experiment in July 2022.

2.2. *Experimental set-up*

We conducted a transplantation experiment in which two factors were crossed: species interactions (i.e., planting in sand couch patches or on bare soil) and extreme heat and drought (hereafter referred to as heatwave treatment), resulting in 4 treatments (bare – ambient, bare – heatwave, sand couch – ambient and sand couch – heatwave, each with eight replicates (Figure 5.1, Figure S5.1).

Marram grass plants were grown from seeds in pot soil (at a plant nursery) for about 5 months and were transplanted to the field the first week of April 2022. A surplus of marram grass was planted on bare soil (n=80) or within sand couch patches (n=80), to have enough living plants in July after the acclimation period and to be able to select similar plants across treatments (n=8 replicates per treatment, resulting in n=16 bare and n=16 sand couch plots). We assigned blocks based on location (e.g., proximity, similar distance to the North Sea and similar elevation) and plant morphology (e.g., shoot numbers and plant vitality) in July (Figure S5.1). Except for one individual, sand couch patches were larger than the 2 x 2 m plots. Therefore, at the start of the experiment, rhizome connections of each sand couch individual (with and without heatwave treatment) were cut to obtain a 2 x 2 m patch.

Next, in the heatwave assigned treatments, we installed greenhouses over the plots that increased temperature and prevented precipitation (Figure 5.1). The greenhouses covered the entire 2 x 2 m plot surface and had a sloping roof with a height of 0.7-0.9m. We used transparent plastic foil (Mevolux E.V.A foil, AMEVO 2000 BV, Dronten, The Netherlands) on the roof and sides of the greenhouse but kept a 0.1m space between the sides and the roof to allow air flow through the structures.

To assess our heatwave treatment effects, we used temperature and light loggers (Onset HOBO Pendant temperature/light logger, n=3 replicates inside and outside the greenhouse, total 6 loggers) attached to bamboo sticks (±50 cm above soil level) that measured every 15 minutes. Furthermore, we used rain gauges to measure rainfall during our experiment (n=3 replicates inside and outside the greenhouse, total 6). Lastly, soil moisture measurements at 0.1, 0.2, 0.4, 0.6 and 1 m depth (using Delta-T PR^2 Profile Probe, n=3 replicates per treatment, total 12) were taken every other day of the experiment.

2.3. Data collection

Every other day during the experiment, we checked marram grass survival. At the start and end of the experiment, morphological characteristics of marram grass (i.e., shoot number and maximum shoot length) were determined. To determine relative water content (RWC) of the marram grass leaves, two leaves were cut off in the early morning of the harvest (i.e., the end of the experiment) and kept cool and sealed. Subsequently, fresh weight was determined, and leaves were placed in sealed zip-lock backs on paper towels soaked in distilled water. After 24h in dark conditions at 4°C, the leaves were weighted for turgid weight after which the leaves were dried (48h, 60°C) and dry weight was determined. RWC was expressed by:

$$RWC\,(\%) = \frac{fresh\ weight - dry\ weight}{turgid\ weight - dry\ weight} * 100$$

At the end of the experiment, the complete marram grass individuals were collected, including roots. The initial pot soil (shaped like the 9*9*9.5 cm pots the plants were reared in) was still present and most roots were located within the pot soil (Figure S5.2). After excavation, we measured maximum length of the shoots from pot soil (correcting for the removed leaves for RWC) and maximum length of roots that expanded from the pot soil. Subsequently, shoots were separated from roots, all parts were washed, and (pot) soil was removed. The shoots and roots were dried (48h, 60°C) and dry weight was determined (shoot biomass was corrected for RWC samples).

2.4. Statistical analyses

We analyzed the data using R (version 4.2.1, R Core Team, 2022). From the shoot numbers we calculated relative growth during the experiment, which was determined as the number of shoots at end divided by the number of shoots at start, and log-transformed to normalize the distribution (i.e., in the log-transformed data zero represents no growth, a positive value growth and a negative value a reduction of shoots). Furthermore, aboveground biomass was square root transformed to obtain normality. Other included variables were normally distributed.

Maximum temperature was determined for each day, after which these daily maxima were compared between heatwave and ambient conditions using a Welch two sample t-test. Since the marram grass transplants rooted in the topsoil layers (up to 20 cm), we focused on the soil moisture level measured at 10 and 20 cm depth. At the start of the experiment, we were one measurement tube short, therefore, the data for one replicate (bare – heatwave treatment) for the first week is missing. Effects of the heatwave treatment and presence of sand couch on soil moisture levels were analyzed with two-way factorial ANOVA’s. To get an impression of the overall change in soil moisture levels, we compared levels at the start and subsequently at the end of the experiment. To assess whether variability in soil moisture levels differed between treatments over time (i.e., rain might cause a larger variation in measures outside of the greenhouses), we calculated the difference between consecutive soil moisture measures and compared the variance between treatments using a Levene’s test.

To examine the effect of the treatments (i.e., heatwave and presence of sand couch) on plant characteristics (i.e., shoot numbers, maximum shoot and root length, shoot and root biomass), we fitted linear mixed-effect models with a Gaussian distribution including block as random factor (package “lme4”, (Bates et al., 2015)). P-values were calculated in a type 3 ANOVA via Satterthwaite's degrees of freedom method (package “lmerTest”, (Kuznetsova et al., 2017)). We considered treatment effects significant at a significance level of P=0.05.

3. Results

3.1. Greenhouse and sand couch environmental effects

On average, our measured daily maximum temperature in ambient conditions was 32.3°C and 36.5°C in heatwave conditions (t=2.38, P=0.01, range in max temperatures: 23.0 – 50.8°C (heatwave) and 21.8 – 47.3°C (ambient), Figure S5.3). At the start of the experiment there were no significant differences in soil moisture levels between treatments. At the end of the experiment, the moisture level at 10 cm depth was significantly lower in the heatwave treatment than in ambient plots (1.8±0.5 % (heatwave) vs 4.9±0.7 % (ambient), $F_{1,8}$=13.3, P=0.006, Figure 5.2). There was little rain during the experimental period (total 12.8 mm, compared to a 30-year average of 69.2 mm for this period, Table S5.1). Still the rain caused variation in soil moisture over time in ambient conditions, which was significantly different from the heatwave treatment (Levene’s Test, $F_{1,205}$=10.1, P=0.001, Figure S5.4). Moreover, variability in soil moisture levels (ambient) was higher at 10 cm depth than at 20 cm depth (Levene’s Test, $F_{1,202}$=13.2, P<0.001). At 20 cm depth, we found no significant effects of the heatwave on soil moisture levels (Figure S5.4). There was also no significant effect of sand couch on soil moisture, independent of measured depth.

3.2. Marram grass survival and growth

All marram grass plants survived irrespective of experimental treatment. No significant effects of the heatwave treatment on morphological characteristics (i.e., shoot numbers, shoot, and root length) were found. Presence of sand couch had a negative effect on growth of marram grass in both ambient and heatwave conditions. Plants on average had a lower growth (i.e., less increase in shoot numbers) (log growth, 0.36±0.1 (bare) vs -0.14±0.1 (sand couch), $F_{1,27}$=8.2, P=0.008, conditional R^2=0.25, Figure 5.3), a lower final number of shoots (11.7±2.3 (bare) vs 6.7±0.8 (sand couch), $F_{1,21}$=4.6, P=0.04, conditional R^2=0.42), and lower maximum shoot and root lengths (max shoot length 50.7±1.5 cm (bare) vs 39.7±2.1 cm (sand couch), $F_{1,19.2}$=20.9, P<0.001, conditional R^2=0.52; max root length 39.9±9.4 cm (bare) vs 14.4±3.8 cm (sand couch), $F_{1,21}$=6.9, P=0.02, conditional R^2=0.29, Figure 5.3). Similarly, total shoot dry weight was lower for marram grass plants planted within sand couch (3.7±0.7 g (bare) vs 1.9±0.3 g (sand couch), $F_{1,21}$=7.7, P=0.01, conditional R^2=0.43, Figure 5.3). However, no

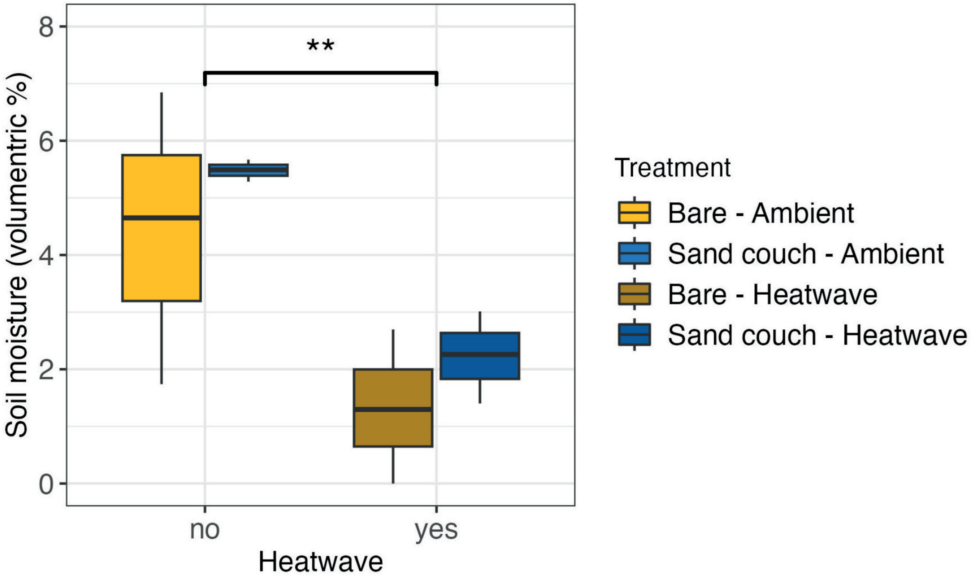


*Figure 5.2: Soil moisture (volumetric %) at 10 cm depth at the end of the experiment (03-08-2022) per treatment, with a significantly higher soil moisture content in ambient conditions than in the heatwave treatment ($P<0.01$ **). The horizontal bars depict median value, box height the first and third quartile and whiskers the minimum and maximum values.*

significant differences in biomass per shoot was found. For the total below ground biomass and shoot:root ratio there was a trend for lower biomass and a lower shoot:root ratio in presence of sand couch (below ground biomass: 0.89±0.1 g (bare) vs 0.62±0.1 g (sand couch), $F_{1,28}=3.7$, $P=0.06$; shoot:root ratio: 4.1±0.6 (bare) vs 3.0±0.3 (sand couch), $F_{1,21}=9.7$, $P=0.05$, Figure 5.3). There were no significant effects of treatment (i.e., sand couch and heatwave) on the relative water content of marram grass leaves (Figure S5.5).

4. Discussion

We examined the effect of heat and drought combined with interspecific interactions with sand couch on the survival and growth of establishing marram grass plants. The extreme heat and drought had no significant effects on growth or survival of establishing marram grass, irrespective of species interactions. This supports that marram grass is an extremely heat and drought resistant species, even in its early establishment (Biel, 2021; Huiskes, 1979). Contrary to our hypothesis, growth of marram grass was significantly reduced by the presence of sand couch and this species interactions did not change in extreme conditions. These findings indicate that for development of establishing marram grass competition with sand couch plays an important role.

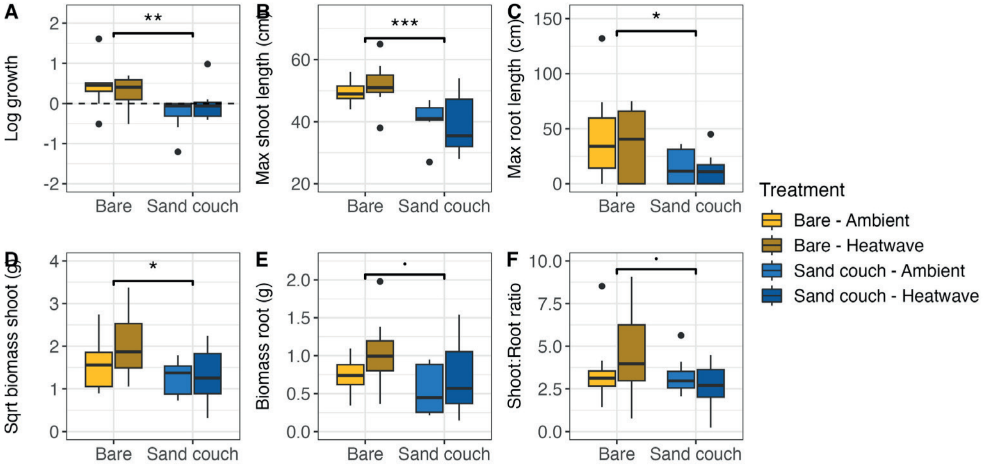


*Figure 5.3: Marram grass morphological characteristics (top) and biomass measures (bottom) for the four different treatments (bars from left to right in every plot: bare – ambient, bare – heatwave, sand couch – ambient, sand couch – heatwave). A) The growth per treatment. The dotted line indicates no growth, positive values indicate an increase in shoot numbers and negative numbers a decrease in shoot numbers. B) Maximum shoot length and C) maximum root length (measured from pot soil). D) The shoot dry biomass (g) and E) the root dry biomass (g) and F) the ratio between dry shoot and root weight. The horizontal bars depict median value, box height the first and third quartile and whiskers the minimum and maximum values. Significance levels are only indicated for sand couch vs bare treatments since there were no heatwave or interaction effects (trend ·, P<0.05 *, P<0.01 **, P<0.001 ***).*

4.1. Heat and drought treatment

The greenhouses efficiently inhibited rainfall and increased average maximum daily temperatures over 4°C, leading to a lower moisture content in the topsoil layer (Figure 5.2). In the deeper soil layers (20+ cm), no effect of the treatment was found, which could be a result of insulation of deeper layers by the dry top soil layer, capillary rise and/or internal dew formation (Maun, 2009; Figure S5.4). Moreover, the higher soil moisture variability at 10 cm depth than at 20 cm depth, suggests that rainfall and evaporation had a larger effect on the topsoil layer than the deeper soil layers (Figure S4). While we expected sand couch to mitigate treatment effects by maintaining higher soil moisture levels, the moisture levels were not significantly different in presence of sand couch (Figure 5.2, Figure S5.4). Conditions in our experiment – even in controls – were very warm and dry compared to 30-year averages from the closest weather station (±11 km from our experiment, Table S5.1). However, there was a large deviation between measured conditions in the experiment and weather data recorded by the Royal Netherlands

Meteorological Institute (KNMI, Table S5.1). We suggest that this difference can be explained by the sand reaching very high temperatures (which affects temperatures up to 160 cm from the soil) and a lack of shading (Baldwin & Maun, 1983). Our measurements show that the beach vegetation experiences extreme conditions, even more extreme than what might be expected based on data from official weather stations.

4.2. Treatment effects on establishing marram grass

While heat and drought did not significantly affect growth of marram grass, a positive effect on growth of sand couch was found (i.e., shoot length, biomass per shoot, and number of runners) (Berghuis et al. in prep). Earlier studies on marram grass and American beach grass (*Ammophila breviligulata*), showed a positive growth response to warming (Biel & Hacker, 2021; Emery & Rudgers, 2014). We expect these different outcomes to be a result of drought, which was not included in the earlier studies. In our experiment, soil moisture levels were only reduced in the topsoil layer. It is likely that sand couch – which had roots reaching deeper soil layers – was not limited in moisture, while the marram grass transplants – which mainly had shallow roots – did experience drought (Berghuis et al. in prep, Figure S5.2). Therefore, potential positive effects of warming on growth of marram grass might have been hampered by drought.

On the other hand, the expected negative effects of the combined drought and heat were also not found. Most likely, growth of marram grass was already hampered in the dry and warm conditions that occurred in our controls during the experiment. Hence, in milder conditions with more precipitation differences between our treatments might have occurred, since growth has been found to increase with summer precipitation (Homberger et al., 2023). Regardless, however, the marram grass survival in extreme heatwave conditions indicates that even relatively young (±8 months) marram grass plants are heat and drought tolerant (Huiskes, 1979). It is likely that the response to heatwave conditions varies between life stages of the plants, with seedlings being more sensitive to desiccation and established vegetation being more resilient (Del Vecchio et al., 2020; Maun, 1994). Therefore, the response of seedlings or established patches might be different from transplants as tested here. Besides, we terminated the experiment directly after our heatwave treatment, while rewatering after drought can also affect species in different ways (Xu et al., 2010). These effects are yet to be determined for dune grasses.

We did not find evidence that the interaction between sand couch and marram grass changed under pressure of heat and drought. Since the marram grass plants were planted in April, the period that sand couch affected marram grass' development is longer than the heat and drought. Therefore, treatment effects of sand couch presence might have been more profound than heat and drought effects. We tried limiting these effects by selecting plants with a similar appearance (i.e., no significant differences in shoot numbers and above sediment shoot length) in July. Clear indications of competition were found as marram grass developed less shoots, shoots and roots were shorter and the shoot biomass was lower in presence of sand couch (Figure 5.3). Surprisingly, the positive growth response of sand couch seemed to not affect growth of marram grass in the heatwave × sand couch treatment (i.e., no significant difference in growth between ambient and heat and drought conditions).

While it has long been assumed that sand couch, as the species that colonizes the bare beach areas first, facilitates the establishment of marram grass (Bakker, 1976; van Puijenbroek, Teichmann, et al., 2017; Westhoff, 1970), our current and previous work highlights negative effects of sand couch on growth of marram grass and on its survival through habitat formation (Chapter 4, Figure 5.3). However, in relatively sheltered conditions, survival of marram grassed increased in presence of sand couch (Chapter 4). We hypothesized that anchoring (i.e., reduced changes of being uprooted or removed by wind/wave motion) or a different microclimate compared to bare soil, such as a lower soil temperature or higher soil moisture level, could be mechanisms through which sand couch locally facilitates marram grass (Chapter 4; Baldwin, 1983). Yet, in our current work we did not find significant effects of sand couch presence on soil moisture levels, rejecting differences in soil moisture as potential mechanism. Additional experiments are needed to determine through which mechanisms sand couch promotes the survival while reducing growth of marram grass.

4.3. Dune restoration and resilience

The marram grass plants we used were about the same age as marram grass transplants used in coastal restoration projects along the Dutch coast (van der Putten, 1990). Therefore, our results suggest that heat and drought is no threat for restoration success and that the best planting strategy is at bare soil. However, seed germination and establishment from rhizome fragments – which is the natural way of establishment – were not tested and might be more sensitive to environmental extremes (Del Vecchio, 2020; Maun, 1994). The neutral (marram grass transplants) to positive (sand couch) effect of heat and drought on dune grasses indicates that heat and drought would not affect, and even might benefit, development of established embryonic dunes. However, if natural establishment of dune grasses is reduced, the development of new embryonic dunes would be reduced. Additional experiments including different life stages of marram grass would be needed to further expand our knowledge on the effect of extreme climatic events on marram grass establishment and subsequent dune development. Overall, the development of embryonic dunes will depend on the balance between erosion and (life stage dependent) plant recovery and sediment accretion.

Acknowledgements

We thank The Fieldwork Company, and especially Jannes Heusinkveld, for their help with the design, construction, placement and removal of the greenhouses and marram grass planting. We thank Mark Bergsma and Veerle Paarlberg for their help with the placement and removal of the greenhouses. We thank Natuurmonumenten for their permission to conduct the experiment at Nationaal park Schiermonnikoog. This work was financially supported by the Netherlands Organization of Scientific Research (NWO-Vidi grant 16588, awarded to TvdH and VR was funded by NWO-Veni grant VI.Veni.212.059) and NIOZ-UU grant 2020.1.

Supplements

Supplementary tables

Table S5.3: Rainfall and temperature data from weather stations (KNMI; https://www.knmi.nl/nederland-nu/klimatologie/monv/reeksen location Schiermonnikoog and https://www.knmi.nl/nederland-nu/klimatologie/daggegevens location Lauwersoog) and measured in our experiment. For the 30-year averages, rainfall is given as average yearly sum of rainfall and the highest max daily temperature as average yearly maximum temperature.

Location	**Period**	**Rainfall (mm)**	**Average max daily temperature (°C)**	**Highest max daily temperature (°C)**
Weather station Schiermonnikoog	1992-2022 (07-07 till 03-08)	69.2	No data	No data
Weather station Schiermonnikoog	2022 (07-07 till 03-08)	35.2	No data	No data
Weather station Lauwersoog	1992-2022 (07-07 till 03-08)	70.1	21.4	28.8
Weather station Lauwersoog	2022 (07-07 till 03-08)	37.6	21.9	35.2
Experiment heatwave	2022 (07-07 till 03-08)	0	36.5	50.8
Experiment heatwave	2022 (07-07 till 03-08)	12.8	32.3	47.3

Supplementary figures

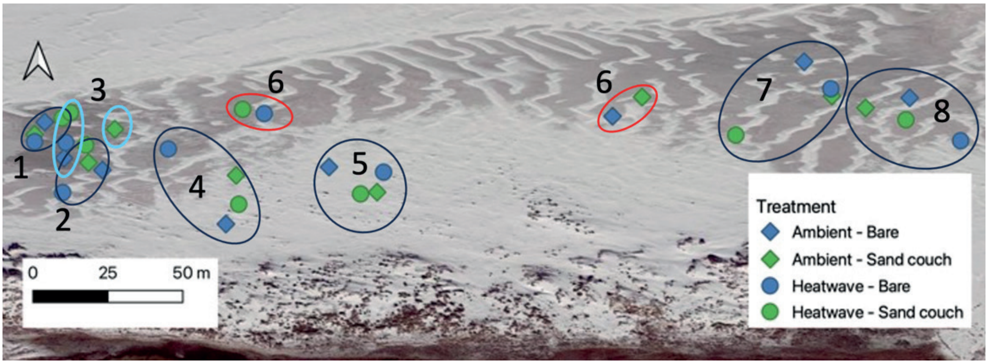


Figure S5.1: Overview of the plots in space with marram grass transplanted in sand couch patches (green marking) and on bare soil (blue marking), in heatwave conditions (round) or in ambient conditions (diamonds). We assigned blocks on location and plant morphology indicated by circles and numbers.

Figure S5.2: Example of a marram grass plant, planted on bare soil, during excavation. At the base of the shoots the darker pot soil, in which the plant was reared, is visible. Most roots that expanded from pot soil were horizontally spreading with little branching.

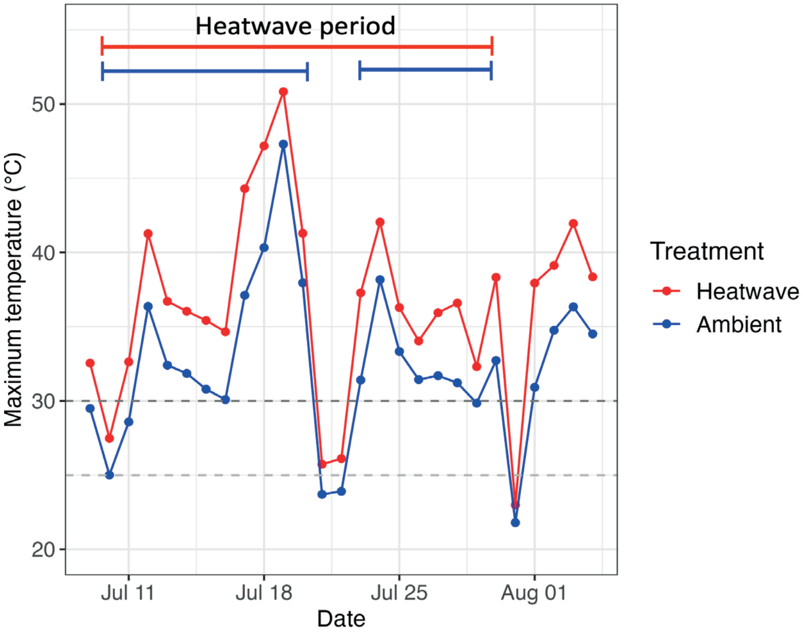


Figure S5.3: Maximum daily temperature inside the greenhouses (i.e., heatwave treatment, in red) and outside the greenhouses (i.e., ambient, in blue). Dotted lines indicate 25°C and 30°C, which are the threshold temperatures for heatwave conditions (heatwave conditions according to the Royal Netherlands Meteorological Institute: 5 days above 25°C including 2 above 30°C, KNMI). The solid lines indicate the length of heatwave conditions in the heatwave treatment (in red) and in ambient conditions (in blue).

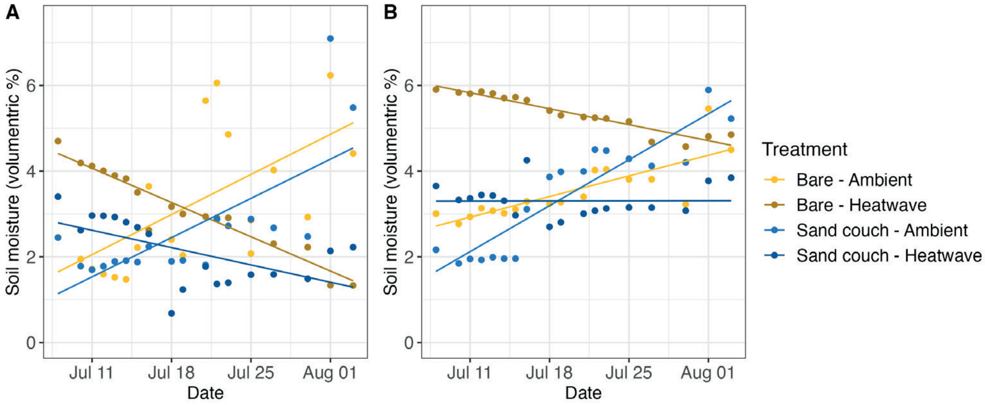


*Figure S5.4: Soil moisture levels over time for 10 cm depth (A) and for 20 cm depth (B). At 10 cm depth, there was no significant effect of sand couch. Over time the soil moisture increased in ambient conditions and decreased inside the greenhouses (i.e., in the heatwave treatment) (repeated measures ANOVA, structure * date, F=2.9, p<0.001). While a similar trend was visible at 20 cm depth, no significant differences between dates, sand couch presence, heatwave treatment or interactions between those was found.*

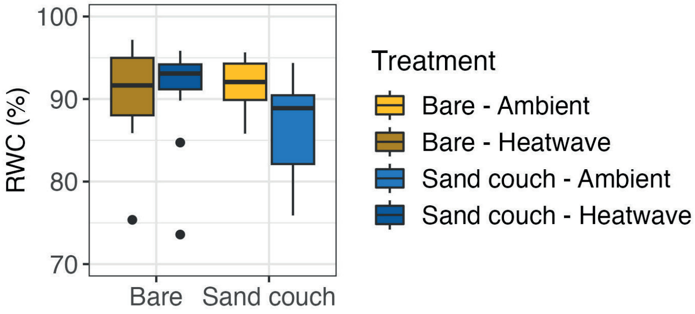
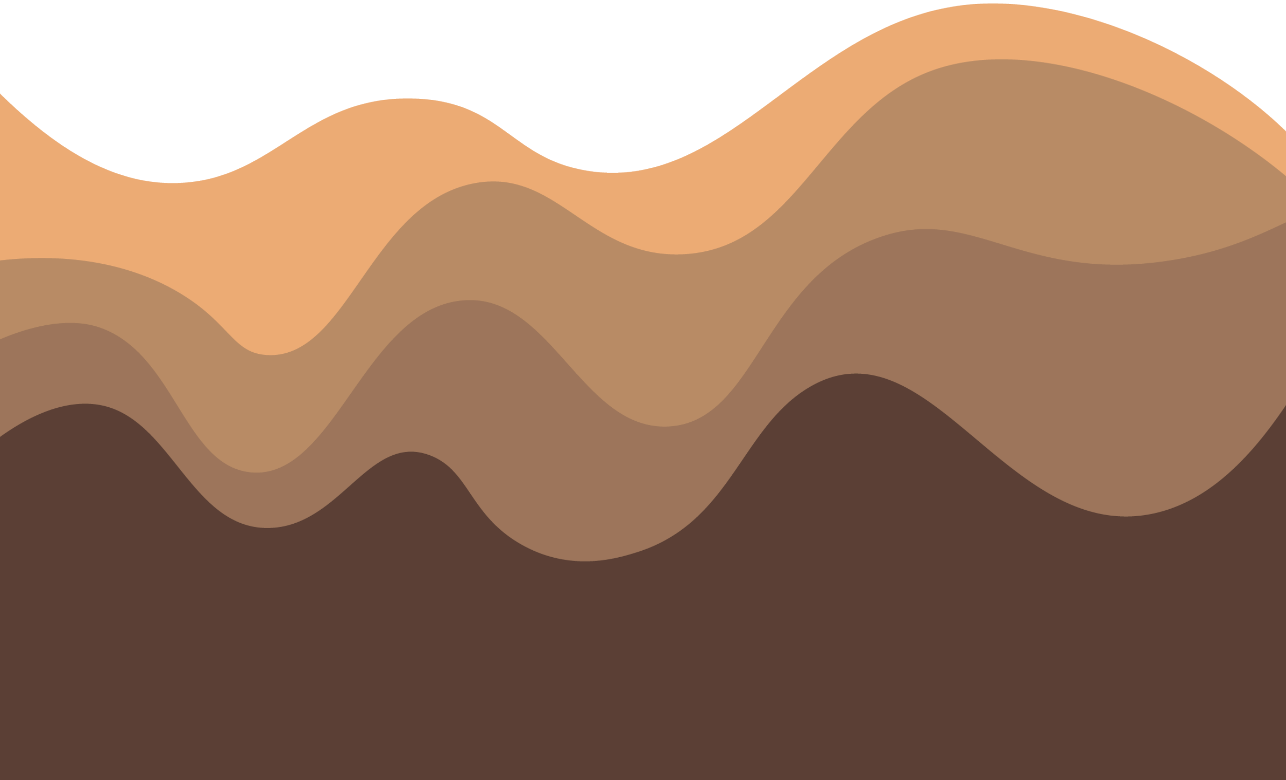


Figure S5.5: The relative water content (RWC %) of marram grass leaves at the end of the experiment. There were no significant effects of treatment on the RWC. The horizontal bars depict median value, box height the first and third quartile and whiskers the minimum and maximum values.

CHAPTER 6

Synthesis



6.1. A short recap: Context and aim of this thesis

Along one third of the world's shoreline coastal dunes occur, where they provide valuable services such as flood protection and drinking water (Martínez et al., 2004, 2007). Like many other coastal systems world-wide, coastal dunes are under threat of local and global change including sea level rise and increased intensity and frequency of extreme climatic events (IPCC, 2022). Ecosystem engineers, most importantly dune grasses, play pivotal roles in coastal dune development (Feagin et al., 2015; Hesp, 1989). They trap sediment, thereby modifying the physical environment and increasing their own growth and survival. Subsequently, they influence establishment and survival of other organisms (Clements, 1916; Hesp, 1989; Maun, 2009). Overall, the emergence and development of coastal dunes is the result of a complex interplay of geomorphic conditions and vegetation, making them so-called biogeomorphic ecosystems (i.e., ecosystems that are shaped by biophysical interactions) (Corenblit et al., 2011; Hesp, 1989; Maun, 2009). Understanding the biophysical processes that drive the emergence and development of coastal dunes can benefit management and restoration strategies of these valuable ecosystems.

The objective of this thesis was to elucidate interactions between dune grasses, environmental conditions, and landscape morphology in early dune development. I focused on the Northwestern European shoreline that is dominated by two co-occurring dune grasses; the early successional species sand couch (*Elytrigia juncea*) and the later successional species marram grass (*Ammophila arenaria*). First, the morphological plant traits that affect ecosystem engineering of these dune grasses, that are associated with different dune morphologies, were compared (Chapter 2). Subsequently, interactions between established dune grasses, their habitat modifying activities, and establishment of conspecifics (Chapter 3) and later successional species (Chapter 4) were determined. Lastly, it was determined whether the interspecific interactions (Chapter 4) changed under pressure of heat and drought (Chapter 5). In this chapter, the most important findings of this thesis are integrated. First, a short summary of the results per chapter are presented. Subsequently, the integrated results of marram grass establishment, including the differences between establishment from seeds, clonal fragments and transplants are discussed. Next, the found local and large-scale effects are compared to other vegetated coastal ecosystems. Lastly, the potential effects of global change and implications for restoration of coastal dunes are presented.

6.2. Clonal expansion strategies and habitat modification

Sediment accretion is the most noteworthy habitat alteration induced via ecosystem engineering by dune grasses (Hesp, 1989; Maun, 1998; Zarnetske et al., 2012). Recently, it was found that the sediment accreting capacity of young, establishing dune grass individuals is fundamentally linked to their clonal expansion strategy (Reijers, Siteur, et al., 2019). Specific clonal expansion strategies generate distinct spatial shoot organizations that in turn determine their ability to modulate wind flow and accumulate sand (Reijers, Siteur, et al., 2019). In a comparison of clonal expansion strategies of sand couch versus marram grass across Northwestern Europe (Denmark – France), I found that most individuals deploy a strategy that deviates from a simple dense vegetation patch and display a patchy shoot organization, balancing clonal expansion and sediment accretion (Chapter 2). However, the pattern characteristics differed between sand couch and marram grass. Sand couch had a more dispersed shoot organization associated with sand capture over a large area, resembling a strategy with maximized total entrapped sand volume (Chapter 2; Reijers, Siteur et al., 2019). On average, marram grass demonstrated a more patchy shoot organization, which is associated with higher local sand-capturing efficiency (i.e., investment in clonal growth versus entrapped sand volume) (Chapter 2; Reijers, Siteur, et al., 2019). Surprisingly, sand couch demonstrated little variation in clonal expansion strategies, whereas marram grass displayed a large variety in shoot organizations, ranging from a dispersed to a clumped organization. Based on the observed plant traits, I hypothesize that sand couch evolved toward building dune landscapes that balance the risk of flooding and erosion (e.g., dislodgement or osmotic stress) with potential benefits of a dispersed growth, such as marine nutrient input through flooding or a (relatively) low burial rate (Reijers, Lammers, et al., 2019), whereas I expect marram grass to have evolved to maximize sand capture and escape flooding completely.

6.3. Habitat modification reduces marram grass' establishment

6.3.1. Habitat formation by marram grass reduces recruitment of conspecifics

In natural conditions, dune grasses establish from seeds (which can be wind and marine dispersed) or marine dispersed clonal fragments (Huiskes, 1977, 1979). Therefore, I first determined availability of marram grass' seeds and rhizome fragments at three locations with different beach-dune morphologies on the Dutch

Wadden island Texel (Chapter 3). Subsequently, I tested shoot emergence from seeds and rhizome fragments at the same locations, in unmodified (beach) and by marram grass modified (embryonic dune) habitats and the effect of burial on seed germination (Chapter 3). Surprisingly, I found no seeds or rhizome fragments, independent of beach-dune morphology or proximity to vegetation (Chapter 3). Seed retention in experimental plots was significantly higher in the unmodified, beach plots than the modified, embryonic dune habitat. The retention of seeds in experimental plots, suggests that a lack of seed input in the unmodified system causes the lack of seeds in natural conditions. However, the low seed retention in the modified habitat suggests that vegetation-induced sediment dynamics reduce seed retention (Chapter 3). Burial of over 3cm significantly reduced germination and shoot emergence from seeds. Moreover, in the field experiment, more shoots emerged in unmodified than in modified conditions, both from seeds and rhizome fragments. Shoot emergence related significantly to sediment dynamics (i.e., less shoots with higher sediment mobility) and for seeds also to elevation (i.e., less shoots with increasing elevation). Our results indicate that vegetation-induced sediment dynamics negatively affect seed availability and shoot emergence from seeds and rhizome fragments, thereby hampering the establishment of conspecifics (Chapter 3).

6.3.2. Sand couch negatively affects marram grass' establishment

Based on field observations, it is assumed that sand couch colonizes bare beach areas and starts dune formation. Marram grass, the later successional species, then establishes after sufficiently large dunes are formed (Bakker, 1976; Westhoff, 1970). However, experimental evidence for this assumption was lacking. Using a field experiment, I tested the role of sand couch and its landscape attributes (elevation, distance to sea and elevation change) on marram grass' establishment (Chapter 4). The results of the field experiment indicate an indirect negative effect of sand couch on survival of establishing marram grass through dune formation. More specific, sand couch elevated the environment, and with an increase in elevation the erosion in winter increased, leading to a higher marram grass' mortality (Chapter 4). Moreover, marram grass' shoot formation was negatively affected by sand couch presence (Chapter 4). While the indirect negative effect occurred independent of location, direct interactions between sand couch and marram grass survival and growth were context-dependent: neutral (growth) to positive (survival) in sheltered conditions, and neutral (survival) to negative (growth) in exposed conditions. Overall, the highest marram grass survival was observed in relatively low-lying, stable, and sheltered areas. I hypothesize that dune formation by sand couch indirectly benefits marram grass establishment by creating these relatively low-lying, stable, and sheltered microsites within the dune landscape, instead of directly through creation of elevation.

Subsequently, I tested whether the observed interactions between sand couch and marram grass, in a sheltered environment (i.e., direct interactions were neutral to positive), changed under pressure of extreme heat and drought (Chapter 5). In a 4-week cross-factorial field experiment, the combined effect of heat and drought and interactions with sand couch on establishing marram grass transplants was tested. The heat and drought did not significantly affect growth or survival of establishing marram grass, irrespective of species interactions. However, marram grass' growth (i.e., shoot formation, shoot length and root length) was significantly lower in presence of sand couch, indicating a competitive relation with sand couch (Chapter 5). These results highlight the context-dependency of the species interaction. Marram grass' growth was unaffected by sand couch in more benign conditions (sheltered conditions, Chapter 4), but this interaction shifted to negative in more stressful conditions such as a more hydrodynamically exposed location or in extreme heat and drought (Chapter 4, Chapter 5).

6.3.3. Interactions between environmental conditions and marram grass establishment from seeds, rhizome fragments and transplants

Overall, marram grass' establishment success is a result of complex interactions between climatic conditions, sediment transport and established vegetation (Figure 6.1). Moreover, establishment success depends on the mode of establishment (i.e., from seeds, rhizome fragments or transplants, hereafter referred to as establishment method) with establishment from transplants being more successful than establishment from seeds or rhizome fragments (van der Putten, 1990; Chapter 3; Chapter 4; Box 1). The prevailing climatic conditions, such as temperature, precipitation, and wind, that were similar across locations within field experiments, are expected to have a direct effect on establishment (e.g. Biel & Hacker, 2021; Homberger et al., 2023; van der Putten, 1990). For example, germination rate is highest with fluctuating day/night temperatures and growth increases in elevated temperatures (Biel & Hacker, 2021; van der Putten, 1990). Next to the direct effect, the climatic conditions will indirectly affect establishment through their influence on sediment transport. For example, in dry conditions more sand will be transported than in wet conditions at similar wind speeds, while during storm conditions chances of erosion increase (Bauer et al., 2009; Hesp & Martínez, 2007). Subsequently, interactions between climatic conditions, sediment

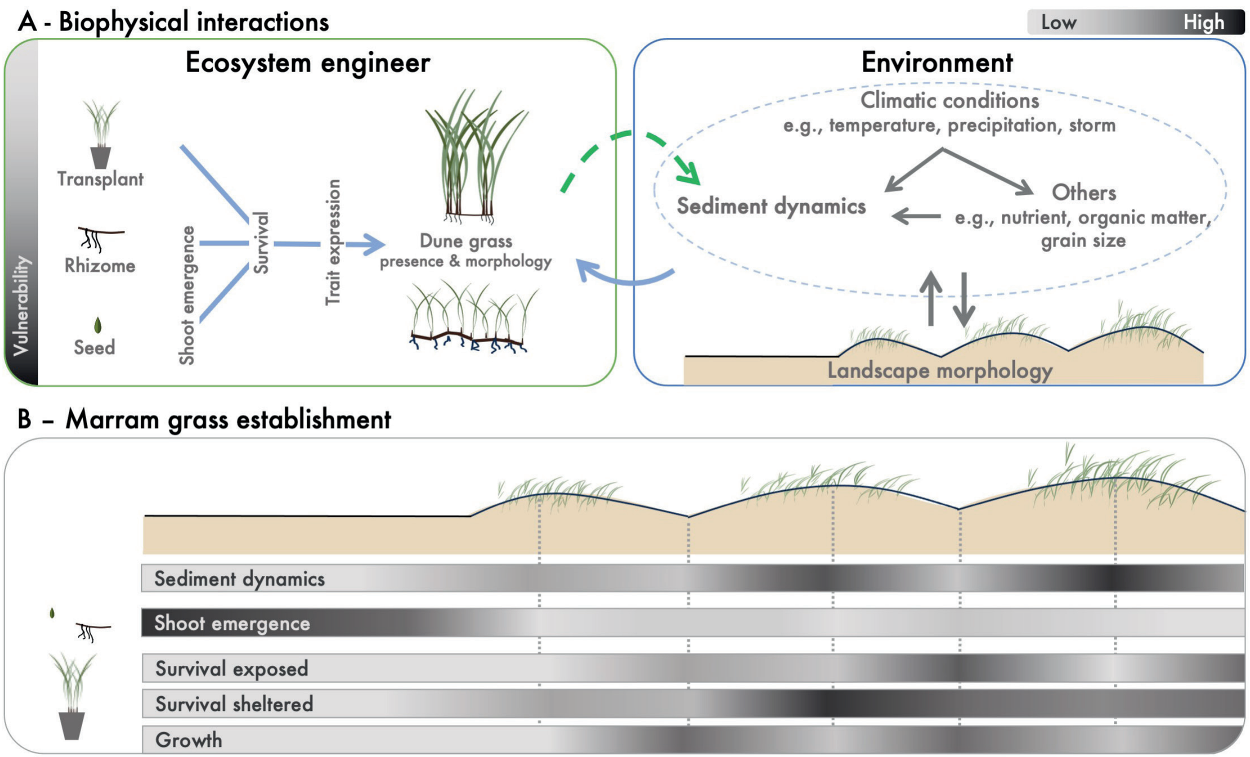


Figure 6.1: A) Most important biophysical interactions in embryonic dunes. Environmental conditions affect dune grass' shoot emergence from seeds or rhizomes, survival, and trait expression, determining their presence and morphology. In turn, dune grass presence and morphology affect environmental conditions, most importantly local sediment dynamics. B) Graphical representation showing how sediment dynamics differs along an embryonic dune gradient. Subsequently, the expected potential for marram grass' shoot emergence from seeds and rhizomes (Chapter 3), transplant survival at locations with differing exposures (Chapter 4) and growth (Chapter 4, Chapter 5) are presented which is related to sediment dynamics, presence of sand couch and position along the gradient. The included factors are presented from relatively low (white) to relatively high (black) values.

transport and vegetation will determine local sediment dynamics, which I found to be a key factor affecting marram grass' shoot emergence from seeds and rhizome fragments, and transplant survival (Chapter 3; Chapter 4; Figure 6.1; Box 1).
I expect that prevailing climatic conditions largely determine germination and plant performance, and that vegetation-induced sediment dynamics forms an additional bottleneck for establishment. For example, I expect that the large difference in germination rate between controlled and field conditions (i.e., 80.4% vs 16.1% maximum germination rate, respectively) are mainly caused by climatic conditions being suboptimal in field conditions, such as little rain combined with high temperatures in the field resulted in low soil moisture levels independent of location or landscape morphology, and that vegetation-induced sediment dynamics is the most important factor resulting in differences between plots (Chapter 3). While it has previously been found that vegetation can change micro-climatic conditions through sediment accretion, such as increased soil moisture levels, nutrients levels and lower temperatures (Baldwin & Maun, 1983), I did not find support for changes in soil nutrient levels (Chapter 2), organic matter content (Chapter 2) or soil moisture levels (Chapter 3; Chapter 5) in within vegetation compared to proximate bare soils in the earliest dune stages. This might be a reason why the expected beneficial effects of vegetation presence for establishment of marram grass were not found.

Sediment dynamics negatively affected marram grass' establishment independent of establishment method, however, different establishment methods differed in their vulnerability. Shoot emergence from seeds and rhizome fragments was more vulnerable to elevation changes in summer (i.e., during the growth season) than transplant survival (Chapter 3; Chapter 4; Box 1). Moreover, survival of shoots emerged from rhizomes during summer (June-September) was about 4 times higher than seedlings (i.e., 46.1±6.9% vs 12.1±3.6%, respectively). These findings highlight that early life stages are the most vulnerable and that disturbance tolerance during establishment differs depending on establishment methods (Balke et al., 2014; Del Vecchio et al., 2020; Figure 6.1). Next to sediment change in summer, conditions in winter strongly affected survival. Very few shoots that emerged from seeds and rhizomes survived winter (Chapter 3; Box 1). However, since conditions in winter were not monitored in this experiment, it cannot be determined which environmental factors affected their survival (Chapter 3). However, conditions in winter were monitored in the experiment with transplant and here, I found that erosion in winter was the most important factor reducing their survival (Chapter 4). Additional research testing tolerance in different life

Box 1. Combined results marram grass establishment

Germination and survival numbers

Shoot emergence from rhizomes and seeds was a much less successful establishment method than using transplants. From the buds of dispersed rhizome fragments only ±0.08% emerged shoots and 0% of them survived winter. Seed germination was relatively more successful with 3.7% of seeds germinating of which 0.7% (i.e., 0.03% of the total sown seeds) survived winter (Chapter 3). In comparison, 33% of the in 2021 transplanted marram grass individuals survived two growing seasons (Chapter 4). However, the survival of transplants in the first months after planting differed greatly between years. Comparing sheltered conditions of the 2021 experiment with survival of transplants in the 2022 experiment (± 4 km between locations, both with a similar beach width and beach-dune morphology), survival between April – July was much higher in 2021 than 2022 with 93% vs 45% survival, respectively (Chapter 4; Chapter 5). Since environmental conditions were not monitored during that period in 2022, I cannot relate survival to environmental conditions. However, I expect a large influence of relatively dry and warm conditions after planting in 2022 compared to 2021 (KNMI).

Sediment dynamics and plot success

Since the experiments testing the effects of habitat-modification took place in different years and at different locations with different morphologies, a one-on-one comparison is not possible. However, comparing the most similar elevation change data (i.e., absolute elevation change between July and October in the first year of the experiment) with 'plot success' (i.e., a seed or rhizome plot is successful if there was at least one shoot in October 2020 (Chapter 3) and one transplant is a 'plot' which is successful if it survived one summer to October 2021 (Chapter 4)) indicates that transplants were less vulnerable to sediment dynamics than seeds and rhizomes, that showed a similar relation to absolute elevation change (Figure 6.2).

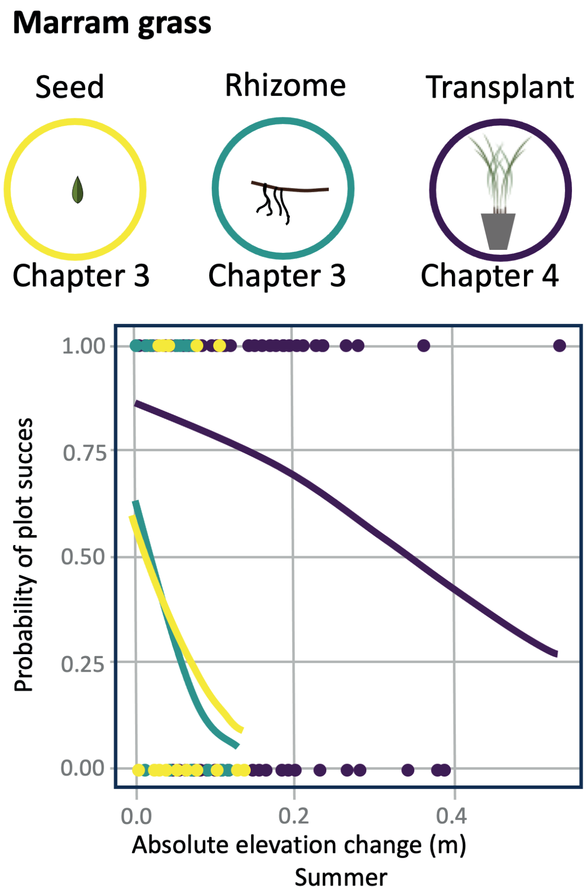


Figure 6.2: The probability of plot success versus the absolute elevation change in meter measured between July - October (2020 for seeds and rhizomes, 2021 for transplants). The seed and rhizome experiment took place on Texel (2020-2021) on the beach and embryonic dunes dominated by marram grass. The transplant experiment took place on Schiermonnikoog (2021-2022) in embryonic dunes dominated by sand couch.

stages and specific relations to disturbances in winter is needed to determine what factors affect long-term establishment of marram grass. Overall, my results indicate that climatic conditions in winter, that are locally affected by vegetation presence and associated dune forms, are the most important in determining the long-term establishment success of marram grass.

6.4. Species interactions, from individual to landscape

In vegetated biogeomorphic systems, such as coastal dunes, seagrass beds and salt marshes, interactions between vegetation and the geomorphic environment determine ecosystem structure and functioning (Balke, 2013; Corenblit et al., 2011). These systems have in common that, at least in early developmental stages, many are shaped by clonal, ecosystem engineering vegetation. On a local scale, the ecosystem engineers benefit their own growth and survival through habitat alterations that are steered by their clonal expansion strategy. Here, young marram grass' context-dependent clonal expansion strategy is hypothesized to benefit their engineering effect and subsequent survival (Chapter 2). While young sand couch in the dunes and cord grasses (*Spartina anglica*) in the salt marsh have a rather inflexible growth strategy, that reduces their local engineering (compared to the most efficient strategy), these strategies are hypothesized to benefit their own survival through limiting burial (sand couch) or erosion (cord grass) (Chapter 2; van de Ven et al., 2023). However, beyond the clonal individual, ecosystem engineers have differing local effects on other individuals (both inter- and intraspecific). For example, while seagrass can locally benefit establishment of conspecifics by increasing soil stability, cord grass (*Spartina alterniflora*) and marram grass limit recruitment of conspecifics as a result of habitat alterations (i.e., increase of sulfide in cord grass and sediment dynamics in marram grass) (Chapter 3; Lambrinos & Bando, 2008; Zipperle et al., 2009). Moreover, the interspecific interaction between dune grasses along the USA coast seem to be largely context-dependent (Biel & Hacker, 2021; Woods et al., 2023; Zarnetske et al., 2013). Similarly, the local effect of sand couch on marram grass' growth and survival ranged from positive to negative depending on the locally prevailing conditions (Chapter 4; Chapter 5). I did not focus on the mechanisms through which sand couch competes with or facilitates marram grass, beyond sediment dynamics. Most commonly, plants compete over limiting resources such as nutrients, water or space. However, in my experiments, competition for nutrients seems unlikely, since marram grass individuals were transplanted including the (nutrient rich) pot soil they were reared in. Moreover, soil moisture levels did not significantly differ between vegetated and non-vegetated plots in the heat and drought experiment, rejecting differences in soil moisture levels as potential mechanism (Chapter 5). To identify mechanisms through which sand couch does compete or facilitate marram grass, and their context-dependency, additional research is needed.

Next to their local effects, ecosystem engineers often have larger, beyond patch, effects. For some ecosystems, such as for salt marshes or arid drylands, the large-scale effects are studied more often than for coastal dunes (e.g., Bouma et al., 2009, 2013; van Wesenbeeck et al., 2008). In these ecosystems, scale-dependent feedbacks (i.e., local positive and large-scale negative or local negative and large-scale positive interactions) play an important role in shaping the environment (e.g., Bouma et al., 2013; Rietkerk & van de Koppel, 2008). For example, cord grasses on coble beaches locally reduce forb establishment while they facilitate establishment on a larger distance, which is expected to explain community structure (van de Koppel et al., 2006) Moreover, scale-dependent feedbacks have been suggested to explain spatial organization of coastal dunes (Baas, 2002). However, these biophysical models only include vegetation growth and not establishment as a biological factor. For growth of dune grasses, the scale-dependent feedback consists of a local positive (i.e., growth increases with sediment accretion and sediment accretion increases with growth) and long-distance negative feedback (i.e., negative effect on growth if sediment deposition is below 0.1 m/year) (Baas, 2002). In contrast, results of this thesis show a local negative effect of dune grasses (sand couch and marram grass) on establishment of marram grass through habitat modifying activities. Moreover, I hypothesize a positive larger-scale effect of dune formation through creation of relatively sheltered and stable microsites (Chapter 4). Overall, the dunes will be shaped by the combined interactions of growth (local positive) and establishment (local negative). Moreover, I expect that the feedback strength (both local and large-scale), and subsequent spatial organization of the dunes, depends on species' traits (e.g., their clonal expansion strategy), species compositions and environmental conditions (e.g., sediment transport). However, since the shaping processes in the coastal dunes, such as wind and storms, are irregular and unpredictable, I expect that the spatial patterns in the coastal dunes are less regular than expected in, for example, salt marshes that are shaped by (regular) tidal motion. To test the posed hypotheses additional research including larger scale interactions and processes would be needed.

6.5. Effects of global change on early dune development

Coastal dunes are predicted to be particularly vulnerable to climate change (IPCC, 2022). Some of the predicted changes, like an increase in temperature, precipitation and nutrient input, benefit growth of dune grasses (Biel & Hacker, 2021; Homberger et al., 2023; Jackson et al., 2019; van der Putten, 1990). While other effects, such as an increase in the frequency of extreme climatic events, or sea level rise, potentially decrease plant growth or increase erosion. In the heat and drought experiment, marram grass transplants were not significantly affected by heat and drought. These results indicate that relatively young, establishing marram grass individuals are highly heat and drought tolerant and suggest little threat of heat or drought for dune development (Chapter 5). However, the response of marram grass to heat and drought is likely life stage dependent, with seedlings or young shoots emerging from rhizomes potentially being more vulnerable than transplants, while adult vegetation is expected to be even more resistant (Del Vecchio et al., 2020; Maun, 1994). Therefore, effects of heat and drought might be larger on natural dune development than expected based on these results. Erosive events like storms might severely or completely erode embryonic dunes. While in general vegetation is expected to reduce erosion, it has recently been found that in extreme storm conditions vegetation can increase erosion (Feagin et al., 2023). Moreover, I found that larger dunes formed by sand couch eroded more than smaller dunes in winter (Chapter 4). Plant morphology partly determines how prone dunes are to erosion, for example, higher shoot densities are associated with less storm erosion and more leaves per shoot with less wave erosion (Charbonneau et al., 2017; Innocenti et al., 2021). Therefore, the clonal expansion strategy not only determines their sediment capturing ability but also partly determines their resistance to erosion. Sand couch, with its dispersed growth, likely leaves the dune body more susceptible to erosion than marram grass that grows more dense (Chapter 2, Feagin et al., 2023; Innocenti et al., 2021; Maximiliano-Cordova et al., 2019).

Depending on storm severity, dune grasses can be severed, dislodged and embryonic dunes can be completely eroded. However, after such a large storm, there are potential benefits for establishment of new individuals. For example, severed parts of clonal individuals can be dispersed (Hilton & Konlechner, 2011; Konlechner & Hilton, 2009). Or seeds buried in the dune body might resurface after erosion, where they add to the ‘effective seedbank’ (i.e., the seeds in the topsoil layer that have the potential to germinate) (Hilton et al., 2019). Moreover, if vegetation is completely removed, sediment dynamics will be lower, increasing the establishment chances from seeds and clonal fragments (Chapter 3). Eventually, the resilience of dune systems will depend on the balance between erosion and vegetation recovery. To further our knowledge in regards of climate change effects on dune development and resilience, additional research into, for example, sensitivity of different life stages to climatic extremes, context dependency of species interactions and recovery time after erosion is needed. However, since global change has opposing effects (e.g., increased growth with increased temperature vs increased erosion due to storms) on dune grasses, the overall effect of global change on coastal dunes development will remain hard to predict.

6.6. Implications for restoration

Traditionally, along the Dutch shore, dune restoration focusses on increasing sedimentation (e.g., with use of groins, wood brush dams or building sand-drift dykes) combined with planting of marram grass to stabilize the sediment (Bochev-Van der Burgh et al., 2011). Nowadays, these practices are often combined with sand nourishment (which happen offshore, onshore and in the form of mega-nourishments) (Ministerie V&W, 2000). The extensive planting of marram grass has reduced the dynamic nature of the dunes. While the high, stable dunes are resistant, increasing the dynamic nature of the dunes likely also increases their resilience (Feagin et al., 2015). Therefore, there is increasing interest in re-enforcing the natural dynamics of the dunes, through vegetation removal or by making notches in the foredunes (Ruessink et al., 2018; van der Valk et al., 2013). However, also in common practices of dune transplantation a more dynamic approach might be applied. For example, sand couch, which is generally ignored in restoration practices, could be included in restoration. Moreover, the focus could shift from reinforcing or creating high foredune ridges to promoting development of embryonic dunes in front of these high dune ridges.

Lower dunes that are formed by faster growing grasses, such as sand couch, might be more resilient than higher dunes formed by slower growing species, such as marram grass, since they likely have a higher recovery after erosive events (Feagin et al., 2015; Pickart, 2021). Therefore, inclusion of sand couch in restoration practice might result in faster dune formation, faster recovery due to its higher growth rate, and a more heterogeneous landscape, which all contributes to coastal resilience. Based on that hypothesis, I would advise testing restoration practices including both sand couch and marram grass. However, I would advise to not plant them in a locally mixed design because sand couch potentially reduces growth of marram grass. However, on a larger scale, dune formation by sand couch might benefit marram grass' establishment. Therefore, a larger-scale design with planting of sand couch closer to the shoreline and marram grass downwind might increase the dynamics and heterogeneity of the landscape and subsequently increase its resilience. One important note is that the suggested measures would only be applicable in specific situations where there is enough space (either towards the sea such as at (mega-) nourishments or by providing more space on the land side through erosion of foredunes) and sediment available (which can be a result of nourishments but could also be accomplished through reactivation of the dunes). In the end, the physical boundary conditions of the system in which restoration is carried out will determine the success of restoration measures.

In the common restoration practices, marram grass is planted in competition limiting arrays (van der Putten, 1990). However, results from Chapter 2 show that the clonal expansion strategy of marram grass is context-dependent, implying that the optimal planting design for marram grass is also context-dependent (Chapter 2; Reijers et al., 2021). To optimize restoration efficacy, we should increase the understanding of the relation between marram grass' shoot organization and its physical environment. Moreover, in restoration of other ecosystems, such as seagrass beds and salt marshes, it was recently found that by increasing intraspecific facilitation restoration yields can increase (Renzi et al., 2019; Silliman et al., 2015). This can be accomplished by mimicking emergent traits (i.e., traits that are not displayed by a single shoot or individual but emerge when there is a larger vegetation patch or species agglomeration), thereby reducing transplant biomass (Temmink et al., 2020). However, effectivity of these measures is also context-dependent (Fischman et al., 2019; van der Heide et al., 2021). While sediment accretion is the emergent trait of dune grasses, mimicking a larger vegetation patch for restoration has been proven ineffective (Box 2), which is in line with the main results on marram grass establishment in presence of vegetation (Chapter 3; Chapter 4). To reduce transplanted biomass in restoration of coastal dunes, it might be beneficial to place structures that create a relatively stable and sheltered environment in their wake, and place transplant in these sheltered microsites.

6.7. Conclusions

In this thesis, I investigated interactions between dune grasses, environmental conditions and landscape morphology. I found that complex biophysical interactions working on a scale from the individual to the landscape determine dune emergence and development. The individual's engineering traits, that are both species-specific and environmental-dependent, determine local engineering effects. Subsequently, these engineering activities affect establishment of other dune grasses. Overall, my results highlight that, to fully understand complex interactions in biogeomorphic systems, inclusion of multiple spatial scales, diverse conditions and timescales are needed. Moreover, increasing our understanding of these interactions might be of vital importance to determine the ecosystem's resilience under pressure of global change, improve management, conservation and restoration practices.

Box 2. Mimicking emergent traits of dune grasses does not increase establishment success

In multiple experiments the potential use of emergent trait mimicry in dune restoration was tested. The experimental design was based on the idea that the emergent trait of dune grasses is sediment accumulation (i.e., a result of their aboveground structures), and the hypothesis that restoration yields would improve if transplants were planted within a larger vegetation patch. In the field experiments, biodegradable structures (50*50*15 cm, BESE-elements see https://www.bese-products.com) were used to mimic dune grass shoots, that locally increased sedimentation. These were outplaced just seaward of the embryonic dunes (on the beach), in spring 2017 on Schiermonnikoog (close to the exposed location of Chapter 5, by Valérie Reijers) and in spring 2019 and 2020 on Texel (close to the wide location of Chapter 3). Both sand couch and marram grass individuals were transplanted within the structures or on bare soil as control (n=6 in 2017 and n=12 in 2019 and 2020).

Overall, the survival of transplants was extremely low in all experiments and across treatments. In 2017, the experiment was terminated after 76 days due to the low survival rate (survival of marram grass 29% (structure) vs 20% (control) and sand couch 0% (structure) vs 17% (control)). In 2019, during the growth season all marram grass individuals died, irrespective of used structure. New transplants were planted in spring 2020, but all these transplants were lost in the summer of 2020. In 2019, sand couch transplants had a much higher survival (79% structure vs 69% control). These plots were followed until spring 2021. In spring 2021, survival within the structures and controls was equal (50% for both) with no significant difference in shoot numbers (9.8±3 (structure) vs 8.3±4 (control)). These results indicate that using biodegradable structures to mimic dune grass shoots does not benefit restoration yields for marram grass and sand couch. Which is also supported by the results from Chapters 3, 4 and 5, that indicate a negative effect of vegetation presence for establishment of marram grass.

Figure 6.2: Examples of an (unsuccessful) marram grass plot (left) and a (successful) sand couch plot (right) after one growing season in 2019 (pictures from 09-10-2019).

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SUMMARY

A sandy symphony

Coastal dunes occur world-wide along sandy shores where they provide vital services such as flood protection, drinking water and recreation. They form and develop through a dynamic interplay between environmental factors, such as sediment movement, and ecosystem engineering plant species. Ecosystem engineering species are species that modify their habitat and benefit from these modifications themselves. In coastal dune systems, dune grasses are the most important ecosystem engineers. They are considered ecosystem engineers because they trap sediment, thereby altering their surroundings and promoting their own growth and survival. As the grasses grow, they trap more sediment which further promotes their growth. In this way the grasses create a so-called self-reinforcing, bio-physical feedback and form the basis of the complete coastal dune ecosystem. Understanding the biophysical processes that drive coastal dune emergence and development is important for effective management and restoration efforts.

In this thesis, I studied the interactions between dune grasses, environmental conditions, and landscape morphology in early dune development, focusing on the Northwestern European shoreline. Here, two co-occurring dune grasses dominate: the pioneer dune grass sand couch (*Elytrigia juncea*) and the later successional marram grass (*Ammophila arenaria*). First, I compared morphological plant traits that affect ecosystem engineering of these dune grass species. Subsequently, I determined how established dune grasses, and their habitat modifying activities, affect establishment of conspecifics and later successional species. Lastly, I tested whether the interspecific interaction (i.e., the interaction between the two species) changed under pressure of combined heat and drought.

One of the most important morphological plant traits of dune grasses that determine the amount of sediment they trap is their clonal expansion strategy. Dune grasses grow clonally by forming rhizomes from which new shoots can sprout. Therefore, their clonal expansion strategy determines the spatial shoot organizations (i.e., specific shoot patterns) that in turn determine their ability to modulate wind flow and accumulate sand. Consequently, the sediment accreting capacity of dune grasses is fundamentally linked to their clonal expansion strategy. In **chapter 2**, I compared the clonal expansion strategies of sand couch and marram grass across a range of coastal dune environments (from Denmark to France). My results reveal that, most individuals deploy a strategy that deviates from a simple dense vegetation patch and display a patchy shoot organization, balancing clonal expansion and sediment accretion. On average, sand couch deployed a more dispersed shoot organization than marram grass, which had a patchy shoot organization. As a result, sand couch (on average) creates lower and broader dunes than marram grass. Whereas sand couch exhibited the same expansion strategy independent of environmental conditions, marram grass demonstrated a large intraspecific variation. Shoot patterns ranged from a clumped organization correlating to relatively high soil organic matter contents, high temperature, and small grain sizes, to a patchy configuration with intermediate conditions, and a dispersed organization with low soil organic matter, low temperature, and large grain sizes. I conclude that marram grass is flexible in adjusting its engineering capacity in response to environmental conditions, while sand couch instead follows a fixed expansion strategy, illustrating that shoot organization results from the interaction of both species-specific and environmental-specific trait expression.

The ecosystem engineering effect of dune grasses does not only affect their own performance but can affect establishment and growth of other species or conspecifics as well. Next to clonal expansion of dune grasses, new individuals can establish from seeds (which can be wind and marine dispersed) or through dispersal of rhizome fragments that can break off from adult vegetation in storm conditions. In **chapter 3**, I investigated how marram grass, through embryonic dune development, affects recruitment of conspecifics from seeds and rhizome fragments. First, I determined natural presence of seeds and rhizome fragments at three dune sites with differing beach widths and dune morphologies. Subsequently, I tested the potential establishment from seeds and rhizomes at the same locations and the effect of habitat modification by marram grass by comparing plots on the beach (no vegetation) and in the embryonic dunes (marram grass vegetation). In addition, I investigated how sediment burial (i.e., the main effect of habitat modification by dune grasses) affected germination and shoot emergence in a controlled experiment. Results show that regardless of habitat modification or beach width, seeds and rhizomes were absent in natural conditions. Moreover, seed retention in experimental plots was significantly higher in the unmodified, beach plots than in the modified, embryonic dune habitat. This suggests that a lack of seed input in the unmodified system causes the lack of seeds in natural conditions. However, the low seed retention in the modified habitat suggests that vegetation-induced sediment dynamics reduce seed retention. In the field experiment, habitat modification negatively affected shoot emergence from seeds (8x less) and rhizomes (4x less). The number of shoots per plot was negatively related to sediment dynamics. Furthermore, fewer seedlings were found with higher elevations. In controlled laboratory conditions, the highest seedling emergence was found with slight burial (0.5-3 cm); both germination and seedling emergence decreased as seeds were buried deeper or shallower. Overall, habitat modification by marram grass negatively affects recruitment of conspecifics through increased sediment dynamics and elevation. Consequently, storm events or eradications programs that include removal of adult vegetation – which leads to an unmodified system – might benefit new recruitment from seeds or clonal fragments.

Generally, it is assumed that sand couch primes the landscape for establishment of marram grass. However, these ideas lack experimental validation, leaving the specific relationship between sand couch, the landscape they form, and marram grass establishment unknown. In **chapter 4**, I experimentally investigated this relationship by planting 975 young marram grass plants in two distinct, sand couch dominated, embryonic dune systems. Using structural equation models, I examined the effect of sand couch and its landscape attributes (elevation, distance to sea and elevation change) on marram grass' establishment. Results show an indirect negative effect of sand couch via landscape modifications on survival of establishing marram grass. Specifically, sand couch elevated the environment and elevated areas in turn eroded more in winter, which was the key factor reducing marram grass survival. Moreover, marram grass' shoot formation was negatively affected by sand couch presence. While the indirect negative effect was found independent of location, direct interactions between sand couch and marram grass survival and growth were context-dependent: neutral (growth) to positive (survival) in more sheltered conditions, and neutral (survival) to negative (growth) in exposed conditions. Overall, I observed the highest survival in the lower areas surrounded by sand couch dunes. Contrary to the idea that created elevation is a prerequisite, I hypothesize that dune formation by sand couch benefits marram grass establishment by creating relatively low-lying, stable and sheltered microsites.

Understanding interactions between species in environmental extremes plays a vital role in predicting ecosystem resilience. Especially, because the occurrence of environmental extremes is predicted to increase due to climate change. In **chapter 5**, I tested whether the observed interaction between sand couch and marram grass in sheltered conditions changed under pressure of extreme heat and drought. In a 4-week field experiment, I transplanted marram grass within sand couch patches or on bare sediment. This plant interaction treatment was combined with a heat and drought treatment that was simulated with greenhouses that inhibited rainfall and increased temperatures (average daily maximum temperature +4 °C). Results show that the presence of sand couch significantly reduced growth (i.e., shoot formation, shoot and root length, and aboveground biomass) of marram grass. By contrast, the heat and drought treatment had no significant effects on growth or survival of marram grass, irrespective of species interactions. The neutral response suggests that even in its early establishment marram grass is highly heat and drought tolerant. My results indicate that the interactions with sand couch play a more important role in marram grass establishment and subsequent dune development than extreme heat and drought.

In conclusion, in this thesis, I investigated interactions between dune grasses, environmental conditions and landscape morphology. I found that biophysical interactions, working on a scale from the individual to the landscape, determine dune emergence and development. The individual's engineering traits, that are both species-specific and environmental-dependent, determine local engineering effects. Subsequently, these engineering activities affect establishment of other dune grasses. Overall, my results highlight that, to fully understand complex interactions in biogeomorphic systems, inclusion of multiple spatial scales, diverse conditions and timescales are needed.

SAMENVATTING

Een zandige symfonie

Duinen komen wereldwijd voor langs zandige kusten waar ze essentiële diensten verlenen zoals overstromingsbescherming, drinkwatervoorziening en recreatie. Ze ontstaan en ontwikkelen zich door een dynamische wisselwerking tussen omgevingsfactoren, zoals zandverplaatsing, en biobouwende plantensoorten. Biobouwende soorten zijn soorten die hun omgeving veranderen en zelf profiteren van deze veranderingen. De belangrijkste biobouwende soorten in de duinen zijn duingrassen. Zij worden als biobouwers beschouwd omdat ze zand invangen en door dit ingevangen zand hun eigen groei en overleving bevorderen. Als het duingras groeit wordt er meer zand ingevangen en door dit ingevangen zand wordt de groei verder gestimuleerd. Op deze manier creëren de grassen een zichzelf versterkende, biofysische terugkoppeling en vormen zij de basis voor het hele duinsysteem. Het begrijpen van de biofysische processen die ten grondslag liggen aan het ontstaan en de ontwikkeling van duinen is belangrijk voor effectief beheer en herstel van duingebieden.

In dit proefschrift heb ik de interactie tussen duingrassen, omgevingsfactoren en landschapsmorfologie in vroege ontwikkeling van duinen bestudeerd, met de nadruk op duingebieden in Noordwest-Europa. In deze gebieden domineren twee duingrassoorten die hier samen voorkomen: de pionierssoort biestarwegras (*Elytrigia juncea*) en het zich later vestigende helmgras (*Ammophila arenaria*). Ten eerste heb ik morfologische plantkenmerken vergeleken die van invloed zijn het biobouwende effect van deze twee soorten. Vervolgens heb ik bepaald hoe gevestigde duingrassen, en de door hen veroorzaakte veranderingen in de omgeving, de vestiging van soortgenoten en zich later vestigende soorten beïnvloedt. Ten slotte heb ik getest of de interspecifieke interactie (dat wil zeggen, de interactie tussen de twee verschillende soorten) verandert tijdens een periode van hitte en droogte.

Een van de belangrijkste morfologische kenmerken van duingrassen die bepalend is voor de hoeveelheid zand die ze vasthouden, is hun klonale uitbreidingsstrategie. Duingrassen groeien klonaal door de vorming van wortelstokken waaruit nieuwe scheuten kunnen ontspruiten. Daardoor is de klonale uitbreidingsstrategie bepalend voor de ruimtelijke scheutorganisatie van het gras (oftewel, het scheutpatroon). De scheutorganisatie bepaalt vervolgens het vermogen om de windstroming te veranderen en als gevolg daarvan hoeveel zand er wordt ingevangen. Daarom is het vermogen van duingrassen om zand in te vangen fundamenteel verbonden aan hun klonale uitbreidingsstrategie. In **hoofdstuk 2** heb ik de klonale uitbreidingsstrategie van biestarwegras en helmgras vergeleken in een scala aan duingebieden (van Denemarken tot Frankrijk). Mijn resultaten laten zien dat de meeste individuen een strategie toepassen die afwijkt van een eenvoudig patroon met een hoge scheutdichtheid en groeien in kleine pollen (of patches) waarbij ze investering tussen klonale groei en het invangen van zand balanceren. Gemiddeld genomen had biestarwegras een meer verspreide scheutorganisatie dan helmgras, dat kleine pollen vormt. Hierdoor zijn de duinen die gevormd worden door biestarwegras gemiddeld genomen lager en breder dan de duinen die helmgras vormt. Terwijl biestarwegras dezelfde uitbreidingsstrategie had onafhankelijk van omgevingsfactoren, vertoonde helmgras een grote intraspecifieke variatie. Scheutpatronen varieerden van een hoge scheutdichtheid die correleerde met een relatief hoge organische stofgehalte in de bodem, hoge temperatuur en kleine korrelgrootte, tot een scheutorganisatie met kleine pollen bij tussenliggende omstandigheden, en een verspreide organisatie bij lage organische stofgehaltes, lage temperaturen en grote korrelgroottes. Hieruit concludeer ik dat helmgras flexibel is in het aanpassen van zijn vermogen om zand in te vangen, terwijl biestarwegras een vaste uitbreidingsstrategie volgt. Dit laat zien dat de scheutorganisatie van duingras het resultaat is van zowel soortspecifieke als omgeving-specifieke expressie van plantkenmerken.

Het biobouwende effect van duingrassen heeft niet alleen effect op hun eigen prestaties, maar kan de vestiging en groei van andere soorten of soortgenoten ook beïnvloeden. Naast de klonale groei van duingras via wortelstokken, kunnen nieuwe individuen zich vestigen uit zaden (die door de wind en via zee verspreid kunnen worden) of doordat stukken wortelstok tijdens stormen worden afgebroken en verspreid. In **hoofdstuk 3** heb ik onderzocht hoe helmgras, door middel van de vorming van embryonale duinen, vestiging van soortgenoten uit zaden en stukken wortelstok beïnvloedt. Op drie locaties die verschillen in kustbreedte en duinmorfologie heb ik bepaald hoeveel zaden en wortelstokken er van nature in de toplaag van de bodem zitten. Daarnaast heb ik op dezelfde locaties experimenteel onderzocht wat de vestigingskansen uit zaden en stukken wortelstok zijn en wat hierbij het effect van duinvorming door helmgras is door proefvlakken op het strand en in de embryonale duinen te vergelijken. Ten slotte heb ik de invloed van begraving (te weten; het belangrijkste biobouwende effect van duingrassen) op de kieming van zaden in gecontroleerde condities bepaald. De resultaten laten zien dat er, ongeacht duinvorming of strand breedte, geen zaden en wortelstokken waren in natuurlijke condities. In de proefvlakken waar zaden waren gezaaid werden na een jaar significant meer zaden teruggevonden op het strand dan in de embryonale duinen. Dit suggereert dat op het strand de toevoer van zaden ontbreekt terwijl de dynamiek in de embryonale duinen het aantal zaden in de toplaag doet afnemen. In het veldexperiment was er een groot verschil in opkomst op het strand en in de embryonale duinen, zowel uit zaden (8x meer scheuten) als uit wortelstokken (4x meer scheuten). De maximum scheutaantallen per proefvlak waren negatief gerelateerd aan zanddynamiek (minder scheuten bij grotere dynamiek) en voor de scheuten die uit zaden ontsproten ook met hoogte (minder scheuten in hogere proefvlakken). In het begravingsexperiment vond ik de hoogste aantal zaailingen bij geringe begraving (tussen de 0.5-3 cm). Zowel de kieming als het verschijnen van zaailingen boven de grond nam af bij minder dan 0.5 cm of meer dan 3 cm begraving. Deze resultaten laten zien dat helmgras een negatief effect heeft op de vestiging van soortgenoten door het vergroten van de zanddynamiek en het creëren van hoogte, dus kortgezegd door hun biobouwende effect. Bijgevolg zouden stormen of uitroeiingsprogramma’s, die ervoor zorgen dat volwassen vegetatie wordt verwijderd en dus leiden tot een kaal stuk strand, de kans op vestiging uit zaden en wortelstokken kunnen vergroten.

Over het algemeen wordt aangenomen dat eerst biestarwegras zich vestigt en helmgras zich hierna pas kan vestigen als biestarwegras embryonale duinen heeft gevormd. Deze aanname is gebaseerd op veldobservaties, maar hiervoor ontbreekt experimentele validatie waardoor de specifieke relatie tussen biestarwegras, de door hen gevormde duinen en vestiging van helmgras onbekend is. In **hoofdstuk 4** heb ik deze relaties experimenteel onderzocht door 975 jonge helmgrasplanten te planten in twee verschillende, door biestarwegras gedomineerde, embryonale duinsystemen op het Waddeneiland Schiermonnikoog. Met behulp van ‘structural equation models’, heb ik het effect van biestarwegras en eigenschappen van het landschap (hoogte, afstand tot zee en veranderingen in de hoogte) op de vestiging van helmgras bepaald. De resultaten laten een indirect negatief effect van biestarwegras op overleving van helmgras zien door landschapsmodificaties. Meer specifiek vond ik dat biestarwegras het landschap ophoogt en deze hogere gebieden vervolgens meer erodeerden in de winter, wat de meest bepalende factor voor overleving van helmgras was. Daarnaast vormde helmgras dat in biestarwegras was geplant minder scheuten. Hoewel de indirecte negatieve effecten onafhankelijk waren van de experimentele locatie, waren de directe interacties omgevingsafhankelijk. In meer beschutte condities waren de directe interactie neutraal (groei) tot positief (overleving) en in meer blootgestelde condities neutraal (overleving) tot negatief (groei). Over het geheel genomen was de helmgras overleving het hoogst in lagere gebieden die omgeven zijn door duinen. Mijn hypothese is dat, in tegenstelling tot het idee dat gecreëerde hoogte van belang is, duinvorming door biestarwegras helmgras vestiging bevordert door het creëren van relatief lage, stabiele en beschutte plaatsen tussen de duinen.

Het begrijpen van interacties tussen soorten in verschillende condities, waaronder weerextremen, is van belang om de veerkrachtigheid van ecosystemen te kunnen voorspellen. Dit is van groot belang omdat verwacht wordt dat de frequentie van extreme weersomstandigheden zal toenemen door klimaatverandering. In **hoofdstuk 5** heb ik getest of de (in hoofdstuk 4 beschreven) directe interacties tussen biestarwegras en vestigend helmgras veranderen onder druk van extreme hitte en droogte. In een veldexperiment van 4 weken werden helmgras planten die geplant zijn in biestarwegrasvegetatie vergeleken met planten die geplant zijn op kale zandbodem. Naast deze plantinteracties werd het gecombineerde effect van hitte en droogte getest door middel van kassen die regenval tegenhielden en de temperatuur verhoogden (gemiddelde dagelijkse maximumtemperatuur +4°C). De resultaten laten zien dat de aanwezigheid van biestarwegras de groei van helmgras significant vermindert (te weten, minder scheutvorming, korte scheuten en wortels, en lagere bovengrondse biomassa). De gecombineerde hitte en droogte hadden daarentegen geen effect op de groei of de overleving van helmgras, onafhankelijk van aanwezigheid van biestarwegras. De neutrale reactie van helmgras op de hitte en droogte laat zien dat zelfs relatief jonge helmgrasplanten erg hitte- en droogte resistent zijn. Deze bevindingen duiden erop dat de interactie met biestarwegras een grotere rol speelt voor de ontwikkeling van helmgras, en dus de ontwikkeling van het duinsysteem, dan extreme hitte en droogte.

Kortom, in dit proefschrift heb ik de interacties tussen duingrassen, omgevingsfactoren en landschapsmorfologie onderzocht. Ik heb gevonden dat biofysische interacties, die werken van individueel tot landschapsniveau, bepalend zijn voor de vorming en ontwikkeling van duinen. De biobouwende kenmerken van individuen, die zowel soortspecifiek als omgevingsafhankelijk zijn, bepalen het lokale biobouwende effect. Vervolgens beïnvloeden deze biobouwende effecten de vestiging van andere individuen. Mijn resultaten laten het belang zien van het meenemen van verschillende ruimtelijke schalen, diverse condities en tijdschalen om deze complexe biofysische interacties te begrijpen.

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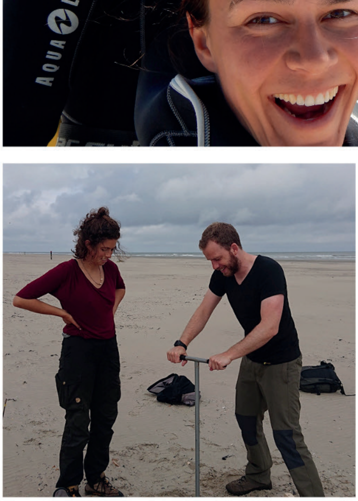










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