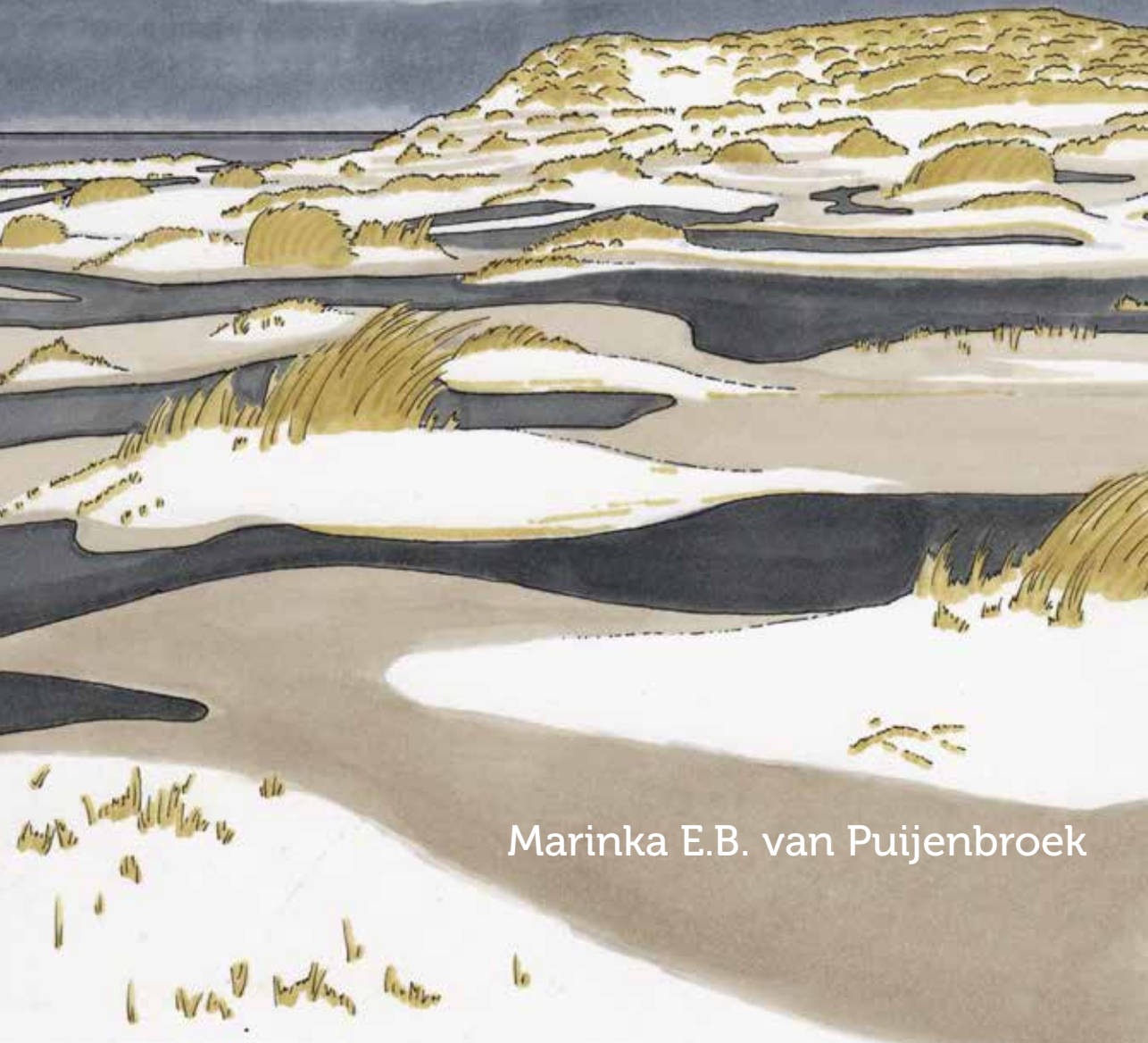


Dunes above and beyond

The interactions between ecological
and geomorphological processes
during early dune development



Marinka E.B. van Puijenbroek

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Dunes, above and beyond

The interactions between ecological and geomorphological processes during early dune development

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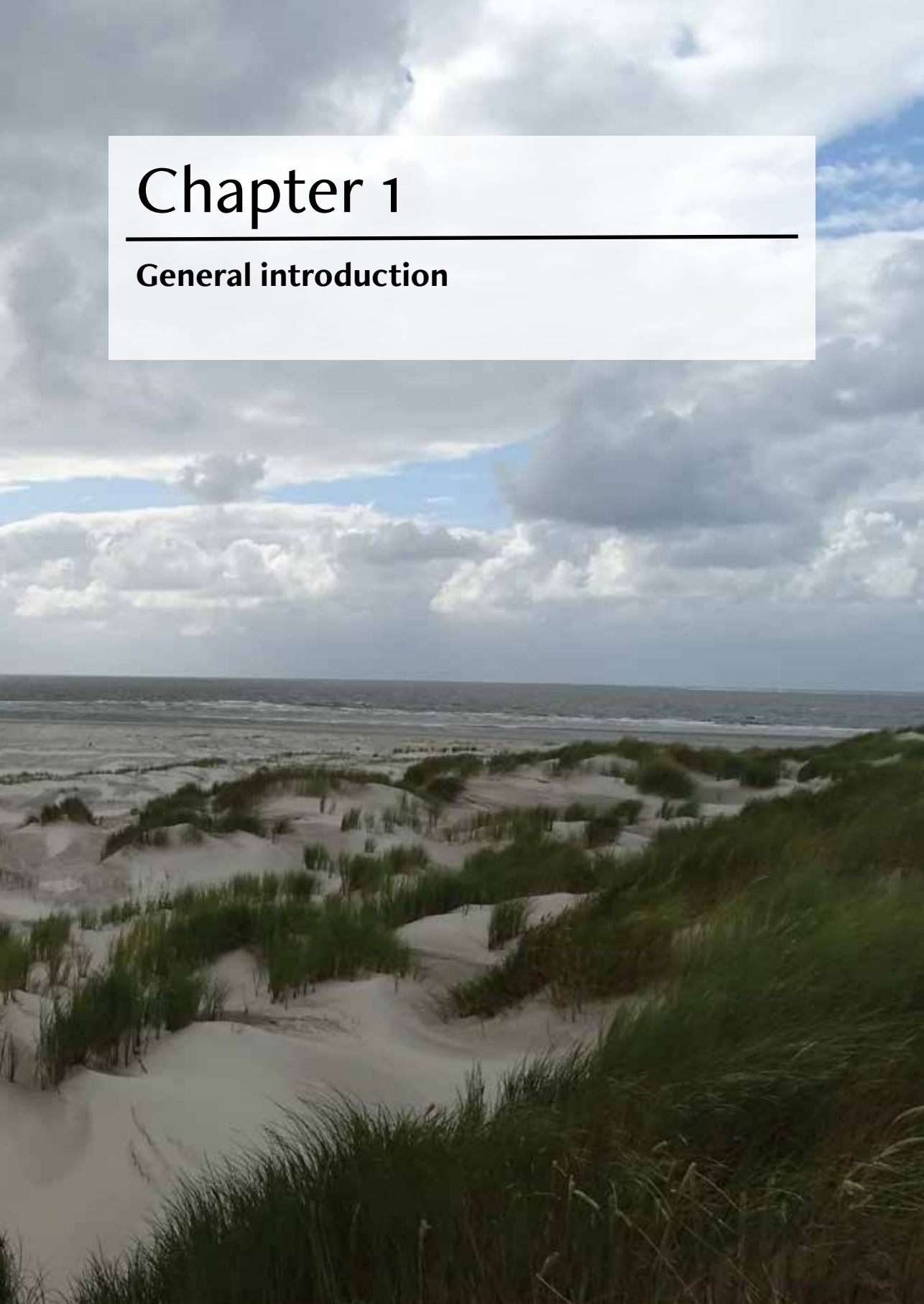
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Chapter 1

General introduction



1.1 Coastal dunes

Coastal dunes are landforms that develop on sandy beaches with sufficient sediment available for transport by wind and vegetation to facilitate sediment fixation (Hesp, 2002). Coastal dunes occur along 34% of the ice-free coasts worldwide (Fig. 1.1; Hardisty, 1994; Martínez and Psuty, 2008), where they serve as the first line of defence against inland flooding by the sea (Coch and Wolff, 1991). As climate change is expected to challenge this natural flood defence (McGranahan et al., 2007; Nicholls and Cazenave, 2010), coastal dune development and its capacity to keep pace with sea-level rise is essential to maintain safe levels of flood protection (Temmerman et al., 2013). Coastal dunes are not only important for coastal protection but also serve as important recreation areas, reservoirs for drinking water and harbour rare plant and animal species (Carter, 1991; Everard et al., 2010). Their importance for biodiversity has been legally recognised by the European Union, as large coastal dune areas have received a protected status as nature reserve within the European Natura 2000 network (European Commission, 2007). Balancing and safeguarding the diverse functions of coastal dunes requires a thorough understanding of the mechanisms underlying coastal dune development, the importance of these mechanisms relative to each other and the time-scales at which they operate.

1.2 Processes involved in early dune development

Vegetation shapes the development of coastal dunes, together with wind and wave action (Fig. 1.2, 1.3, Hesp, 2002; McLean and Shen, 2006; Keijsers et al., 2015). Persistent dune development begins with the establishment of perennial vegetation on the beach (Maun, 1994). The vegetation traps and stabilizes the sand, preventing it from being blown away, which results in a small embryo dune (also known as an incipient foredune or *neбка* dune) (Fig. 1.4, Hesp, 2002; Corenblit et al., 2011). Over time, embryo dunes will transition into established foredunes. The primary foredune may form a dune ridge parallel to the shore (Hesp 2002), turning the previous foredune into a secondary foredune landward of the foredune. In areas with a long-term

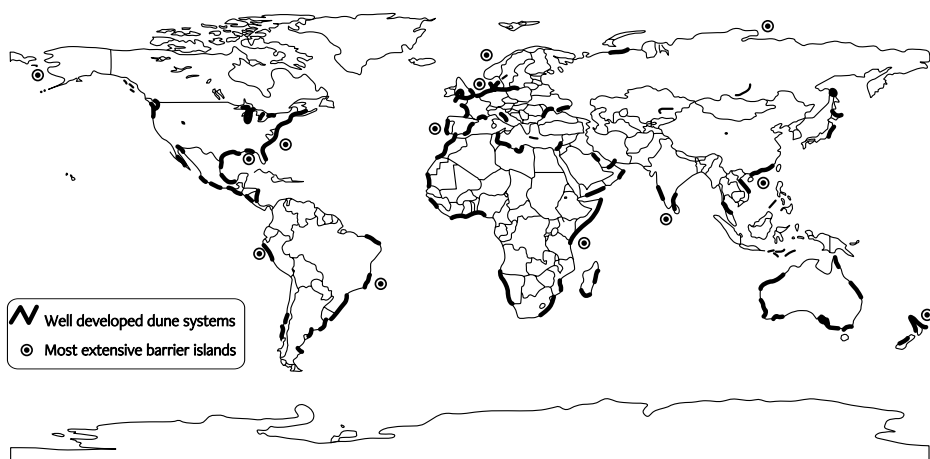
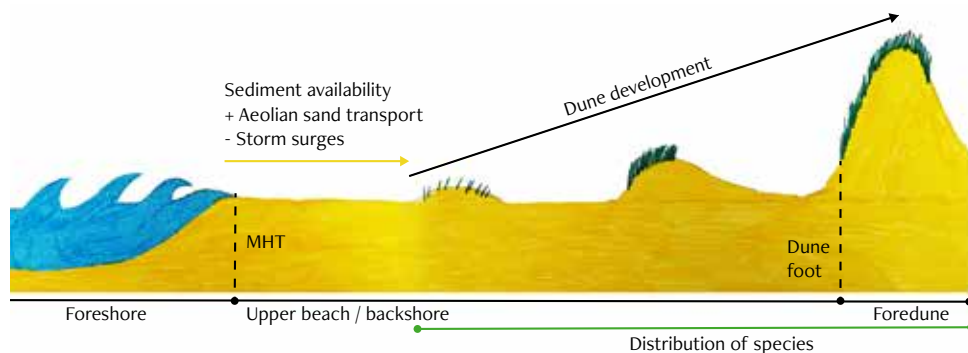


Figure 1.1. Coastal dune areas along the world's coast, and well developed barrier islands (sandy islands with extensive dune systems). Adapted from Martínez and Psuty (2008).

Figure 1.2. Embryo dunes in the Netherlands (Vlieland, 12-09-2013, Marinka van Puijenbroek).



Figure 1.3. Schematic overview of a beach dune system. Dune development is illustrated in time and space, dune size increases from sea to foredune and over time these smaller dunes will increase in size as well. The main processes that determine overall sediment availability are shown. MHT is mean high tide. Artwork by Marinka van Puijenbroek.



accreting, i.e. an expanding, coastline, foredune after foredune may develop from embryo dunes, forming a wide foredune plain (Hesp, 2002; McLean and Shen, 2006). Wide foredune plains offer excellent protection against coastal flooding to the hinterland. Historically the focus has been mainly on maintaining and strengthening the foredune(s), as these offer the main flood protection. More recently however, there has been increasing attention to the function of other landforms. It has for example been hypothesised that embryo dunes contribute to flood defence by attenuating waves, thereby reducing storm erosion of the landward situated foredunes (Montreuil et al., 2013). It has also been suggested that embryo dunes facilitate the establishment of biodiverse rare pioneer plant communities with species such as *Parnassia palustris*, *Liparis loeselii* and *Dactylorhiza incarnate*. However the exact role of embryo dunes on the development of these rare-pioneer communities is unknown.

The development of a bare beach to a foredune depends on three stages: dune formation, dune growth and dune survival, in each of these three stages vegetation plays a large role. Dune formation by plant establishment and dune growth mainly occur in the summer, whereas dune survival mainly depends on the stormy winter season (Montreuil et al., 2013).

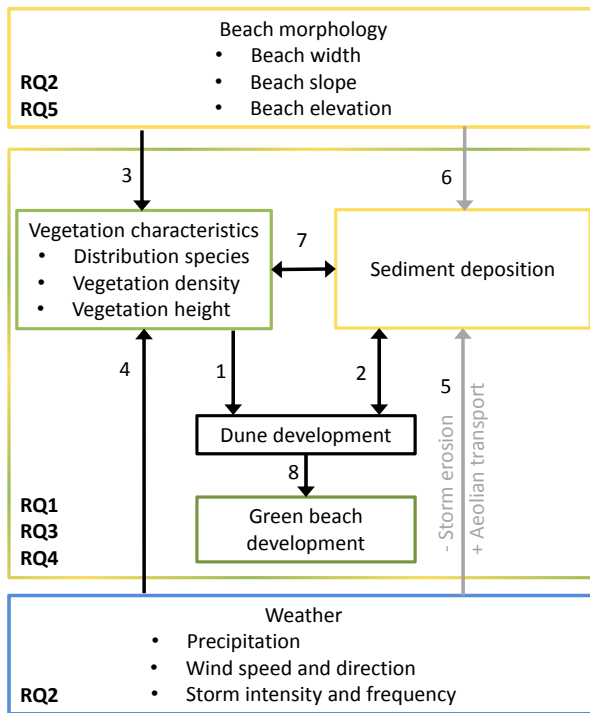


Figure 1.4. Overview of the most important factors and relationships investigated in this thesis. Processes that are the focus in this thesis are in black, in grey processes that have been well studied. RQ indicates the Research Question, in this thesis. Dune development depends on the vegetation characteristics of dune building species (1) and sediment deposition which causes dunes to grow (2). The distribution and growth of dune building species is affected by soil salinity, salt spray and sand burial/erosion, these factors are influenced by beach morphology (3) and weather conditions (4). Sediment deposition is a net result of aeolian transport and storm erosion (5), aeolian transport and storm erosion are modified by beach morphology (6). There is a positive feedback between sediment deposition and vegetation density (7). Dune development creates shelter for the development of species rich green beach vegetation (8).

1.2.1 Dune formation - Plant establishment

Dune development starts with the establishment of perennial dune building species on the beach. Plant establishment takes place via wind or marine dispersed seeds or rhizomes, (Huiskes, 1979; Konlechner and Hilton, 2009) and can be facilitated by wrackline material (wood, seaweed, etc) (Cardona and García, 2008; Eamer and Walker, 2010; Del Vecchio et al., 2017). The establishment and growth of dune building species depend on the abiotic conditions on the beach (Oosting, 1945; Rozema et al., 1985; Hesp, 1991; Maun, 1994, 1998). The beach can be a harsh environment with high soil salinity, low soil moisture, salt spray, sand burial and erosion (Boyce, 1954; Maun, 2009) that vary both spatially and temporally. There is a spatial gradient from sea to dune along which soil salinity and salt spray decrease and sand burial increases (Boyce, 1954; Barbour and DeJong, 1977; Maun 2009). The steepness of the gradient is modified by beach morphology, being most pronounced at short and steep beaches. Temporal variability in abiotic stresses is strongly related to weather conditions, such as precipitation and wind speed and direction (de Jong, 1979; Lichter, 1998). It is generally assumed that the vegetation limit on the beach is determined by soil salinity and salt spray, with sand burial and erosion being sometimes mentioned as alternative drivers (Houle, 1997; Maun, 1998; Gilbert et al., 2008; Konlechner et al., 2013). Salt and sand burial are also thought to drive species zonation from sea to dune (Oosting, 1945; Moreno-Casasola, 1986; Maun and Perumal, 1999; Wilson and Sykes, 1999; Kim and Yu, 2009), as species tolerance to soil salinity, salt spray and sand burial reported from controlled glasshouse conditions (Rozema et al., 1983; Sykes and Wilson, 1988, 1989, 1990) generally correlate with vegetation zonation observed in the field. Until now,



however, field experiments testing these hypotheses are lacking.

1.2.2 Dune development - Plant growth

Once plants have successfully established on the beach, they start affecting wind flow patterns, reducing wind speed around the vegetation (Hesp, 1981; Dong et al., 2004; Nordstrom, 2013). The reduction in wind speed results in sand deposition within and at the leeward side of the vegetation in the shadow zone (Hesp, 1981). The rate of the sand deposition depends on the sand supply by aeolian sand transport and the degree in which wind speed is reduced (Dong et al., 2008; Houser and Mathew, 2011).

Aeolian sand transport depends on weather conditions and beach morphology (Davidson-Arnott and Law, 1996; Saye et al., 2005; Delgado-Fernandez, 2010; de Vries et al., 2012). The main factor determining aeolian sand transport is the wind speed. If the wind speed is above a certain threshold, sand grains can be picked up by the wind and aeolian sand transport takes place (Bagnold, 1942; Arens, 1996). This threshold is higher when the grain size is larger and when the beach surface has a high soil moisture content (Arens, 1996; Davidson-Arnott et al., 2008; Delgado-Fernandez and Davidson-Arnott, 2011). Aeolian sand transport is also modified by beach width and slope, being largest for wide beaches (Jackson and Cooper, 1999; Dong et al., 2004; Aagaard et al., 2004; Anthony et al., 2006; Delgado-Fernandez, 2010) with a gentle slope (Bauer and Davidson-Arnott, 2002).

The reduction in wind speed within and at the lee side of the vegetation is related to vegetation density, and height (Hesp, 1981). It has been shown for foredunes and experimental wind tunnel studies that a dense vegetation reduces wind speed more than sparse vegetation, resulting in higher sand deposition (Buckley, 1987; Gillies et al., 2002; Dong et al., 2004; Burri et al., 2011; Suter-Burri et al., 2013; Keijsers et al., 2015). Also, a taller vegetation can disrupt the wind flow pattern at greater height, which may result in more sand deposition (Hesp, 1981). Indeed, the plant species colonizing the beach determines the very morphology of the dune formed: it has been reported that dunes vegetated with tall dense plant species (e.g. *Ammophila*) have a more hummocky peaked morphology, than dunes vegetated with lower, spreading, rhizomatous plants (e.g. *Spinifex*) (Hesp, 1989, 2002; Hacker et al., 2012; Zarnetske et al., 2012).

The rate of sand deposition interacts with plant growth. For typical dune building species (e.g. *Ammophila arenaria*, *A. brevifolata*, *Elytrigia juncea*) sand burial promotes the growth of the plant species up to a maximum, increasing sand deposition (Disraeli, 1984; Maun and Lapierre, 1984; van der Putten, 1989; Gilbert et al., 2008; Frosini et al., 2012; Qu et al., 2014; Nolet et al., 2017). The positive feedback between sand deposition and plant growth results in the formation and growth of embryo dunes. Indeed, the potential amount of sand captured over longer time periods seems related to a combination of morphological and physiological species traits (Zarnetske et al., 2012). As the vegetation captures more sand and dune volume increases, the differences in elevation also starts to affect wind flow pattern, creating preferential zones of sand erosion and deposition (Li et al., 2008; Barrineau and Ellis, 2013; Hesp and Smyth, 2017). The relative contribution of vegetation and dune size on sediment deposition and subsequently embryo dune development are not well known however, especially since most research on sediment deposition are wind tunnel or model studies.

1.2.3 Dune survival – Plant winter mortality

Erosion of dunes mainly takes place by the sea during winter (Montreuil et al., 2013), and is strongly determined by intensity and frequency of the storms (Guillén et al., 1999; Cooper et al., 2004; Claudino-Sales et al., 2008; Houser et al., 2008; Hacker et al., 2012; Haerens et al., 2012; Keijzers et al., 2014b). Storm intensity is determined by surge level, wave run-up and storm durations (Vellinga, 1982; van de Graaff, 1986). High intense storms occur when the sea water level is pushed above its expected level dictated by the tide by high (onshore) wind speeds, this increase is also known as the surge level. Further water level rise occurs by wave run-up which is the distance water is pushed further ashore by the breaking of the waves on the beach (Stockdon et al., 2006). Local conditions such as beach exposition to the main wind direction, beach width, beach slope, and the shelter of intertidal bars, further modify storm impact (Ruggiero et al., 2001; Anthony, 2013). For example, dissipative beaches with a low and gradual beach slope are less exposed to dune erosion, compared to reflective beaches with a steep beach slope (Short and Hesp, 1982; Wright and Short, 1984; Benavente et al., 2002; Ruggiero et al., 2004). Aside from storm intensity also storm frequency is important as it determines the time-period during which dunes can recover from storm erosion. Thus, more frequent, low-intensity storms could potentially cause the same amount of erosion as a single high-intensity storm (Ferreira, 2006; Pye and Blott, 2008; Gornish and Miller, 2010; Houser et al., 2015; Dissanayake et al., 2015).

Vegetation may modify storm impact by attenuating waves and speeding up recovery of dunes after storms (Carter, 1980; Danielsen et al., 2005; Koch et al., 2009; Zhang et al., 2012; Nobuhisa Kobayashi et al., 2013; Sigren et al., 2014; Blackmar et al., 2014; Feagin et al., 2015; Silva et al., 2016; Charbonneau et al., 2017). Foredunes differing in dune building species have been found to differ in storm erosion (Carter, 1980; Nobuhisa Kobayashi et al., 2013; Charbonneau et al., 2017). This effect has been contributed to differences in wave attenuation by differences in vegetation density based on wave flume experiments (Blackmar et al., 2014; Silva et al., 2016). The recovery of a foredune has been found to depends on the vegetation and storm intensity and frequency: dune recovery will probably be lower, when the vegetation has died or been eroded away (Vergiev et al., 2013; Charbonneau et al., 2017).

The effects of storms on foredune erosion have been well studied (Coch and Wolff, 1991; Claudino-Sales et al., 2008; Houser et al., 2008; Haerens et al., 2012; Anthony, 2013; Keijzers et al., 2014b; Silva et al., 2016) and modelled (Vellinga, 1982; van de Graaff, 1986; van Rijn, 2009), however studies on the effect of storm intensity and frequency on embryo dune erosion are scarce. This knowledge is especially important since embryo dunes occur at shorter distances from the sea where eroding forces can be extremely strong.

1.3 Building with Nature

Since the start of the Holocene, distinct phases of dune building and erosion have been identified in The Netherlands (Jelgersma and van Regteren Altena, 1969) and other coastal areas in Europe (Clemmensen et al., 2009). These phases are related to sea-level rise, changes in sand supply from rivers and changes in wind and wave climate (van Straaten, 1961; Clemmensen et al., 2009, 2014). After the end of the last ice age, sea-level rise resulted into transgression of the Dutch coastline eastward. Around 6000 BP however, the rise of the sea level relative to



the land slowed down to rates that are similar to 0.3 cm/y (Beets and van der Spek, 2000). Together with the large sediment surplus this was enough to result in regression of the coastline westward and the development of coastal dunes (Beets and van der Spek, 2000; Meulen et al., 2007). Nowadays, large parts of the Dutch coast have a sediment deficit, resulting into structural coastal erosion (Ruigt and Louisse 1991, Meulen et al. 2007) that is currently mitigated by sand nourishment, aimed at neutralising the sediment deficit.

Structural coastal erosion threatens approximately 70% of the all sandy beach environments (Bird, 1985; Feagin et al., 2005). Coastal erosion reduces beach width and increases dune erosion and inland flood risk for the landward situated areas (FitzGerald et al., 2008). Before the 1990's in the Netherlands, coastal erosion resulted into dune area loss of 0.2 km² per year (Ruigt and Louisse 1991). At this time, coastal management aimed at reducing beach erosion by the construction of groins and dune stabilisation by planting vegetation and building sand fences (MinV&W, 2000). However, these coastal erosion solutions were not effective. To halt the negative trend of dune erosion, the Dutch government adapted a policy of dynamic preservation in 1990 (MinV&W, 1990). This policy aimed to maintain the coastline at its 1990 position by applying sand nourishments. For sand nourishments, sand is extracted from the deep shore sea floor below -20 m depth and deposited on the nearshore, beach or dune (TAW 2002). Natural aeolian and marine sediment transport processes then redistribute the sand over the beach and land inwards towards the foredunes (Bakker et al., 2012; Arens et al., 2013).

Although sand nourishments have been proved effective in reducing beach and dune erosion (Hamm et al. 2002, van der Wal 2004, van Duin et al. 2004, Bakker et al. 2012, Arens et al. 2013), they have also to be applied every 4 to 5 years to be effective against erosion (TAW, 2002). The high nourishment frequency is costly and reduces the diversity of near shore benthic fauna, which needs 2 to 5 years to recover from sand nourishments (Dalfsen and Essink, 2001; Colosio et al., 2007; Baptist et al., 2009). One way to prolong the effects of sand nourishments that is currently being tested in the Netherlands is to apply 'mega-nourishments', a single large nourishment applied locally that are expected to exist for 20 years or more (Mulder and Tonnon, 2011; Stive et al., 2013; Temmerman et al., 2013; de Vries et al., 2016). It is expected that the longer lifetime will be beneficial for marine biodiversity by allowing longer recovery times. Furthermore, the larger area of the mega-nourishments is expected to be beneficial for terrestrial biodiversity as well by stimulating new dune development. So far the effects of mega-nourishments on new dune development are unknown.

In the Netherlands, three mega-nourishments have been implemented: I) Spanjaardsduin (Het Zuid-Hollands Landschap, 2017), II) the Sandmotor, or Sand Engine (Fig. 1.5B, Rijkswaterstaat and Provincie Zuid Holland, 2017), and III) the Hondsbossche Duinen (Fig. 1.5D, Hoogheemraadschap Hollands Noorderkwartier, 2017). Beside improving flood defence, each of these mega-nourishments have different additional goals, such as improving recreation and biodiversity. The goal of the Spanjaardsduin was to locally strengthen the coast at the location it is constructed, as well as increase biodiversity by the development of a dune slack behind the constructed foredune. Spanjaardsduin has been constructed in 2008 – 2009 with 7.5 million m³ of sand. The Spanjaardsduin follows the profile of a standard dissipative beach in the Netherlands. The goal of the Sandmotor is to improve the sediment budget of adjacent downstream beaches by gradually eroding over a decadal time-scale. Furthermore, the Sandmotor is also designed to improve terrestrial biodiversity and facilitate recreation, such as sun bathing,

swimming and kite surfing. The Sandmotor has been constructed in 2011 with 21.5 million m³ sand and was designed as a large hook-shaped peninsula with a lake (Fig. 1.5B). The beach of the Sandmotor is rather high, it ranges between 0 - 6 m NAP (where NAP is equal to the average sea level), which is high compared to 0 - 2 m NAP for an average beach. Hondsbossche Duinen has a similar goals as the Spanjaardsduin: locally strengthening the coast and increase biodiversity. The Hondsbossche Duinen was constructed in 2013 – 2015 with 35 million m³ of sand seaward from an old “hard defence” seawall (Fig. 1.5C&D).

In the future, mega-nourishments may be used more often to mitigate coastal erosion (Min-V&W 2015). Depending on their function, the design of the mega-nourishment may be different. However ecological consequences of these mega-nourishments on dune development are difficult to predict, especially since not much knowledge is available on the early development of dunes.

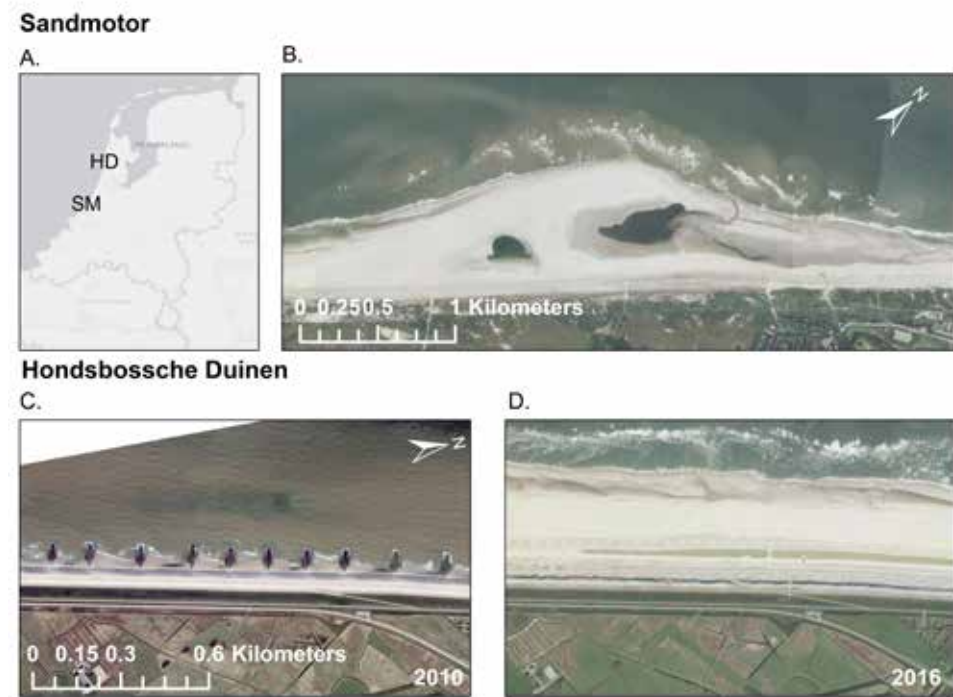


Figure 1.5. Overview of two largest mega-nourishments in the Netherlands. A) Approximate location of the Sandmotor and the Hondsbossche Duinen in the Netherlands, the Spanjaardsduin is seven kilometres to the south-west of the Sandmotor. B) The Sandmotor three years after the construction (Kadaster / Clyclomedia 2016). Clearly visible are the lake and the intertidal area. C) The Hondsbossche Duinen before the mega-nourishment in 2010, the coastline consisted of a hard defence seawall (then known as Hondsbossche Zeewering) (Kadaster / Clyclomedia 2010). D) The Hondsbossche Duinen after the mega-nourishment in 2014 (Kadaster / Clyclomedia 2016), the thin green lake is the area where green beach vegetation is expected to develop.



1.4 Thesis aim and outline

The above shows that the geomorphological processes that determine dune development are relatively well described, as well as factors that influence the vegetation, however there have hardly been any experimental studies on the interaction between the geomorphological and ecological processes on early dune development. Understanding the interaction between the roles of ecological and geomorphological processes in embryo dune development could lead to a well-founded basis for prediction of dune development and coastal safety.

In this thesis we aim to understand the interaction between the ecological and geomorphological processes during early dune development (Fig. 1.2, 1.3) using a combination of scientific approaches ranging from controlled experiments in the glasshouse and field to unmanned aerial vehicle monitoring of a large natural dune field. This thesis is conducted in the Netherlands, of which one-third of the country is below sea level (Louisse and van der Meulen, 1991), and the country relies on dunes for flood defence along most of its coastline. The thesis is organised around five chapters outlined below. The main research questions are summarised in Table 1.1.

Chapter 2 explores the factors that determine the vegetation limit of dune building species on the beach. We hypothesised that salt stress and storm erosion determine the vegetation limit on the beach. This hypothesis was tested with a greenhouse experiment and complementary field transplant experiment with two dune building grasses *Ammophila arenaria* and *Elytrigia juncea*. In the greenhouse experiment we tested the effect of soil salinity and salt spray on the growth and photosynthesis of *A. arenaria* and *E. juncea*. In the field experiment we transplanted plants and monitored soil salinity along a transect from the sea to foredune. Combining the greenhouse and field experiments allowed us to assess whether soil salinity and/or salt spray determined the vegetation limit on the beach. The field experiment also gave insight into the effect of storms on plant survival.

Chapter 3 focusses on the boundary conditions for embryo dune development over a 30 year time-period. We hypothesised that embryo dunes develop on wide beaches with a high sand supply. Furthermore we expected that precipitation would have a positive effect on plant growth and subsequent embryo dune development, whereas storms would have a negative effect on embryo dune development. We tested this hypothesis using a time-series analysis of aerial photographs and combined them with geomorphological monitoring data. These data allowed us to examine the presence and area of embryo dunes in relation to beach width and tidal range, and relate changes in embryo dune area to meteorological conditions.

Chapter 4 explores the relative contribution of dune size and vegetation to growth and erosion of single dunes. We hypothesised that net dune growth would be highest for large dunes with high vegetation density. We monitored dune growth and erosion with an unmanned aerial vehicle over an area of 200 m x 400 m. We related changes in dune volume over a summer and winter period to dune size and vegetation density.

Chapter 5 explores the relationship between embryo dunes and green beach vegetation. We hypothesised that embryo dunes would create sheltered conditions in which species rich green beach vegetation can develop. We measured geomorphology and species composition of eleven transects on the beach of the Dutch barrier island Schiermonnikoog over a time-pe-

riod of ten years. We related the geomorphology to environmental conditions and tested if plant species richness and species turnover at the green beach were influenced by the geomorphological setting and abiotic conditions.

Chapter 6 compares the results of previous chapters with additional measurements and monitoring data on two mega-nourishments and explores how the design of a mega-nourishment can be optimised for new dune development. The chapter ends with future research challenges.

Table 1.1. Research questions and hypothesis and the chapter the research question is answered

Research question	Hypothesis	Chapter
What determines the vegetation limit and growth on the beach?	We expect that soil salinity, salt spray, and storms determine the vegetation limit on the beach. We expect that precipitation determines plant growth.	2, 3
What are the boundary conditions for embryo dune development?	Embryo dunes form on wide beaches with a high sand supply. Storm will have a negative effect on embryo dune development by eroding dunes.	3
How do dune size and vegetation contribute to individual dune growth and erosion?	We expected dune growth to be the highest for larger dunes with a highest vegetation density. Dune erosion is the relatively the highest for smaller dunes and with a low vegetation density.	4
How does embryo dune development contribute to the development of green beach vegetation?	Embryo dune development will create sheltered conditions. Landward of these embryo dunes species rich green beach vegetation can develop, which benefits from the embryo dunes since they reduce sand burial and create a fresh water lens.	5
How can the design of mega-nourishment be optimised for new dune development?	The design determines the vegetation growth and dune erosion. A mega-nourishment that has a high elevation reduces storm erosion, but also reduces germination of dune building species due to low water availability.	6



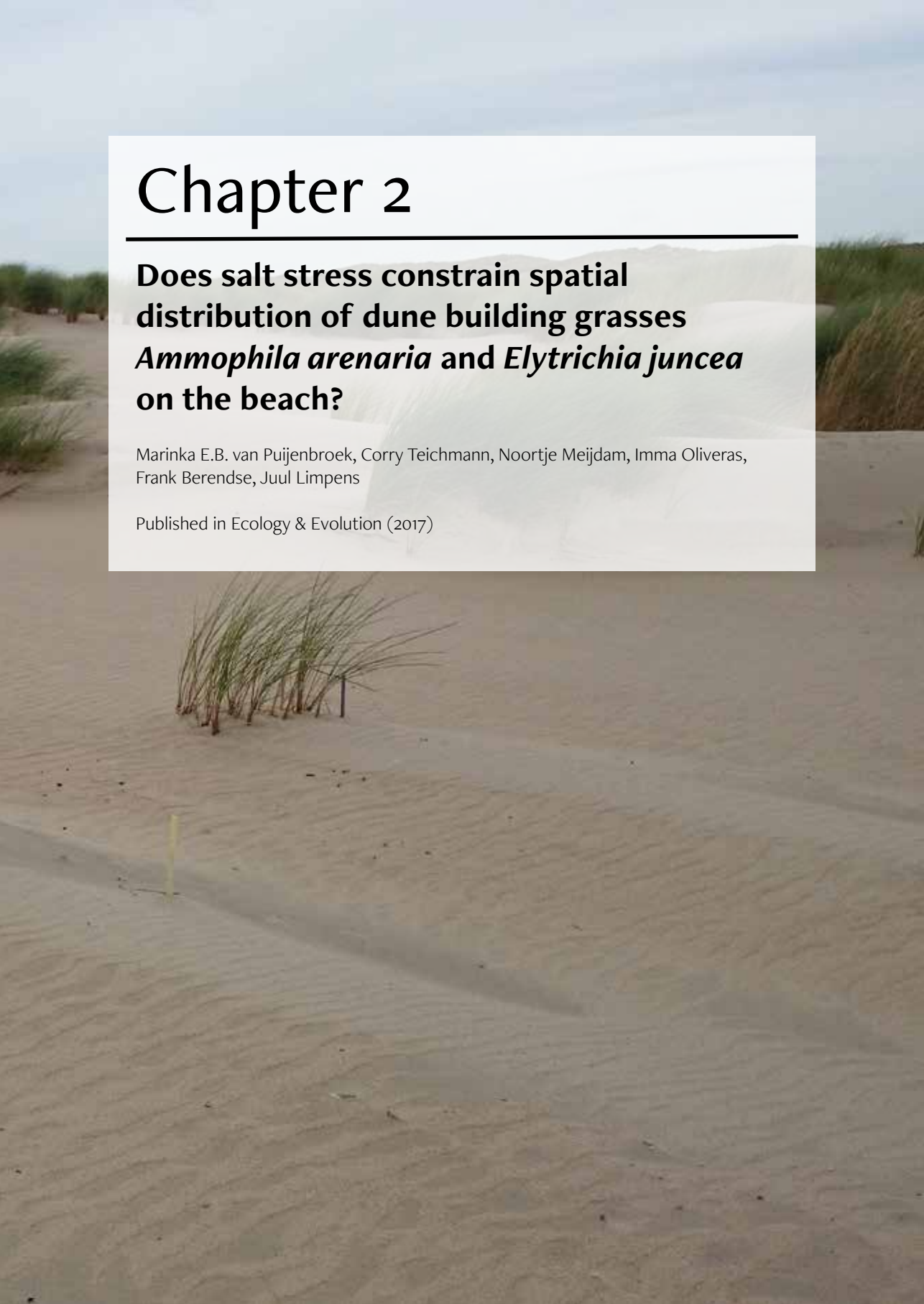


Chapter 2

Does salt stress constrain spatial distribution of dune building grasses *Ammophila arenaria* and *Elytrichia juncea* on the beach?

Marinka E.B. van Puijenbroek, Corry Teichmann, Noortje Meijdam, Imma Oliveras, Frank Berendse, Juul Limpens

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2.1 Abstract

Rising sea levels threaten coastal safety by increasing the risk of flooding. Coastal dunes provide a natural form of coastal protection. Understanding drivers that constrain early development of dunes is necessary to assess if dune development may keep pace with sea-level rise. In this study we explored to what extent salt stress experienced by dune building plant species constrains their spatial distribution at the Dutch sandy coast.

We conducted a field-transplantation experiment and a glasshouse experiment with two dune building grasses *Ammophila arenaria* and *Elytrigia juncea*. In the field we measured salinity and monitored growth of transplanted grasses in four vegetation zones: I) non-vegetated beach, II) *E. juncea* occurring, III) both species co-occurring and IV) *A. arenaria* dominant. In the glasshouse we subjected the two species to six soil salinity treatments, with and without salt spray. We monitored biomass, photosynthesis, leaf sodium and nutrient concentrations over a growing season.

The vegetation zones were weakly associated with summer soil salinity; zone I and II were significantly more saline than zones III and IV. *Ammophila arenaria* performed equally (zone II) or better (zones III, IV) than *E. juncea* suggesting soil salinity did not limit species performance. Both species showed severe winter mortality. In the glasshouse, *A. arenaria* biomass decreased linearly with soil salinity, presumably as a result of osmotic stress. *Elytrigia juncea* showed a non-linear response to soil salinity with an optimum at 0.75‰ soil salinity.

Our findings suggest that soil salinity stress either takes place in winter, or that development of vegetated dunes is less sensitive to soil salinity than hitherto expected.



2.2 Introduction

Sea levels are predicted to rise with 26 – 82 cm in this century, due to climate change (IPCC, 2014). Rising sea levels may lead to higher frequency and intensity of flooding, emphasizing the need for flexible coastal protection (IPCC, 2014; KMNI and PBL, 2015). Coastal dunes provide such a flexible, natural form of coastal protection, while also providing other important ecosystem services such as fresh water supply, recreation and biodiversity conservation (Everard et al., 2010). Understanding the factors that constrain early dune development is essential to predict if natural coastal protection can keep pace with the rising sea level.

Coastal dune formation is the result of vegetation growth and aeolian processes (Hesp 2002). Non-vegetated dunes can form by aeolian transport of sand, but these dunes are transient and will disappear when the wind direction changes. Once vegetation established on the beach, it captures wind-blown sand and forms an embryo dune (also known as an incipient dune) (Hesp, 2002; Maun, 2009; Zarnetske et al., 2012). These vegetated embryo dunes may grow into fore-dunes that are known for their coastal protection function (Maun, 2009). As vegetation plays a key role in capturing and retaining sand, the position, and rate of dune development on the beach are constrained by vegetation establishment and growth (Keijzers et al., 2015; Zarnetske et al., 2012).

Vegetation growth on the beach is limited by the harsh environmental conditions (Maun, 2009), including high salinity (Maun, 1994). Plants experience the saline conditions both aboveground by salt spray and belowground by salt concentration (soil salinity). Both salt spray and soil salinity decrease from beach towards dunes (Gooding, 1947). Salt spray on the beach strongly depends on wind speed and precipitation (Boyce, 1954), while soil salinity is influenced by inundation by seawater, saline groundwater, salt spray, precipitation, moisture content and soil texture (Martin, 1959). Salt spray and soil salinity can disrupt plant–water relations, promote tissue necrosis and leaf loss, reduce photosynthesis, and reduce growth in exposed plants (Boyce, 1954; Breckle, 2002; Munns and Termaat, 1986). Consequently, these factors can have a great impact on the distribution of plant species, and thus potential dune formation, on the beach.

In Western Europe the main two dune building species are *Ammophila arenaria* (L.) Link. and *Elytrigia juncea* (Simonet & Guin.). *Ammophila arenaria* has been introduced in many countries, because of its excellent dune building capabilities (Konlechner et al., 2013). *Ammophila arenaria* creates higher, more hummocky peaked dunes (Hesp, 2002), which can easily withstand flooding (Seabloom et al., 2013). *Elytrigia juncea* creates lower broader dunes and the distribution is more restricted to Europe. *Elytrigia juncea* usually grows closer to the sea than *A. arenaria* (Bakker, 1976). It is generally assumed that dune building starts with *E. juncea* and, once when a fresh water lens is formed, *A. arenaria* plants establish and over time outcompete *E. juncea* (Westhoff et al., 1970). The order in which the grass species occur on the beach corresponds with their salinity tolerance investigated under controlled conditions (Rozema et al., 1985; Sykes and Wilson, 1989, 1988, Appendix 1), suggesting dune building is constrained by soil salinity. However, studies that actually measured both vegetation distribution and environmental conditions in the field (de Jong, 1979; Maun, 2009), conclude that soil salinity on the beach is lower than generally assumed and is unlikely to limit plant growth on the beach. It is yet unclear what explains the discrepancy between spatial plant distribution on the beach, salinity-tolerance

ranges measured in short-term-physiological studies and the actual salinity measured on the beach. Did the physiological studies (Rozema et al., 1985; Sykes and Wilson, 1989, 1988) underestimate the cumulative effect of salt stress (Munns, 2002) due to their short duration (4-10 weeks) or can it be that interactive effects of salt spray and soil salinity explains why plants did not occur under the relatively low soil salinity measured in the field?

In this study we try to bridge the gap between field and glasshouse studies by conducting a field experiment with *A. arenaria* and *E. juncea* transplanted into different vegetation zones and by comparing the field response with a full factorial glasshouse experiment where we subjected the two species to different soil salinities with and without salt spray. Specifically, we attempted to answer the following research questions: 1) what are the interactive effects of salt spray and soil salinity stress on growth of *E. juncea* and *A. arenaria*? 2) Which physiological mechanisms (osmotic stress, ionic stress and nutrient limitation) can explain their biomass response? 3) Does their response to salt spray and soil salinity explain the growth of *A. arenaria* and *E. juncea* in the field?

2.3 Methods

2.3.1 Field transplantation experiment

We conducted a field experiment to assess the plant growth of *Ammophila arenaria* and *Elytrigia juncea* along five transects from beach to dune (Appendix 2) on the Hors on Texel, a barrier island in the Netherlands (coordinates: 52°59'51.97"N, 4°44'04.83"E). The Hors is a wide dissipative beach with much hydrodynamic reworking of the sand, which results in a high transport potential and opportunity for dunes to develop. Due to relatively storm free periods, many dunes have been able to develop on the Hors the last 20 years. Within each transect we selected four locations representing different stages of dune development, zone I) the non-vegetated zone above the mean high water line, 0.78 m – 1.1 m NAP (NAP refers to Amsterdam Ordnance Datum, which is equal to mean sea level near Amsterdam); II) zone with *E. juncea* occurring, 1.17 m – 1.19 m NAP; III) zone with both species co-occurring, 1.42 m – 1.94 m NAP; IV) zone where *A. arenaria* is dominant, 2.06 m – 3.17 m NAP. At each location we established six plots of 50 cm x 50 cm. The minimum distance between the plots was 2 m. Three treatments were randomly assigned to the plots: mono-culture of *A. arenaria*, mono-culture of *E. juncea*, and mixed culture of *A. arenaria* and *E. juncea*. In each plot we planted 20 plants, in the mixed culture we planted 10 plants of each species. The plants, consisting of one shoot, were collected from the same site and stored outside in plastic bags with moist sand for a maximum of two weeks until planting.

After planting, we standardised the leaf height between species and plots by clipping the leaves until the leaves were 3 cm long. We established the experiment in the end of March 2014. We measured the number of leaves for a fixed subplot of 30x30 cm within each plot in May - October 2014, and August 2015.



2.3.2 Soil salinity measurements in the field

We measured the soil salinities at the locations where we established our field experiment. At each location we took soil samples from four depths (5, 10, 25 & 50 cm). The samples were taken back to the lab and dried at 105 °C. The dried soil samples were diluted on a 1:5 mass basis with distilled water. The electrical conductivity of this solution was measured and multiplied with a factor 17 to derive the EC at saturated conditions (EC_e) (Shaw, 1994). When there was groundwater at the sampling depth, we measured groundwater salinity directly in the field with the same instrument as used in the lab. The groundwater depth ranged between 44 cm to > 75 cm below beach surface, depending on location and transect. The measurements were performed on 12, 13 and 14 August 2015. While 12 and 13 August were dry, there was precipitation (15mm) in the early morning of the 14 August which slightly reduced the soil salinity of one of the five transects, increasing the error bars per location.

To explore whether the soil salinity on Texel is comparable to other beaches along the Dutch coast, we complemented our data with soil salinity measurements on two additional beaches: the Hondsbossche duinen, in North Holland (coordinates: 52°44'34.31"N, 4°38'33.14"E; date: September 2015) and on Terschelling, another barrier island (coordinates: 53°24'30.31"N, 5°17'29.25"E, measured in June, August, and November 2015). Both beaches are dissipative beaches, however they have a smaller beach width compared to the Hors. The Hondsbossche duinen is an artificial created mega-nourishment and has the smallest beach width, whereas the beach on Terschelling has a much wider beach width. On Hondsbossche duinen we measured soil salinity at the upper beach and dune foot, 1.9 m – 2.5 m NAP, and on Terschelling we measured at the upper beach, 1.9 – 2.3 m NAP.

The summer of 2014 was warmer and wetter compared to previous years, ideal conditions for plant growth (van Puijenbroek et al., 2017a). The average temperature in June & July was 17.40 °C and the precipitation over the growing season was 361 mm (KNMI, 2015). Over the winter there were two major storms and highest water level was 248 cm NAP, this water level occurs once every two years. This water level is higher than most of our plot locations: only 3 plot locations in zone IV had a higher elevation. However it is likely that also these locations became inundated due to wave run-up, as suggested by the position of the tide-mark. The storm eroded part of the beach, the beach width decreased, but beach elevation did not change.

2.3.3 Glasshouse experiment

2.3.3.1 Plant material

We collected 600 rhizomes equally divided over both *A. arenaria* and *E. juncea*, from the vicinity of our field transplantation experiment on the Hors, Texel. The rhizomes were stored in plastic bags with moist sand in a fridge (c. 4 °C) for three weeks until planting. Just before planting we standardized the rhizomes by cutting all of them to similar length (20 cm), it was not possible to standardize the number of nodes on each rhizome. The range in node number was for *A. arenaria* 6 – 11 and for *E. juncea* 8 – 24. The rhizomes were planted in 196 experimental pots (10 l volume) filled with 14 kg soil which consisted of a mixture of (calcareous) sandy river soil and organic matter (3:1 volume mixture) and 1 litre of water. Three rhizomes of one species were planted in each experimental pot, about 5 cm below the soil surface. All pots were

watered every week to keep the soil moisture content constant, no additional nutrients were provided during this initial phase. Shoots emerged from the rhizomes 1 to 4 weeks after the planting. Four weeks after the planting of the rhizomes, treatments were randomly assigned to all pots where tillers had developed. We ended up with 192 pots for the main experiment (see experimental design below), leaving four pots with living tillers to verify the experimental treatments. The glasshouse climate for both preparation phase and experiment was set to 20°C at day and 15°C at night, standard humidity (about 50 %). Natural light was supplemented by SON-T 400W lamps to guarantee 16 hours day length.

2.3.3.2 Experimental design

A total of 192 experimental pots were used in this experiment with a full factorial design of two factors: soil salinity (six different levels) and salt spray (with/without). For each treatment we had eight replicates, which were distributed over eight replicate blocks. Within each block the treatments were repeated for each species: *A. arenaria* and *E. juncea*. The position of the experimental blocks was randomized three times during the experiment to control for potential variation in light conditions within the glasshouse. For the salt spray treatment the plants were initially sprayed five times from all sides at 70 cm distance with either distilled water or water with 3.5% NaCl concentration (Sykes and Wilson, 1988). After 14 weeks we increased the spraying treatment by spraying ten times from all sides, to ensure that all leaves were sprayed. While spraying, waterproof cardboard was used to shield the other pots from the spraying. For the soil salinity treatment six different saline solutions were prepared with 0%, 0.25%, 0.5%, 0.75%, 1.0%, and 1.5% salt concentration (corresponding to 0, 42.8, 85.6, 128, 171, 214 mM NaCl, and 0.28, 6.0, 11.1, 16.2, 20.2, 33.90 mS/cm EC). The soil salinity treatments were based on the range of soil salinities we found in the field. To ensure there was no effect of salt spray on the soil salinity we applied once every week first the salt spray treatment and then the soil salinity treatment. Since the provided salt can accumulate in the soil, excess saline solution was supplied to the experimental pots to a set weight (16 kg). At this pot weight about one third of the saline solution drained from the pots, preventing accumulation of salt at concentrations higher than the treatment (Poorter et al., 2012; Sykes and Wilson, 1989). The saline solution was directly applied to the soil, to prevent a change in the salt spray on the leaves. Nutrients were added to the different saline solutions in the form of 2.5% Hoagland's solution, to ensure sufficient nutrients for plant growth. This low amount of nutrients represents the field conditions, since dunes are very nutrient poor (Maun, 2009). The plants were harvested after 25 weeks of the start of the treatments, which is more or less similar to the length of the growing season of the two dune building species.

2.3.3.3 Plant growth

Plant growth was measured by counting the number of shoots, leaves (alive, dead) and the height of longest leaf for each experimental pot. Shoots were defined as an individual stem with leaves. Leaves were considered dead when they had no green tissue left. All variables were measured weekly during the first 12 weeks of the experiment and again during week 18 of the experiment. For nine out of the 192 pots all plants died during the experiment, all corresponding to *A. arenaria*. No pots with *E. juncea* experienced mortality, however one experimental pot was planted erroneously with *A. arenaria* and was excluded from the analysis.



We harvested the experiment per block by collecting the whole plant after which we divided it into two fractions: the shoot (including both dead and alive leaves) and root biomass. The roots were carefully separated from the soil by gently rinsing them with flowing tap water. Biomass of both fractions was determined after drying the material at 40° C for three days.

2.3.3.4 Measurements of gas exchange and stomatal conductance

We measured CO₂ gas exchange and stomatal conductance to explore the mechanisms behind the biomass response. From week 21 to week 24 (May 1 – 21 2015), we measured the leaf photosynthesis (CO₂ net exchange) with a cross-calibrated LI-6400 portable photosynthesis system (LI-Cor, Inc, Lincoln, NE, USA) from single leaves of all plants in four randomly selected blocks. The CO₂ net exchange (Asat) was measured under ambient CO₂ concentrations of 400 ppm and photosynthetically active radiation (PAR) flux density at or near 2000 μmol m⁻² s⁻¹. Measurements were made from 08:30 to 12:00 h during the day (CET time) to minimise the risk of declines in gas-exchange rate as a result of stomatal closure, source–sink inhibition or other causes during the afternoon (Pérez-Harguindeguy et al. 2013).

The CO₂ net exchange (Asat) and stomatal conductance were calculated with the following equations from Caemmerer & Farquhar (1981).

$$1. \quad \text{Asat} = (F(C_r - C_s)/100S) - C_s E$$

$$2. \quad g_{sw} = 1/((1/g_{tw}) - (k_f/g_{bw}))$$

Asat is the photosynthesis in μmol m⁻² s⁻¹, F molar flow rate of air (μmol s⁻¹), C_r and C_s are the sample and reference CO₂ concentrations (μmol CO₂ mol air⁻¹), S is leaf area (cm²) and E is the transpiration (mol H₂O m⁻² s⁻¹). g_{sw} is the stomatal conductance in mol H₂O m⁻² s⁻¹, g_{tw} is the total conductance (mol H₂O m⁻² s⁻¹), g_{bw} the boundary layer conductance (mol H₂O m⁻² s⁻¹) and k_f is calculated by k_f = (K² + 1)/(K+1)², where K is the stomatal ratio (estimate of the ratio of stomatal conductance of one side to the leaf to the other side).

Water use efficiency (WUE) was calculated as the ratio between the net CO₂ exchange and the stomatal conductance. During the harvest we measured the Specific Leaf Area (SLA), for the four blocks we measured the single leaf gas exchange. The SLA was measured by scanning five fresh undamaged leaves with a leaf scanner (Li-3100 Area Meter) and weighing the dried leaves (dried at 40°). For each of these five leaves we measured the leaf thickness.

2.3.3.5 Plant chemical analyses

We measured the concentrations of nitrogen (N), phosphor (P), potassium (K) and sodium (Na) in the harvested shoot biomass of all plants in a subset of four randomly selected blocks. The concentrations of plant nutrients N, P and K were measured to explore if nutrient limitation could explain the plant biomass at higher soil salinity (Colmer and Flowers, 2008; Rozema et al., 1983). Concentrations of Na were measured to explore whether ionic stress played a role in explaining the treatment effect (Munns and Termaat, 1986). The harvested shoot biomass, which includes dead and alive biomass, was first gently rinsed with distilled water to remove any residual salt spray. The dried shoot material (70 °C) was pulverised and digested with H₂SO₄, salicylic acid, H₂O₂ and selenium. Subsequently N and P concentrations were measured

colorimetrically using a continuous flow analyser (SKALAR SAN plus system, The Netherlands). K and Na were measured by flame atomic emission spectroscopy (AES) (Walinga et al., 1989).

2.3.3.6 Soil and leaf salinity in experimental pots

To verify that soil salinity at the end of the experiment still matched the treatments we collected soil samples from the experimental pots of four randomly selected blocks and measured the Electrical conductivity (EC) and calculated the Electrical conductivity at saturated conditions (EC_e), using the same methods as for the field samples.

To test how the salt spray treatment affected leaf salinity, we used four planted test pots, which we once sprayed with water which contained 3.5% NaCl. The plants in these test pots were harvested and the leaves were washed with 500 ml distilled water. The difference between the EC of the distilled water before and after the plants were washed was used to calculate the EC on the leaves by correcting it for leaf area. The EC on the leaves after spraying once was 131.1 $\mu\text{S}/\text{cm}$. This value is higher than fresh water levels and since we did not wash the leaves the salinity did accumulated over time.

2.3.4 Statistical analysis

2.3.4.1 Field experiment

Data from the two sub-replicates per location in the field were averaged, to avoid pseudo replication. We analysed the number of living leaves with a linear mixed model, where we account for the repeated measure by using plot number as a random intercept, with culture (mono or mixed), species, zone and month as explanatory variables. We calculated the Chi-squared values with an ANOVA type III SS (Fox and Weisberg, 2011), as it is robust for unequal sample sizes (Quinn and Keough, 2006). We corrected for the number of plants that were planted at the start of the experiment. The unequal sample sizes were a result of anthropogenic disturbance. All plants in the non-vegetated zone (zone I) were pulled out of the plots shortly after the start from the field experiment, preventing inclusion in our analyses. Two additional plots in the zone with only *E. juncea* (zone II) were destroyed in September 2014. We excluded these plots from this time point onward.

2.3.4.2 Glasshouse experiment

For the glasshouse experiment, the numbers of living leaves, tillers and maximum plant height were analysed with a generalised linear model with a negative binominal distribution, and a normal distribution for maximum plant height (Quinn and Keough, 2006). We used species, time, soil salinity and salt spray treatment as explanatory variables. The total biomass, shoot biomass, root biomass and shoot to root ratio was analysed with an ANOVA and with species, soil salinity and salt spray treatments as explanatory variables. Between the different treatments significant differences were calculated by using the Tukey HSD test (Hothorn et al., 2008).

The net CO₂ exchange and stomatal conductance were analysed with an ANOVA type III. Sample sizes ranged between one to six per treatment, because we discarded replicates with negative intercellular CO₂ concentrations from the analyses. We used species, soil salinity



and salt spray treatments as explanatory variables. The N, P, Na and K concentrations in the leaves were analysed with an ANOVA and species, salinity and salt spray treatment were used as explanatory variables.

We did not find any significant difference between the different blocks of the glasshouse experiment. The normality of the data and homogeneity of variance were checked graphically. Variable deviating from normality were transformed with a natural logarithm (stomatal conductance, water use efficiency, Na concentrations, number of living leaves in the field) or a square root (field soil salinity and the salinity in the pots) before analysis. To facilitate interpretation the figures are based on non-transformed data. All statistical analyses were performed with the program R 3.1 (R Core Team, 2016).

2.4 Results

2.4.1 Soil salinity in the field

On Texel, the salinity of both groundwater and soil increased with proximity to the sea ($F_{89,5} = 339.75, p < 0.001$), but were only weakly related to vegetation zones (Fig. 2.1). Zones I and II were saltier than zones III and IV. The salinity of the groundwater was 32.74 ± 6.12 mS/cm (means \pm SE) in zone I and 5.63 ± 1.51 mS/cm in zone III ($F_{11,5} = 19.96, p > 0.001$). Soil salinity increased significantly with depth in zones I and II ($F_{89,5} = 9.47, p < 0.001$), whereas soil salinity was hardly affected by depth in zones III and IV (Fig. 1). Soil salinity on Texel was significantly higher than on the narrower beaches of the Hondsbossche duinen or Terschelling, irrespective of vegetation zone.

2.4.2 Plant growth in field experiment

Plant growth depended on time-of-year, species and zone. The number of leaves increased linearly after planting, levelled off at the end of the 2014 growing season and declined over 2015, irrespective of zone and species. Species did show a different growth pattern over the zones (Fig. 2.2), leading to a significant zone*species interaction (zone*species: $F_{2,338} = 11.06, p < 0.004$). *Ammophila arenaria* generally performed least in zone II, producing fewer leaves over summer and regrowing less after winter than in zones III and IV. *Elytrigia juncea* did not show a clear growth response to zonation: *E. juncea* performed equally well in all zones over summer, but only survived in zone III. There was no significant difference between the mixed and mono culture plots (mono vs mixed *A. arenaria*: 1.87 ± 0.020 vs 1.60 ± 0.017 leaves/planted plant, *E. juncea*: 0.91 ± 0.0095 vs 0.60 ± 0.0064 leaves/planted plant, species * mono/mixed culture: $F_{1,338} = 1.43, p = 0.23$, Appendix 3).

2.4.3 Glasshouse experiment

The treatments resulted in the desired soil salinity concentrations (Appendix 4), irrespective of salt spray ($F_{77,1} = 0.12, p = 0.73$) and species ($F_{77,1} = 0.25, p = 0.62$). Soil salinity concentrations differed significantly between treatments, with soil salinity measured in the pots corresponding to the soil salinity treatment ($F_{77,5} = 91.19, p < 0.001$). Soil salinity in the treatments was within the same order of magnitude as the salinity measured in the field (Fig. 2.1). The 0% salinity treatment corresponded to the soil salinity measured in zones III and IV (Fig. 2.1), whereas the

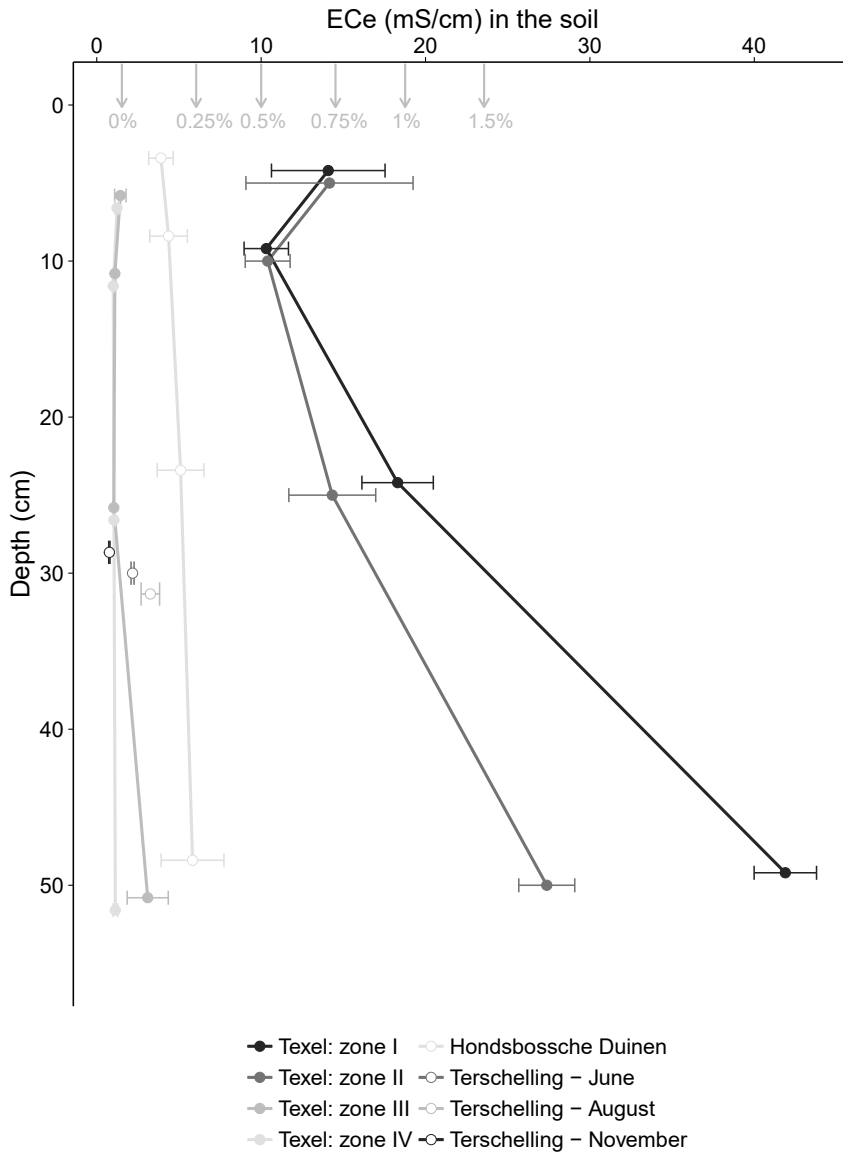


Figure 2.1. The ECe (Electrical conductivity at saturated soil) for different depths in the soil. Closed circles indicate the ECe at different zones at the Hors, Texel. Open circles indicate the ECe at beaches on the Hondsbosse duinen and on Terschelling. Points show the mean and the error bars the standard error. The arrows and the percentages show the ECe value of the specific soil salinity treatment. The EC of the seawater is 50 mS/cm. Zone I is the non-vegetated zone, zone II the zone with only *E. juncea* occurring, zone III the zone with both *E. juncea* and *A. arenaria*, and in zone IV *A. arenaria* is dominant.



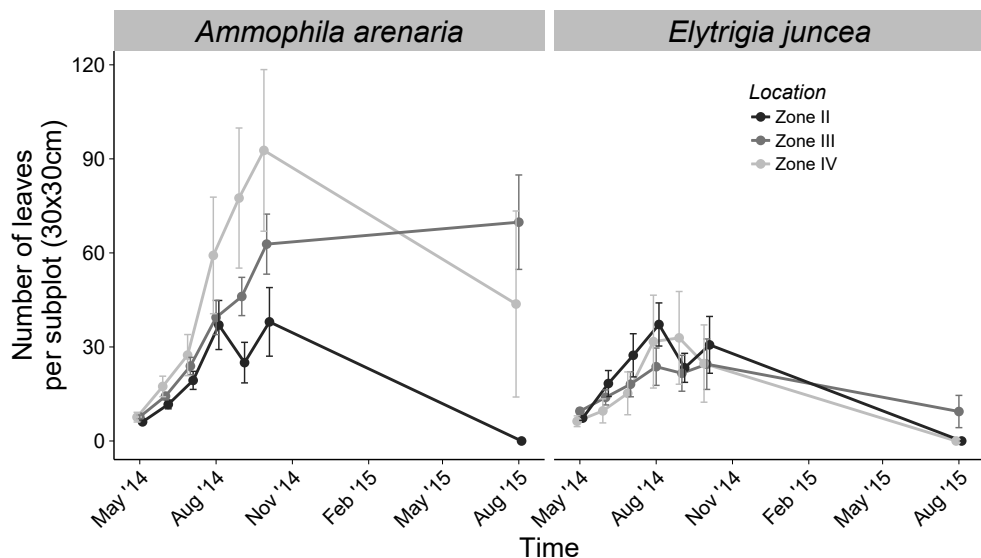


Figure 2.2. The number of living leaves for *A. arenaria* and *E. juncea* per subplot of 30cm x 30cm within a plot at the different zones at the Hors, Texel, over a period of 15 months. The points are means and the error bars are standard errors. Zone II is the zone with only *E. juncea* occurring, zone III the zone with both *E. juncea* and *A. arenaria* and in zone IV *A. arenaria* is dominant.

soil salinity for the 0.5 – 1 % soil salinity treatments corresponded to the salinity measured between 5 – 25 cm depth for zones I and II. The highest soil salinity treatment (1.5%) was found only deeper in the soil (>25 cm) in zones I and II.

2.4.3.1 Impacts on plant growth and biomass

Salt spray had neutral to positive effects on species performance. Salt spray significantly increase the number of leaves and tillers and the maximum plant height for *A. arenaria* (Table 2.1), but did not affect shoot, root, total biomass and fraction of dead leaves of *A. arenaria* and *E. juncea* (Table 2.2). The total biomass for *A. arenaria* was 4.71 ± 0.42 g/pot without salt spray and 5.21 ± 0.45 g/pot with salt spray, whereas it was 8.28 ± 0.40 g/pot and 8.19 ± 0.41 for *E. juncea*. Salt spray interacted with soil salinity resulting in higher number of leaves for the lowest soil salinities (0%, 0.25%) for both species: in week 18 the number of leaves of *A. arenaria* for the 0% soil salinity treatment was 2.38 ± 0.42 without salt spray and 3.25 ± 0.31 with salt spray. Salt spray did not affect plant mortality: of the nine pots where all plants died, five received salt spray. We found no significant interaction effect between salt spray treatment and soil salinity treatment for maximum height, total-, shoot- and root biomass (Table 2.1 & 2.2).

Soil salinity significantly affected plant performance, with the effect strongly depending on species. For *A. arenaria* we found a significant negative effect of soil salinity on the shoot, root and total biomass, number of living leaves (Fig. 2.3 & 2.4), tillers and maximum height (Table 2.1 & 2.2). Treatment effects on living leaves became significant from 50 days onward (Fig. 2.3).

Plant biomass at harvest was negatively related to soil salinity. Biomass decreased by 34% between the 0% and 0.25% treatments. The decrease in biomass was mainly due to the decrease in shoot biomass (Fig. 2.4C). Although the root biomass clearly decreased between 0% and 0.25% salinity, the root biomass did not further decrease at higher soil salinity levels (Fig. 2.4D). Consequently, the decrease of shoot biomass resulted into a lower shoot to root ratio at high

Table 2.1. Statistical models for the plant growth during the greenhouse experiment, with as response variables number of leaves, number of shoots and maximum plant height. The number of leaves and the number of tillers were analysed with a generalised linear model with negative binomial distribution and the deviance (Chi-square test) is shown for the factors. Maximum plant height is analysed with an ANOVA and the F-values are shown.

Factor	df	Number of leaves	Number of shoots	Maximum plant height
Species	1	3,130.82***	717.35***	9.55**
Salinity	5	24.82***	2,405.29***	9.07***
Salt Spray	1	35.30***	18.85***	4.77*
Days	1	1015.39***	66.25***	535.21***
Species x Salinity	5	390.56***	163.92***	11.26***
Species x Salt Spray	1	29.81***	15.14***	5.02*
Species x Days	1	86.61***	110.51***	31.94***
Salinity x Salt Spray	5	132.20***	74.05***	1.11
Salinity x Days	5	22.28***	19.09**	7.25***
Salt spray x Days	1	0.15	0.39	0.075
MSresiduals	2074	-	-	188

df = Degrees of freedom. The asterisk denotes the level of significance (* $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$).

soil salinity (1.0%, 1.5%) (Fig. 2.4B). The fraction of dead leaves increased with soil salinity for *A. arenaria* ($F_{1196,5} = 4.48$, $p < 0.001$), the fraction of dead leaves from 0.17 ± 0.020 alive/dead in the control treatment to 0.39 ± 0.043 alive/dead in the highest soil salinity treatment. Mortality of all *A. arenaria* plants occurred in nine experimental pots (9.4%). Plant mortality for the highest soil salinity treatment was 43.8% (seven out of nine pots that had been subjected to the 1.5% soil salinity treatment). The other two experimental pots were with 0.75% soil salinity treatment and 0.5% soil salinity treatment. Increased soil salinity resulted into smaller and thinner, yet denser leaves, significantly decreasing SLA ($F_{77,5} = 6.54$, $p < 0.001$), from 39.58 ± 3.04 cm/g in the control treatment to 13.99 ± 5.70 cm/g in the highest soil salinity treatment. Leaf thickness ranged from 0.41 ± 0.017 mm in the control treatment to 0.18 ± 0.063 mm in the highest salinity treatment ($F_{37,5} = 5.72$, $p < 0.001$). The ratio between dead and total shoot biomass was significantly affected by the soil salinity treatment ($F_{81,5} = 15.47$, $p < 0.001$), the ratio between dead and total shoot biomass was 0.08 ± 0.048 g/g for the control treatment and 0.50 ± 0.094 g/g for the highest soil salinity treatment. We found no significant relationship between the dead leaves biomass and Na concentration ($F_{44} = 1.33$, $p = 0.25$).



Table 2.2. ANOVA model for the total biomass, shoot/root ratio, shoot biomass, root biomass. The values shown are the F values.

Factor	df	Total Biomass	S/R ratio	Shoot biomass	Root biomass
Species	1	96.73***	109.00***	174.39***	15.23***
Salinity	5	36.47***	0.81	7.87***	11.85***
Salt Spray	1	0.39	0.00	0.14	0.48
Species x Salinity	5	35.91***	44.58***	10.89***	9.79***
Species x Salt Spray	1	0.55	1.03	0.79	0.50
Salinity x Salt Spray	5	0.07	0.01	0.68	0.78
MSresiduals/SSresiduals	172	5.77	0.12	1.9	1.47

df = Degrees of freedom. The asterisk denotes the level of significance (***) $p < 0.001$.

In contrast to *A. arenaria*, increasing soil salinity generally improved performance of *E. juncea*. The number of living leaves, tillers and maximum plant height increased linearly with soil salinity (Table 2.1 & Fig. 2.3), and the fraction of dead leaves was higher at low salinity (0.48 ± 0.022 alive/dead) than high salinity (0.26 ± 0.0011 alive/dead, $F_{1227,5} = 18.01$, $p < 0.001$). Plant biomass at harvest showed an optimum at a soil salinity of 0.75%. At this salinity level the total biomass was 37.7% higher than for the 0% salinity treatment (Fig. 2.5A). At the highest soil salinity level (1.5%) the total biomass was about equal to that of the control treatment with 0% soil salinity. The effect of soil salinity on the total biomass of *E. juncea* was mainly driven by the effect on shoot biomass (Fig. 2.4C). The root biomass did not show a significant increase at the soil salinity levels of 0.25 to 1.0%, but decreased at 1.5% soil salinity (Fig. 2.4D). Consequently, the shoot to root ratio increased with increasing soil salinity for this species (Fig. 2.4B), again a response opposite to that of *A. arenaria*. Increased soil salinity also resulted in smaller and denser leaves, decreasing the SLA from 93.49 ± 6.56 cm/g in the control treatment to 64.26 ± 3.53 cm/g in the highest soil salinity treatment ($F_{77,5} = 6.54$, $p < 0.001$). In contrast to *A. arenaria*, soil salinity did not affect leaf thickness for *E. juncea* ($F_{35,5} = 2.11$, $p = 0.087$, leaf thickness control treatment: 0.31 ± 0.016 , highest salinity treatment: 0.29 ± 0.015). For *E. juncea* no distinction has been made between the dead and alive biomass, however from the data collected during the experiment it seemed that the number of dead leaves was similar to that of *A. arenaria*.

2.4.3.2 Impacts on photosynthesis

Photosynthesis (Asat) was affected by both soil salinity and species, with salt spray having no effect (Table 2.3, Fig. 2.5A). Photosynthesis linearly decreased with soil salinity for both species (Table 2.3, Fig. 2.5A), with *A. arenaria* showing a stronger response than *E. juncea*. Photosynthesis of *A. arenaria* was completely suppressed (i.e. there was respiration instead of CO₂ accumulation, reflected by negative values) at soil salinity levels of 0.75% and higher, whereas of *E. juncea* kept photosynthetically active in all treatments. Stomatal conductance decreased with soil salinity, irrespective of species (Table 2.3, Fig. 2.5B). As a result the water use efficiency of both species decreased with increasing soil salinity, dropping below zero at soil salinity levels of 0.75% or higher for *A. arenaria*, and at a soil salinity of 1.5% for *E. juncea* (Fig. 2.5C).

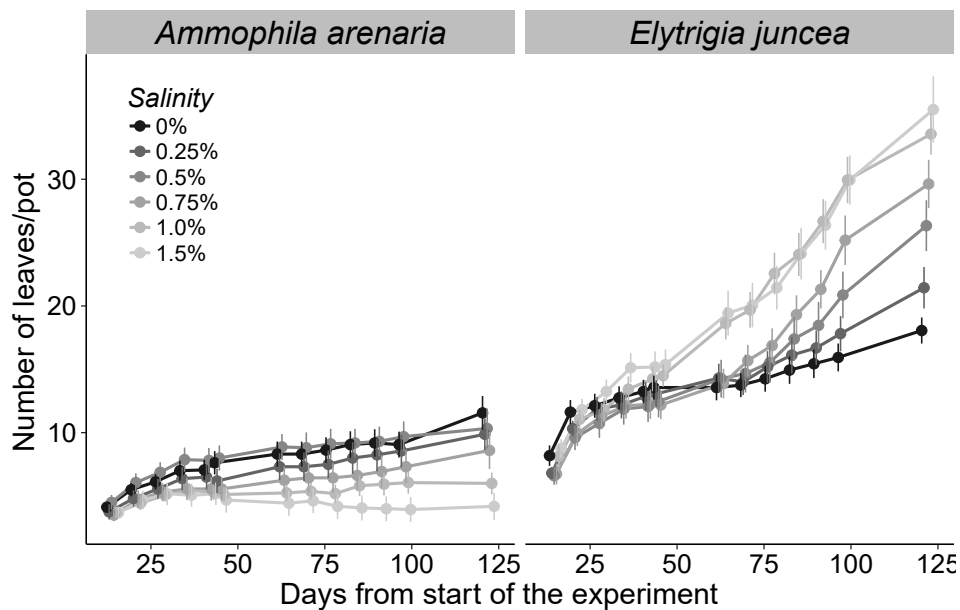


Figure 2.3. The number of living leaves per pot for *A. arenaria* and *E. juncea* over the first 125 days of the experiment at the different soil salinity levels. The points are means and the error bars are standard errors.

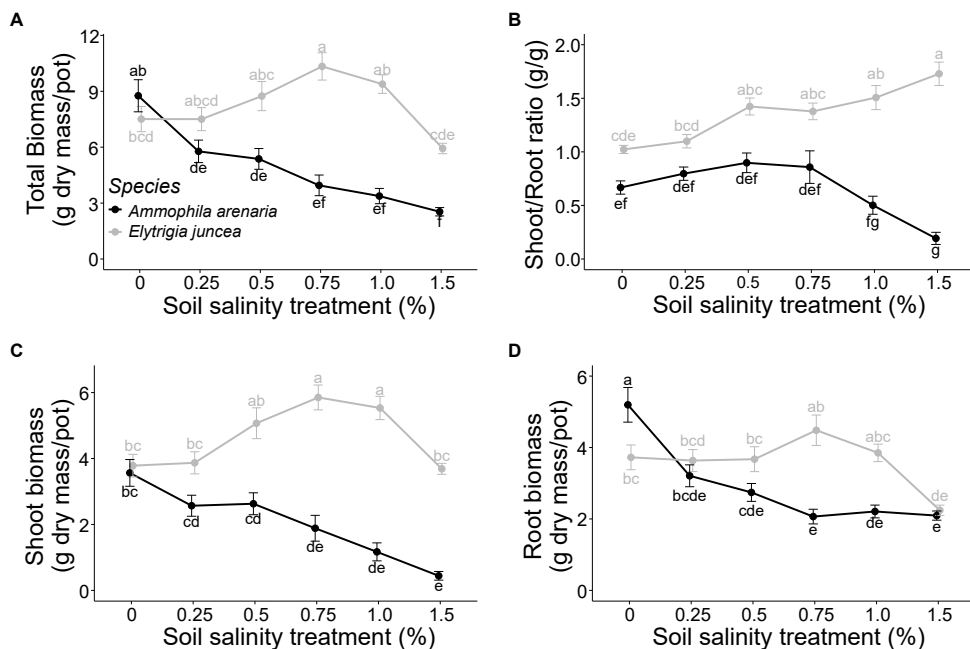


Figure 2.4. The effect of soil salinity (%) and species (*A. arenaria* and *E. juncea*) on: A) total biomass (g dry mass/pot); B) Shoot/Root ratio (g/g dry mass); C) Shoot biomass (g dry mass/pot); D) Root biomass (g dry mass/pot). The points are the means and the error bars the standard error. The letters denote the significance between the different salinity levels (Tukey HSD test).



2.4.3.3 Leaf nutrient concentrations

Leaf nutrient (N, P and K) concentrations were comparable between the two grass species and N and P concentrations increased with soil salinity, while K concentrations decreased with soil salinity (Table 2.4, Fig 2.6 A-C). Leaf Na concentrations differed between species, with *A. arenaria* having significantly higher leaf Na concentration compared to *E. juncea*. This species effect was mainly caused by the effect of salt spray on leaf Na concentration: salt spray increased the leaf Na concentration of *A. arenaria* but not affect *E. juncea*. Leaf Na concentrations increased with soil salinity for both species at approximately the same rate (Table 2.4, Fig. 2.6D). The leaf Na and K concentrations were negatively correlated to each other ($K = 0.75 - 0.46*Na$, $p = 0.009$, $R^2 = 0.06$).

Table 2.3. An overview of the model outcome of the Photosynthesis, Stomatal conductivity and Water use efficiency (WUE). The data was analysed with an ANOVA type 3. The values shown are the F values.

Factor	df	Photosynthesis	Stomatal conductivity	WUE
Species	1	0.017	0.032	0.00
Salinity	5	4.23**	2.81*	2.94*
Salt Spray	1	0.96	0.15	2.85
Species x Salinity	5	0.16	0.28	0.57
Species x Salt Spray	1	1.13	0.0091	0.57
Salinity x Salt Spray	5	0.50	0.38	0.94
SSresiduals	25	562.42	8.46	20.87

WUE = water use efficiency ($\mu\text{mol}/\text{mol}$), df = degrees of freedom. The asterisk denotes the level of significance (* $p < 0.05$, ** $p < 0.005$).

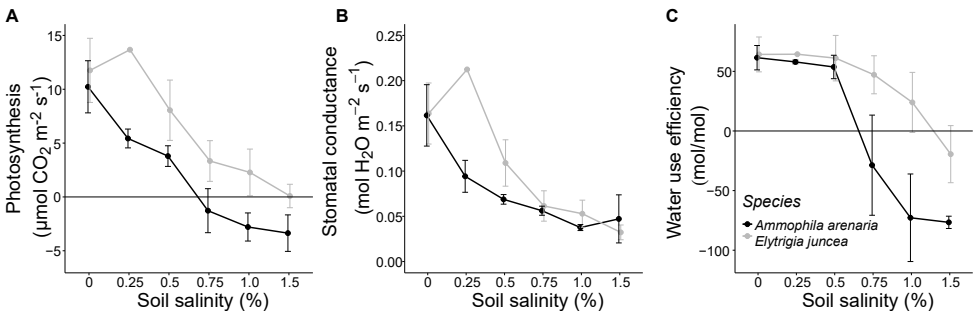


Figure 2.5. The mean and standard error of A) the Photosynthesis (Asat) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), B) the Stomatal conductance ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and C) the water use efficiency ($\mu\text{mol}/\text{mol}$) for *A. arenaria* and *E. juncea* at different soil salinity levels. There were no significant differences between the different species and soil salinities.

Table 2.4. An overview of the model outcome of the N, P, K, Na concentrations in the leaves. The data was analysed with an ANOVA. The values shown are the F values.

Factor	df	N	P	K	Na
Species	1	0.97	2.78	0.039	8.66**
Salinity	5	19.83***	2.92*	16.28***	46.07***
Salt Spray	1	2.88●	0.059	0.79	5.04*
Species x Salinity	5	7.36***	0.65	4.87***	1.92
Species x Salt Spray	1	2.34	0.68	4.80*	3.73●
Salinity x Salt Spray	5	1.17	1.13	2.90*	1.94●
MSresiduals	74	0.041	0.0026	0.17	0.31

df = Degrees of freedom. The asterisk denotes the level of significance (● $p < 0.1$ * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$).

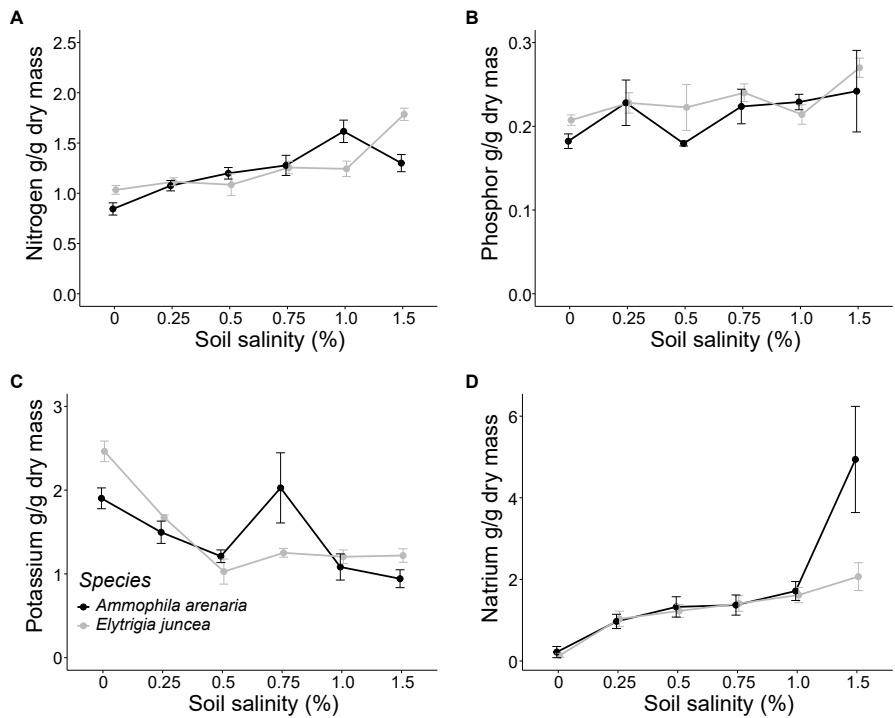


Table 2.6. The mean and standard error of A) N concentration (g/g dry mass), B) P concentration (g/g dry mass), C) K concentration (g/g dry mass) and D) Na concentration (g/g dry mass) of *A. arenaria* and *E. juncea* for different soil salinity levels. Since there was a significant effect of the salt spray treatment on the Na concentration, for graph 6D we only present data without the salt spray treatment. There were no significant differences between the different species and soil salinities.



2.5 Discussion

In this study we tried to explain the discrepancy in current literature between spatial plant distribution on the beach, salinity-tolerance ranges measured in short-term-physiological studies and the actual salinity measured on the beach. We hypothesised that the discrepancy was either related to 1) the interactive effects of aboveground salt spray stress and belowground salinity stress or 2) the short experimental duration of most glasshouse experiments. Contrary to our expectations we found in our glasshouse experiment that salt spray did not interact with soil salinity. Moreover, despite species being up to three times more sensitive to soil salinity in our 176 day glasshouse experiment than in a similar 32 day glasshouse experiment (Sykes and Wilson, 1989), the concentrations found to limit species performance in the glasshouse were still several orders of magnitude higher than observed in the field. Below we try to answer the questions to what extent soil salinity restricts the spatial distribution of dune-building species, and thereby the development of vegetated dunes, on the beach.

2.5.1 Salt spray

Salt spray did not affect growth of the main dune-building species in our glasshouse experiment, also at high soil salinity concentrations. The absence of an effect is unlikely to be an artefact of the concentrations used in our study. Although we did not control the droplet size in our study (Boyce, 1954), the leaf salt concentration that the plants were subject to in our experiment are likely to exceed the concentrations experienced by plants in the field, because of the absence of precipitation in the glasshouse. In the field salt stress is often reduced by precipitation, as the rain removes build-up of salt from the leaves (Boyce, 1954). The tolerance for salt spray of species growing on the beach has also been found in other studies (Rozema et al., 1983; Sykes and Wilson, 1988) and has been mainly attributed to the structure of the epicuticular wax layer (Ahmad and Wainwright, 1976), which can reduce the uptake of Na⁺ and Cl⁻ deposited by salt spray.

2.5.2 Mechanisms explaining biomass response to saline conditions

We explored to what extent the species biomass responses to increasing soil salinity in the glasshouse could be attributed to nutrient limitation, osmotic stress and ionic stress, as this could, perhaps, shed more light on species responses in the field. Of these three mechanisms, nutrient limitation is unlikely. Leaf N and P concentrations remained constant or increased with increasing soil salinity levels. Leaf K concentration did decrease with soil salinity, suggesting K limitation as a potential explanation for a negative biomass response to high salinity. However, as K concentration decreased irrespective of species, and leaf K concentrations remained within field ranges (1%), K deficiency as driver of the biomass response seems unlikely. The decline in K was positively related to the increase in leaf Na concentration, presumably due to the competition between K and Na uptake at the root surface (Amtmann and Sanders, 1998; Colmer and Flowers, 2008). This leaves osmotic stress and ionic stress as alternatives to explain the negative biomass responses. Soil salinity stress occurs in two stages for a plant (Munns and Tester, 2008). First a rapid response to increase in external osmotic pressure (osmotic stress), and secondly over time a response to the accumulation of Na⁺ in the leaves (ionic stress) (Munns and Termaat, 1986). Osmotic stress characteristically results in the re-

duction of shoot growth (Weimberg et al., 1984) while ionic stress leads to leaf mortality. Very likely both processes played a role, with osmotic stress being important for both *A. arenaria* and *E. juncea*, while ionic stress may have contributed to the biomass response of *A. arenaria* only.

For both species stomatal conductance decreased with increasing soil salinity, the decrease being steeper for *A. arenaria* than for *E. juncea*. The reduction of stomatal conductance, which indicates stomatal closure, is often associated with osmotic stress (Lovelock and Ball, 2002; Munns, 1993). For *A. arenaria* the reduction in leaf stomatal conductance was accompanied by a steep decline in leaf photosynthesis for soil salinities until 0.75%. The decline in photosynthesis mirrored the pattern observed for shoot biomass, suggesting the species increasingly suffered from osmotic stress. For *E. juncea*, photosynthesis declined less steeply, remaining positive until the highest soil salinity treatment of 1.5%. Surprisingly, the physiological response did not mirror the response in shoot biomass, which showed an optimum at 0.75% soil salinity. The above suggests that *E. juncea* also experienced increasing osmotic stress with increasing soil salinity, but was better able to compensate for it than *A. arenaria*. The reason for the discrepancy between the biomass and photosynthetic responses is as yet unclear, and could perhaps be related to a time lag-effect between photosynthetic rates and biomass production suggesting cumulative stress.

Ionic stress is caused by the Na^+ accumulation in the leaves until toxic levels are reached, causing senescence (Munns and Termaat, 1986; Munns and Tester, 2008). Both *A. arenaria* and *E. juncea* showed a similar increase in the Na concentration in the leaves, but only *A. arenaria* displayed increasing leaf mortality with increasing soil salinity. For *E. juncea* however, the proportion of dead leaves was higher at low salinity levels. The above suggests that for the soil salinity range we studied, ionic stress may have been an issue for *A. arenaria*, but not for *E. juncea*. Perhaps *E. juncea* could be more tolerant to Na by storing it in different cell organs, for example the vacuole (Flowers et al., 1977).

2.5.3 Distribution and growth in the field

Vegetation distribution on the beach has often been hypothesised to depend on soil salinity (Westhoff et al., 1970), as the species zonation corresponds to different degrees in salinity tolerance of dune-building species investigated under controlled conditions. Our results from the field transplantation experiment suggest that there is an abiotic factor restraining plant survival in winter, but not in summer. In summer, the growth of *A. arenaria* in zone II was limited by soil salinity, but not that of *E. juncea*. *Elytrigia juncea* showed no significant difference in plant growth in the field between the three different zones with different soil salinity. Unfortunately, we do not have any results on plant performance of transplants in zone I due to anthropogenic disturbance. Nevertheless, as soil salinity in the un-vegetated zone I was comparable to *E. juncea* occupied zone II, it seems reasonable to assume that a factor other than salt stress prevented vegetation development in this zone. Perhaps more regular inundation by the sea in zone I and associated mechanical stress or, alternatively, higher extremes in soil salinity, could explain the pattern.



In our study we measured salt concentrations at one moment in time, whereas soil salinity is known to vary extensively in the field, due to changes in sea level, salt spray, and precipitation (de Jong, 1979; Maun, 2009). Of course it is possible that plant distributions reflect higher salt concentrations that are reached after periodic drought in summer (Ayyad, 1973), or perhaps, directly after storm inundation in winter (Barbour and DeJong, 1977). Furthermore our results are only based on the Hors, Texel, and the soil salinity could be different at other beaches. Yet, despite the limitation of our study described above soil salinity at two other beaches differing in morphology was even lower than the level we found on the Hors, Texel. This is also consistent with the few other studies that measured soil salinity on the beach, which reported soil salinity levels between 0.0008% – 0.04% (Boyce, 1954; de Jong, 1979; Gooding, 1947; Kearney, 1904; Olsson-Seffer, 1909). At these beaches where soil salinity remains well below 0.25%, the dune development of *A. arenaria* is probably not limited by soil salinity. In general, beach soil salinity probably depends on beach morphology. Shorter beaches, with a steep slope, and a higher elevation, might have lower soil salinity levels compared to wide beaches, with a gradual slope and a lower elevation. Further research should be conducted on the variation of soil salinity on the beach, and its relationship to beach morphology and extreme events, such as drought and inundation.

Our field experiment suggests that the survival of dune building grasses is determined in the winter season. In zone II no plants of either species survived the winter. The low survival of both species is most likely associated with the occurrence of a storm that winter, which resulted in high water levels. Storms can severely erode dunes (Claudino-Sales et al., 2008; Haerens et al., 2012; Keijsers et al., 2014b) and have been found to be a limiting factor for embryo dune development (van Puijenbroek et al., 2017a). The storm affected probably all experimental plots, however the zones closer to the sea were probably longer and/or more deeply inundated by high water compared to zones further from the sea (Barbour and DeJong, 1977). Even though the transplanted plants did not survive the winter period in our field experiment, natural *E. juncea* dunes do occur in zone II. Why our transplanted plants did not survive while the natural plants did, we cannot say for sure. It is possible that the better developed root system, the higher cover and/or bigger dune size of the natural plants increased their storm resistance.

2.5.4 (Dis)similarities between field and glasshouse

The plant species differed in vigour between glasshouse and field: in the field *A. arenaria* grew much better than *E. juncea* at the same soil salinity than in the glasshouse experiment. This difference between the glasshouse and field experiment is most likely caused by factors that are important for species growing in the field, but were not included in the glasshouse experiment, such as sand burial, precipitation, and storm erosion. With sand burial *A. arenaria* can escape soil pathogens, which promotes the growth of *A. arenaria* (Maun, 1998; van der Putten, 1989). Although we used sterile river sand for our glasshouse experiment, pathogens could have been introduced with the rhizomes which we collected in the field (de Rooij-van der Goes et al., 1998). Furthermore sand accumulation might decrease the soil salinity by increasing elevation. *Elytrigia juncea* is not known to suffer from negative soil feedback in the field but can suffer from the high rates of sand burial during winter, particularly in zones close to the dunes, such as zone IV (Sykes and Wilson, 1990). In the field both species trapped sand, however the amount was not much, between 10 – 20 cm in elevation change, and did not differ

much between the species.

In the field, *A. arenaria* decreased in the number of leaves in response to increasing soil salinity over summer, however the decrease was not so pronounced as in the glasshouse given equal salinity. Perhaps this difference can be explained by the temporary dilution of soil salinity, and thus alleviation of salt stress, by precipitation in the field (Seeliger et al. 2000; Greaver & Sternberg 2007).

In the field, both species declined dramatically in performance over winter. This decrease was probably caused by a large storm that occurred during our study period. Storms have two main effects, they cause mechanical erosion of the dunes and they increase the salinity in the soil by seawater inundation (Charbonneau et al., 2017; Feagin et al., 2015; Sigren et al., 2014). Seawater has a high salinity of 3.5%, that could have a detrimental effect on the growth of both *A. arenaria* and *E. juncea* (Konlechner et al., 2013). However the inundation of seawater by storms mainly occurs during the winter season, and it is not clear how detrimental this increased salinity is for plants when they are not growing. A worthwhile avenue for future research is to study the effect of inundation and resulting increase in soil salinity on the survival and growth of dune building grasses during the growing season and winter season. In zone III *E. juncea* had a lower survival compared to *A. arenaria*, whereas the results from our glasshouse experiment suggest that *E. juncea* is more resistant to soil salinity than *A. arenaria*. Consequently, the low survival of *E. juncea* and *A. arenaria* is most likely caused by the mechanical erosion of the dunes and vegetation. The higher survival of *A. arenaria* compared to *E. juncea* in zone III is most likely due to the higher vegetation density of *A. arenaria*, which enables the species to better withstand mechanical erosion by storms. However, the higher vegetation density was partly the result of a lower productivity of *E. juncea* compared to *A. arenaria*. From this study it is difficult to predict if the differences in winter survival of *A. arenaria* and *E. juncea* would be similar if they had equal number of leaves. However since *E. juncea* had a lower growth rate compared to *A. arenaria* in the field, our results still suggest that mechanical erosion by storms is more likely to limit the distribution of *E. juncea* than soil salinity, however we cannot totally excluded the effect of episodic increase in soil salinity during storms.

2.5.5 Implication for dune development

Although some research has been conducted on factors that determine plant succession in dunes, research on factors that determine the vegetation limit on the beach are scarce. *Ammophila arenaria* has been introduced in many countries for its dune building capabilities, therefore understanding the factors that determine its vegetation limits would be beneficial. Dune development starts with the establishment of vegetation on the beach making it dependent on establishment of dune-building species from rhizome or seeds (Harris and Davy, 1986; Hilton and Konlechner, 2011; Maun, 1981). Although glasshouse results show clear differences in salt tolerance between both dune-building species, beach salinity and performance of transplanted species on the beach suggest that salt stress is unlikely to drive species distribution or limit dune building on the beaches we studied. We cannot exclude however that on some beaches salt salinity does affect distribution of *A. arenaria*, provided soil salinity on the beach reaches concentrations above 0.25%. Especially, the high soil salinity could prevent the germination of *A. arenaria* seeds, as seedlings are more vulnerable to soil salinity (Sykes and Wilson, 1989). A limited germination of *A. arenaria* could explain why only *E. juncea* dunes occur in zone



II. In contrast to *A. arenaria*, distribution of *E. juncea* is unlikely to be limited by salt stress as illustrated by its natural distribution that shows the species can establish and survive in zone II, which had equal salinity to zone I. As both species facilitate dune development, our results suggest that net dune building on the beach is not limited by soil salinity.

Instead of soil salinity, dune development seems more limited by the storms in the winter season. Storms during the winter season result in mechanical erosion, where vegetation can be completely removed by waves. The sensitivity to mechanical erosion could differ between dune-building species however, with denser vegetated species being less sensitive to mechanical erosion, than species forming a more sparse vegetation (Charbonneau et al., 2017; van Puijenbroek et al., 2017b). Sensitivity to mechanical erosion also depends on the root network, although this has hitherto not been investigated for coastal dunes (Feagin et al., 2015). Both of the species studied expand with rhizomes and, as a results, most shoots are connected to each other. The rhizome network likely promotes stabilisation of sediment and reduces storm erosion, potentially increasing survival over winter. In our field experiment we planted individual plants, which might have made them, more sensitive to mechanical erosion than vegetated dunes in the field. Rhizomes are also known to be quite resistant against high soil salinity, rhizomes have been found to be viable after floating 70 days in seawater (Konlechner and Hilton, 2013). Therefore, storm erosion could result in the mortality of the shoots, but next growing season vegetation growth might occur from the rhizomes. Taken together, our results suggest that there is no fixed vegetation limit on the beach, but rather a combination of continuous summer recruitment and stochastic winter mortality, with net expansion of dune-building species and dunes depending on storm characteristics of the winter season. The limits for vegetation establishment on the beach are important for modelling coastal dune development (de Groot et al., 2012; Durán and Moore, 2013).

2.6 Conclusion

The purpose of this study was to assess to what extent soil salinity restricts the spatial distribution of dune-building species, and thereby lower the limit for development of vegetated dunes on the beach. Performance of dune-building species did change with soil salinity in the glasshouse, confirming salt stress as a potential limit for vegetation growth, but field measurement on plant performance and summer soil salinity suggest that mortality of dune-building grasses is rather a function of mechanical erosion in winter, rather than summer soil salinity. Consequently, our findings suggest that soil salinity stress either restricts recruitment from seeds, takes place in winter, or that development of vegetated dunes is less sensitive to soil salinity than hitherto expected.

2.7 Acknowledgement

We would like to thank Maurits Gleichman and Frans Moller for the help with the experiments. We would like to thank Jan van Walsem for the nutrient analysis. We would like to thank the technology foundation STW for funding the project NatureCoast which made this research possible. Finally, the authors thank the two anonymous reviewers and editor for their useful and extensive comments on a previous draft of the manuscript.

Appendix 2.1 Overview table with literature on the response of *A. arenaria* and *E. juncea* on salt spray and soil salinity.

Table A2.1. Overview table with literature on the response of *A. arenaria* and *E. juncea* on salt spray and soil salinity. The treatment indicates the abiotic conditions the authors tested experimentally.

Authors	Treatment	Method	Species	Results
Salt Spray				
Rozema et al, 1983	Distilled water and seawater	Once every two days Experiment duration: 2.5 months	<i>E. juncea</i>	No effect of salt spray on biomass, only slight increase of Cl ⁻ concentration in the leaves
Sykes & Wilson, 1988	Distilled water and 3.5% NaCl	Once every 5 days Experiment duration: 21 days	<i>A. arenaria</i>	No effect on biomass, seedling were affected.
			<i>E. juncea</i>	No effect on biomass
Soil salinity				
Rozema et al 1983	0 mM NaCl = 0% 60 mM NaCl = 0.35% 150mM NaCl= 0.87% 300mM NaCl = 1.74%	Aerated hydro-culture Experiment duration: 6 weeks	<i>E. juncea</i>	Overall decrease in growth. Decrease in K ⁺ concentration in the leaves, increase in Na ⁺ and chloride concentration in the leaves.
Sykes & Wilson 1989	0%, 0.25%, 0.5%, 0.75%, 1%, 2%	Pots were drained Experiment duration: 32 days	<i>A. arenaria</i>	Significant decline with higher soil salinities, RGR significantly different at 0.75% soil salinity
			<i>E. juncea</i>	Shows an optimum at 0.75% soil salinity, no overall significant difference
Konlechner et al 2013	3.5% sea water	Immersed for 3 hours Growth assessed for a week	<i>A. arenaria</i>	No survival when immersed with seawater, some plants survived if they were washed with fresh water.



Appendix 2.2 Overview of the field site Hors at Texel.



Figure A2.1. Overview of the field site on the Hors at Texel. The dots indicate the different zones where we conducted the field transplantation experiment and measured the soil salinity. The star in the map indicates the location of the field site in the Netherlands. Zone I is the non-vegetated zone, zone II the zone with only *E. juncea* occurring, zone III the zone with both *E. juncea* and *A. arenaria*, and in zone IV *A. arenaria* is dominant. Map source: Image © DigitalGlobe, Data SIO, NOAA, U.S. Navy, NGA GEBCO, 2017 Google, image taken at 30-06-2015.

Appendix 2.3 Plant growth of mono and mixed culture in the field experiment

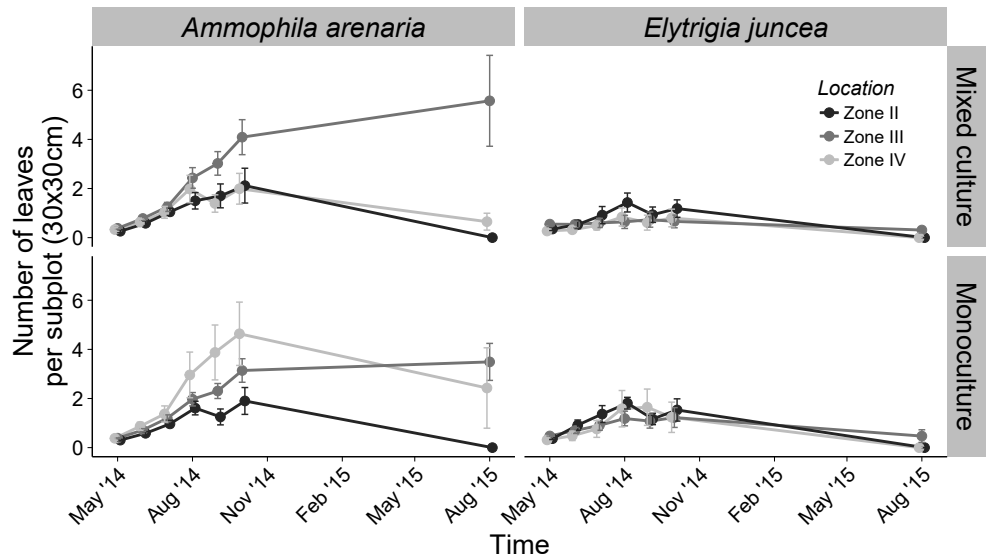


Figure A2.2. The number of living leaves/plant for *A. arenaria* and *E. juncea* and mixed and mono culture per subplot of 30cm x 30cm within a plot at the different zones at the Hors, Texel, over a period of 15 months. The points are means and the error bars are standard errors. Zone II is the zone with only *E. juncea* occurring, zone III the zone with both *E. juncea* and *A. arenaria* and in zone IV *A. arenaria* is dominant.

Appendix 2.4 The ECe (mS/cm) of the experimental plots

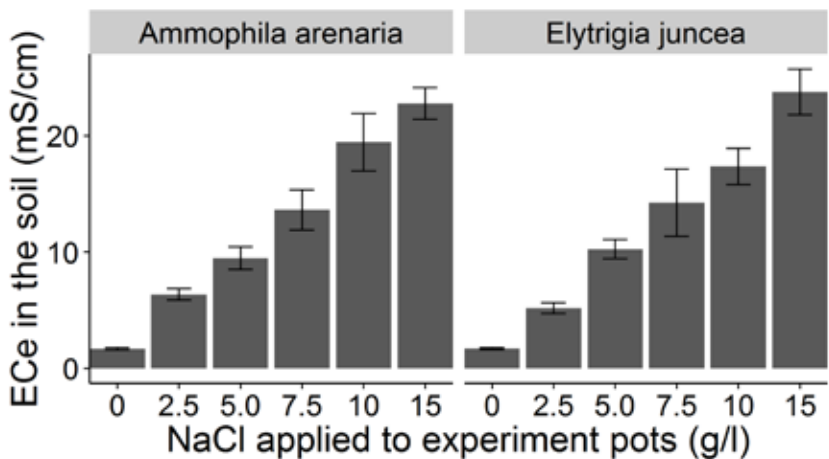
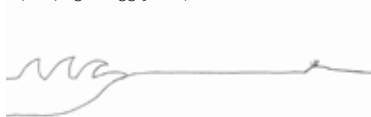


Figure A2.3. The mean \pm SE ECe (mS/cm) for the different soil salinity treatments for both *A. arenaria* and *E. juncea*. The saline solutions that were applied to the pots were: 0‰ = 0.28 mS/cm, 0.25‰ = 6.0 mS/cm, 0.5‰ = 11.1 mS/cm, 0.75‰ = 16.2 mS/cm, 1.0‰ = 20.2 mS/cm, 1.5‰ = 33.9 mS/cm.



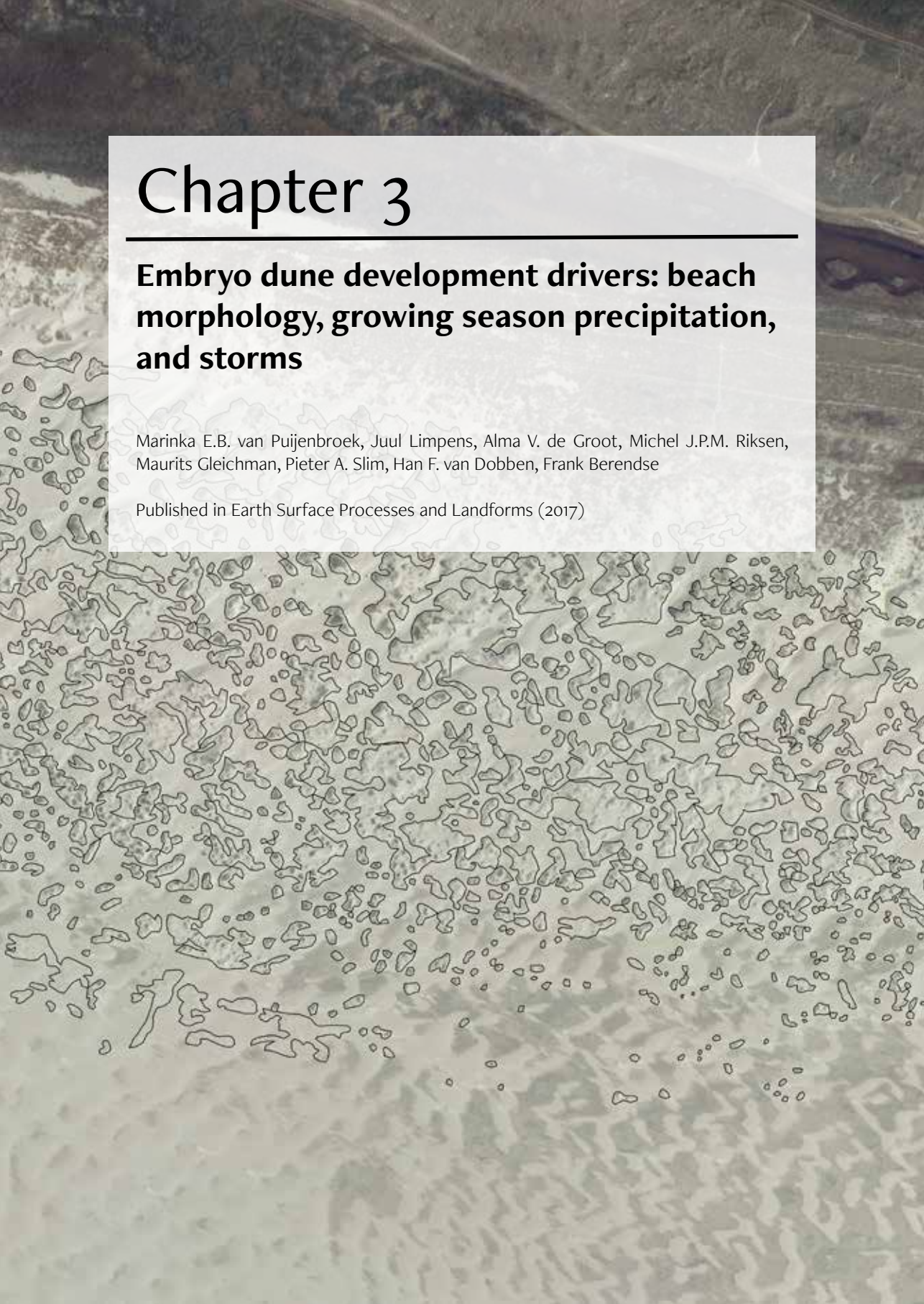


Chapter 3

Embryo dune development drivers: beach morphology, growing season precipitation, and storms

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3.1 Abstract

For development of embryo dunes on the highly dynamic land-sea boundary, summer growth and the absence of winter erosion are essential. Other than that, however, we know little about the specific conditions that favour embryo dune development. This study explores the boundary conditions for early dune development to enable better predictions of natural dune expansion.

Using a 30 year time series of aerial photographs of 33 sites along the Dutch coast, we assessed the influence of beach morphology (beach width and tidal range), meteorological conditions (storm characteristics, wind speed, growing season precipitation, and temperature), and sand nourishment on early dune development. We examined the presence and area of embryo dunes in relation to beach width and tidal range, and compared changes in embryo dune area to meteorological conditions and whether sand nourishment had been applied.

We found that the presence and area of embryo dunes increased with increasing beach width. Over time, embryo dune area was negatively correlated with storm intensity and frequency. Embryo dune area was positively correlated with precipitation in the growing season and sand nourishment. Embryo dune area increased in periods of low storm frequency and in wet summers, and decreased in periods of high storm frequency or intensity.

We conclude that beach morphology is highly influential in determining the potential for new dune development, and wide beaches enable development of larger embryo dune fields. Sand nourishment stimulates dune development by increasing beach width. Finally, weather conditions and non-interrupted sequences of years without high-intensity storms determine whether progressive dune development will take place.



3.2 Introduction

Coastal dunes occur along the sandy shores of most continents (Martínez and Psuty, 2008) and serve functions such as coastal defence, recreation, reservoirs for drinking water, and hotspots for biodiversity (European Commission, 2007; Everard et al., 2010). The quality and resilience of coastal dunes is threatened, however, by climate-induced sea-level rise (Carter, 1991; Feagin et al., 2005; Keijsers et al., 2016). This threat may be mitigated by the spontaneous formation of new dunes on beaches where and when conditions are favourable. To predict the future of dunes and coastal evolution, knowledge about early dune development is essential. Yet, despite the obvious importance of dunes, we know surprisingly little about the mechanisms that underlie early dune development.

Embryo dunes (also referred to incipient dunes) (Hesp, 2002; Maun, 2009) are the first stage of dune development. Embryo dunes are formed when sand is deposited within discrete clumps of vegetation or individual plants (Hesp, 2002). It starts with establishment of dune-building plant species above the high water line. Driftwood material may form a nucleus for vegetation establishment and sand deposition (Del Vecchio et al., 2017; Eamer and Walker, 2010). Once vegetation becomes established on a bare beach, it serves as a roughness element that facilitates sand deposition and reduces erosion. An embryo dune is thus the result of an interaction between vegetation and aeolian processes. Embryo dunes increase in size by deposition of more sand, as a result of the reduced flow velocities caused by vegetation roughness (Hesp, 2002; Maun, 2009). In time, embryo dunes may develop into a foredune that forms the first line of coastal defence.

Previous research has focused on either the ecology of dune-building vegetation or on factors driving sediment supply to embryo dunes (Anthony, 2013; Maun, 2009; Montreuil et al., 2013; Olivier and Garland, 2003). Few studies have investigated the relative importance of plant- and sand-related drivers for embryo dune development. Montreuil et al. (2013) found that embryo dune development has a seasonal cycle, with summer accumulation and autumn-winter erosion. Dune-building plant species become established in the summer months and are strongly influenced by soil salinity, soil moisture, and sand erosion/burial (Maun, 2009; Sykes and Wilson, 1989). The supply of sediment for development of embryo dunes depends on the transport capacity of the dominant wind direction, beach morphology and sediment availability (Anthony, 2013; Montreuil et al., 2013; Olivier and Garland, 2003). Sediment supply is related to both local factors, such as surface moisture (Anthony, 2013; Delgado-Fernandez and Davidson-Arnott, 2011; Saye et al., 2005; de Vries et al., 2012), and to regional factors, such as the welding of intertidal bars (Aagaard et al., 2004). The relative importance of these factors for embryo dune growth is nonetheless still unclear.

As, noted, embryo dunes grow mainly in summer, and erode in winter due to increased storm frequency (Montreuil et al., 2013). Yet, studies of the effects of storms on embryo dune development are scarce, so impacts of storms on embryo dune development must largely be deduced from research on foredune development. Foredune erosion is influenced by storm intensity and beach morphology (Claudino-Sales et al., 2008; Haerens et al., 2012; Houser et al., 2008; Keijsers et al., 2014b). Storm intensity is a product of regional characteristics and meteorological conditions, which determine surge levels, wave conditions, and storm durations (van de Graaff, 1986; Vellinga, 1982). Local factors, such as the direction of onshore winds, beach

width, beach slope, and presence of intertidal bars, modify storm impact, as they co-determine wave energy and wave run-up (Anthony, 2013; Ruggiero et al., 2001). Beach morphology affects dune erosion. For instance, dissipative beaches with a low and gradual beach slope are less subject to dune erosion than reflective beaches with a steep beach slope (Short and Hesp, 1982; Wright and Short, 1984). The extent that storms constrain embryo dune development, however, remains unknown.

Although embryo dune formation precedes foredune development, surprisingly little is known about the factors that determine their dynamics. In this study, we explored boundary conditions for early dune development to better predict natural dune expansion. Using a 30-year time series of aerial photographs of the Dutch coast we investigated: (1) the relation between beach morphology and presence and area of embryo dunes, (2) the effect of sand supply, storm characteristics, and other climatic factors on changes in embryo dune area.

3.3 Methods

3.3.2 Study area

We selected 33 sandy dissipative beach sites, each 2.5 km long, along the coast of three geographic areas in the Netherlands: the West Frisian barrier islands (N=20), the Holland mainland (N=7), and the south-western delta (N=6) (Fig. 3.1). The beaches on the West Frisian islands had the largest range in beach width, which is why most sites were selected there. The sites were separated by at least 2 km, to avoid spatial autocorrelation between them (de Vries et al., 2012). The 33 sites represent a wide variety in beach morphology, with beach widths ranging between 50 m and 1,400 m. All three geographic areas contained both accreting and eroding sites. Mean tidal ranges varied between 1.6 m and 2.7 m, depending on the area. Sediment mean grain size ranged between 190 μm and 400 μm (Arens, 1996; Stuyfzand et al., 2012).

All study sites were backed by a continuous foredune ridge covered largely by the grass *Ammophila arenaria* (L.) Link (Appendix 1). At many sites, foredune ridges had been created, or reinforced, by vegetation plantings and sand fences. All sites had embryo dunes seaward of the foredune at one time. Embryo dunes were covered by the grass *Elytrigia juncea* (L.) Nevski with some *A. arenaria*. Some of the sites experienced intensive recreational use and tourism and were mechanically cleaned by the municipality during summer. That cleaning resulted in the removal of drift material and, potentially, seedlings or ramets of dune-building grasses (Dugan and Hubbard, 2010).

3.3.2 Data collection

Presence and area of embryo dunes were extracted from aerial photographs spanning the years 1979 through 2010 (AIS, 2005; Dunea, 1975; Kadaster / Clyclomedia, 2010; PWN, 1987; Rijkswaterstaat, 1979). The time interval between consecutive photographs (referred to here as the time period) depended on what photographs were available for the individual sites (Table A3.1). The average interval was 6 years. Hard-copy photos of coastal areas for the years 1978, 1979, 1982, 1983, and 1988 had a scale of 1:4,000, and were scanned at 400 dpi. These digital photographs were georeferenced by matching 10 recognisable objects (e.g., beach poles,



road intersections) on the beach and in the dune area to a topological map. To georeference the images we applied a spline transformation using ArcGIS software (ESRI, 2013). The resulting spatial resolution of the photographs was between 0.20 m and 1 m (Table A3.2). Embryo dunes smaller than about 1 m² could not always be recognised, leading to conservative estimates of embryo dune area.

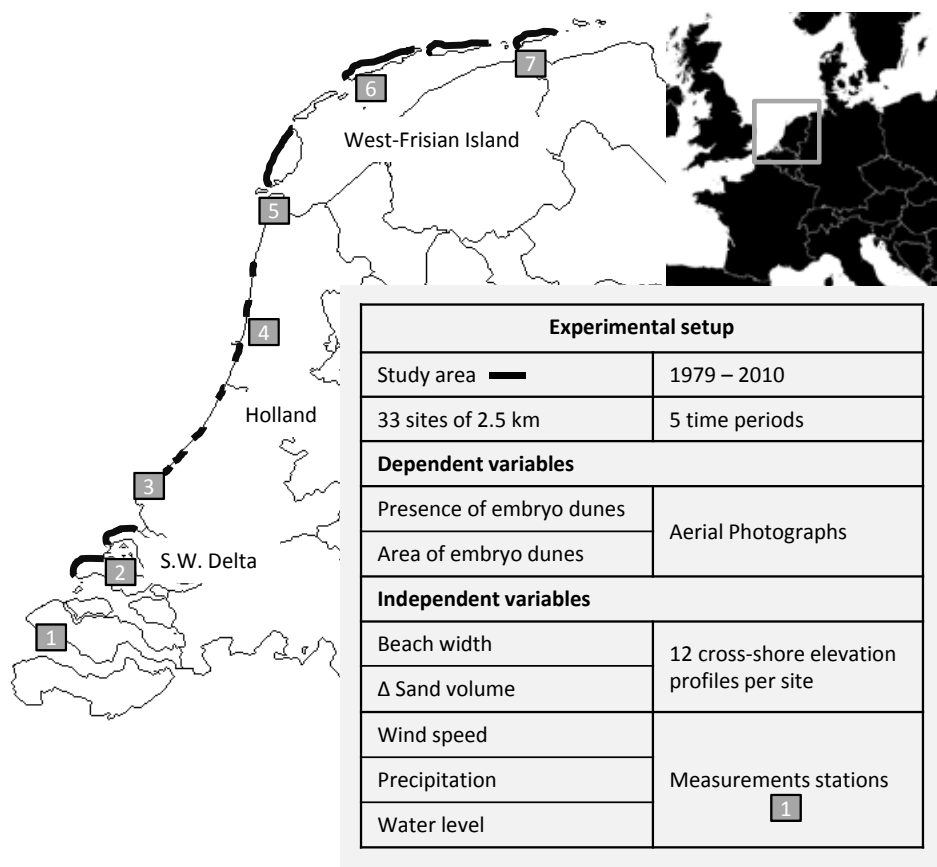


Figure 3.1. Study areas along the coast of the Netherlands. Each thick line represents a subset of in total 33 sites, of 2.5 km each. For the West Frisian islands and the south western delta 2 km distance was retained between sites to avoid autocorrelation. For the data used, see table. Squares denote measurement stations along the Dutch coast: (1) Vlissingen, (2) Brouwershavense Gat o8, (3) Hoek van Holland, (4) IJmuiden Buitenhaven, (5) Den Helder / De Kooy, (6) West Terschelling, (7) Schiermonnikoog.

3.3.3 Embryo dune area

The outlines of individual embryo dunes were manually digitised using ArcGIS. With 2010 as the starting point, we combined information from the aerial photographs and a LiDAR-derived digital elevation model (AHN2) (Programmasecretariaat AHN, 2013). Embryo dunes could thus be identified based on their vegetation structure (aerial photographs) and height (digital elevation model) (Fig. 3.2B). In the Netherlands, foredunes are higher than approximately 8 m NAP (NAP refers to Amsterdam Ordnance Datum, which is equal to mean sea level near Amsterdam). Patches with discrete clumps of vegetation at an elevation less than +6 m NAP in the 2010 aerial photographs were classified as embryo dunes.

Vegetation structure was used to distinguish between embryo dunes and low foredunes, which are more continuously covered with vegetation. Polygons were drawn around the vegetation patches at a standard resolution (1:600). We included no buffer around the vegetation. Subsequently, we identified embryo dunes on the photographs from the preceding years, using the 2010 embryo dunes as baseline.

For earlier years, no digital elevation model was available. We therefore used vegetation structure only to identify embryo dunes. In these earlier years some sparsely vegetated foredunes might have been falsely identified as embryo dunes, potentially increasing measurement error. After analysing all aerial photographs for a certain site, we verified the embryo dunes by comparing the most recent years with previous years. We took a conservative approach, discarding all embryo dunes that overlapped previous year's foredunes: i.e. we did not distinguish between eroding foredunes and newly developed embryo dunes in the same space. The maximum error in our assessment of the embryo dune area per site was 20% for 0.2 m resolution photographs and 5% for 1 m resolution photographs. This was determined after digitising the same subsample of sites 5 times at high resolution and 5 times at low resolution. The area covered by embryo dunes was summed per site per year and used for the statistical analysis.

3.3.4 Beach morphology

Beach width (BW in m) and beach volume (V in m³/m) were derived from 8 to 12 cross-shore elevation profiles for each year in which we also had photographs. Cross-shore elevation profiles from 1970 to 2010 were obtained from the JarKus database (Rijkswaterstaat, 2014a). This database contains annual elevation measurements covering dune, beach, and foreshore, and has been used in several studies addressing coastline dynamics from an annual to a decadal scale (Bochev-van der Burgh et al., 2009; Keijzers et al., 2014b, 2015; de Vries et al., 2012). The cross-shore distance between the JarKus profiles is 200 m to 250 m. The distance between elevation measurements along each profile is 5 m (Fig. 3.2A). Profile elevation was measured for the respective time periods using the following methods: levelling (1975 - 1977), stereo photography (1978 - 1995) and laser altimetry (1995 - 2010). The reported accuracy of the measurement techniques differed substantially, ranging from 0.01 m for levelling (Oosterwijk and Ettema, 1987), to 0.1 m for photogrammetry and laser altimetry (De Graaf et al., 2003; Minneboo, 1995; Sallenger et al., 2003).



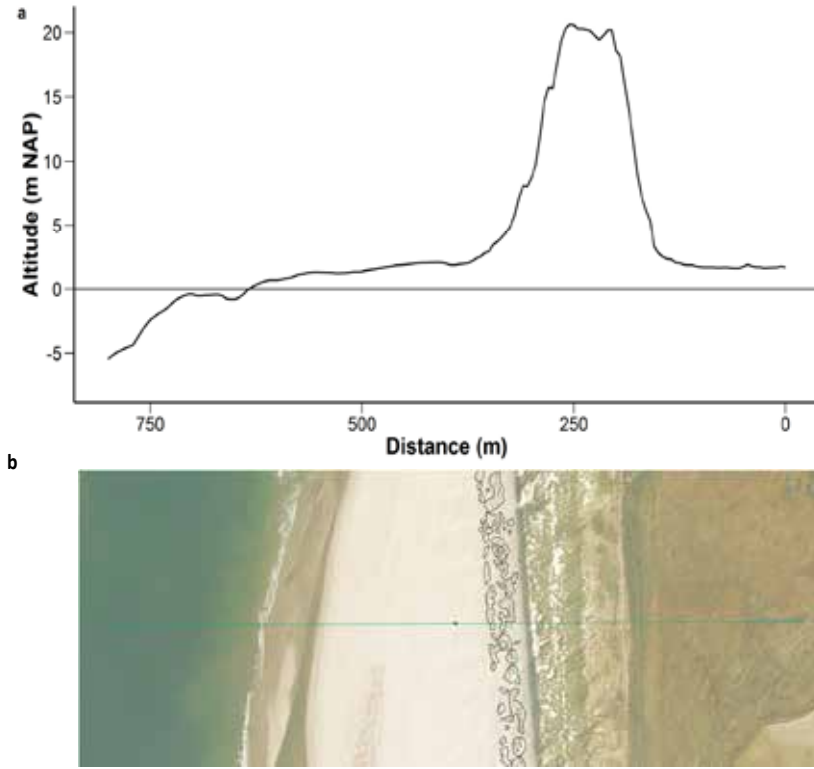


Figure 3.2. A) An example cross-shore elevation profile from the Jarkus database with the altitude in m NAP (Dutch Ordnance Datum). B) Aerial photograph (AIS, 2005) with areas outlined in black representing manually assigned embryo dunes. Cross-shore line represents the location of cross-shore elevation profile shown in A. Data from Terschelling in 2005.

Each site contained 12 profiles on average, though more profiles were available on dynamic beaches. Each profile was inspected for measurement errors and omitted if errors were found (i.e. if measurement points were missing or an unrealistically high elevation was measured). This resulted in a minimum of 8 profiles per site. From the available profiles we calculated beach width (BW) and beach volume (V). Beach volume was calculated as the area (m^3/m) under the curve of the profile to a depth of -5 m NAP. We defined beach area as the expanse between the shoreline and the dune foot (also known as the toe), i.e. between 0 and +3 m NAP (Keijsers et al., 2014; de Vries et al., 2012). Beach width was calculated for both the intertidal beach (between 0 and +1 m NAP, BW_{0-1}) and the dry beach (between +1 and +3 m NAP, BW_{1-3}). Beach volume was calculated for both the intertidal and dry beach, as well as for the whole beach between 0 m and 3 m NAP. The change in beach volume was calculated for each time interval between consecutive photographs, again distinguishing between the intertidal beach (ΔBV_{0-1}), the dry beach (ΔBV_{1-3}), and the entire beach (ΔBV_{0-3}). If a site had a positive change in beach volume (ΔBV_{0-3}), it was classified as an accreting beach.

3.3.5 Meteorological conditions

3.3.5.1 Water level and storm characteristics

Dune erosion results from combination of strong onshore winds, high energy waves, high water levels, and high wave run-up (Haerens et al., 2012; Vellinga, 1982). In the absence of wave height data, we used observed water levels as a proxy for storm intensity and thus potential dune erosion (Guillén et al., 1999; Keijzers et al., 2014; Ruessink and Jeuken, 2002). We derived hourly water level data from six tidal measurement stations along the Dutch coast (Rijkswaterstaat, 2014b): Brouwershavense Gat 08, Hoek van Holland, IJmuiden buitenhaven, Den Helder, West Terschelling and Schiermonnikoog, Fig. 1). For each site we used the nearest measurement station.

We created four water level exceedance classes (i.e. storm intensity classes, I-IV), based on water level return periods from the tidal measurement stations. These were high water levels of a severity that occurs once every (I) 1-2 years, (II) 2-5 years, (III) 5-10 years, and (IV) >10 years. For each station, we calculated the number of hours per time period (between consecutive aerial photographs) that the water level fell within one of these exceedance classes. The hours for each storm intensity class were abbreviated as $T_{\text{WLRT}(1-2y)}$, $T_{\text{WLRT}(2-5y)}$, $T_{\text{WLRT}(5-10y)}$, $T_{\text{WLRT}(>10y)}$.

Additionally, we calculated the storm interval, defined as the uninterrupted time period that the water level remained below the first storm intensity class ($T_{\text{WLRT}(1-2y)}$). If a storm interval was shorter than 24 hours, we considered the event represented to be one continuous storm. Most time periods had multiple storm events. We therefore, calculated the average storm interval for each time period. Tidal range was used as an additional factor in the analysis, defined as the difference between the average high tide and low tide levels, calculated from the daily highest and lowest water levels.

3.3.5.2 Wind speed, Precipitation and temperature

Data on wind speed, precipitation, and temperature were derived from two meteorological stations along the Dutch coast and operated by the Royal Dutch Meteorological Institute (KNMI, 2015). These two measurement stations (De Kooy, Vlissingen, Fig. 1) were the only ones from which hourly values were available for the study period.

Wind speed was used as a proxy for potential sand supply to the dunes. We calculated the number of hours that wind speeds were equal to or greater than 7 m s^{-1} within a time period. This threshold value was based on field measurements along the Dutch coast (Arens, 1996) and corresponds to the saltation threshold of 6.6 m s^{-1} for the average grain size in our study. We did not take wind direction into account, since embryo dunes are separated features in the landscape and therefore aeolian sand transport from several directions may contribute to embryo dune growth (Montreuil et al., 2013).

We calculated the total precipitation (mm) in the growing season (April to September) for each time period. Since higher temperatures during the growing season may enhance plant growth, we also calculated the average temperature ($^{\circ}\text{C}$) in June and July for each time period.



3.3.6 Sand nourishment

Most of the sites had been nourished to compensate for ongoing erosion. Beach nourishment was the most common method among our study sites, although dune and nearshore nourishment had also been applied (Nordstrom, 2013). For each site we checked if sand nourishment had been applied, using the presence or absence of sand nourishment as a variable. Data on sand nourishments in the Netherlands were provided by Rijkswaterstaat (Rijkswaterstaat, 2014c).

3.3.7 Statistical analyses

We explored, first, factors that influenced the presence and area of embryo dunes per site for each year in which we had aerial photographs. Second we investigated factors that influenced changes in the area of embryo dunes per site between consecutive time periods. The binominal presence/absence data of embryo dunes was analysed using a binominal linear mixed statistical model (Bolker et al., 2009), with beach width (BW_{0-1} & BW_{1-3}) and tidal range as explanatory variables. The mixed model was employed to account for variation between sites; we therefore used site as a random variable in the model (Zuur et al., 2009). We analysed embryo dune area with a general linear mixed model, after log transforming embryo dune area to ensure normality of the data. For this model, we also used beach width (BW_{0-1} and BW_{1-3}) and tidal range as explanatory variables and site as a random variable. Both models were simplified to include only the variables with a statistically significant contribution using a backward selection method with either Akaike Information Criterion (AIC) or a Bayesian Information Criterion (BIC). The total data set contained 188 replicates (observations). For both models we calculated the marginal and conditional R^2 (Nakagawa and Schielzeth, 2013). The marginal R^2 is the variance explained by the explanatory variables and the conditional R^2 is the variance explained by the entire model (including the random variables).

We calculated the change in embryo dune area as a relative value. All the variables in the models were corrected for the number of years between the time periods. The increase or decrease of embryo dune area between consecutive photos was tested with a binominal linear model, using as explanatory variables changes in beach volume (ΔBV_{0-3} , ΔBV_{0-1} , ΔBV_{1-3}), hours wind speed ($WS \geq 7 \text{ m s}^{-1}$), temperature in summer, precipitation in the growing season, storm intensity ($T_{WLRT(1-2y)}$, $T_{WLRT(2-5y)}$, $T_{WLRT(5-10y)}$, $T_{WLRT(>10y)}$), storm interval, beach width (BW_{1-3}), and the occurrence of sand nourishment. No random variables were included in the model, because we did not have enough replicates ($n = 150$), compared to the number of random effects levels. For the binominal linear model we calculated the Nagelkerke R^2 (Nagelkerke, 1991).

The relative change in embryo dune area was calculated as $\ln(t) - \ln(t-1)$ and analysed with a linear model using as explanatory variables beach volume (ΔBV_{0-3} , ΔBV_{0-1} , ΔBV_{1-3}), hours wind speed ($WS \geq 7 \text{ m s}^{-1}$), temperature in summer, precipitation in the growing season, storm intensity ($T_{WLRT(1-2y)}$, $T_{WLRT(2-5y)}$, $T_{WLRT(5-10y)}$, $T_{WLRT(>10y)}$), storm interval, beach width (BW_{1-3}), and the occurrence of sand nourishment. No random variable was included. Model complexity was reduced by forward or backward selection with AIC or BIC. We were mainly interested in the relative importance of the variables and therefore calculated the standardised estimates for all the models (Gelman, 2008). The normality and homogeneity of variance of the data was visually checked. All statistical analyses were done in the statistical program R (R Core Team, 2016).

3.4 Results

3.4.1 Presence and area of embryo dunes

All sites contained embryo dunes in one or more years between 1970 and 2010. On only 30 of the 188 aerial photographs (16%) we did not find any embryo dunes. The embryo dune area per site differed significantly between geographic area and year ($F_{185} = 11.5, p < 0.001$; $F_{185} = 18.9, p < 0.001$, respectively). The West-Frisian islands had on average the most embryo dunes with $11 \pm 2 \text{ m}^2/\text{km}$ (mean \pm SE), and the Holland mainland coast had the lowest embryo dune area with $2 \pm 0.5 \text{ m}^2/\text{km}$. The south western delta took an intermediate position with $4 \pm 1 \text{ m}^2/\text{km}$. The differences found could be due to the corresponding significant differences in beach widths in the three geographic areas (West Frisian island: $182 \pm 15 \text{ m}$, south western delta: $125 \pm 17 \text{ m}$, Holland mainland coast: $45 \pm 3 \text{ m}$; $F_{185} = 17.1, p < 0.001$). Indeed, embryo dune area and presence were positively related to beach width at between 1 m and 3 m NAP (Table 3.1), with the largest dune fields occurring when the width of the dry beach (BW_{1-3}) exceeded 300 m or more (Fig. 3.3). Neither beach width at between 0 m and 1 m NAP (BW_{0-1}) nor tidal range had a significant effect on the presence or area of embryo dunes (Table 3.1).

3.4.2 Temporal variation in environmental factors

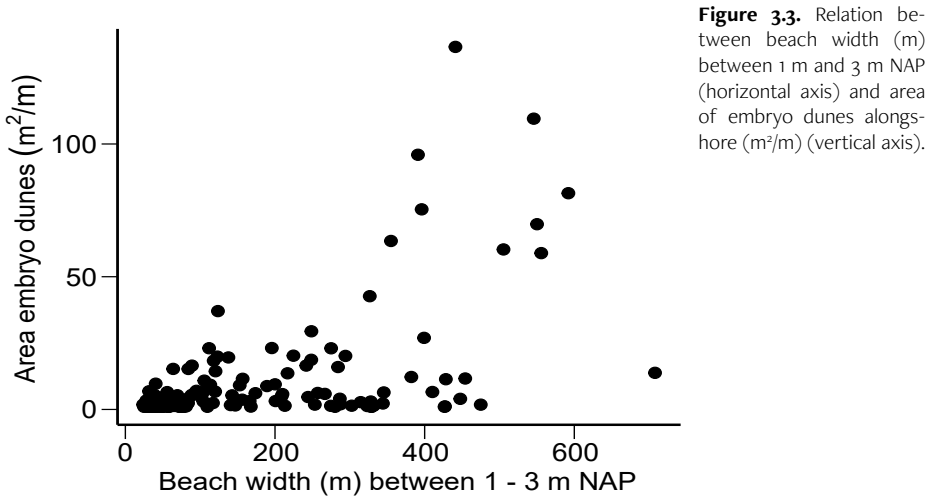
The environmental variables into our models – hours wind speed ($\geq 7 \text{ m s}^{-1}$), temperature, precipitation, storm intensity, beach volume changes, and sand nourishment – showed considerable temporal variation in the 30-year period covered by our study. Temperatures in June and July increased steadily over the years, ranging from 14.0°C to 19.2°C ($F_{39} = 13.91, p < 0.001$) (Fig. 3.4B). Precipitation during the growing season also showed a steady rise over the years, ranging from 154 mm year^{-1} to 490 mm year^{-1} ($F_{39} = 4.27, p = 0.045$, Fig. 3.4C). Storm intensity varied from year to year, showing no consistent pattern over time, unlike precipitation and

Factors	Full model	AIC backward	BIC backward
<i>Presence/absence of embryo dunes, n=188</i>			
$BW_{1-3 \text{ m}}$	1.85 •	1.63 •	
$BW_{0-1 \text{ m}}$	-0.52		
Tidal range (m)	0.18		
Marginal R^2	0.11	0.10	-
Conditional R^2	0.46	0.49	-
<i>Total area of embryo dunes, n=188</i>			
$BW_{1-3 \text{ m}}$	2.87***	2.70***	2.70***
$BW_{0-1 \text{ m}}$	-0.19		
Tidal range	-0.62		
Marginal R^2	0.14	0.14	0.14
Conditional R^2	0.39	0.39	0.39

Table 3.1. Statistical models for the presence or absence of embryo dunes and total embryo dune area. All time periods are included and the 33 sites were used as a random factor. The standardized estimates are shown for the models. Next to the full model, two additional methods were used for model selection: backward model selection with Akaike Information Criterion (AIC) and a backward model selection with Bayesian Information Criterion (BIC). The best BIC model for the presence or absence of embryo dunes did not select any explanatory factors. BW, beach width.

Note: Levels of significance: • $p < 0.1$, * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$.





temperature. The time periods with the most severe storms were 1988 - 1996 and 2005 - 2010 (Fig. 3.4D). The highest storm intensity ($T_{\text{WLRT}(>10\text{y})}$) occurred three times in our dataset. Precipitation during the growing season and a high storm intensity ($T_{\text{WLRT}(>10\text{y})}$) were auto-correlated (Pearson correlation: -0.32, t-value = -4.53, $p < 0.001$). As the correlation was not very strong, we used both variables in our statistical analyses (see methods). Wind speed did not change significantly over the years ($F_{39} = 0.031$, $p = 0.85$) (Fig. 3.4A), wind speeds equal to or above the 7 m s^{-1} threshold were quite common, occurring between 2300 and 3900 hours/year. The most common wind direction was south-south westerly (onshore) to westerly (alongshore), ranging between 195 degrees and 285 degrees (Fig. A3.1).

Changes in beach volume (ΔBV_{0-3} , ΔBV_{0-1} , ΔBV_{1-3}) did not vary significantly over time (Fig. 3.4E) and ranged between -209 and +180 $\text{m}^3 \text{ m}^{-1} \text{ y}^{-1}$. The number of nourished sites increased after 1990 as a result of changes in coastal management, rising from 5 between 1979 and 1983 to 14 between 2005 and 2010. Nourishment was applied more often on narrow beaches than on wide beaches. The average beach width where sand nourishment was applied was 68 m (± 7 (SE)), whereas the average beach width without sand nourishment was 180 m (± 16 (SE)).

3.4.3 Changes in embryo dunes over time

Embryo dune area changed significantly over time ($F_{134} = 2.01$, $p = 0.02$). During the first time period (1979 - 1983) embryo dune area decreased on most sites (Fig. 3.5). This was followed by a steady increase over the next three time periods (1983 - 1988, 1988 - 1996, 1996 - 2005), with a decrease in the last time period (2005 - 2010). Despite large differences between the sites in embryo dune area, we found no significant effect of sites on embryo dune area and development ($F_{117} = 0.34$, $p = 1.00$).

Periods with an increase in embryo dune area had relatively high precipitation during the growing season and a low frequency of high-intensity storms ($T_{\text{WLRT}(>10\text{y})}$). We included both these variables in all four binomial models using either BIC or AIC as selection criteria (Table 3.2).

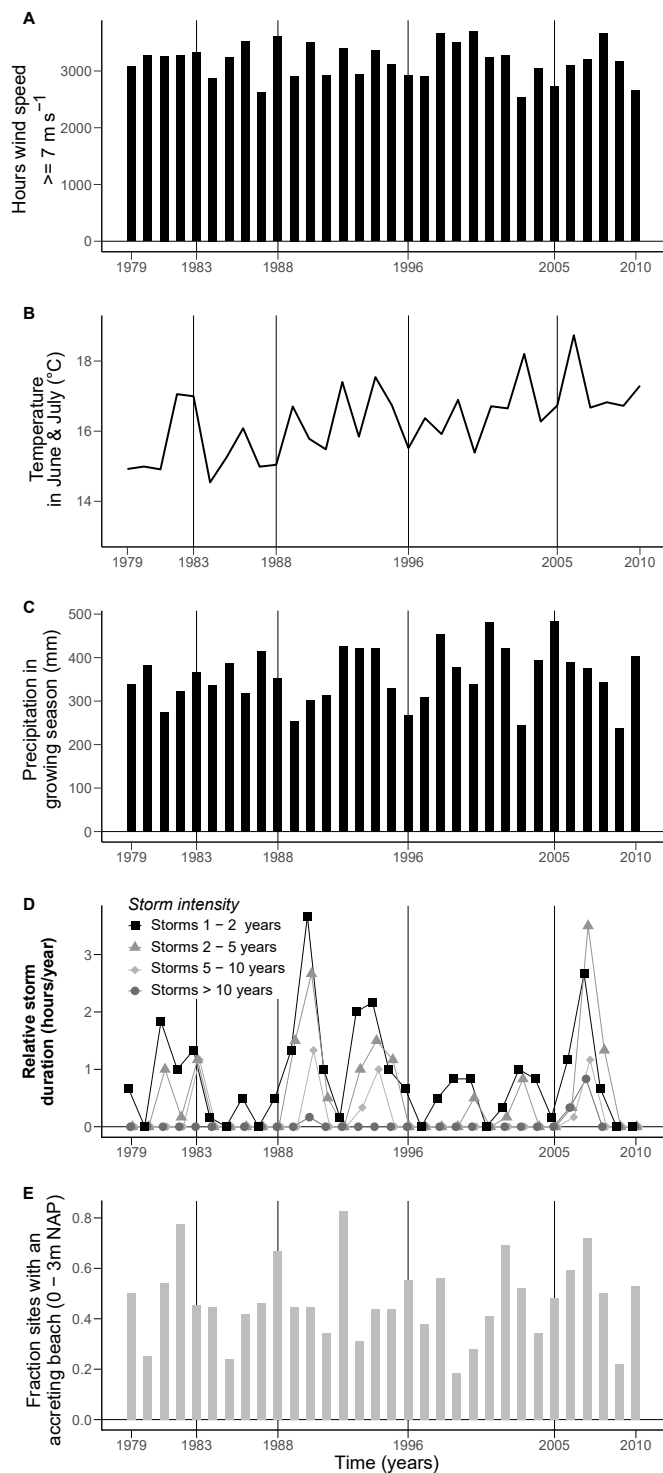


Figure 4. Environmental conditions over the study period. The vertical line represents the time points of the aerial photographs. The weather data is the mean of the two weather stations. A) Hours that the wind speed was equal to or greater than 7 m s^{-1} . B) Average temperature in June and July ($^{\circ}\text{C}$). C) Total precipitation during the growing period (mm). D) Occurrence of storm intensity (based on water levels, averaged over six tide stations), where the different shades and shapes represent the different storm intensity classes. E) Fraction of sites with an accreting beach (0-3 m NAP).



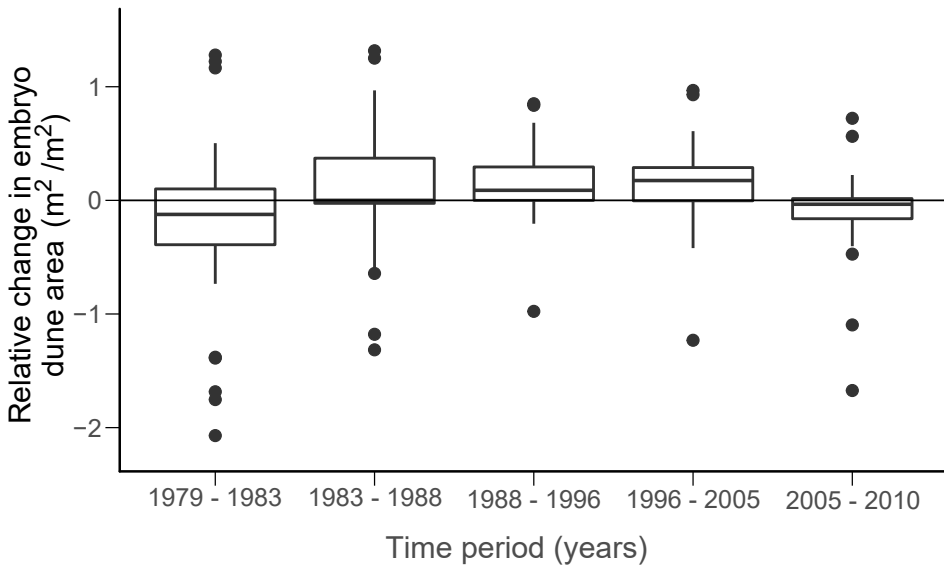


Figure 3.5. Boxplots showing relative change in embryo dune area (m^2/m^2) over five time periods. The middle line in the boxplot is the median, whereas the lower and upper hinges represent the 25% and 75% quartiles. The upper whisker extends from the hinge to the highest value that is within $1.5 \times$ the interquartile range of the hinge. The dots represent the values outside the $1.5 \times$ interquartile range.

Sand nourishment and storm intensity $T_{\text{WLRT}(5-10y)}$ were included only in the models with AIC as selection criteria. Embryo dune area increased more on beaches with sand nourishment than on beaches where no sand nourishment had taken place (Fig. 3.6A). An increase in the area of embryo dunes was positively correlated to growing season precipitation (Fig. 3.6B), whereas decreasing embryo dune area was correlated with high-intensity storms ($T_{\text{WLRT}(5-10y)}$ and $T_{\text{WL-RT}(> 10y)}$) (Fig. 3.6C+D). Changes in sand volume, hours wind speed ($WS \geq 7 \text{ m s}^{-1}$), temperature, storm interval, and beach width (BW_{1-3}) did not significantly affect the change in embryo dune area.

The relative change in embryo dune area (m^2/m^2 per site) responded to similar environmental drivers as the absolute change in embryo dune area (Table 3.2; Fig. 3.7). The relative change in embryo dune area was overall positive when the interval between storms was 100 weeks or longer. The explained variance in these linear models with relative change in embryo dune area (13%-16%) was much smaller than the variance explained in the binomial models with change in embryo dune area (25%-30%). It is possible that the long time periods between consecutive photographs, combined with the high stochasticity of the dune ecosystem, masked any relationship between the initial area of embryo dunes at the start of a period and the change in area observed over that period.

Table 3.2. Model selection for the increase or decrease in embryo dune area (binomial model) and the relative change in embryo dune area (linear model). All time periods were included in the models; the standardized estimates are shown. Four methods were used for model selection: a forward and backward model selection with Akaike Information Criterion (AIC) and a forward and backward model selection with Bayesian Information Criterion (BIC).

Factors	Full model	AIC forward	AIC backward	BIC forward	BIC backward
<i>Increase/ decrease in embryo dune area over time period, n=150</i>					
$\Delta BV_{1-3\text{ m}}$	0.27				
$\Delta BV_{0-1\text{ m}}$	-0.01				
$\Delta BV_{0-3\text{ m}}$	0.16				
Hours $WS \geq 7\text{ m s}^{-1}$	-0.79				
Temperature	0.37				
Precipitation	0.98	0.92*	0.92*	1.40***	1.40***
$T_{WLRT(1-2y)}$	0.50				
$T_{WLRT(2-5y)}$	0.25				
$T_{WLRT(5-10y)}$	-1.16	-0.94*	-0.94*		
$T_{WLRT(>10y)}$	-1.70	-1.80*	-1.80*	-1.90*	-1.90*
Storm interval	1.07				
Sand nourishment	1.07*	1.02*	1.02*		
$BW_{1-3\text{ m}}$	0.82	0.83●	0.83●		
Nagelkerke R^2	0.32	0.29	0.29	0.25	0.25
<i>Change in embryo dune area over time period, n=150</i>					
$\Delta BV_{1-3\text{ m}}$	0.23●	0.15●	0.18*		
$\Delta BV_{0-1\text{ m}}$	0.06				
$\Delta BV_{0-3\text{ m}}$	-0.08				
Hours $WS \geq 7\text{ m s}^{-1}$	-0.20●		-0.14		
Temperature	0.16				
Precipitation	0.24●	0.31***	0.31***	0.29**	0.29**
$T_{WLRT(1-2y)}$	0.05				
$T_{WLRT(2-5y)}$	0.06				
$T_{WLRT(5-10y)}$	-0.11				
$T_{WLRT(>10y)}$	-0.18		-0.13		
Storm interval	0.37*	0.26**	0.28**	0.26**	0.26**
Sand nourishment	0.03				
$BW_{1-3\text{ m}}$	0.04				
R^2	0.19	0.15	0.17	0.13	0.13
Adjusted R^2	0.10	0.13	0.14	0.12	0.12

Note: abbreviations: ΔBV , change in beach sand volume; WS , wind speed; T_{WLRT} , hours between water level return time, indicates storm intensity; BW , beach width. Levels of significance: ● $p < 0.1$, * $p < 0.05$, ** $p < 0.005$, *** $p < 0.001$.



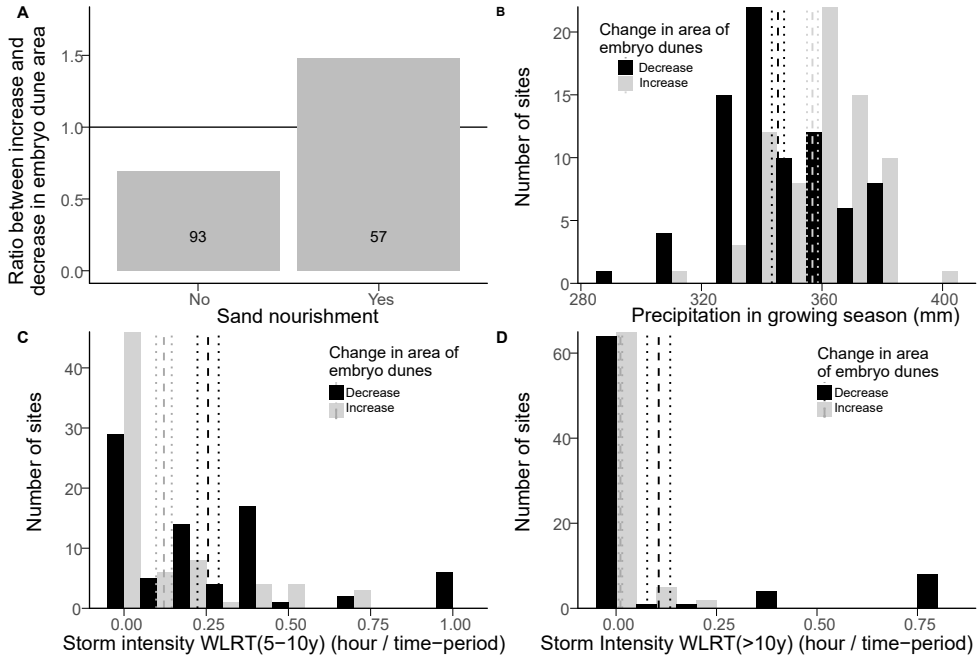


Figure 3.6. A) Ratio between increase and decrease in embryo dune area, for sites without (no) and with (yes) sand nourishment. Values above 1 indicate a net increase in embryo dune area. Values below 1 indicate a net decrease in embryo dune area in the time period analysed. The numbers indicate the quantity of replicates. B) Precipitation (mm) during the growing season for either an increase or decrease in embryo dune area. Dashed line indicates the mean and the dotted line the standard error. C) Storm of an intensity that occurs every 5-10 years (hours / time period $T_{WLRT(5-10y)}$) for either an increase or a decrease in embryo dune area. WLRT = water level return time. D) Storm of an intensity that occurs less than once every 10 years (hours/time period $T_{WLRT(>10y)}$) for either an increase or decrease in embryo dune area.

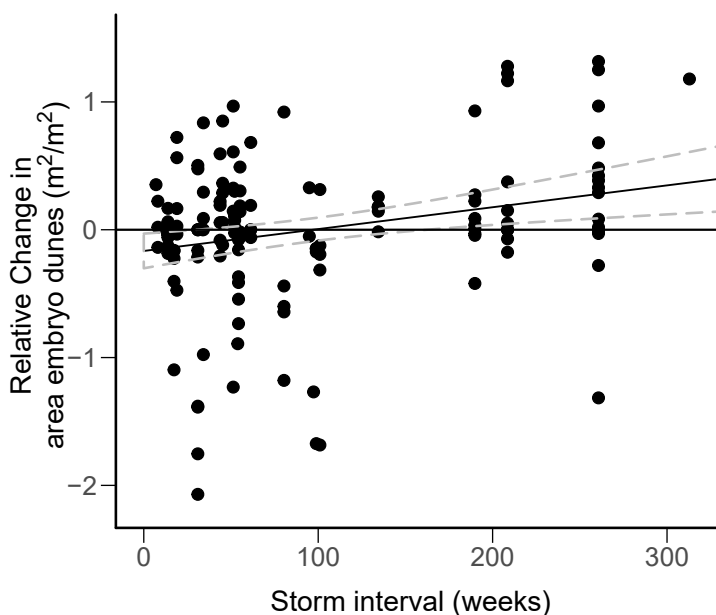


Figure 3.7. Relative change in embryo dune area (m^2/m^2) as a function of storm interval in weeks. The solid line represents the predicted values from a model with the storm interval as explanatory variable, the grey dashed line is the 95% confidence interval. $Y = 0.0017X + 0.165$, $p = 0.001$, $R^2 = 0.06$.

3.5 Discussion

3.5.1 Embryo dune development and environmental factors

This study explored boundary conditions for early dune development with the aim of enabling better prediction of natural dune expansion. Our results show a positive relationship between embryo dune area and beach width. Growth of embryo dune area was negatively correlated with storm frequency and intensity, and positively correlated with growing season precipitation and sand nourishment.

3.5.1.1 Beach morphology

We found embryo dune area to be most closely related to beach width. Among our study sites, large embryo dune complexes developed on beaches wider than 300 m, suggesting a high potential for the development of a new foredune ridge. There were a few locations where this was not the case, including sites having a small embryo dune area on a wide beach. Yet, these beach widths had only recently increased and vegetation had not had enough time to become established and thus not enough time for the formation of embryo dunes to begin.

The positive relationship found between beach width and embryo dune development points to several conclusions. First, the fact that only beach widths at between 1 m and 3 m NAP had an effect on embryo dune development suggests that the space available for embryo dunes to



develop, the accommodation space, is a key factor. Second, a minimum beach width, or fetch length, may be needed for maximum aeolian transport. On narrow beaches, the fetch length is shorter than on wide beaches, resulting in less aeolian transport (Davidson-Arnott et al., 2008; Nordstrom and Jackson, 1992) and less sand available for dune development. Previous research has shown the critical fetch distance for maximum aeolian transport to lie between 10 m and 50 m (Delgado-Fernandez, 2010; Dong et al., 2004; Shao and Raupach, 1992). This distance is much smaller than the beach width that we found necessary for maximum embryo dune development, suggesting that the fetch length was not the limiting factor in our study areas. Third, increased beach width could protect embryo dunes against storms, for example, by attenuating wave energy (Ruggiero et al., 2001). In our study it was not possible to separate these three factors. It is, however, clear that in the areas we investigated beach width strongly determined the potential for embryo dunes to develop.

Recent work by Durán and Moore (2013) suggests a relationship between beach width and foredune height, with wide beaches generally having higher foredunes than narrow beaches. Interestingly, we found an opposite relationship for our sites: wide beaches had lower foredunes than narrow beaches. This discrepancy may be related to beach morphology, as our study covered only dissipative beaches, whereas Durán and Moore (2013) examined a mix of dissipative and reflective beaches. An alternative explanation for the relationship we found between foredune height and beach width is the presence of embryo dunes. Embryo dune fields may constrain the height of foredunes by starving them of sand (Hesp, 1989; Montreuil et al., 2013). We explored whether using the width-height ratio might improve the fit of our statistical models. We found that large embryo dune fields occurred on beaches with a width to foredune height ratio of 10 m/m and larger. However, the relationship between this ratio and the area of embryo dunes was weaker than the relationship between beach width and embryo dune area, indicating that beach width is the better explanatory variable for our study region.

3.5.1.2 Storm characteristics

We found that high-intensity storms, occurring no more than once every 5 years, constrained embryo dune development, whereas low-intensity storms had no effect on embryo dune development. This suggests that the erosion caused by low-intensity storms was rapidly offset by aeolian sand caught by the vegetation in the following growing seasons. Additionally, we found that the storm interval influenced embryo dune development, as the erosion caused by storms occurring in rapid succession might be much greater than that from a single, larger storm (Dissanayake et al., 2015; Ferreira, 2006; Forbes et al., 2004; Lee et al., 1998). The effect of storm interval on embryo dunes indicates that recovery time is very important for the coastal system. Of course, recovery time cannot be seen independently of the regional storm climate of our study sites. For example, recovery times are likely to be far longer for hurricane-impacted coastlines, where embryo dune fields are likely to be completely eroded (Claudino-Sales et al., 2008).

3.5.1.3 Meteorological conditions

We found precipitation to stimulate embryo dune development, presumably because of its positive effect on the growth of dune-building plant species. Sandy beaches can become very

dry during summer (Lichter, 1998), precipitation increases soil moisture, water availability, and reduce soil salinity (Gooding, 1947). This benefits the growth of dune-building species, such as the grasses *A. arenaria* and *E. juncea*, and may even act as a trigger for germination (Maun, 2009; Sallenger et al., 2003).

We found no effect of wind speed on embryo dune development. A number of possible factors may explain for the absence of this correlation. First, aeolian sand transport may not be the limiting factor in the growth of embryo dunes. The amount of sand that vegetation can capture is determined by vegetation density and height (Zarnetske et al., 2012). If vegetation density and height do not change between consecutive transport events, the vegetation cannot capture more sand. The embryo dune is then in equilibrium condition, and does not increase in size. Second, the effect of storms may have overshadowed the effect of aeolian transport over our time periods. Third, the 7 m s^{-1} threshold proxy we used for aeolian sand transport may not have describe the actual transport at our sites, as it did not consider local conditions such as surface moisture and lag deposits (Davidson-Arnott et al., 2008; van der Wal, 1998). Furthermore, the vegetation's effectiveness at capturing sand depends on the wind speed (Buckley, 1987; Zarnetske et al., 2012). The effectiveness decreases at higher wind speeds, and at very high wind speeds, during storm events, erosion can occur. Our study used only a single threshold. Obtaining data to create multiple wind speed categories could yield different results for the effect of wind speed on embryo dune development. This would be, worthwhile avenue for in future research.

3.5.1.4 Sand nourishment

Sites with sand nourishment had an overall net increase in embryo dune area over the study period, whereas sites without sand nourishment had an overall net decrease. This pattern suggests that sand nourishment reduces erosion or promotes growth of embryo dunes. Sand nourishment is known to increase or stabilise beach width (Arens et al., 2013; van Duin et al., 2004; Grunnet and Ruessink, 2005). The wider beach, in turn, provides more accommodation space for embryo dune development, while perhaps also attenuating wave energy during storms and reducing wave erosion of embryo dunes (Ruggiero et al., 2001). Sand nourishment was primarily applied to the narrow beaches in our dataset. Although sand nourishment increases beach width, it does not create the very wide beaches that, our findings show, allow for large increases in embryo dune area. Still, sand nourishment on average increased dune development on narrow beaches.

The net effect of sand nourishment on embryo dune development likely depends on the type of nourishment applied. Beach nourishment was the most common type of nourishment in the period of our study. Beach nourishment generally results in an immediate increase in beach width. In contrast, nearshore nourishment has a more diffuse effect on beach width: beach width might merely be stabilised or might increase slowly over time (Hamm et al., 2002). Consequently the effect of such nourishment on the development of embryo dunes would likely be less strong than that observed in our study.



3.5.2 (Dis)similarities between embryo dune and foredune development

We found that embryo dune development was determined by beach morphology, storm intensity and interval, and precipitation during the growing season. These factors have been reported as drivers of foredunes development too. The biggest differences between findings on foredunes and our results lies in the strength of the relationships, as we found embryo dunes to generally be more sensitive particularly to storms. Moreover, precipitation effects on foredune growth have not been reported, although moisture plays an important role in dune vegetation growth (Greaver and Sternberg, 2010; Maun, 2009; Seeliger et al., 2000).

The positive relationship found in our study between beach width and dune development has also been reported in studies on foredunes (Anthony, 2013; Keijsers et al., 2014b; Saye et al., 2005), but the nature of the relationship differs. We found a linear relationship between beach width and embryo dune area for beaches wider than 300 m. However, Keijsers et al. (2014b) found that for foredunes the positive relationship between beach width and foredune development was no longer significant for beaches wider than 200 m. This suggests that embryo dunes are more sensitive to storm erosion than foredunes.

3.5.3 Windows of opportunity for embryo dune development

Our study suggests that embryo dune development depends on embryo dune survival over the storm season. Dune development is limited by storms, since small dunes can be completely eroded by wave run-up and storm surge. Bigger dunes, stand a better chance of surviving storm events (Claudino-Sales et al., 2008). This indicates that storm-free periods represent windows of opportunity (Balke et al., 2014; Durán Vinent and Moore, 2015) for embryo dune development, enabling new dunes to form and existing dunes to grow large enough to survive storm erosion. The required length of this window of opportunity depends on the lag time between storm erosion and the rebuilding of embryo dunes. Our results suggest that frequent precipitation during the growing season may reduce this lag time, as high precipitation stimulates plant growth and therefore embryo dune development.

The window of opportunity represents a useful concept for understanding embryo dune development in a changing climate. To take the next step, to predict embryo dune development according to climatic variables (e.g. storm interval and intensity, precipitation), we need to further examine the relationships between climatic variables and plant establishment, as well as the relationships between characteristics of embryo dunes and dune fields (e.g., volume and height) and their responses to dune erosion by wave run-up and storm surge. For example, we know very little about the effect of wave run-up and storm surge on different embryo dune sizes and whether such effects may be modified by plant species due to their wave attenuation effects, which reduce the wave energy (Koch et al., 2009).

3.5.4 Management implications

Sand nourishment is often applied locally on severely eroding coasts and has to be repeated frequently. With accelerated sea-level rise due to climate change, sand nourishment is likely to become more prevalent in the future. In the Netherlands, a large-scale ‘mega-nourishment’ pilot project under way that mimics the onshore migration of a large intertidal bar (the project

is called the 'Sandmotor', Stive et al., 2013; Temmerman et al., 2013). Such mega-nourishments create very wide beaches and thus accommodation space for dune development, possibly leading to development of a new foredune ridge. The effect of beach morphology on embryo dune area can be applied to predict how embryo dunes will develop in large mega nourishment projects.

Climate change will have a substantial impact on coastal areas (McGranahan et al., 2007; Nicholls and Cazenave, 2010). Climate change-induced sea-level rise combined with strong storms could lead to severe erosion of dunes (IPCC, 2014). Altered precipitation patterns may affect the lag period needed for dune to recover from storm erosion, as precipitation during the growing season stimulates embryo dune growth and rebuilding after storms. Embryo dune development might be constrained in areas where precipitation is expected to decrease, whereas embryo dune development might increase where precipitation is expected to rise. Coastal managers may thus be able to anticipate changes in embryo dune regeneration times by monitoring projected precipitation patterns in their region.

3.6 Conclusions

The purpose of this study was to explore the boundary conditions for embryo dune development. Our results show that, first, beach widths at between 1 m and 3 m NAP correlate positively with embryo dune development, suggesting that accommodation space is a key development factor. Second, beach nourishment stimulates embryo dune development by increasing beach width. Third, precipitation in the growing season enhances embryo dune development by increasing vegetation growth. Fourth, low-frequency and high-magnitude storms constrain embryo dune development by increasing recovery time. These results indicate that on wide beaches progressive dune development depends on precipitation and non-interrupted sequences of years without heavy storms.

3.7 Acknowledgements

We thank Rijkswaterstaat, Dunea and PWN for the use of their aerial photographs. We thank Rijkswaterstaat and KNMI for the use of their databases on beach morphology and climate variables. We further thank the technology foundation STW (grant number STW 12689 S4) for funding the NatureCoast project, which made this research possible. Finally, we thank the two anonymous reviewers for their useful and extensive comments on a previous draft of the manuscript.



Appendix 3.1 Photographs to illustrate the study site



Figure A3.1. Large embryo dune field on the Hors, Texel, The Netherlands (14-03-2014, photo by Marinka van Puij-enbroek).



Figure A3.2. Embryo dunes and foredune on Vlieland, the Netherlands (12-09-2013, photo by Marinka van Puijenbroek).



Figure A3.3. Large embryo dune field on Vlieland, the Netherlands (12-09-2017, photo by Marinka van Puijenbroek).



Appendix 3.2 The aerial photographs for each site

Table A3.1. For the 33 sites along the Dutch coast the years we have aerial photographs

Site	Years aerial photographs
Schouwen 1	1979, 1983, 1988, 1996, 2005, 2010
Schouwen 2	1979, 1983, 1988, 1996, 2005, 2010
Schouwen 3	1979, 1983, 1988, 1996, 2005, 2010
Goeree 1	1979, 1983, 1988, 1996, 2005, 2010
Goeree 2	1979, 1983, 1988, 1996, 2005, 2010
Goeree 3	1979, 1983, 1988, 1996, 2005, 2010
Zandmotor	1979, 1983, 1988, 1996, 2005, 2010
Den Haag	1979, 1983, 1988, 1996, 2005, 2010
Meijndel	1975, 1980, 1985, 1990, 1995, 2001, 2005, 2010
Noordwijk	1979, 1983, 1988, 1996, 2005, 2010
Ijmuiden	1979, 1983, 1988, 1996, 2005, 2010
Castricum	1979, 1983, 1987, 2005, 2010
Bergen aan Zee	1979, 1983, 1987, 1996, 2005, 2010
Texel 1	1996, 2005, 2010
Texel 2	1978, 1982, 1988, 1996, 2005, 2010
Texel 3	1978, 1982, 1988, 1996, 2005, 2010
Texel 4	1978, 1982, 1988, 1996, 2005, 2010
Texel 5	1978, 1982, 1988, 1996, 2005, 2010
Texel 6	1978, 1982, 1988, 1996, 2005, 2010
Terschelling 1	1979, 1983, 1996, 2005, 2010
Terschelling 2	1979, 1983, 1996, 2005, 2010
Terschelling 3	1979, 1983, 1996, 2005, 2010
Terschelling 4	1979, 1983, 1996, 2005, 2010
Terschelling 5	1979, 1983, 1996, 2005, 2010
Terschelling 6	1979, 1983, 1996, 2005, 2010
Ameland 1	1979, 1983, 1988, 2005, 2010
Ameland 2	1979, 1983, 1988, 1996, 2005, 2010
Ameland 3	1979, 1983, 1988, 1996, 2005, 2010
Ameland 4	1979, 1983, 1988, 1996, 2005, 2010
Ameland 5	1979, 1983, 1988, 1996, 2005, 2010
Schiermonnikoog 1	1979, 1983, 1988, 1996, 2005, 2010
Schiermonnikoog 2	1979, 1983, 1988, 2005, 2010
Schiermonnikoog 3	1979, 1983, 1988, 2005, 2010

Table A3.2. Resolution of aerial photographs

Time period	Average resolution of Aerial Photographs (m)
1979 - 1983	0.25
1983 - 1988	0.25
1988 - 1996	0.63
1996 - 2005	1
2005 - 2010	0.7



Appendix 3.3 Wind speed and direction over the 30 year time-series

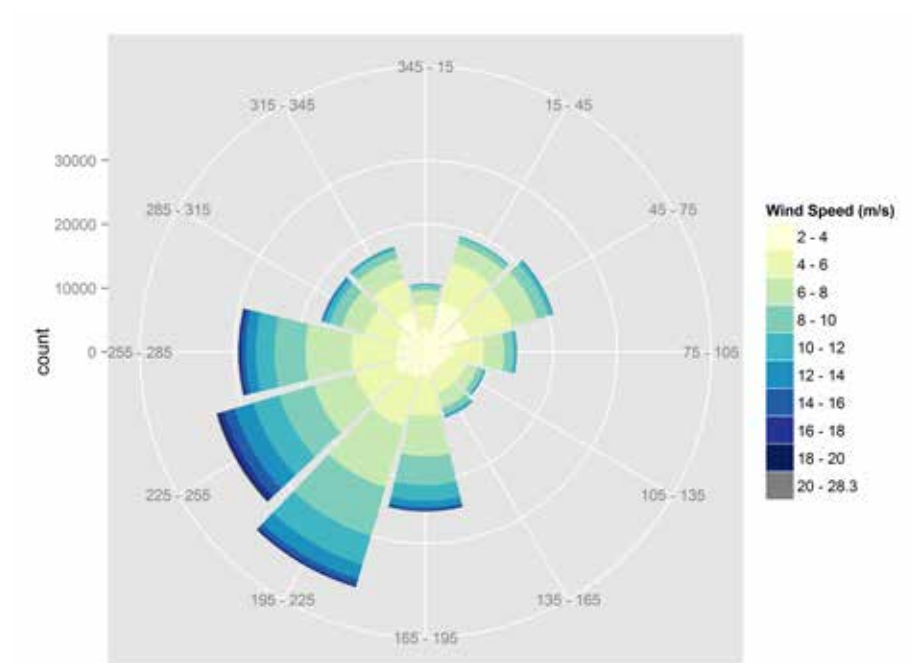


Figure A3.4. The wind speed and direction over the 30 year time-series. The wind rose shows the hours the wind came from a certain direction. The colours show the wind speed in m s^{-1} .



An aerial, black and white photograph of a desert landscape. The image shows numerous sand dunes of varying sizes, some with distinct ridges and troughs. Scattered across the dunes are dark, clumpy patches of vegetation, likely shrubs or small trees. The overall texture is granular and undulating. A white rectangular box is overlaid on the upper portion of the image, containing the chapter title and author information.

Chapter 4

Exploring the contributions of vegetation and dune size to early dune building using unmanned aerial vehicle (UAV)-imaging

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4.1 Abstract

Dune development along highly dynamic land-sea boundaries is the results of interaction between vegetation and dune size with sedimentation and erosion processes. Disentangling the contribution of vegetation characteristics from that of dune size would improve predictions of dune development under a changing climate, but has proven difficult due to scarcity of spatially continuous monitoring data.

This study explored the contributions of vegetation and dune size to dune development for locations differing in shelter from the sea. We monitored a natural dune field of 8 hectares, along the coast of the island Texel, the Netherlands, for one year using an Unmanned Aerial Vehicle (UAV) with camera. After constructing a Digital Surface Model and orthomosaic we derived for each dune 1) vegetation characteristics (species composition, vegetation density, and maximum vegetation height), 2) dune size (dune volume, area, and maximum height), 3) degree of shelter (proximity to other dunes and the sheltering by the foredune). Changes in dune volume over summer and winter were related to vegetation, dune size and degree of shelter.

We found that a positive change in dune volume (dune growth) was linearly related to dune volume over summer but not over winter. Big dunes accumulated more sand than small dunes due to their larger surface area. Exposed dunes increased more in volume than sheltered dunes over summer, while the opposite occurred over winter. Vegetation characteristics did not significantly affect dune growth in summer, but did significantly affect dune growth in winter. Over winter, dunes dominated by *Ammophila arenaria*, a grass species with high vegetation density throughout the year, increased more in volume than dunes dominated by *Elytrigia juncea*, a grass species with lower vegetation density. The effect of species was irrespective of dune size or distance to the sea.

Our results show that dune growth in summer is mainly determined by dune size, whereas in winter dune growth was determined by vegetation. In our study area the growth of exposed dunes was likely restricted by storm erosion, whereas growth of sheltered dunes was restricted by sand supply. Our results can be used to improve models predicting coastal dune development.



4.2 Introduction

Coastal dunes occur along the sandy shores of most continents (Martínez and Psuty, 2008), and are important to protect these coasts against flooding, provide areas for recreation, store drinking water and shelter unique biodiversity (Everard et al., 2010). Coastal dunes and their services are threatened by climate-induced sea-level rise (Carter, 1991; Feagin et al., 2005; Keijsers et al., 2016). However, dunes also provide self-adapting systems of coastal protection, since the threat by sea-level rise can be mitigated by the development of new dunes. Despite the obvious importance of dunes, we know surprisingly little about the factors that determine early dune development. Understanding these factors is essential for predicting dune development, and for safeguarding their services.

Dune development is the result of an interaction between vegetation and aeolian processes and starts above the high-water line by the establishment of dune-building plant species (Maun, 2009). Once vegetation establishes on the bare beach, it forms a roughness element that facilitates local sand deposition and reduces erosion, forming a small dune within discrete clumps of vegetation (Hesp, 2002). At the lee side of these small clumps of vegetation a shadow dune develops by sand deposition, this shadow dune has a ridge parallel to the wind direction (Hesp, 1981). Vegetation and shadow dune together are known as embryo dunes, or incipient dunes (Hesp, 2002; Hesp and Smyth, 2017). Their further development strongly depends on the balance between summer accumulation of sand and vegetation growth and winter erosion of sand and loss of vegetation (Montreuil et al., 2013). Summer growth and winter erosion depend on weather conditions, such as wind speed, precipitation and storm intensity (Montreuil et al., 2013; van Puijenbroek et al., 2017a). As a result, net dune growth can differ from year to year. Over time the smaller vegetated dunes can develop into an established foredune that forms the first line of coastal defense against flooding.

Most research on coastal dune growth and erosion have focussed on processes and factors that influence the supply of sand to the dunes and the effect of storm intensity on dune erosion (Anthony, 2013; Haerens et al., 2012; Houser et al., 2008; Keijsers et al., 2014; Saye et al., 2005; de Vries et al., 2012). However, how coastal dune growth and erosion rates are influenced by the individual dune characteristics, such as dune size, vegetation and degree of sheltering are less well studied. Dune size affects the wind flow pattern, thus affecting sand deposition (Walker and Nickling, 2002) for example increasing height or length of the shadow dune (Hesp, 1981; Hesp and Smyth, 2017). Dune size also influences storm erosion: Claudino-Sales (2008) found that foredunes with a higher volume were less sensitive to erosion. Whether the latter also applies to embryo dunes, is unknown. Differences in vegetation density between plant species are known to modify sand deposition, storm erosion, dune morphology, and growth (Charbonneau et al., 2017; Hacker et al., 2012; Seabloom et al., 2013; Zarnetske et al., 2012). Sheltering by other dunes can decrease the sand supply but can also reduce erosion by waves (Arens, 1996; Montreuil et al., 2013). Although dune size, vegetation and sheltering are known to be important for individual dune development, the relative contributions of these factors are unknown.

In this study, we explored the contribution of vegetation and dune size to dune development. Using an unmanned aerial vehicle (UAV) with camera we monitored a natural dune field for one year. From the aerial images we constructed a digital terrain model (DTM) and an orthomosaic.

From the DTM and orthomosaic we extracted detailed data on dune size (dune area, volume and maximum height), vegetation characteristics and the degree of sheltering. We related dune size and vegetation to changes in dune volume over a summer (April - August) and winter period (November - April). We expected dune growth to be a function of dune size and vegetation density, dune growth being the largest for big dunes with high vegetation density. We also expected that the effect of sheltering on dune growth would depend on season: exposed dunes growing faster in summer, but slower in winter.

4.3 Methods

4.3.1 Study area

We monitored 8 hectares (200 m x 400 m) of a natural dune field with a large range of dune sizes at 'the Hors', the southern tip of the barrier island at Texel, the Netherlands, coordinates: 52°59'43.70"N, 4°43'47.53"E (Fig. 4.1). The Hors is a wide dissipative beach with a high degree of hydrodynamic reworking of the sand, which results in a high transport potential and opportunity for dunes to develop. In the last 20 years many vegetated dunes have developed on the beach. At this area permanent dunes are formed by plant species *Ammophila arenaria*, *Elytrigia juncea* or a mixture of both species. These three types of vegetated dunes occurred at similar distances from the sea, making this area ideal for testing the effects of dune size and species composition on dune growth. *A. arenaria* and *E. juncea* differ in their vegetation characteristics: *A. arenaria* grows in dense patches, whereas *E. juncea* has a more sparse growth form. This difference in growth form probably also results into a different dune morphology: *A. arenaria* forms higher 'hummocky' shaped dunes, whereas *E. juncea* builds broader and lower dunes (Bakker, 1976; Hacker et al., 2012). The monitoring area is bisected by a low, continuous foredune ridge that runs parallel to the shore. The dunes that occur at the seaward side of this foredune are more exposed to the sea, while the dunes occurring at the landward side of the foredune are more sheltered from the sea, enabling us to explore whether the effects of dune size and vegetation are modified by the degree of shelter. The foredune in our monitoring area has a maximum height of 7 m NAP (NAP refers to Amsterdam Ordnance Date, which refers to mean sea level near Amsterdam).

Summer conditions during our study period were similar to previous years, while winter conditions were calmer than usual (Appendix 1). The precipitation during the growing season was 276 mm, and the average temperature in June and July was 16 °C. The most common wind direction was South to South-West. The most common wind speed in summer was 4 - 5 m s⁻¹, and the maximum wind speed was 13 m s⁻¹. In winter the wind speed was higher compared to summer, the most common wind speed was 5 - 6 m s⁻¹ and the maximum wind speed was 19 m s⁻¹. We registered one storm during the study period. This storm, however, could be classified as relatively weak. The highest water level was 211 cm NAP; compared to 248 cm NAP and 254 cm NAP from previous years. The storm, which was the first of the season, occurred after the beginning of our mapping campaign.





Figure 4.1. Overview of the Hors on Texel, the Netherlands. The white lines show the flight path for the four different flights. The points show the position of the ground control markers. The white polygon is the monitoring area, which is 200 m x 400 m. Map source: Image © DigitalGlobe, Data SIO, NOAA, U.S. Navy, NGA GEBCO, 2017 Google, date: 30-05-17

4.3.2 Data collection

Three UAV flights in November (2015), April (2015) and August (2016) were carried out with a rotary octocopter UAV system (Aerialtronics Altura Pro AT8 v1) and camera equipment of WageningenUR Unmanned Aerial Remote Sensing Facility. The octocopter was equipped with a Canon EOS 700D single-lens reflex camera with a 28mm f/2.8 Voigtländer Color Scopar SL-II N objective. The camera sensor was modified to give a false colour output. The red channel of the camera had been converted to be sensitive in the near-infrared, with centre point around 720 nm. The blue channel of the camera had been extended to also cover the UV region of the spectrum. The green channel was left with almost original response. The false colour modification enabled the calculation of a modified Normalised Difference Vegetation Index (NDVI), a commonly used measure for vitality and/or cover of the vegetation (Carlson and Ripley, 1997). Aerial images were acquired by auto-piloted flights at an altitude of 80 m at 4 – 5 m s⁻¹ velocity. The camera was set to take one image per second. The auto-piloted flights enabled us to have the same flight paths for each of the three mapping campaigns.

The flight paths ensured that images had a minimum of 85% forward and 65% side-way overlap. Four flights of 10 minutes were needed to cover the study area, yielding up to 900 RAW false colour images per mapping campaign. Five ground control points were permanently placed in the flight area and measured with a RTK-DGPS Trimble R6 Model 3 (TSC3) to calibrate our images with coordinates. During our mapping campaign, a Spectralon reference panel was measured with our camera immediately before take-off and after landing.

4.3.3 Radiometric calibration

In order to compare the images over the time, they were calibrated and converted from RAW to 16 bit tiff format. First, we ensured that each individual pixel within an image was comparable, by converting the RAW digital number into radiance units using a pixel-wise dark current and flat field calibration. Second, each radiance image was calibrated to a reflectance factor image in order to correct for changes in incident irradiance on different flight days. This calibration was done by using a Spectralon panel with a known reflectance factor. The radiometric calibration is described in more detail by Suomalainen et al. (2014).

The images were subsequently converted into NDVI images. Usage of the standard NDVI was not possible due to lack of red channel in the false color modified camera. Thus we used a custom NDVI equation (Eq. 1), which was recommended by the company that modified the sensor. On their website (MaxMax.com) this equation was shown to be just as effective for green vegetation as the traditional NDVI formula ($R^2 = 0.77$), where the red band is taken as the absorption channel.

$$1) \quad NDVI = \frac{(NIR + G) - (2B)}{(NIR + G) + (2B)}$$

Where NIR, G, and B are the near-infrared, green and blue bands of the false colour image respectively. For photogrammetric reconstruction, the NDVI image layer was stacked with the original green and blue bands to form a three-color image.

4.3.4 Photogrammetric reconstruction

The large overlap between the consecutive images was necessary for photogrammetric software to successfully process the aerial images into a 3D point cloud. The 3D point cloud was generated using Agisoft Photoscan Professional (v. 1.2.6), using the Structure-from-Motion (SfM) and Multi-View Stereo (MVS) algorithms (Fonstad et al., 2013; Westoby et al., 2012). The correlated 3D points are georeferenced to match the ground control points, and contain pixel intensity values of the input imagery. From this 3D point cloud we interpolated a 5 cm pixel size digital surface model (DSM) and a 1 cm pixel size orthomosaic image. The vertical error distribution of a DSM produced by UAV photogrammetry is expected to be equivalent to airborne LIDAR data and terrestrial laser scanning (Hugenholtz et al., 2013; Mancini et al., 2013). The DSM included also vegetation, which resulted in a vertical error in dune height in areas where vegetation is present. We removed the vegetation from the point cloud by identifying and removing the vegetation points. Vegetation points were removed by distinguishing vegetation from sand using k-means clustering of the 3-D point cloud with NDVI using the Hartigan and Wong (1979) algorithm in R (R Core Team, 2016). The holes in the point cloud that arose by removing the vegetation were filled by using LAStools (the tool Blast2dem) (Isenburg, 2016), which resulted in a Digital Terrain Model (DTM) without vegetation.



4.3.5 Defining dunes

To be able to relate dune growth to characteristics of an individual dune, we first had to define individual dunes from the DTM. We followed a step-wise procedure for each of our mapping campaigns (November, April, and August) using ArcGIS 10.3 (ESRI, 2016) that resulted into different polygons in which each individual dunes expanded or decreased in volume over the study period. Dune size and growth were later calculated using the same polygons for each measurement campaign through time (see next section). To define the polygons we used the step-wise procedure described below: 1) we constructed a baseline raster by calculating the average elevation in a circle of 5 m radius around each pixel in the DTM. A higher or lower radius resulted in either a too low or too high baseline. 2) We then qualified pixels of the DTM as dunes, if they were 5 cm above a baseline raster, or had a slope of 15° or higher. From these selected 'dune' pixels we created dune polygons. 3) Dune polygons of consecutive campaigns were overlaid to construct the largest dune-covered area during the study period. 4) Each polygon was visually checked for minimum size and presence of vegetation: dunes consisting of only one clump of vegetation (0.4 m² or smaller) and dunes with no vegetation were discarded.

4.3.6 Variables

For each dune and for each mapping campaign we extracted dune volume (m³), max height (m) and horizontal area (m²) from the dune polygons (see previous section) in the DTM. We calculated the absolute change in dune volume by subtracting the current dune volume from the volume of the previous mapping campaign, and we corrected for the number of weeks between the mapping campaigns. To explore relationships irrespective of dunes size, we also calculated the relative change in dune volume per week as $(V_t/V_{t-1})/\text{week}$. Where V_t is the dune volume and V_{t-1} the dune volume of the previous mapping campaign.

We manually identified the species composition on each dune from the orthomosaic. Species identification was verified in the field for a random subset of 100 dunes (23%). To this end we created 2 transects from the southwest border to the northeast border of the area. For these transects we determined the species on each dune in the field in May 2016. We compared the presence of species in the field with the orthomosaic, and adjusted the species composition if necessary. In our dataset, dunes have either *A. arenaria*, *E. juncea* vegetation, or a mixture of both species. A dune was defined as covered by a mixture of both species, when it had distinct vegetation patches of both species present. For each dune and mapping campaign we also extracted the vegetation density and the maximum plant height. To assess vegetation density we first distinguished vegetated pixels from non-vegetated pixels based on the orthomosaic using k-means classification of the NDVI using the MacQueen (1967) algorithm. Hereafter, the vegetation density (NDVI/cm² dune) was calculated by summing the NDVI values of all vegetated pixels within the dune polygon and then dividing this summed NDVI by the total number of cm² pixels within the dune polygon. The maximum plant height was calculated by subtracting the DTM (with vegetation) from the DSM (without vegetation).

Sheltering can affect the sand supply and storm erosion. We used two methods to define the extent of sheltering. Firstly, we distinguished whether a dune was seaward or landward from the foredune. Secondly we determined how much a dune was clustered with other dunes. We

extracted the degree of clustering for each dune by calculating the mean height from the DTM in a 25 m radius around the dune. All data extraction from the DSM, DTM and orthomosaic were done in R (R Core Team, 2016).

4.3.7 Statistical analysis

First we explored if dune area, volume, maximum dune height, clustering (mean height in a 25 m radius around the dune), vegetation density and maximum plant height depended on species composition using August 2016 data. As the number of dunes per species composition was unequal, we used an ANOVA type III SS, to compensate for the unequal sample size (Fox and Weisberg, 2011) and then used a Tukey HSD test (Hothorn et al., 2008) to determine significant differences between the dunes with different species compositions.

Secondly, we tested how absolute changes in dune volume over winter (November – April) and summer (April – August) periods related to the dune volume at the beginning of the period at location with different degree in sheltering with a linear regression model.

Thirdly, we analysed how the relative changes in dune volume over winter and summer depended on dune size and vegetation characteristics in separated linear mixed models (Pinheiro et al., 2009). To correct for spatial autocorrelation and species distribution we ran this analyses on a subset of 236 (54%) dunes. To this end we first explored the degree of spatial autocorrelation in our dataset by creating a variogram. To account for the spatial autocorrelation of 25 m in our dataset we imposed a 50 m x 50 m grid over our study area; all dunes that were located within a grid cell (referred to as block) were assumed to show spatial autocorrelation to some extent. This spatial autocorrelation was corrected for in our statistical model by including block as a random intercept. We had 10 blocks seaward from the foredune and 11 blocks landward from the foredune (Fig. 2), in which all species combinations occurred (*A. arenaria* dunes, *E. juncea* dunes and *A. arenaria* + *E. juncea* dunes). By only including dunes that were located within a block in the analysis, our selection was biased towards smaller dunes, since larger dunes often fell within multiple blocks. We do expect that the effect of vegetation is more apparent for these smaller dune compared to larger dunes. To better distinguish between effects of species compositions and vegetation structure we used two different models. The effect of species composition was tested in a model with dune volume, maximum dune height, clustering and species, whereas the effect of vegetation structure was tested in a model with dune volume, maximum dune height, dune clustering, vegetation density and maximum plant height as explanatory variables. Within each model we used the initial conditions for the explanatory variables, with initial conditions being the values at the start of each measurement campaign. We included all two-way interactions. We selected the best model by using Akaike information criterion (AIC). As we were mainly interested in the importance of the explanatory variables relative to each other, we calculated the standardised estimates for all the models by scaling the explanatory data.

The normality and homogeneity of the variance of the data was visually checked. All statistical analyses were conducted in R (R Core Team, 2016). In the results we use statistic notation to show the results of the ANOVA and linear regression models. We mention the F-value (ANOVA) or t-value (linear regression), which indicates the difference of the explanatory variable to the



variation in the data. The p -value indicates the probability that the null-hypothesis is correct, we used a p -value of 0.05 as a cut off to reject the null-hypothesis. The number in subscript indicates the degrees of freedom.

4.4 Results

4.4.1 Dune characteristics

Within the 8 hectare dune field we distinguished 434 polygons that were covered with dunes for at least one moment during our mapping campaigns. Most of the dunes were *E. juncea* dunes (50.23%), followed by *A. arenaria* dunes (28.11%) and mixed dunes (22.66%) in August 2016. Species composition of the dunes changed along a gradient from sea to land. Close to the sea dunes were vegetated by *E. juncea*, while, further from the sea, dunes were also vegetated by *A. arenaria* alone, or in a mix with *E. juncea* (Fig. 4.2). Landward of the foredune dunes were also vegetated by *E. juncea*, *A. arenaria* alone, or a mix of both species. The foredune bisecting our study area was mainly vegetated with *A. arenaria*.

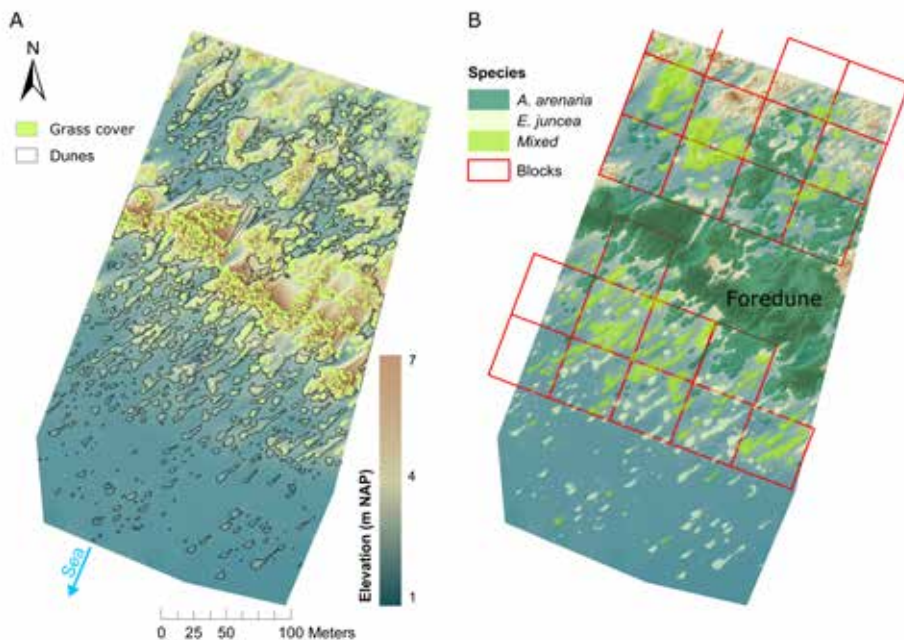


Figure 4.2. Overview of the monitoring area. A) The elevation is shown with the Digital Terrain Model (m NAP), the green pixel indicates grass cover and the polygons indicate the dunes. B) The colour indicates the species present on the dune and the squares the blocks. The foredune in the middle of the monitoring area is excluded from the statistical analysis. Some dunes that were cut-off by the edge of the DTM, we discarded these dunes.

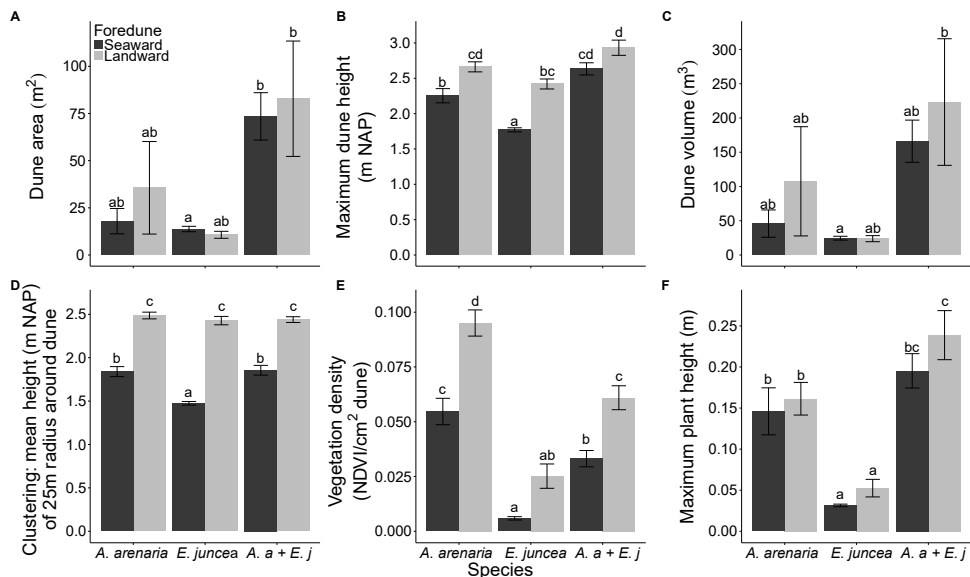


Figure 4.3. Different dune characteristics for dunes in August with *A. arenaria*, *E. juncea* and a mix of both species separated for dunes seaward and landward of the foredune: A) Dune area, B) Maximum dune height, C) Dune volume, D) Clustering: mean height around a 25 m radius around the dune, E) Vegetation density, F) Plant height. The letters denote the significant difference between the bars. Seaward of the foredune there were 41 *A. arenaria* dunes, 198 *E. juncea* dunes, and 53 dunes with both species, landward of the foredune there were 81 *A. arenaria* dunes, 23 *E. juncea* dunes, and 41 dunes with both species. NAP refers to Amsterdam Ordnance Date, which refers to mean sea level near Amsterdam

In August 2016 dune area, volume and maximum height differed significantly between dunes differing in species composition (volume: $F_{2,428}=3.05$, $p=0.048$; max. height: $F_{2,428}=59.6$, $p < 0.001$), but did not differ between dunes contrasting in shelter. Dunes with a mix of *E. juncea* and *A. arenaria* had overall the highest volume and maximum height, whereas *E. juncea* dunes had the lowest volume and height. *Ammophila arenaria* dunes had the largest range in dune volume (Fig. 4.3A, B, C). For *E. juncea* dunes seaward from the foredune the distance between dunes was higher compared to *A. arenaria* dunes and dunes with both species ($F_{2,428}=52.5$, $p < 0.001$), the distance between dunes landward from the foredune was overall smaller than dunes seaward from the foredune (Fig. 4.3D, $F_{1,428}=70.2$, $p < 0.001$). The dune volume did not significantly differ between dunes seaward and landward from the foredune (volume: $F_{1,428}=0.76$, $p=0.39$), but the dune height above NAP was significantly higher for dunes landward from the foredune ($F_{1,428}=15.9$, $p < 0.001$).

For the statistical model with relative change in dune volume as response variable, we had to correct for species distribution and spatial autocorrelation. We created a grid, with blocks of 50 m x 50 m, and we selected dunes that fell within a block. In total, we selected 236 dunes, which consisted of 41.95% of *E. juncea* dunes, 36.02% of *A. arenaria* dunes, and 22.03% of dunes with both species. These subset of dunes had an overall lower dunes size compared to all the dunes, but had overall similar dune morphology and vegetation characteristics (Appendix 2).

Vegetation characteristics depended on the plant species dominating the dunes and on the degree of shelter. *E. juncea* dunes had significantly the lowest vegetation density, *A. arenaria* dunes the highest and dunes which consisted of both species had an intermediate vegetation density (Fig. 4.3E, $F_{2,428}=49.30, p<0.001$). Similar to vegetation density, *E. juncea* dunes also had the lowest maximum plant height, whereas *A. arenaria* and dunes consisting of both species had the highest maximum plant height (Fig. 4.3F, $F_{2,428}=42.70, p<0.001$). Dunes landward from the foredune had significantly higher vegetation densities compared to seaward dunes ($F_{1,428}=45.7, p<0.001$). There was no significant difference in maximum plant height between dunes seaward and landward from the foredune ($F_{1,428}=0.41, p=0.52$).

4.4.2 Change in dune number and volume

The number of dunes within the measurement area changed over time, with dune numbers declining over winter and increasing during summer. The degree of dynamics depended on season, species and degree of sheltering.

4.4.2.1 Summer

Of the 434 dunes present in August 2016, 22.36% appeared over summer (April – August). Most of these new dunes (65.93%) were *E. juncea* dunes, 31.87% were *A. arenaria* dunes and only 2.20% were mixed dunes. Most (73.63%) new dunes developed seaward from the foredune and were quite small in size with a volume of $2.72 \pm 0.29 \text{ m}^3$ (mean \pm SE). We assumed that most of these dunes established over the growing season, as the orthomosaic showed a large amount of wrack line material (plant material, woody debris, rope etc.) in their polygon in November and April. However we cannot exclude that part of the large increase in the smaller *E. juncea* over summer is a result of their poor recognition in November and April.

Over summer, most dunes increased in dune volume, including the foredune which increased over summer with 0.28% per week, reaching a volume of $64,444 \text{ m}^3$ in August. Only 4.15% of the dunes showed a small decrease in the volume with a mean of $-0.041 \pm 0.014 \text{ m}^3/\text{week}$. Changes in dune volume were positively related to dune volume (Fig. 4.4A, $t\text{-value}_{430} = 57.20, p<0.001$) and were higher for dunes seaward of the foredune compared to dunes landward of the foredune, resulting in a significant effect of shelter ($t\text{-value}_{430} = -41.70, p<0.001$).

Over summer, the relative change in dune volume was mainly influenced by sheltering, where the relative change in dune volume was higher seaward of the foredune compared to landward of the foredune (Fig. 4.5A). We found no significant difference in relative change in dune volume between dunes with different species composition (Fig. 4.5A, Table 4.1). In our statistical model plant height had a statistically significant effect on the relative dune growth. However, when tested in a single linear mixed model with block as random intercept, plant height had a R^2 of 0.0038, thus hardly explaining any variation in relative dune growth (Table 4.2). Several dune size variables were significant, but the individual variation explained by dune volume, and dune height was very low, their R^2 ranging between 0.05 – 0.0033. The significant interactions between variables were mostly caused by the slight correlations between the explanatory variables. The clustering of dunes did not significantly affect the relative dune growth. We tested

whether the effect of clustering was masked by the use of blocks as random intercept, since the amount of clustering was different between the blocks. We re-analysed the data without the blocks as random factor and found again no effect of clustering on the relative growth rate of dunes.

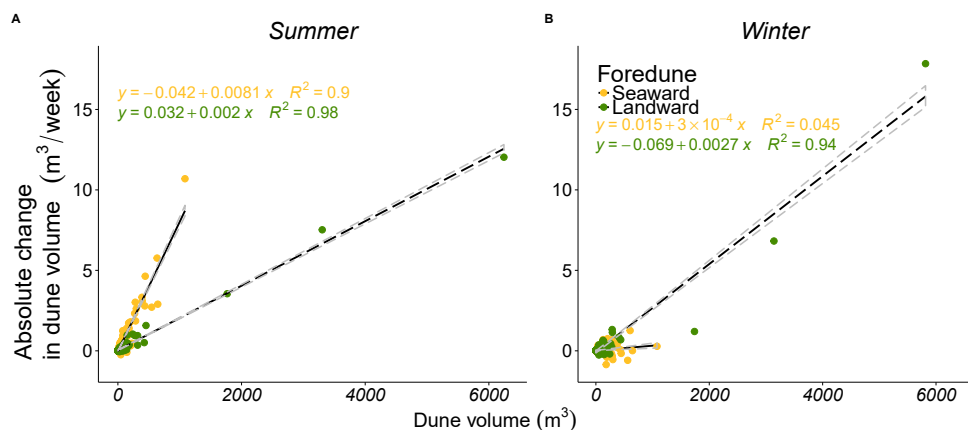


Figure 4.4. The relationship between dune volume (m³) and the absolute change in dune volume (m³/ week) for: A) summer (April – August); B) winter (November – April). The data is shown for dunes seaward and landward of the foredune. The black line shows the regression prediction, the grey dashed line the 95% confidence interval. The formulas are the result of a linear regression model.

4.4.2.2 Winter

Over winter (November – April) 7.85% of the 344 dunes disappeared, of which 40.74% were *E. juncea* dunes, 55.56% were *A. arenaria* dunes and 3.70% dunes with both species. These dunes disappeared both seaward (40.74%) and landward (59.26%) from the foredune and were overall quite small with an average volume of 2.23 ± 0.19 m³.

Over winter dunes still increased in volume, the large foredune even increased with 0.22% per week. However on average the changes in dune volume was less positive than over summer, 21.20% of the dunes decreased -0.061 ± 0.015 m³/week in volume, particularly seaward of the foredune. 25.00% of these decreased dunes were covered with *A. arenaria*, 50.00% with *E. juncea* and 25.00% with both species. The absolute change in dune volume between November and April was positively related to dune volume in November (Fig. 4.4B, $t\text{-value}_{430} = 2.1$, $p = 0.033$), but was only significant for dunes landward of the foredune. Dunes seaward of the foredune showed no relationship between absolute change in dune volume and the dune volume in November (shelter: $t\text{-value}_{430} = 16.37$, $p < 0.001$).

The relative change in dune volume was influenced by species composition and degree of shelter (Table 4.1). Dunes with *E. juncea* increased relatively less in volume than *A. arenaria* dunes (Fig. 4.5B); this effect was only significant for dunes seaward of the foredune. We found no significant relationship between relative change in dune volume and vegetation density or maximum plant height (Table 4.2). There was a significant interaction between vegetation density and sheltering by the foredune, which could be related to the higher vegetation density



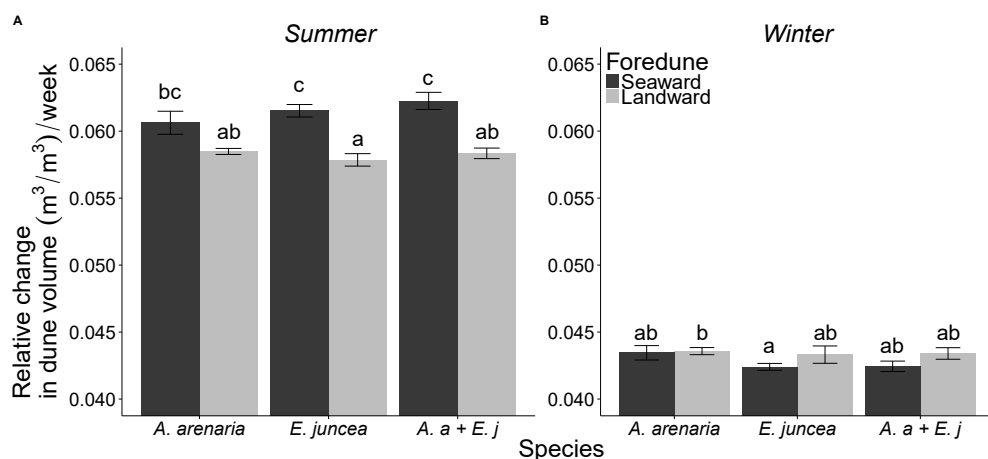


Figure 4.5 Relative change in dune volume ($\text{m}^3/\text{m}^3/\text{week}$) for dunes with *A. arenaria*, *E. juncea* and a mix of both species and separated for dunes seaward and landward of the foredune for: A) summer, April – August; B) winter, November – April. The letters denote the significant difference between the bars. Seaward of the foredune there were 28 *A. arenaria* dunes, 77 *E. juncea* dunes, and 28 dunes with both species, landward from the foredune there were 57 *A. arenaria* dunes, 22 *E. juncea* dunes, and 25 dunes with both species.

at the dunes landward of the foredune. Dune volume, the position relative to the foredune, had a significant negative effects on the relative change in dune volume, whereas clustering had a positive significant effect, but the relationship was very weak (R^2 between 0.002 – 0.05).

4.4.3 Net dune growth

Net absolute dune growth per week over the whole observation period November – August was higher at the seaward side of the foredune than at the sheltered landward side (slope seaward dunes: 0.37%, slope landward dunes: 0.25%, dune volume*position from foredune: $t\text{-value}_{430} = -11.7, p < 0.001$). Seaward dunes also had a slightly higher relative change in dune volume over November to August compared to the landward dunes (seaward dunes: 0.27 ± 0.00009 ($\text{m}^3/\text{m}^3/\text{week}$), landward dunes: 0.026 ± 0.0001 ($\text{m}^3/\text{m}^3/\text{week}$), $F\text{-value}_{1,230} = 18.51, p < 0.001$).

Table 4.1. Statistical models for the relative change in dune volume between April – August (summer) and November – April (winter). In this model we tested the effect of species, dune size, and degree of sheltering. The data was analysed with a general linear mixed model with blocks as random intercept. The standardized estimates and level of significance are shown for the models. Model selection was performed with AIC (Akaike information criterion) as selection criteria. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Model with species	Dependent variable			
	Relative change in dune volume			
	Summer		Winter	
	Full model	Model selection	Full model	Model selection
<i>Main effects</i>				
Intercept	1.18***	1.17***	0.92***	0.94***
<i>E. juncea</i>	-0.02		0.005	-0.02**
Mix	0.02		0.02	-0.003
Dune volume	6.10	8.27***	-6.0*	-3.43**
Clustering	-0.22	-0.18	0.22	0.23
Max. dune height	-0.25	-0.31*	0.15	0.087
Sheltering by foredunes	0.29*	0.31**	-0.31**	-0.31**
<i>Interaction effects</i>				
<i>E. juncea</i> * Dune volume	0.90		1.90	
Mix * Dune volume	-0.11		1.41	
<i>E. juncea</i> * clustering	0.11		0.04	
Mix * clustering	0.01		-0.006	
<i>E. juncea</i> * max. dune height	-0.08		-0.09	
Mix * max. dune height	-0.02		-0.033	
<i>E. juncea</i> * Shel. by foredune	-0.05		0.03	
Mix * Shel. by foredune	-0.02		0.001	
Dune volume * clustering	-4.64*	-5.65**	4.44**	4.10**
Dune volume * max. dune height	-1.16	-2.01*	0.62	
Dune volume * Shel. by foredune	1.85	2.00*	-1.11	-1.31*
Clustering * max. dune height	0.31	0.34*	-0.29	-0.27*
Clustering * Shel. by foredune	-0.12	-0.17*	0.12	0.13
Max. dune height * Shel. by foredune	-0.20*	-0.18*	0.19**	0.19**
Marginal R^2	0.31	0.31	0.25	0.23
Conditional R^2	0.34	0.33	0.39	0.39
Observations	236	236	236	236
Akaike Inf. Crit.	-632.60	-685.45	-673.10	-709.11
Bayesian Inf. Crit.	-555.08	-641.04	-595.57	-661.35

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$



Table 4.2. Statistical models for the relative change in dune volume between April – August (summer) and November – April (winter). In this model we tested the effect of vegetation characteristics, dune size and degree of sheltering. The data was analysed with a general linear mixed model with blocks as random intercept. The standardized estimates and significance values are shown for the models. Model selection was performed with AIC as selection criteria. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Model with vegetation characteristics	Dependent variable:			
	Relative change in dune volume			
	Summer		Winter	
	Full model	Model sel.	Full model	Model sel.
<i>Main effects</i>				
Intercept	1.24***	1.24***	0.90***	0.81***
Vegetation density	-0.003		-0.05	-0.03
Max. plant height	0.15	0.14**	0.04	
Dune volume	8.65***	6.62***	-2.72	-3.67**
Clustering	-0.21	-0.23	0.29	0.40**
Max. dune height	-0.44*	-0.41**	0.07	0.17
Sheltering by foredune	0.26*	0.29*	-0.28*	-0.25**
<i>Interaction effects</i>				
Veg. density * max. plant height	-0.01		0.001	
Veg. density * dune volume	0.83		0.92	
Veg. density * clustering	-0.03		0.078	0.06
Veg. density * max. dune height	0.04		-0.03	
Veg. density * Shel. by foredune	-0.005		-0.03	-0.04**
Max. plant height * dune volume	-0.58		-0.19	
Max. plant height * Clustering	0.02		-0.06	
Max. plant height * max. dune height	-0.11	-0.10**	0.04	
Max. plant height * Shel. by foredune	0.004		-0.01	
Dune volume * clustering	-6.37**	-6.30***	4.51**	4.65***
Dune volume * max. dune height	-1.54		-1.11	
Dune volume * Shel. by foredune	1.63	1.95*	-2.23*	-1.82**
Clustering * max. dune height	0.40*	0.41**	-0.32	-0.42**
Clustering * Shel. by foredune	-0.15	-0.17*	0.05	
Max. dune height * Shel. by foredune	-0.16	-0.16*	0.28**	0.31***
Marginal R^2	0.33	0.31	0.24	0.21
Conditional R^2	0.37	0.35	0.42	0.40
Observations	236	236	236	236
Akaike Inf. Crit.	-622.85	-674.05	-656.46	-704.97
Bayesian Inf. Crit.	-542.07	-626.28	-575.68	-657.20

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

4.5 Discussion

The aim of this study was to explore the contributions of vegetation and dune size to dune development and how these effects are modified by the degree of shelter. We expected dune growth to be a function of dune size and vegetation density, dune growth being the largest for big dunes with high vegetation density. We also expected that the effect of sheltering on dune growth would depend on season: exposed dunes growing faster in summer, but slower in winter. Our results show that the contribution of vegetation and dune size depended on season and degree of shelter. In summer dune volume change was explained by dune size and to a lesser extent by dune height, while species composition, vegetation height or density had no effect. In winter dune volume change was explained by vegetation and dune size, depending on the degree of shelter. Exposed dunes with sparsely growing *E. juncea* grew less in volume than exposed dunes with densely growing *A. arenaria*. In contrast, growth of sheltered dunes was a function of dune volume. These findings are the first to show the relative contribution of vegetation and dune size for dune development over a winter and summer season, and these results can be used for modelling coastal dune development.

4.5.1 Dune size

4.5.1.1 Summer growth

We found a positive linear relationship between dune volume and the absolute change in dune volume over summer. It is known that dunes affect sedimentation by changing the wind flow patterns (Dong et al., 2004; Li et al., 2008). Previous studies have found that with increased dune volume the area where the wind speed is reduced increases, which result in higher sedimentation rates (Hesp, 1981; Hesp and Smyth, 2017). The linear relationship between dune volume and dune growth found in our study indicates that different dune sizes have similar effect on the wind flow pattern per unit of area. This result has also been found in a modelling study by Walmsey and Howard (1985), who found that different sized desert barchan dunes experienced similar disruptions of wind flow patterns, suggesting similar relative rates of deposition and erosion.

Our study focussed on a relatively small size range. It is likely that the linear relationship between dune volume change and dune size will saturate when dunes continue to grow and processes other than wind speed reduction become important. The latter is supported by the volume change of the low foredune bisecting our study area. Over summer the large foredune increased 0.28% per week in volume, which is much lower than the overall increase of 0.81% per week of the dune seaward of foredune. Therefore, we expect that there is a critical dune size at which the relationship between dune volume and absolute dune growth is no longer linear. However, what exactly the critical dune size is, is difficult to predict, it probably depends on multiple factors such as available sediment supply and vegetation growth. The wind flow patterns are not only influenced by dune volume, but also by maximum dune height (Walker and Nickling, 2002). In our study we found a significant, albeit weak effect of the maximum dune height on the relative growth, suggesting differences in height did not have a large effect on the wind flow pattern and the subsequent deposition of sand.



The positive linear relationship between dune volume and dune growth was modified by sheltering; dunes landward of the foredune increased 0.60% per week less in volume than dunes seaward of the foredune. This reduction in dune growth rate is likely the result of decreased sand supply landward of the foredune; presumably a large amount of the sand was captured by the foredune as was also observed for other foredunes (Arens, 1996). In our study the decrease in sand transport was less sharp as observed by Arens (1996), however the difference in foredune sink strength between the foredune in our study and those measured in Arens (1996) could be related to its smaller size, its relatively low height and/or its sparse vegetation cover of 29% (Keijsers et al., 2015). Clustering of dunes did not have any significant effect on the relative growth rate, which suggests that these smaller dunes do not significantly reduce the sand supply to the landward situated dunes.

4.5.1.2 Winter

In winter dune size was only a good predictor for growth of the dunes occurring landward of the foredune. For these sheltered dunes, growth again followed a linear relationship with dune volume. The absence of a relationship between dune size and dune growth for the exposed dunes occurring seaward from the foredune, suggests that dune erosion is less dependent on dune size than dune growth. Dune erosion has mainly been attributed to wave run-up during storms (Haerens et al., 2012; Vellinga, 1982). Therefore, it seems reasonable to assume that the degree of erosion depends on whether the dune can be reached by high energy waves. Large dunes that are reached by high water levels can erode substantially, whereas small dunes can have no erosion if they are protected by other dunes from the high water.

Interestingly, the sheltered dunes had a slightly higher dune growth in winter compared to summer. This increase in dune growth can perhaps be explained by more frequent and/or intensive aeolian transport events during winter resulting into higher sand supply to the sheltered dunes.

4.5.2 Vegetation characteristics

Vegetation characteristics were a poor predictor of dune volume change over the summer period, but were a significant predictor for dune volume change over winter. Over summer dune growth did not differ between dunes covered by different dune building plant species when corrected for dune size. Similarly we did not find a clear effect of vegetation density and plant height on dune growth. This results contrast with other studies that report a significant difference in the ability of species to trap sand mediated by differences in shoot density and cover (Keijsers et al., 2015; Zarnetske et al., 2012). Perhaps the discrepancy with our study can be explained by the differences in spatial scale used between studies. We studied dune volume change at the scale of a dune, whereas the other studies focussed on the scale of the vegetation patch, where species specific effects are probably more pronounced than at the scale of the whole dune. Also Al-Awadhi and Al-Dousari (2013) found that the effects of vegetation on dune growth are scale dependent for coastal dunes. They found that the linear relationship between shrub vegetation characteristics and dune morphology levels off for bigger dunes. In our statistical models we selected the smaller dunes, which was a consequence of only selecting dunes that were located within one block. However even for these smaller dunes vegetation had no significant effect on relative dune growth.

Over winter *E. juncea* dunes had a significantly lower relative growth rate than *A. arenaria* dunes, presumably because of their higher sensitivity to erosion. This species-effect might be related to the sparser growth form of *E. juncea* in comparison to *A. arenaria* as dense vegetation has been found to reduce the amount of dune erosion, by more effective wave attenuation (Charbonneau et al., 2017; Koch et al., 2009; Silva et al., 2016). However, the effect of vegetation density was not significant in our model suggesting that the species effect might be due to other species differences, such as differences in rooting pattern. Another explanation is that the vegetation density measurement did not reflect the real vegetation density, *E. juncea* was difficult to detect due to the low NDVI values. The species effect was only significant for dunes situated at the exposed, seaward side of the foredune where erosion by water likely occurred during the single storm covered by our study period. Despite being statistically significant, the differences in relative growth rate between exposed *A. arenaria* and *E. juncea* dunes was not very large. Nevertheless the species effect might become more pronounced with higher erosion pressure during more stormy winters (Charbonneau et al., 2017).

Interestingly, our species did show differences in dunes size. On average, *A. arenaria* dunes were higher than *E. juncea* dunes, that were broader (Bakker, 1976; Zarnetske et al., 2012). This difference in dune morphology suggests a higher sand catching efficiency of *A. arenaria* that might be masked by using dune volume, mean height or dune area as explanatory variables. We explored whether there is an effect of species composition on the change in maximum dune height over summer, but found no consistent effect. Perhaps the difference in dune morphology could be a result of differences in erosion between the dune types over winter.

4.5.3 Implication for dune development

4.5.3.1 Net dune growth

Exposed dunes had an overall higher net growth compared to sheltered dunes, indicating that summer growth offset winter erosion in our study period which was characterised by an average summer and calm winter. This balance might have been different if winter conditions had been more severe.

During winter, storms determine the erosion of dunes seaward of the foredune. Multiple low-intensity storms can lead to more erosion than one high-intensity storm (Dissanayake et al., 2015; Ferreira, 2006; van Puijenbroek et al., 2017a). Whether exposed dunes have a higher net dune growth compared to dunes landward from the foredune depends mainly on the storm intensity and frequency. A single high-intensity storm can erode all the sand that exposed dunes have accumulated over a whole summer, and in such case sheltered dunes could have a higher growth rate than the exposed dunes. The exact relative growth rate over summer depends on the number of aeolian transport events. Linking the number of aeolian transport event to the relative growth rate over summer would be a worthwhile avenue for future research.

Sand supply and storm intensity are also affected by local conditions as beach morphology. A minimum beach width is needed to reach maximum aeolian transport, the fetch length (Delgado-Fernandez, 2010; Dong et al., 2004; Shao and Raupach, 1992). Our study site had a wide beach (0.9 km wide), and we assume that the maximum aeolian transport was reached. The net growth of our foredune was approximately 30 m³ per m foredune parallel to the sea for a



period of 10 months. This growth rate does also occur at other places along the Dutch coast, but is not very common (Keijzers et al., 2014). Storm intensity is also influenced by beach morphology. The presence of intertidal bars and a wide beach can reduce the storm intensity by wave attenuation (Anthony, 2013; Ruggiero et al., 2004). Therefore we can assume that the net dune growth we found in our study will depend on the beach morphology. On smaller beaches we expect the net dune growth to be lower compared to wider beaches, due to the lower sand supply by reduced fetch length and higher storm erosion of dune (van Puijenbroek et al., 2017a)

4.5.3.2 Vegetation

For coastal dune development vegetation is essential, however the species-composition of the vegetation seems less important than we assumed: species did not seem to affect dune growth over the summer, but did affect dune growth over winter. We did find differences in dune morphology between the species, which indicates an effect of species composition on dune morphology. However, this difference in dune morphology is probably also caused by vegetation succession. In Western Europe, the primary succession of coastal dunes is generally assumed to start with *E. juncea*. Only after a fresh water lens has developed in the *E. juncea* dune, *A. arenaria* will establish (Westhoff et al., 1970). Over time *A. arenaria* will outcompete *E. juncea*. This assumed succession pathway matches part of the spatial patterns that we found in our study site and explains why dunes with only *E. juncea* are relatively small. Over time these small dunes merge together after which *A. arenaria* is assumed to establish. However, we found that *A. arenaria* has a large range in dune volume suggesting that, contrary to current assumptions, *A. arenaria* can also establish on the bare beach without *E. juncea*, as long as the soil salinity is not too high.

At our study site only two dune building species occur, however there are many different dune-building species. It could very well be that other dune building species do have a significant effect on the dune growth over summer. For further research it would be interesting to study if these results are similar in another dune system with different plant species.

4.5.3.3 Application

To our knowledge, we are the first to report on the relationship between dune volume and dune growth in the field. The linear relationship that we found in our studies can be incorporated in mathematical models that predict dune development. Furthermore, our research shows that for predicting dune growth species identity does not matter during the summer, however it does matter during the winter. This indicates that for dune building models, species identity is especially important when winter survival of dunes is modelled. Furthermore, for the construction of an artificial dune it appears to be crucial to plant the more storm resistant species.

Despite the presence of smaller dunes seaward of the foredune, the foredune showed a large increase in volume compared to similar foredunes along the Dutch coast. This indicates that sand supply to the foredune was not seriously hampered by the presence of the small vegetated dunes, while the smaller dunes seaward of the foredune likely added to the protection of the foredune against storm erosion. For coastal management it could be beneficial for foredune growth to have embryo dunes seaward of the foredune given a high sand supply.

4.6. Conclusions

The purpose of this study was to explore the contribution of vegetation and dune size on dune development at locations differing in shelter from the sea. Our results show that 1) the contribution of vegetation and dune size depend on season and degree of shelter. 2) Species composition does not affect dune growth over summer, but does affect dune growth during winter, particularly at exposed sites. 3) During early dune development, dune growth is linearly related to dune volume, whereas dune volume does not seem to matter for dune erosion. 4) Sheltering by a foredune reduces both sand supply and dune erosion; the net effect of shelter on dune growth therefore likely depends on beach morphology and weather conditions. These results can be incorporated in models predicting dune development and can be used by managers to determine coastal safety.

4.7 Acknowledgements

We thank Ministry of Defence and Staatsbosbeheer to allow UAV flights in their nature area. We thank the technology foundation STW (grant number STW 12689 S4) for funding the NatureCoast project, which made this research possible.



Appendix 4.1 Weather conditions

Table A4.1. Weather conditions in the years 2013 – 2016. For temperature the average is shown, and the precipitation was summed. For the precipitation in summer we summed the precipitation between the months April - August

Year	Temp. June & July (°C)	Temp. Januari & Februari (°C)	Total precipitation (mm)	Precipitati-on Summer (mm)
2013	15.67	2.25	553.2	163.1
2014	17.40	5.96	714.8	360.6
2015	15.98	4.47	804	283.8
2016	16.38	4.90	708.2	275.9

Table A4.2. Storm intensity in the years 2013 – 2016. The storm duration is calculated as the time the water level is above the water level recurrence of once a year.

Year	Storm duration (min)	Maximum water level (cm)
Winter 2013 - 2014	530	254
Winter 2014 - 2015	410	248
Winter 2015 - 2016	10	211



Figure A4.1. The wind speed and direction for the years 2013 - 2016. The wind rose shows the percentage the wind came from a certain direction over the time-period 2013 - 2016. The colours show the wind speed in m s^{-1} .

Appendix 4.2 Dune morphology selected dunes

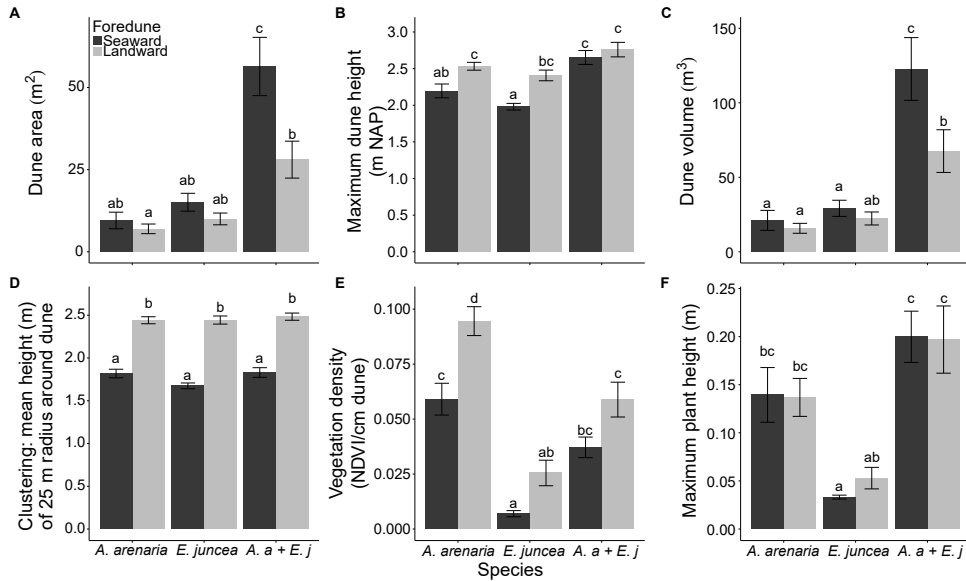


Figure A4.2. Different dune characteristics for dunes within the blocks and separated by species and sheltering: A) Dune area (m²), B) Maximum dune height (m NAP), C) Dune volume (m³), D) Clustering: mean height (m NAP) around a 25 m radius around the dune, E) Vegetation density (NDVI/cm dune), F) Plant height (m). The letters denote the significant difference between the bars.





Chapter 5

Can beach morphology explain green beach vegetation and species turn-over?

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5.1 Abstract

Questions 1) How does beach geomorphology affect the abiotic soil conditions in the rooting zone? 2) Which abiotic conditions drive diversity and turn-over of green beach vegetation?

Location West-Frisian Barrier Island Schiermonnikoog, the Netherlands.

Methods We set out 107 plots along 11 transects from beach to dune. We characterised transect geomorphology (elevation, distance to the sea, volume of embryo dunes and volume of secondary dunes). Within the plots we measured environmental conditions (soil salinity and organic layer thickness) and characterised the vegetation (species composition, species richness, Shannon-Wiener diversity index, evenness, and cover) in 2006 and 2016. Plant species composition and species turn-over were related to geomorphological setting and abiotic conditions.

Results In 2006 beach width was an important factor in explaining total species richness, with the highest number of species occurring at the shorter beaches. More specifically, dune slack and salt-marsh species were separated along a gradient of soil salinity and had the highest species richness on beaches with a large volume of embryo dune. In 2016, species richness was positively associated with the build-up of soil organic matter. Declines in species richness and species turn-over were accompanied by an increase in elevation as a result of sand burial and an expansion of taller grasses and shrubs. For dune-slack species the decline was associated with expansion of embryo dune volume.

Discussion We conclude that the geomorphological setting influenced the vegetation indirectly by affecting the abiotic factors soil salinity and sand burial. We found that plant species richness declined less at sheltered conditions, where there is a build-up of organic matter and no sand burial. Our results suggest a non-linear relationship between embryo dunes volume and plant species richness: embryo dunes can be a source of shelter, thus increasing plant species richness, but can also compete for space, thus lowering plant species richness. The net effect of embryo dunes most likely depends on the sediment budget of the beach and storm intensity, illustrating the need for linking vegetation development to sediment dynamics and wider coastal setting. This study can be used to better predict the development of green beaches.



5.2 Introduction

Sandy beaches occur along the coastline of many continents and are either accreting or eroding depending on the sand budget (Short & Hesp, 1982). Accreting beaches continuously create space for primary plant succession, which usually starts with the development of embryo dunes. At some locations, embryo dune development is accompanied by the establishment of rare pioneer communities, forming so-called green beaches or green strands (Edmondson et al., 2001; Bakker et al., 2005). As these green beaches are high in biodiversity compared to other coastal habitats (Speybroeck et al., 2008), they significantly contribute to the overall plant biodiversity of the regional coastal ecosystem, thus representing a high conservation value (European Commission, 2007; Acosta et al., 2009). At present we do not know how abiotic soil conditions and the geomorphological setting, such as shelter by embryo dunes, affect the plant diversity and species turn-over in green beach vegetation.

Species occurrence in coastal ecosystems is mainly determined by gradients in salinity, sand burial, moisture and soil development, which in turn are related to beach and dune morphology (Rozema et al., 1983; Packham & Willis, 1997; Maun, 2009). It is generally assumed that green beaches develop at locations that are slightly sheltered from the erosive force of the sea and heavy sand deposition. Indeed, historically green beaches have been recorded from wide beaches or beaches sheltered behind intertidal bars (Edmondson et al., 2001; Bakker et al., 2005; Kers & Koppejan, 2005; van Tooren & Krol, 2005) or constructed sand drift dykes (Joenje & Thalen 1968). Although wide beaches are often associated with high rates of sand transport (Wright & Short, 1984), they may also attenuate waves better than a narrow beach (Ruggiero et al., 2001), thus providing shelter against sea erosion. It has been hypothesised that the development of embryo dunes may facilitate green beach development by offering additional shelter against sea erosion and sand burial (Bakker et al., 2005), but until now this has not been backed up by evidence.

Embryo dunes do not only potentially offer shelter, but may also act as sources of fresh water seepage within the saline environment (Röper et al., 2013). They may thus act in concert with the larger secondary dune complexes at the landside of the green beach (Stuyfzand, 2016), enabling the coexistence of salt-sensitive dune slack species and salt-tolerant salt-marsh species (Lammerts & Grootjans, 1998; Grootjans et al., 2002).

Once plants have established, plant growth will result in the development of an organic layer. With the increase in organic matter, nutrient availability may increase, eventually enabling the more competitive species to become dominant (Berendse et al., 1998). The successional pathways can change due to changes in beach morphology. Sand burial and storm erosion can fully set-back succession (Maun, 1998; Feagin et al., 2005; Silva et al., 2016) but can also change the direction of succession by changing abiotic conditions related to elevation or reduced shelter by eroding embryo dunes (Maun & Perumal, 1999).

Consequently, vegetation succession depends on stress factors and stochastic disturbance events which have the potential to set-back vegetation succession or change the direction of the successional pathway. The reduction of stress and disturbance by dunes on a wide beach allows for quicker succession. Highest species diversity is predicted to occur under intermediate disturbance conditions, where succession can take place under sheltered conditions, but

is reset by a disturbance event before competitive species can become dominant (Connell, 1978). However, if disturbance is accompanied by changes in abiotic conditions it might not result in higher plant diversity, as is suggested by this theory. To what extent a change in beach morphology affects the succession of green beaches has not yet been investigated.

In this study we explored the relative importance of abiotic soil conditions as affected by the geomorphological setting on the diversity and species turn-over of green beach vegetation. We addressed the following questions: 1) how does beach geomorphology affect the abiotic conditions in the rooting zone? 2) Which abiotic conditions drive green beach vegetation and its turn-over? To answer these questions we set out 107 plots along 11 transects from beach to dune on the Dutch barrier island Schiermonnikoog. We characterised transect geomorphology (elevation, distance to the sea, volume of embryo dunes and volume of secondary dunes), and within the plots measured environmental conditions (soil salinity and organic layer thickness) and characterised the vegetation (species composition, species richness, Shannon-Wiener index, evenness, and cover) in 2006 and 2016.

5.3 Methods

5.3.1 Study site and plot selection

The West-Frisian barrier island Schiermonnikoog has wide dissipative sandy beaches with a high degree of hydrodynamic reworking of the sand, which results in a high aeolian transport potential and a concomitantly high potential rate of sand burial. The westward facing beaches on Schiermonnikoog are facing the tidal inlet between the West-Frisian islands Ameland and Schiermonnikoog (Fig. 5.1). The northward facing beaches are facing the North Sea. The beaches on Schiermonnikoog have been accreting since the period 1980 – 1990, which has resulted in wide beaches, compared to other Dutch beaches. Especially the westward facing beaches are very wide, in 2016 the beach width ranged between 1040 m and 2545 m. The northward facing beaches were narrower, but still had a beach width between 375 m and 815 m, wide enough to support large embryo dune complexes (van Puijenbroek et al., 2017a). At all beaches a foredune was present, most beaches also had secondary dunes landward from the foredunes, except for the most eastern part of the island. At these beaches only an man-made foredune was present. We established 11 transect along the beaches on Schiermonnikoog (Fig. 5.1). These transects represent the variation in beach morphology on Schiermonnikoog. Along all transects, the establishment of green beach vegetation started around the year 2000 ((Bakker et al., 2005), with the development of microbial mats (Stal et al., 2010, Bolhuis et al., 2013).

We selected 107 plots positioned along the 11 transects in 2006, which we revisited in 2016. In 2006 the transects started at the foot of the foredune and every 20 m along the transect a plot of 2 m x 2 m was established, and the last plot was at the edge of the vegetation limit. In 2016, the transect started again at the foot of the foredune and every 20 m we established a plot, the last plot was either the last plot measured in 2006 or at the edge of the vegetation limit. For 6 out of 11 transects this difference in the end of the transect resulted in less plots in 2016 compared to 2006. We only included plots that were measured in both years in our analyse, resulting in 107 plots and 8 – 14 plots per transect.



5.3.2 Transect morphology

Beach width (m) and embryo dune volume (m^3/m) were derived for each transect by using cross-shore elevation profiles for 2006 and 2015. The cross-shore profiles correspond precisely with the position of the transects. Cross-shore elevation profiles for 2006 and 2015 were obtained from the JarKus database (Rijkswaterstaat, 2014a). This database contains annual elevation measurements covering foredune, beach, and foreshore, and has been used in several studies addressing coastline dynamics from an annual to a decadal scale (Bochev-van der Burgh et al., 2009; de Vries et al., 2012; Keijsers et al., 2014b; Keijsers et al., 2015; van Puijenbroek et al., 2017a). The distance between elevation measurements along each profile is 5 m. Profile elevation was measured using laser altimetry, which resulted in an accuracy of 0.1 m (De Graaf et al., 2003; Sallenger et al., 2003).

We calculated beach width and embryo dune volume from the profiles for each transect. To calculate beach width, we defined the beach area as the expanse between the shoreline and the foredune, i.e. between 0 m and +6 m NAP (NAP refers to Amsterdam Ordnance Datum, which is equal to mean sea level near Amsterdam), the length of the beach area being the beach width. The beach width was subtracted from the distance of the plot from the foredune to calculate the distance to the sea for each plot. Embryo dune volume per transect was calculated as the area (m^3/m) under the curve of the beach area between +2 m and +6 m NAP,



Figure 5.1. Aerial photograph of our study area Schiermonnikoog in 2016 (Kadaster / Clyclomedia 2016). The grey part of the lines indicate the position and orientation of the transects, and the red part of the lines the plot locations. The texts indicates the transect number and the beach width of the transect. Transects I-III are westward facing, transects IV-XI are northward facing.

as well as the change in embryo dune volume between 2006 and 2015.

Volume of secondary dunes for each transect was calculated by creating a profile extending 500 m from each transect landward, including the foredune. To create the profile we measured the elevation at 5 m interval from a digital elevation model of 2014 (Rijkswaterstaat, 2014d). We only used the digital elevation model of 2014, since we did not expect any significant changes in the volume of secondary dunes between different years (Arens et al., 2013). The volume of secondary dunes was calculated as the area under the curve (m^3/m) for each profile.

The GPS-coordinates (Garmin eTrex GPS Basic, 4 m – 5 m accuracy) for each plot were used to obtain the approximate elevation from laser altimetry data of the coast from 2006 and 2016 (Rijkswaterstaat, 2006; Rijkswaterstaat, 2015). We calculated the change in elevation between 2006 and 2016 by subtracting the elevation data.

5.3.3 Environmental characterisation of the rooting zone

Not all abiotic variables were measured for both years. In 2006 none of the plots had an organic matter layer, so no soil development had taken place. In 2016, some soil development had taken place and therefore we measured organic layer thickness. For the measurement of the organic layer thickness we took three soil cores of 5 cm diameter up to 50 cm depth, and we averaged the organic matter layer thickness over the three cores. Since all plots in 2006 had no organic matter layer, the change in organic layer thickness equalled the organic layer thickness in 2016.

The measurement of soil salinity differed as well between 2006 and 2016. In 2006, groundwater salinity was measured as Electrical conductivity (EC) with an EC meter (Eurotech instruments, EcoScan, COND 6+). In the 41 plots where the groundwater was below 60 cm, no salinity measurements were performed, leading to a lower sample size for soil salinity. We ran two different analyses exploring the effects of salinity on species diversity: one analysis with the deep-groundwater table plots set as missing values and one analysis for which we exchanged the missing values with the lowest value of groundwater salinity that was measured in our plots (0.05 mS/cm). The latter choice was based on the significant negative relationship between groundwater depth and groundwater salinity (Ibrakhimov et al., 2007), which we also found for other Dutch beaches with similar geomorphological settings ($t\text{-value} = -3.52$, $p=0.0047$, $R^2=0.53$). In 2016 we measured the soil salinity with an EC meter. The soil salinity was measured by making a compound soil sample using rhizosphere soil (10 – 40 cm depth) from the three soil cores. Samples were weighted, dried at 105°C for 18 hours, and weighted again to determine the gravimetric soil moisture content. Dried samples were diluted on a 1:5 mass basis with distilled water and shaken for 2 hours, after which the EC was measured. Values were multiplied with a factor 17 to derive the E_{ce} at saturated conditions (Shaw, 1994). We did not calculate the change in soil salinity from 2006 to 2016 since groundwater salinity and soil salinity are not directly comparable.



5.3.4 Vegetation sampling

Vegetation assessments of each plot were made using the extended Braun-Blanquet scale for the estimation of coverage (van der Maarel, 1979). Nomenclature of plant species followed van der Meijden et al. (2005). Nomenclature of plant communities is according to Weeda et al. (2003). For the calculation of the diversity and the statistical analyses, ordinal scale measurements were later transformed to interval type cover percentages (van der Maarel, 2007).

We calculated the species richness, species evenness, cover as well as the Shannon-Wiener diversity index; these indices provide information on vegetation patterns and species diversity and are commonly used in vegetation science (Shannon, 1948; Mulder et al., 2004). We calculated the indices for 1) all species and for subsets of species characteristic of 2) young dune slacks, 3) salt marsh and 4) green beaches (subset 2 and 3 together). For young dune slack we considered the following plant community associations to be characteristic: Parnassio-Juncetum articipilli, Junco baltici-Schoenetum nigricantis, and Cicendietum filiformis. For the salt marshes we used the plant community associations within the orders Thero-Salicornietalia and Glauco-Puccinellietalia. From these plant community associations we selected species that had a 10% faithfulness for that particular association (Appendix 5.1, for an overview of all species), using the software package SynBioSys (Hennekens et al., 2010). Out of the in total 126 recorded species, 42 species were considered characteristic of green beaches. Of these 42 species 15 species were characteristic of dune slack vegetation whereas 30 were characteristic of salt-marsh vegetation. Three species *Odontites vernus* subsp. *serotinus*, *Parapholis strigosa*, and *Carex distans* were characteristic of both salt-marsh and dune-slack vegetation. The dune-slack species mainly encompassed stress tolerant short herbs and grasses, of nutrient poor and moist soils with low salinity (Ellenberg et al., 1991). Ten of these fifteen species are endangered and highly protected in the Netherlands, such as *Liparis loeselii*, *Schoenus nigricans*, and *Sagina nodosa*. The salt-marsh species mainly encompassed short grasses and herbs (*Artemisia maritima*, *Limonium vulgare*, and *Puccinellia maritima*) of moist, saline and basic soils, but also included more taller and competitive grasses and shrubs (*Elytrigia atherica*, *Juncus maritimus*, *Festuca rubra*, and *Salix pentandra*) (Ellenberg et al., 1991).

We calculated the change in species richness, Shannon-Wiener diversity index, cover, and evenness between 2006 and 2016 for all species, as well as for green beach, dune-slack, and salt-marsh species separately. Furthermore we analysed the impacts of factors that caused plant mortality. Therefore we calculated the species turn-over, the fraction of stable species in each plot, which is the number of species that occurred in the same plot in 2006 and 2016 divided by the total number of species in 2006.

5.3.5 Statistical analyses

5.3.5.1 Abiotic factors

For the statistical analysis we explored how the abiotic factors were correlated with beach morphology. We analysed the electrical conductivity, moisture content, organic layer thickness and change in elevation with a linear regression model. The electrical conductivity, moisture content, and organic layer thickness were analysed with elevation, distance to the sea, and embryo dune volume as explanatory variables. For this analysis we used the data from 2016. For

the electrical conductivity and moisture content we also included the volume of the secondary dunes and organic layer thickness as explanatory variables. The change in elevation between 2006 – 2016 was analysed with elevation, distance to the sea, and embryo dune volume as explanatory variables, these variables were measured in 2006.

5.3.5.2 Vegetation composition

First, we explored the factors that influenced the composition of the vegetation of 2006 and 2016 separately. The species richness of all species, green beach and salt-marsh species was analysed with a generalised linear mixed model with Poisson distribution and transect as a random intercept (Bolker et al., 2009). We also analysed the Shannon-Wiener diversity index, evenness and cover of all species, green beach and salt-marsh species with a general linear mixed model with transect as a random intercept (Pinheiro et al., 2016). Dune-slack species occurred in only a few plots and consequently the species richness of dune-slack species data contained many zeros (Zeros 2006: 62%, 2016: 55%). Therefore, we analysed presence and absence of dune-slack species with a binomial generalized linear mixed model with transect as random intercept (Bolker et al. 2009). The explanatory variables for the models for plant species richness, Shannon-Wiener diversity index, evenness and cover in 2006 and 2016 were electrical conductivity, elevation, distance to the sea, embryo dune volume and the volume of secondary dunes. In the 2016 models we also included the organic layer thickness as an explanatory variable. We did not include soil moisture content in our statistical model, because it was highly correlated with elevation (Pearson correlation: - 0.75, $t\text{-value}_{105} = -11.54$, $p < 0.001$).

Secondly, detrended correspondence analysis (DCA) was used to extract the dominant patterns of variation in composition of the vegetation. DCA is an indirect gradient analysis which ordinales only the species data and does not include environmental factors (ter Braak & Verdonschot, 1995). We used a DCA method because the data showed an unimodal response (Oksanen et al., 2017). We plotted the species and plots on the first and second axes of the DCA. In order to relate the plant species composition and abiotic variables directly, we fitted the abiotic factors onto the ordination. We included the following abiotic variables: elevation, embryo dune volume, secondary dune volume, soil salinity, and distance to the sea. In 2016 we also included moisture percentage, and organic matter layer thickness.

Thirdly, we analysed the change in species richness, diversity, evenness, and cover of all species, green beach species, dune-slack species and salt-marsh species between 2006 and 2016 and the fraction of stable species, with a general linear mixed model with transect as random intercept. As explanatory variables we used the change in elevation, distance to the sea, embryo dune volume, organic matter layer thickness between 2006 and 2016, and the volume of secondary dunes.

We were mainly interested in the relative importance of the variables and therefore calculated the standardized estimates for all models. For all mixed models we calculated the marginal and conditional R^2 (Nakagawa & Schielzeth, 2013). The marginal R^2 is the variance explained by the explanatory variables and the conditional R^2 is the variance explained by the entire model (including the random variables). The normality and homogeneity of variance of the data was visually checked. We transformed green beach species Shannon-Wiener diversity index in 2016, salt-marsh species Shannon-Wiener diversity index in 2016, evenness in 2006 and 2016,



vegetation cover in 2006, salt-marsh vegetation cover in 2016, and electrical conductivity in 2016 with an \ln transformation. Organic layer thickness was transformed with a square root transformation. All statistical analyses were done in the statistical program R (R Core Team, 2016).

5.3 Results

5.3.1 Beach and dune morphology

In 2006 embryo dune volume differed between transects (Fig. 5.2). The northward facing transects IV – XI had an overall larger volume of embryo dunes, and thus a higher degree of shelter, than westward facing transects I – III, with the exception of transect I. Transect I had the largest embryo dune volume off all transects, but since embryo dune was located at the edge of the foredune foot it did not provide shelter to the vegetation on the green beach, which was located seaward from that embryo dune. Between 2006 and 2016, most beaches eroded (on average: -84.2 ± 12.7 m (mean \pm SE), Fig. 5.2), only transects X and XI increased in beach width with 110 and 115 m, respectively. The erosion of the beach did not hamper embryo dune development, as on most transects embryo dune volume in 2016 was higher than in 2006, increasing with 40.2 ± 3.6 m³/m, except in transect I and II. The largest embryo dune erosion likely took place in the winter of 2012/2013 during a severe storm, with a return frequency of once every 15 years (Rijkswaterstaat 2014c). Between 2006 and 2016 also the position of the embryo dunes shifted land inward, reducing the area of beach sheltered between embryo dunes and foredunes (Fig. 5.2B). Moreover, on beaches with a high embryo dune volume there was overall a positive change in elevation on the beach (Fig. 5.3B). Increase in elevation of the beach mainly occurred on northward facing beaches on locations with initially low elevation (Table 5.1, Fig. 5.3A).

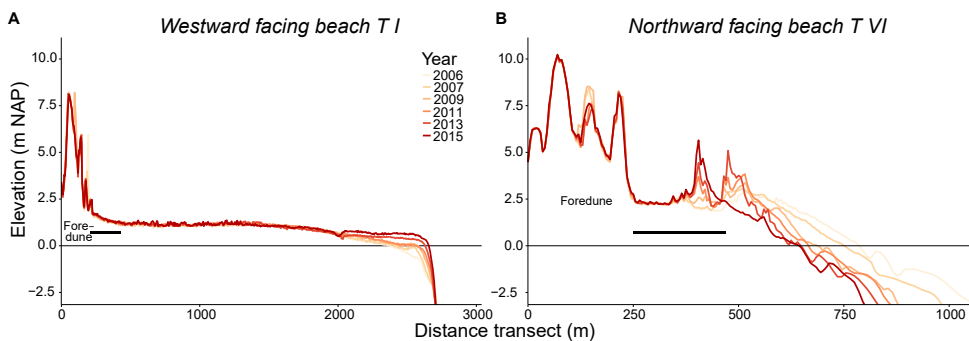


Figure 5.2. Cross-shore profiles of the beach-foredune system for the years 2006, 2007, 2009, 2011, 2013 and 2015 at the position of A) The westward facing transect 1, B) northward facing transect 6. These two transects illustrate the range in beach morphology on Schiermonnikoog: a very wide beach with no embryo dune development (A) to a beach with well-developed embryo dunes (B). The black line below the profiles indicates the length of the transect covered by the present study and its vegetation plots. NAP refers to Amsterdam Ordnance Datum, which is equal to mean sea level near Amsterdam.

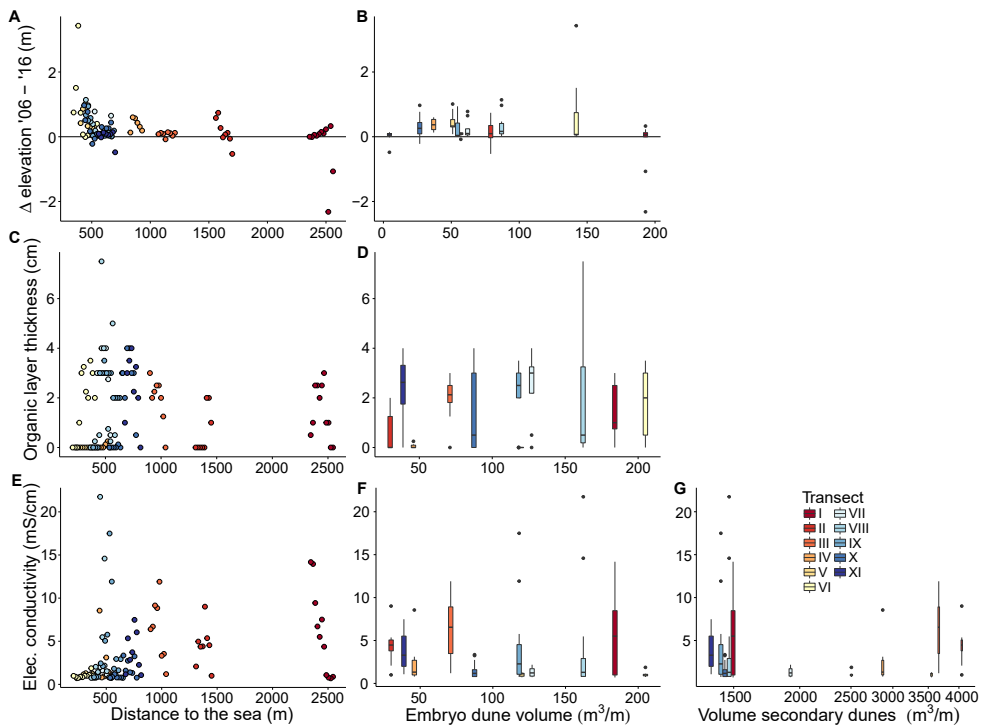


Figure 5.3. A) The relationship between distance to the sea and the change in elevation between 2006 – 2016. B) A boxplot of change in elevation between 2006 and 2016 for each transect related to the embryo dune volume in 2006. C) The relationship between the distance to the sea and the organic layer thickness in 2016. D) A boxplot of the organic layer thickness for each transect related to the embryo dune volume in 2016. E) A relation between distance to the sea and the electrical conductivity of the soil in 2016. F) A boxplot for the electrical conductivity for each transect related to the embryo dune volume in 2016. G) A boxplot for the electrical conductivity for each transect related to the volume of secondary dunes. The different colours indicate the different transects. The middle line in the boxplot is the median, whereas the lower and upper hinges represent the 25% and 75% quartiles. The upper whisker extends from the hinge to the highest value that is within $1.5 \times$ the interquartile range of the hinge. The dots represent the values outside the $1.5 \times$ interquartile range. Transects I-III are westward facing, transects IV-XI are northward facing.

5.3.2 Environmental conditions in the rooting zone

The environmental conditions were clearly influenced by beach and dune morphology. We found that soil salinity, moisture content and organic layer thickness were negatively correlated with elevation (Table 5.1). Wider beaches had overall higher soil salinity and moisture content than narrow beaches (Fig. 5.3E). The volume of secondary dunes had no significant effect on the soil salinity and moisture content, but the small volume of secondary dunes on transect VIII – XI could explain the high soil salinity in these transects (Fig. 5.3G). The volume of embryo dunes on the beach had a weak albeit significant positive effect on the organic matter thickness (Table 5.1; Fig. 5.3D).



Table 5.1. Statistical models for the EC, moisture content, organic layer thickness in 2016 and change in elevation between 2006 - 2016. For EC, moisture content, organic layer thickness the explanatory data was from 2016, for the change in elevation the explanatory data was from 2006. All the data was analysed with a general linear model. The standardized estimates and level of significance are shown for the models. Abbreviations: ED: embryo dune, EC: electrical conductivity.

Abiotic variables	Dependent variable:			
	EC	Moisture content	Organic layer thickness	Δ Elevation
Intercept	1.20***	14.31***	2.24***	1.13***
Elevation	-0.33***	-4.430***	-0.42***	-0.38***
Distance Sea	0.17**	1.10*	-0.0001	-0.0005***
ED volume 2 - 6 m NAP	-0.008	-0.64	0.003**	0.004***
Volume secondary dunes	0.10●	0.82	-	-
Organic layer thickness	0.14*	3.81***	-	-
Observations	107	107	107	107
R ²	0.48	0.71	0.25	0.35
Adjusted R ²	0.45	0.70	0.22	0.33
Residual Std. Error	0.500	4.649	0.42	0.43
F Statistic	18.37***	49.87***	11.14***	18.72***

Note: ● $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

5.3.3 Vegetation in 2006

In 2006 the vegetation had a sparse cover ($27.8 \pm 2.2\%$) and mainly consisted of short herbs and grasses with a small contribution of woody shrubs ($0.3 \pm 0.1\%$, Table 5.2). The vegetation was dominated by characteristic green beach species and species characteristic of dry dunes, with green beach species accounting for $61.2 \pm 3.1\%$ of the total vegetation cover. Most of the green beaches species were salt tolerant species characteristic of salt marshes ($14.2 \pm 1.5\%$ cover), with only a few fresh water species characteristic of young dune slacks ($2.9 \pm 0.7\%$ cover).

In 2006 vegetation composition and species richness differed slightly between transects, with transects I, II, III and, in particular, transect XI differing in composition from the other transects. The vegetation composition of the wider westward facing transects I, II, and III was quite similar, and mainly consisted of salt-marsh species, whereas the other transects contained a more mixed group of species (Fig. A5.1). Transect XI was most dissimilar in composition from the other transects. The relatively short northward facing transect V, VI and VII had the highest species richness and Shannon-Wiener diversity index, irrespective of focus group (all species, green beach species, dune-slack species or salt-marsh species). Species rich plots had also the highest vegetation cover, since there was a significant positive correlation between species richness and vegetation cover (Pearson correlation: 0.78, $t\text{-value}_{105} = 12.79$, $p < 0.001$).

Environmental conditions or beach morphology explained only a small part of the variation in species composition and species richness per plot (Table 5.3). The species richness of all species was negatively related to beach width, with the highest richness occurring on the short northward facing beaches (Table 5.3, Fig. 5.4A). The Shannon-Wiener diversity index

Table 5.2. Top 10 species with on average the highest cover in 2006 and 2016, the highest net increase over the period 2006-2016 and the highest net decrease over the period 2006-2016. Summed cover of the top ten species and total vegetation cover are given at the bottom of the table. Type indicates their growth form.

Top 10 vegetation cover 2006			Top 10 vegetation cover 2016		
Species	Type	%	Species	Type	%
<i>Agrostis stolonifera</i>	G,LP	2.5	<i>Festuca rubra</i>	G, HP	16.6
<i>Leontodon saxatilis</i>	H,LP	2.1	<i>Hippophae rhamnoides</i>	W, HP	11.0
<i>Elytrigia atherica</i>	G,HP	1.9	<i>Agrostis stolonifera</i>	G, LP	9.7
<i>Festuca rubra</i>	G, HP	1.8	<i>Elytrigia atherica</i>	G, HP	7.6
<i>Glaux maritima</i>	H, LP	1.7	<i>Juncus maritimus</i>	G, HP	5.7
<i>Odontites vernus</i>	H, LP	1.4	<i>Glaux maritima</i>	H, LP	3.6
<i>Leymus arenarius</i>	G, LP	1.0	<i>Salix repens</i>	W,HP	3.5
<i>Plantago coronopus</i>	H,LP	0.9	<i>Carex extensa</i>	G,LP	2.7
<i>Sonchus arvensis</i>	H,LP	0.8	<i>Juncus gerardii</i>	G,LP	2.6
<i>Plantago maritima</i>	H,LP	0.7	<i>Phragmites australis</i>	G,HP	2.5
Top 10 cover		14.9	Top 10 cover		65.7
Total cover		27.8	Total cover		89.9
Top 10 increase 2006 - 2016			Top 10 decrease 2006 - 2016		
<i>Festuca rubra</i>	G,HP	14.8	<i>Leymus arenarius</i>	G,LP	0.8
<i>Hippophae rhamnoides</i>	W,HP	10.8	<i>Plantago coronopus</i>	H,LP	0.7
<i>Agrostis stolonifera</i>	G,LP	7.2	<i>Puccinallia distans</i>	G,LP	0.7
<i>Elytrigia atherica</i>	G,HP	5.7	<i>Salicornia europaea</i>	H,LP	0.5
<i>Juncus maritimus</i>	G,HP	5.7	<i>Leontodon saxatilis</i>	H,LP	0.5
<i>Salix repens</i>	W,HP	3.3	<i>Sonchus arvensis</i>	H,LP	0.4
<i>Phragmites australis</i>	G,HP	2.4	<i>Puccinellia maritima</i>	G,LP	0.4
<i>Schoenus nigricans</i>	G,LP	2.3	<i>Centaurium pulchellum</i>	H,LP	0.4
<i>Carex extensa</i>	G,LP	2.2	<i>Odontites vernus</i> subsp. <i>serotinus</i>	H,LP	0.3
<i>Juncus gerardii</i>	G,LP	2.1	<i>Parapholis strigosa</i>	G,LP	0.3
Top 10 increase in cover		56.4	Top 10 decrease in cover		5.0
Total increase in cover		62.1	Total decrease in cover		9.1

Abbreviations: G = grasses, H = herbs, W = woody shrubs, LP = low productive, HP = high productive.

of all species was positively, albeit weakly related to elevation (Appendix 5.2). Green beach species Shannon-Wiener diversity index (dune-slack and salt-marsh species) was positively related to embryo dune volume. Similar to the species richness of all species, the presence of dune-slack species was negatively correlated with the distance to the sea, dune-slack species mainly occurred on the northward facing beaches (Table 5.3, Fig. 5.4B). Furthermore, the presence of dune-slack species was negatively correlated with groundwater salinity (Table 5.3). The species richness and Shannon-Wiener diversity index of salt-marsh species was unrelated to groundwater salinity, elevation, distance to the sea, embryo dune volume and secondary



Table 5.3. Statistical models for the species richness in 2006 of all plant species and the species characteristic of green beaches, dune slack and salt marshes. Species richness per plot for all species, green beach, and salt-marsh species were analysed with a generalised linear mixed model with a Poisson distribution and transect as random intercept. The dune-slack species were analysed with a generalised linear mixed model with binomial distribution and transect as random intercept. The standardised estimates and level of significance are shown for the models. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Plant species richness 2006	Dependent variable:			
	All species	Green beach species	Dune-slack species	Salt-marsh species
Intercept	2.32***	1.90***	-0.29	1.79***
EC	-0.028	0.013	-0.78*	0.054
Elevation	0.039	-0.004	-0.096	-0.015
Distance Sea	1.38**	-0.15	-2.63***	-0.11
ED volume 2 – 6 m NAP	-0.86	0.25*	0.58	0.23
Volume secondary dunes	-0.34	0.064	-0.24	0.072
Marginal R^2	0.33	0.13	0.28	0.10
Conditional R^2	0.95	0.27	0.28	0.25
Observations	107	107	107	107
Akaike Inf. Crit.	659.56	615.58	104.00	602.88
Bayesian Inf. Crit.	678.27	634.29	122.71	621.59

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: EC: electrical conductivity, ED: embryo dune.

dune volume. The evenness of all species, green beach, dune-slack and salt-marsh species was not affected by any of the environmental factors (all p -values were above 0.12, conditional $R^2 = 0.07\%$). Similar to species richness, vegetation cover was negatively related to beach width (t -value₉₃ = -2.58, $p = 0.012$) and groundwater salinity (t -value₉₃ = -3.36, $p = 0.0011$). When we re-ran species richness analysis excluding the missing groundwater salinity values (see methods), many explanatory variables lost their significance, although the direction of their effects remained unchanged. The richness of all species was no longer significantly associated with distance to the sea but to (higher) elevation instead. Richness of green beach species was no longer significantly related to embryo dune volume and the presence of dune-slack species was no longer significantly related to groundwater salinity.

5.3.4 Vegetation in 2016

Species composition across the transects was more similar in 2016, as compared to 2006 (Fig. A5.2). The species richness varied between the transects, with the highest species richness in transect VII, III, and XI (17.4 ± 2.2 , 14.0 ± 0.7 , and 13.5 ± 0.6 , respectively). Dune-slack species had the highest species richness in transect VII (4.5 ± 1.1) and only in transect IV no dune-slack species were present. The highest species richness for characteristic salt-marsh species was in transects III and XI (8.4 ± 1.1 and 7.9 ± 1.0 , respectively). Similar to 2006, species richness was positively correlated to vegetation cover, although the correlation was less strong than it was in 2006 (Pearson correlation: 0.65, t -value₁₀₅ = 8.83, $p < 0.001$).

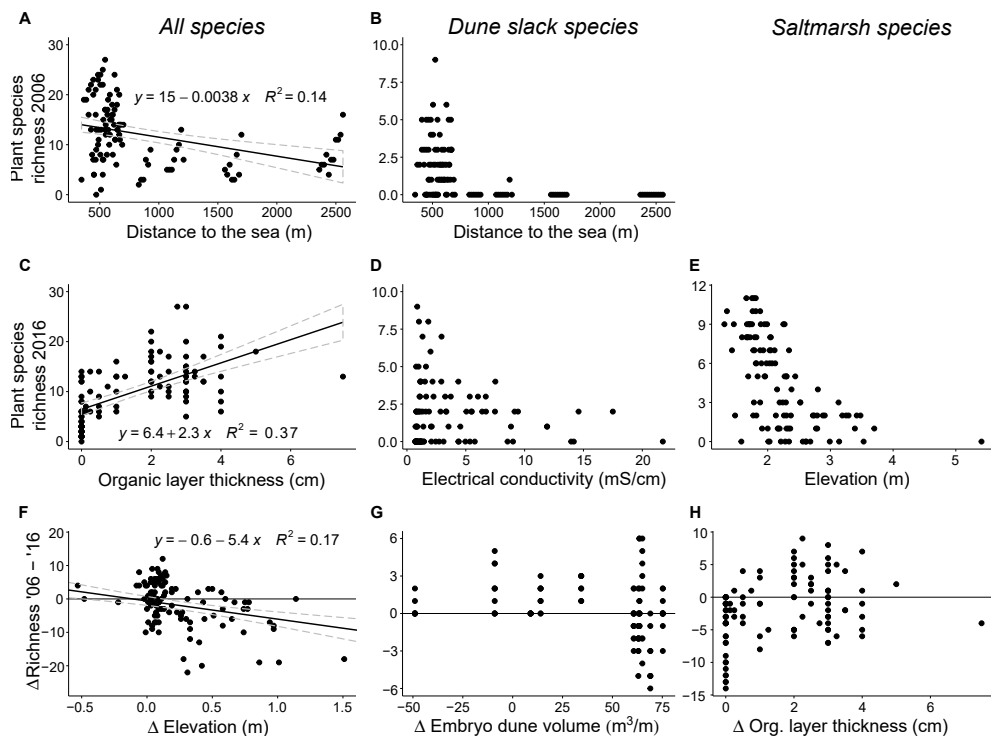


Figure 5.4. The relationship between A) distance to sea and the species richness of all plant species in 2006; B) distance to the sea and the species richness of the dune-slack plant species in 2006; C) organic layer thickness and the species richness of all plant species in 2016; D) electrical conductivity and species richness of dune-slack plant species in 2016; E) elevation and species richness of salt-marsh plant species in 2016; F) change in elevation and change in species richness of all plant species between 2006 and 2016, 3 outliers have been removed; G) Change in embryo dune volume and change in species richness of dune-slack plant species between 2006 and 2016; H) change in organic layer thickness and change in species richness of salt-marsh species between 2006 and 2016.

In 2016 plant species richness and cover were significantly correlated with organic layer thickness, with more organic matter leading to more species as well as higher coverages (cover: estimate₉₂ = 35.38, $p < 0.001$; Table 5.4, Fig. 5.4C). Beside organic layer thickness, the species richness of all species had a significant positive relationship with distance to sea, and a negative relationship with elevation and electrical conductivity, although these relationships were very weak. The evenness of all species was unrelated to any environmental factor. Similar to all species, the number and evenness of characteristic green beach species increased with organic layer thickness (evenness: estimate₉₂ = 2.31, $p < 0.001$) and decreased with elevation (evenness: estimate₉₂ = -1.34, $p < 0.001$; Table 5.4). On these low elevation plots the soil salinity determined whether there was a high Shannon-Wiener diversity index of dune-slack or salt-marsh species (Fig. 4D, Appendix 5.2). The evenness of salt-marsh species was higher with a thicker organic layer (estimate₈₀ = 0.12, $p < 0.001$) and at wider beaches (estimate₈₀ = 0.076, $p = 0.29$).



Table 5.4. Statistical models for the species richness in 2016 of all plant species and the species characteristic of green beaches, dune slacks and salt marshes. Species richness per plot for all species, green beach, and salt-marsh species were analysed with a generalised linear mixed model with a Poisson distribution and transect as random intercept. The dune slack species were analysed with a generalised linear mixed model with binomial distribution and transect as random intercept. The standardised estimates and level of significance are shown for the models. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Plant species richness 2016	Dependent variable:			
	All species	Green beach species	Dune-slack species	Salt-marsh species
Intercept	2.20*	1.53***	0.51●	1.29***
Elevation	-0.24***	-0.47***	-0.71●	-0.41***
Distance Sea	2.93***	0.12	0.33	0.11
ED volume 2 – 6 m NAP	-0.035	0.023	-0.17	-0.064
Volume secondary dunes	-0.008	-0.048	-0.40	0.001
Organic layer thickness	0.15***	0.34***	1.70***	0.38***
EC	-0.097*	-0.062	-0.59●	0.036
Marginal R^2	0.36	0.62	0.28	0.66
Conditional R^2	0.44	0.66	0.28	0.69
Observations	107	107	107	107
Akaike Inf. Crit.	651.37	531.88	108.64	456.94
Bayesian Inf. Crit.	672.75	553.27	130.02	478.32

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: EC: electrical conductivity, ED: embryo dune.

5.3.5 Change in vegetation

The vegetation cover increased from 2006 to 2016 (cover 2016: $89.9 \pm 5.6\%$) and consisted in 2016 mainly of shrubs with an average cover of $13.3 \pm 3.9\%$ and highly productive grass species of later successional salt-marsh and dune habitats (Table 5.2), such as *Festuca rubra*, *Hippophae rhamnoides*, and *Elytrigia atherica*. Furthermore, the ten most common species in 2016, which were mainly highly productive grasses or shrubs, also accounted for a large portion of the total vegetation cover (table 5.2). In contrast, the green beach species accounted for half ($50.7 \pm 3.0\%$) of the total vegetation cover in 2016, which was slightly less than in 2006. As in 2006, most green beach species were species characteristic of salt-marshes, with only a few characteristic dune slack species with a low cover.

The top 10 species that decreased in cover were low productive short grasses and herbs, for example *Plantago coronopus*, *Puccinellia distans*, and *Leontodon saxatilis*. Net declines in the cover of species were smaller than the net increases in cover. Overall, less species per plot were found in 2016 than in 2006 (2006: 11.9 ± 0.6 , 2016: 10.1 ± 0.6 , $t\text{-value}_{211} = -2.24$, $p = 0.026$). The green beach species richness was significantly lower in 2016, compared to 2006 (2006: 5.8 ± 0.4 , 2016: 4.6 ± 0.3 , $t\text{-value}_{211} = 2.29$, $p = 0.023$). This decline in species characteristic of green beaches was driven by the decline in characteristic salt marsh species (2006: 6.4 ± 0.4 , 2016: 4.6 ± 0.3 , $t\text{-value}_{211} = 3.60$, $p < 0.001$), the species characteristic of dune slacks had a similar

Table 5.5. Statistical models for the change in plant species richness of all plant species and the species characteristic of green beaches, dune slacks, and salt marshes only. Statistical model for the fraction of stable species (species present in 2006 and 2016) compared to all species in 2006. All data was analysed with a general linear mixed model with transect as random intercept. The standardized estimates and level of significance are shown for the models. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Δ in plant species richness between 2006 - 2016	Dependent variable:				
	All species	Green beach species	Dune-slack species	Salt-marsh species	Fraction stable species
Intercept	-1.77	-1.14	0.26	-1.63	0.23***
Δ Elevation	-1.63**	-0.80	-0.47*	-0.35	-0.050**
Δ Distance Sea	-1.21	0.39	-0.081	0.59	-0.090**
Δ ED volume 2 - 6 m NAP	-3.28	-2.28	-0.98*	-2.02	0.020
Δ Organic layer thickness	0.38	1.00*	0.26	0.88*	0.050**
Volume secondary dunes	-2.86	-1.74	-1.00	-1.10	-0.049
Marginal R^2	0.27	0.26	0.29	0.21	0.26
Conditional R^2	0.63	0.56	0.29	0.50	0.37
Observations	107	107	107	107	106
Akaike Inf. Crit.	653.63	617.96	458.04	601.79	-56.38
Bayesian Inf. Crit.	674.55	638.88	478.96	622.71	-35.54

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: ED: embryo dune.

species richness in 2016, compared to 2006 (2006: 1.4 ± 0.2 , 2016: 1.6 ± 0.2 , $t\text{-value}_{210} = -0.82$, $p = 0.42$). The species richness declined in 5 transects (V, VI, VIII, IX and X), transect V had the highest decline in species richness (-15.5 ± 2.15). The highest increase in species richness was in transect III (6.38 ± 3.70).

Species turn-over and changes in species richness between 2006 and 2016 were related to similar abiotic conditions that resulted in high species richness in 2016, such as the change in elevation and the increase in organic layer thickness (Table 5.5, Fig. 5.4H). The decrease in species richness between 2006 and 2016 was associated with an increase in elevation, although this relationship was not very strong and driven by two outliers (Table 5.5, Fig. 5.4F). The change in species richness of dune slack species was only negative in transects with an increase in embryo dune volume (Fig. 5.4G). The fraction of stable species (turn-over of species) had a positive relationship with organic layer thickness and a negative relationship with change in elevation and distance to the sea (Table 5.5). The evenness and cover showed similar result as the species richness and the species diversity.



5.4 Discussion

The aim of our study was to explore the relative importance of different abiotic soil factors as affected by beach and dune morphology in determining vegetation and species turn-over of green beaches. More specifically we expected that green beach vegetation would be positively associated with the presence and development of embryo dunes, as they potentially provide shelter against storm erosion and sand burial, and may act as a source of fresh seepage water into the saline beach, enabling coexistence of salt-intolerant dune-slack species and salt-tolerant salt-marsh species. Although embryo dunes were positively associated with richness of salt-intolerant dune slack species, species turnover showed an opposite response with the highest species losses occurring on beaches with high embryo dune volume. Furthermore our results indicate that embryo dune development can take over dune slack habitat by sand burial and thereby reduce the occurrence of these dune-slack species. Consequently, our results suggest a non-linear relationship between embryo dune volume and plant species richness: embryo dunes can be a source of shelter, thus increasing plant species richness, but can also compete for space, thus lowering plant species richness.

5.4.1 Coupling beach and dune morphology to environmental conditions

The abiotic factors soil salinity and sand burial were mainly determined by beach morphology. Soil salinity is an important factor that determines the occurrence of either dune-slack or salt-marsh vegetation. The soil salinity depends on multiple factors such as elevation, beach width, embryo dune volume and secondary dunes volume, which makes it hard to make generalisations about the spatial distribution of soil salinity on the beach (de Jong, 1979; Maun, 2009). In our study we found a significant effect of beach width on soil salinity. Wider beaches had overall higher soil salinity, and when plots were situated closer to the sea the soil salinity was higher. Transect I - III had very wide beaches and on these transects high soil salinity values were measured. Transects I - IV were also rather low in elevation, their elevation was 1.13 – 1.52 m NAP on average for the whole beach, which is rather low considering that the mean high tide is 1.05 m NAP. These beaches are much more influenced by the tides than transect V – XI which were on beaches with an average elevation between 1.69 – 2.18 m NAP.

Another factor that could influence soil salinity is the fresh water seepage from secondary dunes (Grootjans et al., 2002; Bakker et al., 2005; Groot et al., 2016; Kooijman et al., 2016). The volume of secondary dunes had no significant effect on the soil salinity. It might, however, explain the high soil salinity in transects VIII and IX. These transects had only the established foredune, while no secondary dunes were present near these transects. The absence of a clear effect of the volume of secondary dunes could be related to the 2-dimensionality in our method that was used to calculate secondary dunes volume. In reality, the fresh seepage availability depends on the surface area of the dunes. Therefore our method might not be a sufficient indicator for the amount of fresh seepage water.

The amount of sand burial was greatest on plots at narrow beaches, which all had a northward orientation and overall the highest embryo dune volume. Sites at low elevation also endured more sand burial compared to sites at high elevation, which seems to indicate that these areas served as sand sinks. High waves during storms likely eroded the small dunes on the beach

depositing the eroded sand closer to the foredune, effectively levelling the beach. Therefore, sand burial might also depend on the occurrence of storms.

5.4.2 Factors controlling vegetation and species turnover

The green beach of Schiermonnikoog was in 2006 still in an early stage of succession, considering the low vegetation cover and dominance of short herbs and grasses. The highest plant cover was measured at the higher elevated areas. A possible explanation for this result is that these higher areas are less likely to erode by high water levels during storms. Erosion by storms can cause mortality of vegetation and setback succession. On higher parts this is less likely to occur which resulted in most plots in a higher vegetation cover. The highest species richness was on narrow beaches. These beaches were all sheltered by embryo dunes which protected the vegetation against severe disturbances such as high water inundation.

The characteristic green beach species had higher species richness on beaches with a larger embryo dune volume, emphasizing the importance of embryo dunes to reduce disturbance. The characteristic green beach species consist of dune-slack and salt-marsh species. Dune-slack species occurred in 2006 only on the northward facing beaches of Schiermonnikoog. These northward facing beaches had well developed embryo dunes and some transects had a large volume of secondary dunes, which might have increased fresh water seepage (Röper et al., 2013), whereas the availability of freshwater had positive effects on the occurrence of dune-slack species.

In 2006 salt-marsh species occurred at all transects, indicating that these species can occur in a broad range of abiotic conditions. No environmental factor affected the salt-marsh species richness and diversity. The absence of the effects of any environmental factor on salt-marsh species richness, could be explained by the large variation in salt tolerance within this group which includes extremely stress-tolerant species, such as *Salicornia* sp. and *Spartina anglica*, but also less tolerant, more competitive species, such as *Elytrigia atherica* and *Juncus maritimus*. Another explanation can be the different starting dates of succession between transects and the different distances to source populations limiting the dispersal of some species, thereby causing differences in species richness and Shannon-Wiener diversity index between transects (Ozinga et al., 2005). Transect as a random factor in our model accounted for 10% to 60% of the variation, depending on the selected model. This indicates that transects were clearly different from each other and that different starting dates or different distances to be covered by dispersal might explain some of the patterns we found.

In 2016, most ecosystems were clearly in a later stage of succession, with higher vegetation cover and dominated by taller grasses and shrubs. The overall plant species richness and Shannon-Wiener diversity index per plot was lower in 2016 compared to 2006, indicating that either plants experienced more stress, which resulted in more mortality or that more competitive species had established. Most likely a combination of both processes occurred, where in some areas plants experienced more stress by for example sand burial, whereas in other areas more competitive plants had established, which also explains the reduction in evenness. Plant species richness and Shannon-Wiener diversity index was significantly higher in plots with more developed soils. This indicates that a negative effect of soil development is not yet apparent,



as was expected in later stages of succession, and that the system is instead in an intermediate stage of succession (Berendse et al., 1998; Houle, 2008). This seems to indicate that soil development has a positive effect in early stages of succession, although organic matter layer thickness and the time the vegetation had to develop are of course naturally strongly correlated. Consequently, the positive effect of soil development could also be an artefact of the undisturbed time species had to establish, after the start of succession.

Furthermore an increase in organic matter indicates no disturbances, such as sand burial, therefore it could be that soil development has a positive effect on species richness since it indicates the absence of disturbances. We found that an increase in elevation had a negative effect on the species richness and diversity. This indicates a negative effect of sand burial on plant species richness. While it is known that there are coastal species that profit from minor amounts of sand burial (Hesp, 1989; van der Putten, 1989; Maun, 1998), large amount of sand burial would cause mortality in a large number of species (Moreno-Casasola, 1986; Sykes & Wilson, 1990; Maun & Perumal, 1999; Forey et al., 2008; Gilbert et al., 2008). The number of species that occurred in the same plot between 2006 and 2016 was also lower with an increase in elevation. This gives further evidence that sand burial results in major negative effects on plant species richness through plant mortality. Species that did not seem to suffer by sand burial, and increased their cover since 2006, have often a strong potential for vegetative growth, for example: *Agrostis stolonifera*, *Hippophae rhamnoides*, and *Phragmites australis*. The vegetative growth capacity gives these species the ability to expand rapidly into disturbed patches (Ecke & Rydin, 2000). Furthermore, sand burial also influences site specific variables related to elevation, such as moisture and salinity (Maun & Perumal, 1999). Soil moisture levels were mainly determined by elevation in our study, and as such an increase in elevation due to sand burial would lower moisture levels and create a less suitable environment for characteristic green beach species, since they had the highest species richness in the lower elevated areas.

The characteristic dune-slack species richness and Shannon-Wiener diversity index was on average similar between 2006 and 2016, and in 2016 the dune slack species were not any longer restricted to only the northward facing beaches, indicating that on more transects fresh water conditions had developed. The species richness and diversity of characteristic dune slack species mainly decrease at transects with a large increase in embryo dune volume. On most transects the embryo dunes are situated closer to the foredune in 2016 compared to 2006. These embryo dunes might have formed in areas that were once suitable habitat for the dune-slack species. The migration of these embryo dunes landward indicates a reduction of suitable habitat for dune-slack species by sand burial, and results in a lower species richness and diversity of dune-slack species. In 2016, the characteristic dune-slack species mainly occurred in areas with an organic matter layer. Characteristic dune-slack species most likely benefitted from the absence of sand burial as indicated by the organic matter layer in the plots where these species occur, but an increase of the organic matter layer did not increase the diversity and species richness of characteristic dune-slack species. This is most likely because these dune-slack species mainly occur in nutrient-poor areas (Berendse et al., 1998).

The diversity and species richness of salt-marsh species was higher in 2006 compared to 2016. This decrease is most likely related to the increase of more competitive species, such as *Elytrogia atherica* and *Juncus maritimus*. Logically, we found a significant positive effect of soil salinity on the diversity of salt-marsh species. However, soil salinity did not affect the species richness.

In plots with low soil salinity but still high salt-marsh species richness more brackish species could occur or the salinity just decreased, and the salt-tolerant species were still present.

5.4.3 Implications for the diversity of coastal habitats

The future of the species rich dune slack and salt-marsh communities on the green beach on Schiermonnikoog seems to be mainly determined by a delicate balance between two processes: sand burial and succession. On the one hand disturbance via sand burial set back succession towards more competitive vegetation. On the other hand disturbance via sand burial causes mortality and also indirectly lowers characteristic green beach diversity by changing abiotic factors by an increase in elevation. Furthermore, due to the continuous increase in organic matter and further succession towards more competitive vegetation, it is likely that the characteristic green beach diversity will decline over the next coming years. Of the characteristic green beach species, we especially expect dune-slack species to be particularly sensitive to being replaced by dune species, competitive grasses and especially shrubs such as *Hippophae rhamnoides* (Isermann et al., 2007).

In a natural barrier island system, populations of green beach species would shift over space and time as new areas continuously emerge, develop, are buried or are washed away, thus maintaining vital populations even with only limited suitable areas available during short time windows (Grootjans et al., 2002; Groot et al., 2016). This would, however, require large areas of dynamic nature (Groot et al., 2016). Management will either need to allow for the creation of new suitable areas by allowing a more complete set of dynamics, with disturbance events including erosion, over space and time or retard further succession for as long as possible using artificial measures such as mowing or removal of the soil organic layer to slow down or prevent vegetation succession (Grootjans et al., 2002).

The window of opportunity for green beaches to develop likely depends on a combination of storm-erosion and wider coastal setting. Most of the beaches were eroding during our study period, which results in more dune erosion during storms, since narrow beaches can attenuate waves less than wider beaches (Short & Hesp, 1982; Ruggiero et al., 2001). If the beach had been accreting, most likely new dunes seaward of the embryo dunes would have developed, reducing storm erosion and sand burial to the area landward of these new embryo dunes. Moreover, on an accreting beach, new embryo dune development seawards of these dunes would ensure that green beach species always have new habitat to establish. Such a repeating pattern of dune formation on an accreting beach, has been found to have a positive effect on green beach species in general and dune-slack species in particular on other West-Frisian islands, such as Texel and Terschelling (Grootjans et al., 2002; European Commission, 2007; Bitton & Hesp, 2013; Kooijman et al., 2016).



5.6 Conclusion

Our study shows the close interrelationship between beach morphology, sedimentation dynamics and green beach diversity and species turnover. Key findings of this research were: 1) the geomorphological setting of the beach influences plant species richness on the green beach by affecting the amount of sand burial and soil salinity. 2) Plant species richness increased with soil organic layer thickness and decreased with sand burial, illustrating the importance of shelter for plant species on the green beach. 3) Sand burial decreases habitat suitability for dune-slack and salt-marsh species by increasing elevation, which in turn decreases soil moisture and salinity. 4) Dune-slack species mainly occur on beaches with large embryo dune complexes, however embryo dune development reduces the area suitable for dune-slack species due to the associated increase in sand burial. This study can be used to better predict the occurrence and succession of green beach vegetation.

5.7 Acknowledgements

We would like to thank Jan van Walsem for assistance with the soil sampling analysis and Sanne Hagedoorn for her assistance with fieldwork. We would like to thank Natuurmonumenten for permission to do fieldwork in the National park Schiermonnikoog. We would like to thank the technology foundation STW for funding the project NatureCoast (grant number STW 12689 S4) which made this research possible.

Appendix 5.1 Table with all the recorded species.

Table A5.1. List of all recorded species and whether they were a green beach species, dune slack or salt-marsh species, a one indicates that the species fall within the category.

Species	Green beach	Dune-slack	Salt-marsh
<i>Agrostis stolonifera</i>	0	0	0
<i>Ammophila arenaria</i>	0	0	0
<i>Arabidopsis thaliana</i>	0	0	0
<i>Arenaria serpyllifolia</i>	0	0	0
<i>Armeria maritima</i>	1	0	1
<i>Artemisia maritima</i>	1	0	1
<i>Aster tripolium</i>	1	0	1
<i>Atriplex litoralis</i>	0	0	0
<i>Atriplex portulacoides</i>	1	0	1
<i>Atriplex prostrata</i>	0	0	0
<i>Bellis perennis</i>	0	0	0
<i>Betula pubescens</i>	0	0	0
<i>Blysmus rufus</i>	1	0	1
<i>Bolboschoenus maritimus</i>	1	0	1
<i>Bromus hordeaceus</i>	0	0	0
<i>Cakile maritima</i>	0	0	0
<i>Calamagrostis baltica</i>	0	0	0
<i>Calamagrostis epigejos</i>	0	0	0
<i>Carex arenaria</i>	0	0	0
<i>Carex distans</i>	1	1	1
<i>Carex extensa</i>	1	0	1
<i>Carex flacca</i>	0	0	0
<i>Carex nigra</i>	1	1	0
<i>Carex oederi</i> subsp. <i>oederi</i>	1	1	0
<i>Carex panacea</i>	0	0	0
<i>Centaurium littorale</i>	1	1	0
<i>Centaurium pulchellum</i>	1	0	1
<i>Cerastium fontanum</i> subsp. <i>vulgare</i>	0	0	0
<i>Cerastium semidecandrum</i>	0	0	0
<i>Chamerion angustifolium</i>	0	0	0
<i>Cirsium arvense</i>	0	0	0
<i>Convolvulus sepium</i>	0	0	0
<i>Eleocharis palustris</i>	0	0	0
<i>Eleocharis quinqueflora</i>	1	1	0
<i>Eleocharis uniglumis</i>	1	0	1
<i>Elytrigia atherica</i>	1	0	1
<i>Elytrigia juncea</i>	0	0	0
<i>Elytrigia repens</i>	0	0	0
<i>Epilobium hirsutum</i>	0	0	0
<i>Epilobium palustre</i>	0	0	0
<i>Epipactis palustris</i>	1	1	0
<i>Eupatorium cannabinum</i>	0	0	0
<i>Euphrasia stricta</i>	1	1	0
<i>Festuca arenaria</i>	0	0	0
<i>Festuca rubra</i>	1	0	1
<i>Galium saxatile</i>	0	0	0
<i>Galium verum</i>	0	0	0
<i>Glaux maritima</i>	1	0	1



Species	Green beach	Dune-slack	Salt-marsh
<i>Hieracium umbellatum</i>	0	0	0
<i>Hippophae rhamnoides</i>	0	0	0
<i>Holcus lanatus</i>	0	0	0
<i>Honkenya peploides</i>	0	0	0
<i>Hydrocotyle vulgaris</i>	0	0	0
<i>Hypochaeris radicata</i>	0	0	0
<i>Jacobaea paludosa</i>	0	0	0
<i>Jacobaea vulgaris</i>	0	0	0
<i>Juncus alpinoarticulatus</i>	1	1	0
<i>Juncus ambiguus</i>	1	0	1
<i>Juncus articulatus</i>	0	0	0
<i>Juncus gerardii</i>	1	0	1
<i>Juncus maritimus</i>	1	0	1
<i>Leontodon autumnalis</i>	0	0	0
<i>Leontodon saxatilis</i>	0	0	0
<i>Leymus arenarius</i>	0	0	0
<i>Limonium vulgare</i>	1	0	1
<i>Linaria vulgaris</i>	0	0	0
<i>Linum catharticum</i>	1	1	0
<i>Liparis loeselii</i>	1	1	0
<i>Lolium perenne</i>	0	0	0
<i>Lotus corniculatus</i>	0	0	0
<i>Lythrum salicaria</i>	0	0	0
<i>Matricaria spec.</i>	0	0	0
<i>Melilotus albus</i>	0	0	0
<i>Mentha aquatica</i>	0	0	0
<i>Myosotis spec.</i>	0	0	0
<i>Odontites vernus subsp. serotinus</i>	1	1	1
<i>Oenothera deflexa</i>	0	0	0

Species	Green beach	Dune-slack	Salt-marsh
<i>Oenothera oakesiana</i>	0	0	0
<i>Parapholis strigosa</i>	1	1	1
<i>Parnassia palustris</i>	1	1	0
<i>Phleum arenarium</i>	0	0	0
<i>Phleum spec.</i>	0	0	0
<i>Phragmitis australis</i>	0	0	0
<i>Plantago coronopus</i>	0	0	0
<i>Plantago lanceolata</i>	0	0	0
<i>Plantago major</i>	0	0	0
<i>Plantago maritima</i>	1	0	1
<i>Poa annua</i>	0	0	0
<i>Poa pratensis</i>	0	0	0
<i>Poa trivialis</i>	0	0	0
<i>Potentilla anserina</i>	0	0	0
<i>Prunella vulgaris</i>	0	0	0
<i>Puccinellia distans subsp. distans</i>	1	0	1
<i>Puccinellia maritima</i>	1	0	1
<i>Ranunculus flammula</i>	0	0	0
<i>Ranunculus repens</i>	0	0	0
<i>Rubus caesius</i>	0	0	0
<i>Rumex crispus</i>	0	0	0
<i>Sagina maritima</i>	1	0	1
<i>Sagina nodosa</i>	1	1	0
<i>Salicornia europaea</i>	1	0	1
<i>Salix cinerea</i>	0	0	0
<i>Salix pentandra</i>	1	0	1
<i>Salix repens</i>	0	0	0
<i>Salsola kali</i>	0	0	0
<i>Samolus valerandi</i>	0	0	0

Species	Green beach	Dune-slack	Salt-marsh
<i>Schoenoplectus tabernaemontani</i>	0	0	0
<i>Schoenus nigricans</i>	1	1	0
<i>Sedum acre</i>	0	0	0
<i>Senecio inaequidens</i>	0	0	0
<i>Senecio viscosus</i>	0	0	0
<i>Senecio vulgaris</i>	0	0	0
<i>Sonchus arvensis</i>	0	0	0
<i>Spartina anglica</i>	1	0	1
<i>Spergula arvensis</i>	0	0	0
<i>Spergularia media</i>	1	0	1
<i>Spergularia salina</i>	1	0	1
<i>Suaeda maritima</i>	1	0	1
<i>Taraxacum spec.</i>	0	0	0
<i>Trifolium arvense</i>	0	0	0
<i>Trifolium fragiferum</i>	0	0	0
<i>Trifolium pratense</i>	0	0	0
<i>Trifolium repens</i>	0	0	0
<i>Triglochin maritima</i>	1	0	1
<i>Triglochin palustris</i>	0	0	0
<i>Vicia cracca</i>	0	0	0



Appendix 5.2 Statistical models testing Shannon-Wiener diversity index

Plant species richness 2006	Dependent variable:		
	All species	Green beach species	Salt-marsh species
Intercept	1.95***	1.52***	1.40***
EC	-0.075	-0.009	0.050
Elevation	0.18**	-0.014	-0.030
Distance Sea	-0.15	-0.056	0.045
ED volume 2 – 6 m NAP	0.083	0.18	0.13
Volume secondary dunes	-0.054	0.011	0.018
Marginal R ²	0.22	0.18	0.28
Conditional R ²	0.45	0.49	0.28
Observations	107	107	107
Akaike Inf. Crit.	191.36	231.82	104.00
Bayesian Inf. Crit.	212.28	252.74	122.71

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: EC: electrical conductivity, ED: embryo dune.

Table A5.2. Statistical models exploring patterns of Shannon-Wiener diversity index in 2006 of all plant species and the species characteristic of green beaches and salt-marsh. The species richness per plot of all species, green beach, and salt-marsh species were analysed with a general linear mixed model with transect as random intercept. The standardised estimates and level of significance are shown for the models. Marginal R² is the variation explained by the fixed factors, whereas the conditional R² is the variation explained by the fixed and random factors.

Plant species richness 2016	Dependent variable:		
	All species	Green beach species	Salt-marsh species
Intercept	1.51***	0.63***	0.562***
Elevation	-0.10	-0.078*	-0.062●
Distance Sea	0.11	0.068	0.057
ED volume 2 – 6 m NAP	-0.023	-0.023	-0.035
Volume secondary dunes	-0.042	-0.016	0.004
Organic layer thickness	0.33***	0.23***	0.23***
EC	-0.095	0.023	0.058*
Marginal R ²	0.22	0.18	0.13
Conditional R ²	0.45	0.49	0.42
Observations	107	107	107
Akaike Inf. Crit.	203.83	66.94	56.90
Bayesian Inf. Crit.	227.28	90.38	80.35

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: EC: electrical conductivity, ED: embryo dune.

Table A5.3. Statistical models exploring patterns of Shannon-Wiener diversity index in 2016 of all plant species and the species characteristic of green beaches and salt-marshes. Species diversity per plot of all species, green beach, and salt-marsh species were analysed with a general linear mixed model with transect as random intercept. The standardised estimates and level of significance are shown for the models. Marginal R² is the variation explained by the fixed factors, whereas the conditional R² is the variation explained by the fixed and random factors.

Table A5.4. Statistical models exploring the change in Shannon-Wiener diversity index of all species and the species characteristic of green beaches, dune slack and salt marshes. All data was analysed with a general linear mixed model with transect as random intercept. The standardized estimates and level of significance are shown for the models. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

Δ in plant species richness between 2006 - 2016	Dependent variable:			
	All species	Green beach species	Dune-slack species	Salt-marsh species
Intercept	-1.77	-1.14	0.26	-1.63
Δ Elevation	-1.63**	-0.80	-0.47*	-0.35
Δ Distance Sea	-1.21	0.39	-0.081	0.59
Δ ED volume 2 - 6 m NAP	-3.28	-2.28	-0.98*	-2.02
Δ Organic layer thickness	0.38	1.00*	0.26	0.88*
Volume secondary dunes	-2.86	-1.74	-1.00	-1.10
Marginal R^2	0.27	0.26	0.29	0.21
Conditional R^2	0.63	0.56	0.29	0.50
Observations	107	107	107	107
Akaike Inf. Cri Δ t.	653.63	617.96	458.04	601.79
Bayesian Inf. Crit.	674.55	638.88	478.96	622.71

Note: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: ED: embryo dune.



Appendix 5.3 Ordination graphs

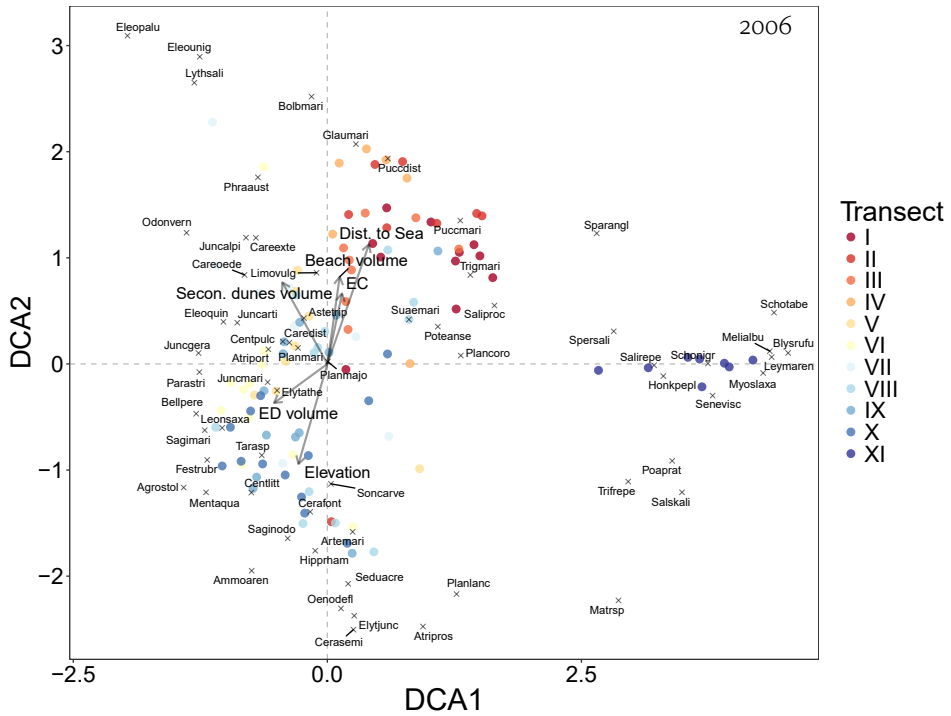


Figure A5.1. A detrended correspondence analysis for all the plots, species and environmental data in 2006. The points are the different plots, with different colours indicating the different transects. Crosses indicates the different species and are indicated with the first four letters of their genus and species names, only the 65 most common species are shown, for these species their abundance is higher than half of the medium abundance. The arrows indicate the factors, distance to the sea, beach volume, volume secondary dunes, embryo dune volume, elevation and EC (electrical conductivity). The small black lines show the location of the labels for the different species.

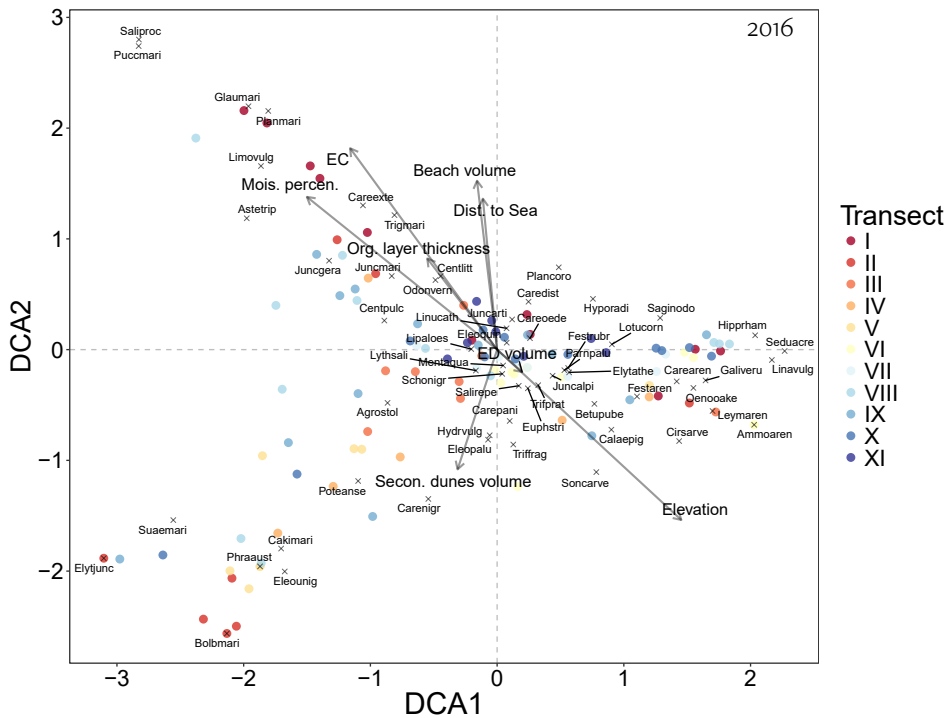


Figure A5.2. A detrended correspondence analysis for all the plots, species and environmental data in 2016. The points are the different plots, with different colours indicating the different transects. Crosses indicates the different species and are indicated with the first four letters of their genus and species names, only the 59 most common species are shown, for these species their abundance is higher than half of the medium abundance. The arrows indicate the factors, distance to the sea, beach volume, volume secondary dunes, embryo dune volume, elevation, organic layer thickness, moisture content and EC (electrical conductivity). The small black lines show the location of the labels for the different species.



An aerial photograph of a coastal landscape. A diagonal line of green, bushy vegetation runs from the bottom left towards the top right, separating a sandy area from a body of water. The water is a light, milky color, suggesting sediment. The sand is a pale, uniform color with some subtle textures. The vegetation consists of small, rounded green shrubs planted in a regular pattern.

Chapter 6

Synthesis: summary of results and implications for future dune development and mega-nourishment design.

This thesis presents results of an experiments under controlled glasshouse conditions, field experiments, analyses of time-series of aerial photographs, and field monitoring. With these studies we aimed to understanding how the interactions between ecological and geomorphological processes determine early dune development, and to what extent embryo dunes facilitate development of species-rich green beach vegetation. Below we summarise our main results and compare them with additional measurements and monitoring data of two mega-nourishments, exploring how the design of a mega-nourishment can be optimised for new dune development. The chapter ends with future research challenges.

6.1 Embryo dune development

6.1.1 Boundary conditions for embryo dune growth

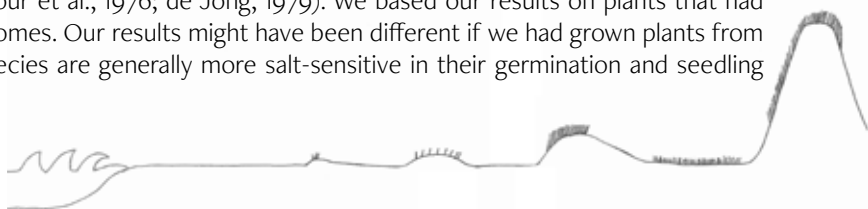
One of the main aims of this thesis was to determine the boundary conditions for embryo dune development. By analysing changes in embryo dune area over a 30 year time period we found that beach morphology determined the potential for dune development (chapter 3). Large embryo dune complexes occurred only on beaches with an upper beach wider than 300 m. This is probably caused by the larger available space, in combination with reduced erosion by storms as wide beaches reduce wave energy (Ruggiero et al., 2001). The maximum area of embryo dunes that can develop on wide beaches does, however, depend on soil salinity, salt spray, and storm erosion. These factors determine the lowest limit at which dune building species can survive on the beach. If the lowest limit of dune building vegetation on the beach is close to the sea, more embryo dunes can develop, than when the vegetation limit is further from the sea.

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Beach morphology determines the potential for dune development. Large embryo dune complexes occur on upper beaches wider than 300 m.

Thus, to predict further new dune development it is important to understand which factors determine the vegetation limit on the beach. Using a greenhouse and a field experiment, we assessed the effects of soil salinity and salt spray on the growth of two dune building species and compared these effects with actual plant growth and soil salinity in the field (chapter 2).

Soil salinity affected *A. arenaria* and *E. juncea* differently; *A. arenaria* was much less salt resistant than *E. juncea*. However, in contrast with our hypothesis (chapter 1), and despite differences in soil salinity tolerance between the two dune building species, soil salinity during summer did not explain plant survival and growth in the field. The observation that soil salinity does not explain the vegetation limit of these dune building species, could be explained by these beaches being less saline than expected. A similar explanation was suggested by Maun (2009) for beaches in North and Central America and Australia (Kearney, 1904; Olsson-Seffer, 1909; Gooding, 1947; Barbour et al., 1976; de Jong, 1979). We based our results on plants that had developed from rhizomes. Our results might have been different if we had grown plants from seeds instead, as species are generally more salt-sensitive in their germination and seedling



stages (Seneca, 1969; Seneca, 1972; Maun, 1981; Greipsson and Davy, 1994; Debez et al., 2004). However, since dispersal via vegetative fragments, such as rhizomes, are common in dynamic environments (Huiskes, 1977; Konlechner and Hilton, 2009; Gornish and Miller, 2010; Hilton and Konlechner, 2011), it seems unlikely that salt sensitivity of seedlings would determine the lowest vegetation limit on the beach. It could however determine the rate of vegetation expansion of salt-sensitive species at the upper beach. A negative effect of soil salinity on the germination of dune building species could partly explain the positive effect of precipitation on embryo dune growth (chapter 3). Precipitation results in lower soil salinity and higher soil moisture content which are both beneficial for plant growth (Lichter, 1998; Yizhaq et al., 2007; Tsoar et al., 2009).

In the field experiment the survival of the transplanted plants decreased in winter, most likely due to the high water level during storms (chapter 2). Plants transplanted close to the sea did not survive, clearly indicating that the vegetation limit on the beach could be a result of inundation by high water during storms. This suggests that the vegetation limit is variable each year and depends on the storm intensity and frequency (Gagné and Houle, 2002). In a year with only low intensity storms or no storms at all, vegetation can establish much closer to the sea, compared to a year with more severe storms. Storms may cause a sudden increase in soil salinity by sea water inundation and can lead to mechanical erosion. The effect of a salinity increase due to seawater inundation on plant survival likely depends on the time of year of the inundation (Harris and Davy, 1986; Baye, 1990; Vergiev et al., 2013; Konlechner et al., 2013). As storms in temperate regions mainly occur during winter, it seems unlikely that sea-water inundation caused the mortality of *A. arenaria* and *E. juncea* in the field experiment. Plant mortality is most likely related to mechanical erosion instead. In contrast to models of dune development by Durán and Moore (2013, 2015) that use a fixed vegetation limit to determine the location where dunes can develop on a beach, our results suggest that a dynamic vegetation limit, which depends on storm intensity, might be more realistic.

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The lower limit of dune-builder *E. juncea* depends on storm erosion, whereas the lower limit of *A. arenaria* may be related to soil salinity.

6.1.3 Embryo dune development over time

In temperate regions, embryo dunes show a pattern of sediment accumulation in summer and erosion in winter (Montreuil et al. 2013). In this thesis we found the same pattern of summer accumulation and winter erosion for our dunes on Texel (chapter 4).

We found no effect of species composition and vegetation density on dune growth over summer (chapter 3). Although the presence of vegetation is needed to fix the sand, dune volume ultimately determined sediment deposition, in contrast to our hypothesis (chapter 1). There are several explanation for the absence of an effect of vegetation height, density or species composition on sediment deposition in our study. First, vegetation might have only an effect on sediment deposition within a vegetation patch (Zarnetske et al., 2012; Keijsers et al., 2014b)

and not at a larger spatial scale itself. Secondly, the effect of vegetation on dune growth might only be measurable over time scales longer than that of a single summer season, since its effects on sediment deposition are rather small (Zarnetske et al., 2015). Thirdly, the two dune building species that were grown in our study site are both grasses and might be too similar in growth form and density to lead to a difference in sediment deposition (Baas, 2002; Baas and Nield, 2007). Finally, it could be that the size of the vegetated area determines sand deposition rather than vegetation density or height. In an additional field experiment, which has not been included in this thesis, we planted *A. arenaria* at the same density in 1 m² and 4 m² plots on the beach. After three months, the larger plots had caught more sand and had a higher elevation compared to the smaller plots suggesting variation in vegetated area may have (partly) masked the effect of the other vegetation characteristics in our study (Fig. 6.1).

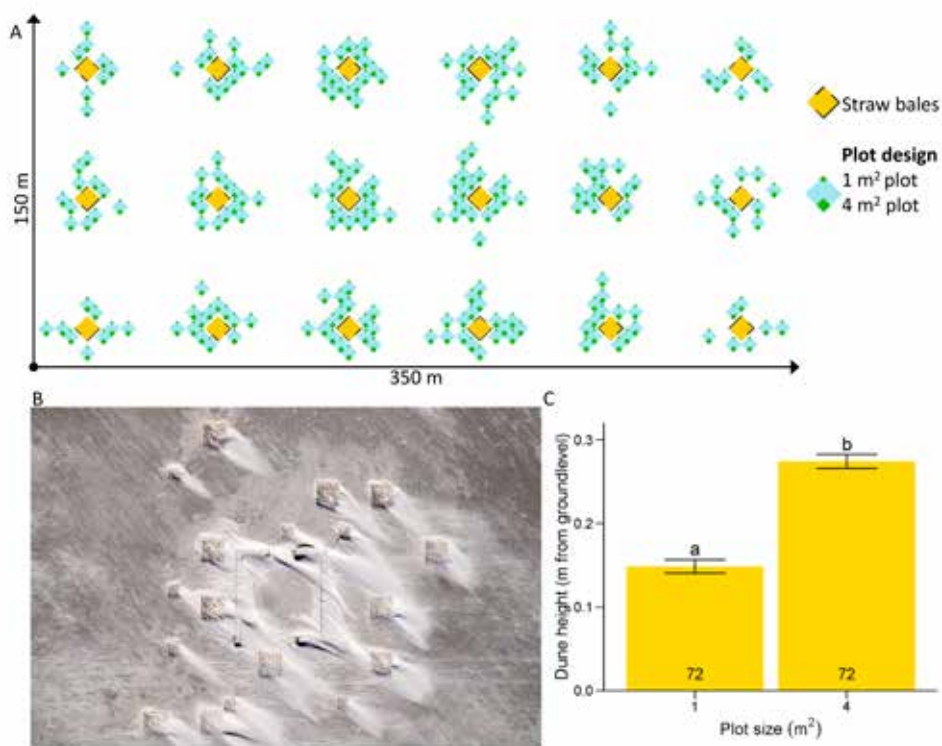


Figure 6.1. Large scale plant experiment on the Dutch barrier island Terschelling where *Ammophila arenaria* was planted in 1 m² and 4 m² plots in April 2016. The experiment was part of an exhibition on landscape art, to visualize dune development (Windwerk: <http://www.slem.org/projecten/windwerk>). A) Overview of the experimental design, the direction of the sea is to the top of the picture. The experiment consisted of 18 blocks with a varying number of paired plots (large, light grey square) of 1 m² and a 4 m² plots (small, dark grey squares). For artistic reasons, a square of straw bales was placed in the middle of each block. We randomly selected 72 plots of each size class (144 in total) and measured the maximum height above ground level with a levelling device in June 2016. B) Picture of one of the blocks in Windwerk. C) Effect of plot size (m²) on average dune elevation after three months since planting (generalised linear model, with distance to straw bale as random effect; $p=0.009$). Large plot size results in more sand deposition and a higher elevation, compared to the lower plot size.

Over summer, embryo dunes were found to grow at a constant rate per unit of area, with the rate of growth depended on the sand supply (chapter 4). Interestingly, foredunes have also been found to have a linear growth rate per area over a decadal time-scale, which suggest that variation in aeolian transport between years averages out over longer time-periods (de Vries et al., 2012; van der Weerd and Wijnberg, 2016). These results also suggests that dunes grow at a constant rate over longer time periods and that the average rate is determined by the beach morphology. It would be interesting to link the rate of dune growth to the actual aeolian transport or to a proxy for aeolian transport, such as wind speed. However, no significant effect of wind speed on dune development has been found in this thesis or in other studies (chapter 3, de Vries et al., 2012; Keijzers et al., 2014). Aeolian transport is notoriously difficult to predict from wind speed alone, since aeolian sand transport can be supply limited by high surface moisture, crust formation and lag deposits (e.g. shells, coarser grains etc.)(Nordstrom and Jackson, 1992; Arens, 1996; Davidson-Arnott et al., 2008; Delgado-Fernandez, 2010; Lynch et al., 2013). Furthermore, the sand deposited by aeolian transport might partly be eroded away after storm events, which will reduce the correlation between aeolian sand transport and dune development over longer time-periods.

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Embryo dune growth over summer is mainly determined by dune size and sand supply rather than by vegetation height, density or species composition.

Although vegetation characteristics did not affect summer growth, it did affect dune erosion over winter (chapter 4). Keeping distance to the sea constant, dunes with the lower density grass *E. juncea* had a lower growth rate in winter than dunes with the higher density grass *A. arenaria*. In the field transplant experiment (chapter 2), winter survival of *E. juncea* was also lower, compared to *A. arenaria*. These results suggest that dune erosion and plant survival therefore depend on species traits (Charbonneau et al., 2017). Our study species differed in vegetation density (chapter 4). It has been shown that vegetation can dissipate more wave energy if it is denser (Augustin et al., 2009; Silva et al., 2016). However, vegetation density did not have a significant effect on the dune growth in winter, which suggest that species traits other than density, such as plant height and the flexibility of the vegetation could play a role (Koch et al., 2009; Tanaka, 2008; Kobayashi et al., 2013). Whether plants are completely eroded away by mechanical erosion, or survive to regrow in spring also depends on their rooting structure (Feagin et al., 2015). A vegetation patch with an extensive root system, where tillers are connected by rhizomes is better protected against mechanical erosion than a just established plant with a single root system. Besides directly affecting sediment erosion, plants can also indirectly reduce erosion by increasing organic matter build-up (Feagin et al., 2009). More research on how vegetation mediates storm erosion in dune systems is needed to better predict dune erosion and survival.

Dune size had no effect on the amount of sediment erosion or dune survival (chapter 4). The absence of an effect of dune size suggests that there might not be a critical dune size, which dunes need to survive storms over winter (Balke et al., 2014). Multiple reasons could explain why dune size did not affect dune erosion. Firstly, vegetation may have a larger effect on dune erosion than dune size, thus masking the effect of dune size. Secondly, water follows

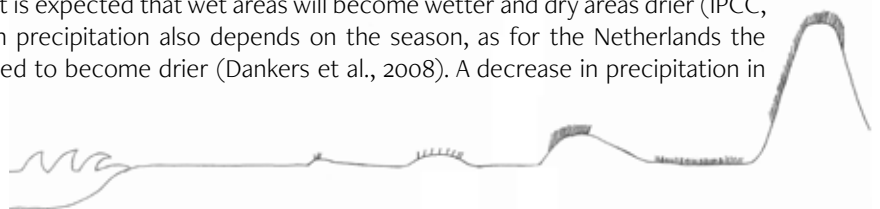
the path of least resistance and therefore the dune erosion also depends on whether the high sea-water will reach these dunes, as they can be sheltered by other dunes. Thirdly, vegetation and dunes alter water flow patterns over a large scale and can therefore affect patterns of sedimentation. Vegetation has been found to have local positive feedback effects on sedimentation by reducing dune erosion, but negative feedback effects at longer distances, for example by the formation of erosion troughs (Bouma et al., 2009). Finally, the effect of dune size and vegetation on storm erosion most likely depends on the storm intensity. The storm that we monitored in chapter 4 was relatively weak and therefore might not have had that large an effect on dune erosion, allowing the small dunes to survive.

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Storm erosion of embryo dunes in winter can be modified by vegetation composition: *E. juncea* has more dune erosion and lower plant survival compared with *A. arenaria*, which had higher vegetation density and plant height.

Overall, net dune growth depends on the balance between summer growth and winter erosion. This balance depends on the wind speed during summer and the storm intensity and frequency during winter: dune growth will be highest in years with windy summers with regular precipitation and mild winters without any storms and negative in years with extremely dry and wind-still summers and winters with a high intensity or frequency of storms (Fig. 6.2). Sand supply and storm intensity are also modified by beach morphology (Klijn, 1990; Jackson and Cooper, 1999; Ruggiero et al., 2001; Bauer and Davidson-Arnott, 2002; Delgado-Fernandez, 2010; Keijsers et al., 2014b). At shorter beaches the sand supply may be lower while the attenuation of waves will be less. For this reason dune growth on narrow beaches might be lower compared to wider beaches. The variation in storm intensity among years will most likely be the cause of most of the variability between years in net dune growth. A high-intensity storm that occurs once every 5 years or less can even set back dune development for many years (chapter 3). Ultimately, the regional storm climate will determine the severity of high intensity storms, and so affect dune erosion. Hurricanes for example, will result in extreme dune erosion (Coch and Wolff, 1991; Claudino-Sales et al., 2008; Charbonneau et al., 2017). The net dune growth may differ between dunes that are dominated by different plant species, since some species are more resistant against storm erosion than others and will therefore survive storms better. Overall, net embryo dune growth per year likely peaks at wide beaches with a high sand supply and low storm intensity.

In the future, climate change will affect the balance between dune growth in summer and dune erosion in winter (Jackson and Cooper, 2011; Katsman et al., 2011). The expected sea level rise of 18 to 59 cm will result in more intense storms, so that net dune growth might be less or even negative in the future (Corre, 1991; FitzGerald et al., 2008; IPCC, 2014; KMNI and PBL, 2015). Climate change might also affect vegetation establishment and growth by affecting precipitation patterns. In general, it is expected that wet areas will become wetter and dry areas drier (IPCC, 2014). The change in precipitation also depends on the season, as for the Netherlands the summers are expected to become drier (Dankers et al., 2008). A decrease in precipitation in



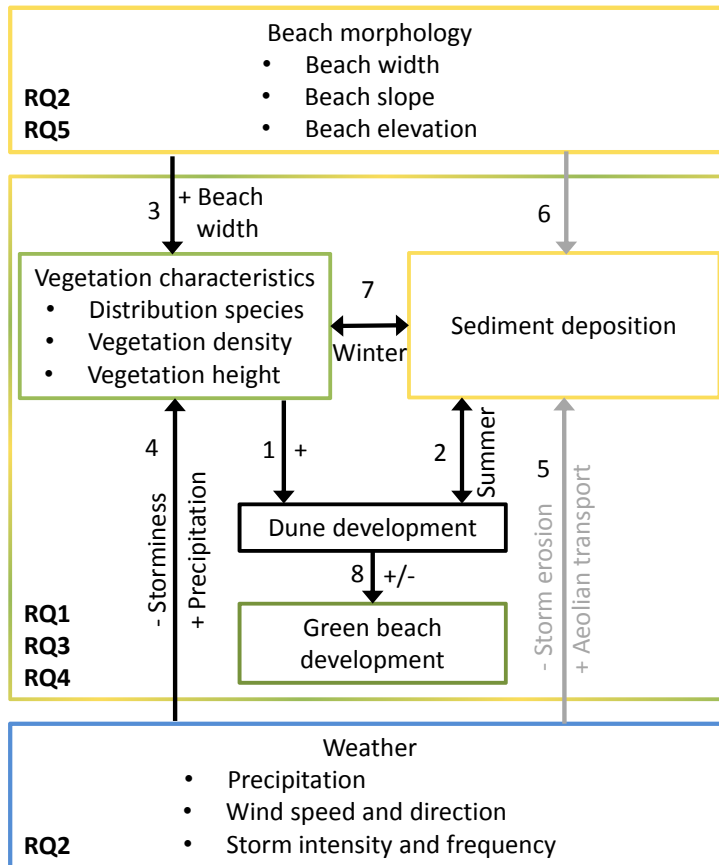


Figure 6.2. Overview of the most important factors that are involved in embryo dune development and subsequent green beach development. Dune development depends on the vegetation characteristics of dune building species (1) and sediment deposition which occurs in summer and causes dunes to grow in size (2). The distribution and growth of dune building species is affected by precipitation and storm erosion (4), these factors are influenced by beach width and elevation (3). Sediment deposition is a net result of aeolian transport and storm erosion (5), aeolian transport and storm erosion is influenced by beach morphology (6). Vegetation composition only affected dune erosion during winter, vegetation composition did not affect sand deposition during summer (7). Dune development can give shelter for the development of species rich green beach vegetation on accreting beaches, however on eroding beaches embryo dunes compete for space with green beach vegetation (8). Black lines are processes that were studied in this thesis and grey lines are not extensively researched in this scheme. RQ indicates the research question.

the growing season may reduce establishment and growth of dune building species and subsequently reduce embryo dune development (Yizhaq et al., 2007; Tsoar et al., 2009; Greaver and Sternberg, 2010). Vegetation recovery might also be lower with decreased precipitation. Not only the amount of precipitation is expected to change, but also more extreme rain events are predicted (Allen and Ingram, 2002; O’Gorman and Schneider, 2009). What the effect of these extreme rain events will be on dune development is difficult to predict, but since water leaches easily from the sandy soil (Greaver and Sternberg, 2010), extreme rain events might not benefit the vegetation as much as more frequent, but less intense rain events.

6.2 Implication for dune functions

6.2.1 Coastal safety

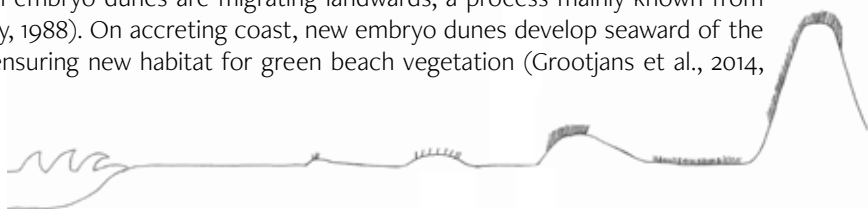
Currently it is not well known, whether the formation of embryo dunes in front of a foredune increases or decreases coastal safety. In the short term embryo dunes can either reduce the foredune growth by reducing the sand supply or reduce foredune erosion during storms by attenuating waves (Arens et al., 1995; Montreuil et al., 2013). It is unknown how the net foredune growth is affected by embryo dune development. The monitored foredune in chapter 5 had a lower growth rate compared to the seaward situated embryo dunes, indicating that embryo dunes may reduce sand supply to the foredune. However, the foredune also did not show net erosion in winter, probably because the embryo dunes protected the foredune (Fig. 6.3). Overall net foredune growth was quite high, compared to other foredunes along the Dutch coast, which suggests that embryo dunes do not really restrict foredune development. In the longer term embryo dunes will increase coastal safety by developing into a new foredune, while the old foredune would become a secondary dune (Hesp, 2002; Goldstein et al., 2017).

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Embryo dunes can be a source for shelter for green beach vegetation, but can also compete for space, reducing the area suitable for green beach vegetation. Accreting beaches that continuously provide area for the development of new embryo dunes provide the best potential for green beach development.

6.2.2 Green beach vegetation

The presence of embryo dunes is assumed to benefit the development of species rich green beach vegetation by creating shelter (Edmondson et al., 2001; Bakker et al., 2005; van Tooren and Krol, 2005; Barrett-Mold and Burningham, 2009). However, our research showed that there can be competition for space between the embryo dunes and green beach vegetation. The increase in elevation by embryo dune development, is detrimental for green beach vegetation and especially the dune slack vegetation, since burial by sand changes the abiotic conditions to a drier habitat. Competition for space between embryo dunes and green beach vegetation only occurs when embryo dunes are migrating landwards, a process mainly known from eroding coasts (Psuty, 1988). On accreting coast, new embryo dunes develop seaward of the old embryo dunes, ensuring new habitat for green beach vegetation (Grootjans et al., 2014,



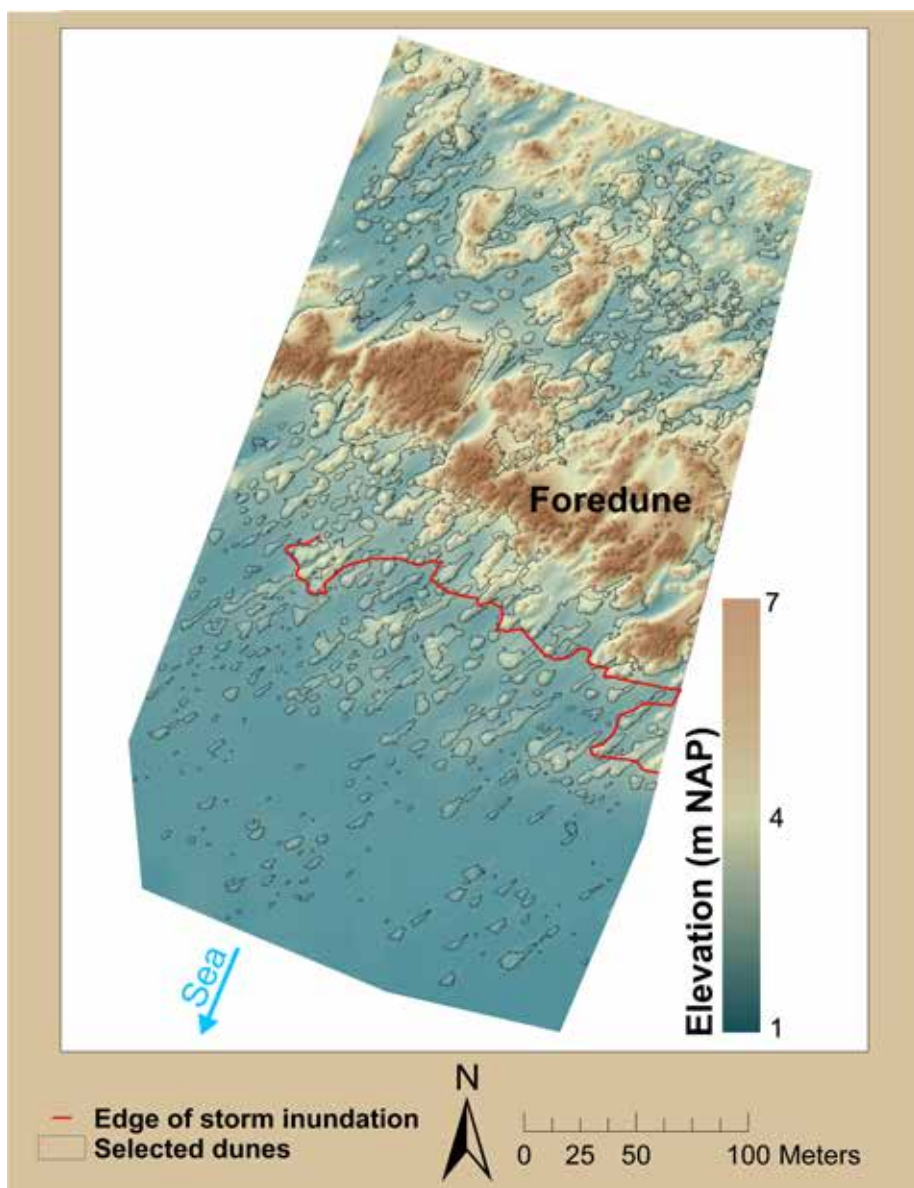


Figure 6.3. The map shows the digital surface model of a natural dune field at the Hors on Texel. Digital surface model is constructed from aerial photographs taken in August 2016, for methods see chapter 4. The red line indicates the edge of the high water inundation during a storm at 13 January 2017. The edge of the higher water inundation was measured with a hand-held GPS (Sony mobile phone, accuracy 4-5 m). The highest water level was 213 cm NAP. The graphs illustrates that embryo dunes may help to protect the foredune against flooding. Inundation of high water was stopped by embryo dunes, so that the high water could not reach the foredune.

Shahrudin, 2014). The potential for new development is restricted to accreting beaches or beaches that recently have been accreting and have a wide beach available for embryo dune development. In the Netherlands, areas where green beach vegetation can develop or increase in area are north of Schouwen, north eastern of Goeree, IJmuiden, south and north of Texel, west of Terschelling, north-west of Ameland, and the west of Schiermonnikoog.

6.2.3 Recreation

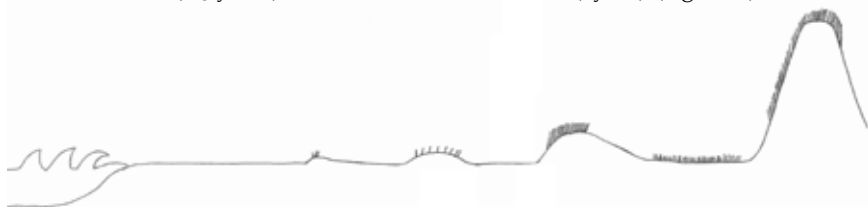
In the Netherlands, people visit the beach for a day for over 6.5 million times per year (CBS, 2017). This amount of recreation on the beach can also compromise new dune development. On a natural coast (Texel) human disturbance resulted in plant mortality in the field transplant experiment (chapter 2 and this synthesis). Recreation can reduce vegetation establishment and thereby constrain embryo dune development (McAtee and Drawe, 1981; Purvis et al., 2015). In our field experiment, human trampling and cars driven on the beach especially resulted in severe plant mortality and may have reduced the establishment of dune building species and green beach species on the beach (McAtee and Drawe, 1981; Casu et al., 2006; Santoro et al., 2012). Another factor constraining vegetation establishment is the mechanical cleaning of the beach during the summer season, since mechanical cleaning removes plant material (Dugan and Hubbard, 2010). This indicates that there is a trade-off between the recreation and dune development functions on the beach. On some beaches, the recreation pressure might be too high for new dune development to occur.

6.3 Mega-nourishments and embryo dune development

The recent construction of mega-nourishments to mitigate structural coastal erosion raises questions regarding their potential for nature development (Mulder and Tonnon, 2011; Stive et al., 2013; Temmerman et al., 2013). A high biodiversity on the beach is related to embryo dune development and the establishment of pioneer vegetation of green beaches (Acosta et al., 2009). Below we discuss the potential development of embryo dunes and green beaches for each of the mega-nourishment that we studied and we conclude with a guideline on how the design of a mega-nourishment will affect potential development of embryo dunes and green beaches.

In this thesis we mainly focussed older natural beaches where vegetation has had the time to develop. Furthermore, we studied two mega-nourishments (Sandmotor and Hondsbossche Duinen) to facilitate the translation of the results concerning embryo dune development on natural beaches, to mega-nourishment.

To understand how the ecological processes are influenced by the design of a mega-nourishment the natural establishment and growth of dune-building species was monitored on the Sandmotor in 5 transects over a period of 2 years (Box 6.1.1, Fig. 6.4A). In addition we compared patterns in growth and survival of two main dune building grasses *A. arenaria* and *E. juncea* in a field transplant experiment (Box 6.1.2) on a natural coast (chapter 2) with that on two mega-nourishments: Sandmotor (2.5 years) and Hondsbossche Duinen (1 year) (Fig 6.4D).



Box 6.1. Field transplant experiment and monitoring natural vegetation establishment

1.1 Monitoring natural establishment (collected by B. Arens & K. Vertigaal, 2015)

The establishment and growth of three dune-building species, *A. arenaria*, *E. juncea*, and *Leymus arenaria*, were monitored in five transects on the Sandmotor (Fig. 6.4A). The area and presence of vegetation was measured in October 2013, March and October 2014 and March and October 2015. Some transects were skipped at one measurement moment; in October 2014 transect one was skipped, and in March 2015 transects four and five were skipped. The area of vegetation patches was measured with an accurate RTK-DGPS Trimble R6 Model 3 (TSC3). For small vegetation patches (less than 20x20 cm) a single GPS point was measured. For each vegetation patch we calculated the elevation, distance to the sea and groundwater table depth relative to the surface for each measurement moment. Elevation and the distance to the sea were calculated from Lidar data of the Sandmotor (Rijkswaterstaat, 2017), the groundwater table depth was extracted from a hydrological model of the Sandmotor (Huizer et al., 2017).

To explore the relationships between vegetation, elevation and moisture we tested whether vegetation only occurred on the lower elevated parts of the Sandmotor. Firstly, we related the presence of dune building species in the five transects on the Sandmotor to the elevation. Secondly, we followed vegetation patches over time, and related the changes in vegetated area per patch to the species, the elevation, the change in elevation, the distance to the sea, the groundwater table depth, and precipitation. Thirdly, we summed the area of vegetation patches per transect and related changes in vegetation area to species and precipitation. We corrected the changes in area and precipitation for the number of months between the monitoring moments. Vegetation patches that were planted for the field experiment (see Box 6.1.2) were discarded from the dataset.

1.2 Comparing growth and survival between natural coast and mega-nourishment (Field transplant experiment)

We conducted a field transplant experiment to assess the plant growth of *A. arenaria* and *E. juncea* along five transects from sea to dune. This field experiment was conducted at three locations: a natural coast, the Hors on Texel, a barrier island in the Netherlands (included in chapter 2) and two mega-nourishments: the Sandmotor and Hondsbossche Duinen. We studied whether patterns in growth and survival of dune building species on a mega-nourishment were similar to that on a natural beach. On the Hors, we selected four locations within each transect representing different stages of dune development; (I) the non-vegetated zone above the mean high water line; (II) zone with *E. juncea* occurring; (III) zone with both species co-occurring; and (IV) zone where *A. arenaria* is dominant (Appendix 1.2). On the Sandmotor, we selected four locations from sea to dune within the transects. These locations were selected to represent the whole Sandmotor (Fig. 4D). On the Hondsbossche Duinen we selected three locations within each transect representing different zones on the beach to foredune; (I) the non-vegetated zone above the mean high water line; (II) zone at the dune foot of the foredune; (III) zone within the foredune in non-vegetated areas.

At each location, we established four plots of 50 × 50 cm. The minimum distance between the plots was 2 m. Two treatments were randomly assigned to the plots: a monoculture of *A. arenaria*, and a monoculture of *E. juncea*. In each plot, we planted 20 plants. The plants, consisting of one shoot, were collected from the Hors and stored outside in plastic bags with moist sand for a maximum of 2 weeks until planting.

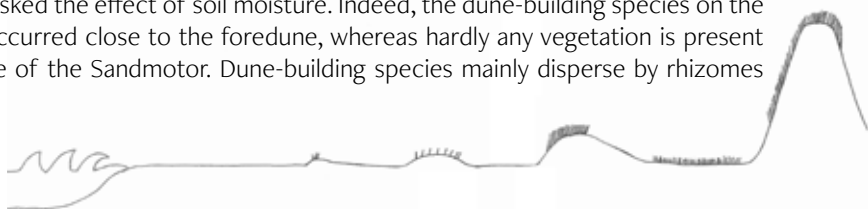
After planting, we standardized the leaf height between species and plots by clipping the leaves until the leaves were 3 cm long. On the Hors and the Sandmotor we established the experiment at the end of March 2014, whereas for the Hondsbossche Duinen the experiment was established in September 2015. We measured the number of living tillers for the Hors and the Sandmotor in August 2014, March 2015, August 2015 and 2016. The Hondsbossche Duinen experiment was measured in March and August 2016.

Additionally we measured soil salinity and soil moisture at the location in our field transplant experiment on the Sandmotor in August 2015. At each location we measured we took samples at five depths (5, 10, 25, 50 and 75 cm). Samples were weighted, dried at 105 °C for 18 hours, and weighted again to determine the gravimetric soil moisture content. Dried samples were diluted on a 1:5 mass basis with distilled water and shaken for 2 hours, after which the EC was measured. The electrical conductivity was multiplied with a factor 17 to derive the EC at saturated conditions (ECe) (Shaw, 1994).

6.3.1 Sandmotor

The goal of the Sandmotor mega-nourishment was to supply the adjacent beaches with sand by gradual erosion over time. Therefore the Sandmotor was designed with a large amount of sand in a small area, which resulted in a wide beach with a high elevation. Since beach width determines the potential for embryo dune development, the Sandmotor has a large potential for embryo dune development. Moreover the high elevation means that a large part of the Sandmotor is safe from storms, potentially increasing suitability for further embryo dune development. Despite the latter, a high beach elevation is also often accompanied by low soil moisture (chapter 5), which could slow down vegetation establishment. In particular, the absence of sea inundation might reduce the chance of establishment of sea-carried vegetative fragments, limiting plant establishment sources to more environment-sensitive germination of wind-carried seeds instead.

Our results showed that over the past 5 years, dune-building grasses established spontaneously on the Sandmotor. Taking all five transects together, dune-building grasses covered an area of 1307 m², of which 76.2% was covered with *A. arenaria*, 23.3% by *E. juncea*, and 0.5% by another dune building species *Leymus arenaria*, corresponding to the low soil salinity of the beach (ECe was between 0.58 – 2.08 mS/cm). We expected a negative relationship between elevation and the presence and growth of dune building species as a results of low soil moisture at higher elevations. Although, the soil moisture was indeed quite low (between 1.84% and 7.59%), it was not related to elevation (linear model: soil moisture ~ elevation, $t\text{-value}_{14} = -0.13$, $p = 0.90$). The lack of a relationship between soil moisture and elevation could be due to the limited range in soil moisture as a result of the high overall elevation of our sample locations on the Sandmotor (2.43 m NAP to 6.27 m NAP). Furthermore, the distribution of naturally occurring dune-building species did not reflect this expectation either. Dune-building species mainly occurred at higher elevation rather than at lower elevations (Fig. 6.5). Moreover, there was no correlation between the presence of dune-building species and groundwater depth (Fig. 6.4B, linear mixed model with change in embryo dune area related to groundwater depth, with transect as random intercept; $t\text{-value}_{244} = 1.37$, $p = 0.17$). Despite the absence of a relationship with elevation or groundwater, soil moisture did seem to contribute to vegetation development, as suggested by a positive correlation between monthly vegetation growth and precipitation (Fig. 6.6, ANOVA with change in embryo dune area per month related to precipitation per month; $F\text{-value}_{45,1} = 10.4$, $p = 0.002$). The lack of a relationship could be because other drivers such as dispersal, masked the effect of soil moisture. Indeed, the dune-building species on the Sandmotor mainly occurred close to the foredune, whereas hardly any vegetation is present on the seaward ridge of the Sandmotor. Dune-building species mainly disperse by rhizomes



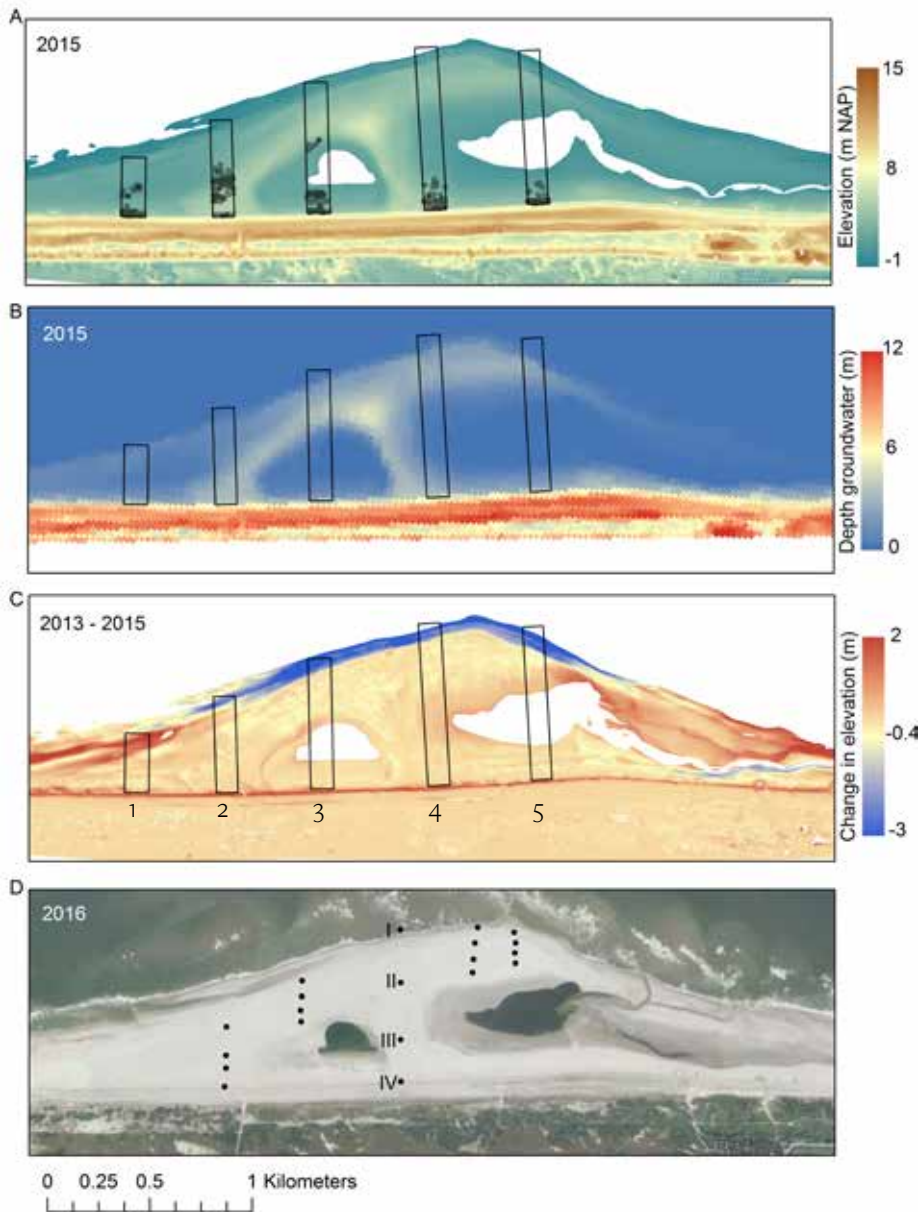


Figure 6.4. Overview Sandmotor. A) The natural distribution of dune building species on the Sandmotor occur mainly close to the existing foredune. Elevation (m NAP) of the Sandmotor (Rijkswaterstaat 2017), the points indicate the presence of natural vegetation in 2015. The squares are the monitored transects for the natural establishment of dune building species, for method see Box 6.1.1. B) The groundwater depth (Huizer et al. 2017). C) The change in elevation between 2013 - 2015. On the seaward ridge of the Sandmotor, slight erosion occurred, deposition occurred mainly at the dune foot. The numbers indicate the transect numbers. D) Aerial photograph Sandmotor (Kadaster / Clyclomedia 2014), the points indicate the plots in our field translocation experiment, the numbers indicate the locations numbers, for method see Box 6.1.2.

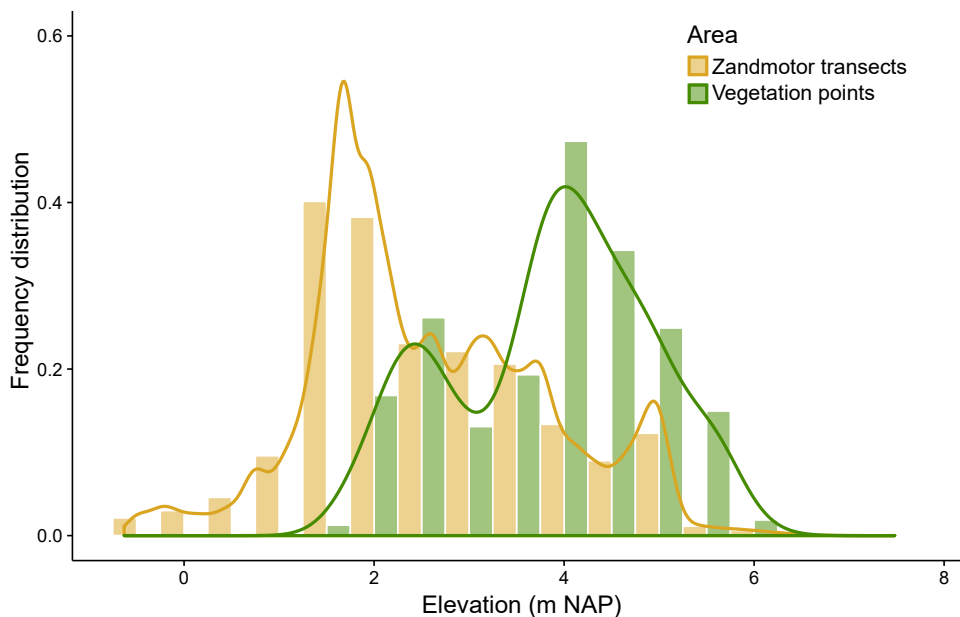
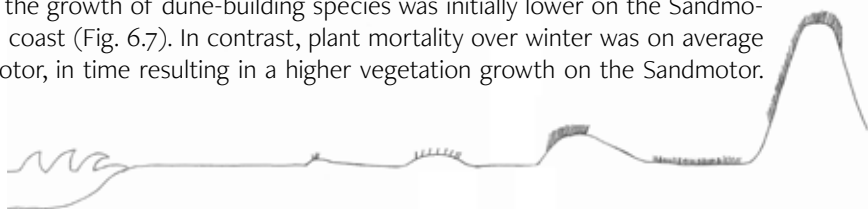


Figure 6.5. Frequency distribution of the elevation (m NAP) estimated by a kernel density estimation for both the whole of the monitored transects and for points where natural vegetation actually established on the Sandmotor. Vegetation mainly occurred at higher elevations than lower elevations at the Sandmotor. For more detail on the method see Box 6.1.1.

and seeds. Rhizomes are mainly dispersed after large storms, when the rhizome is broken off from the maternal material. The rhizome can then establish on the location it washed up and initiate the development of a new dune. Some authors have proposed that disturbance by storms is not a threat to dune-building species but rather a chance to increase their distribution (Gornish and Miller, 2010; Feagin et al., 2015). A large part of the Sandmotor is not reached by high water during storms, which means that plant material of dune-building species cannot be deposited there. This could also explain the absence of vegetation on the seaward ridge of the Sandmotor. The seeds of *A. arenaria* and *E. juncea* are relatively small and it is unlikely that these seeds cannot reach the whole of the Sandmotor by wind dispersal. However the seeds might be trapped by the lake present in the middle of the Sandmotor, which might reduce seed availability. The seaward ridge at the Sandmotor has been eroding over the last 2 years (Fig. 6.4C), which could have a negative effect on seeds germination, as seeds might be blown away from the seaward ridge or seedlings might experience mortality due to sand erosion.

From the above we can conclude that the distribution of dune-building species on the Sandmotor is not limited by elevation or moisture. However, which factor does explain the distribution of dune-building grasses is unclear. As the distribution of dune building species is potentially limited by dispersal, we conducted a field transplantation experiment, which neutralized the effect of dispersal limitation and allows comparison with a natural coast. The first summer after transplantation the growth of dune-building species was initially lower on the Sandmotor than on a natural coast (Fig. 6.7). In contrast, plant mortality over winter was on average lower on the Sandmotor, in time resulting in a higher vegetation growth on the Sandmotor.



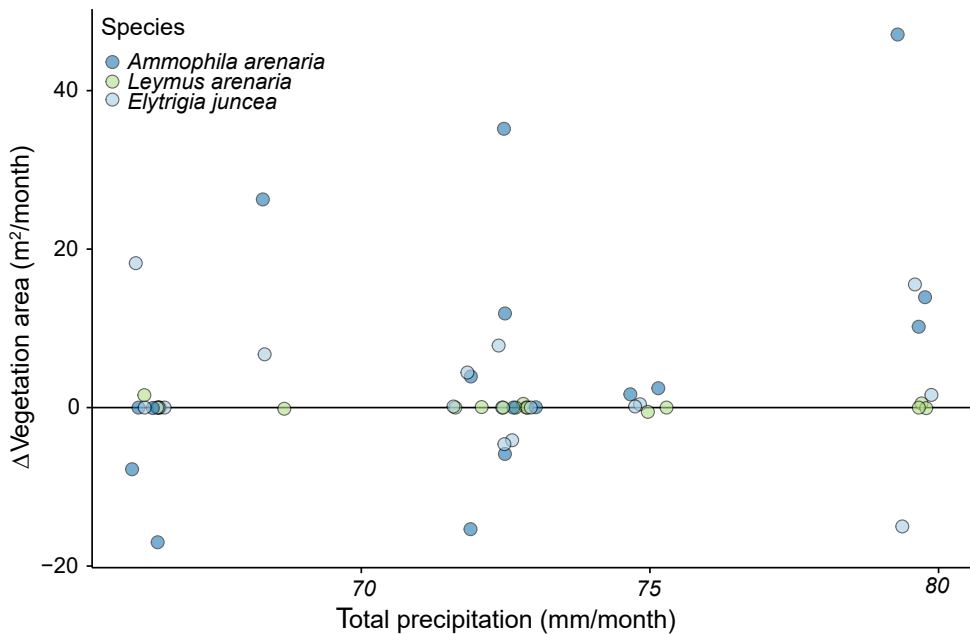


Figure 6.6. Changes in area of patches of dune building species on the Sandmotor related to precipitation during the time period. The changes in vegetation area and the precipitation were corrected for the number of months over which the patches were observed. For more methodological detail see Box. 6.1.1.

An exception to the above were the transplant locations closest to the sea. Here vegetation disappeared due to the structural erosion of the Sandmotor by the sea.

The absence of storm erosion on most of the Sandmotor area means that species traits are less important for dune development than on a natural coast (chapter 4). The monitored vegetation patches showed a positive relationship between sand deposition and the change in area of the vegetated patches (linear mixed model, with transect as random intercept; $t\text{-value}_{248}: 3.21, p = 0.001$), illustrating the positive feedback between sand deposition and vegetation growth (Maun, 1998).

6.3.2 Hondsbossche Duinen

In contrast to the Sandmotor, the Hondsbossche Duinen mega-nourishment was designed to maintain the coast line and therefore follows a standard beach – dune profile. As the design of the Hondsbossche Duinen is similar to a natural coast, we expected that growth and survival of dune-building species would be mainly limited by storm erosion.

As expected, our results suggest that storm erosion had a large influence on plant survival; at the zone close to the sea (non-vegetated zone I) all plants died over winter due to storm erosion (Fig. 6.7). In contrast most transplanted plants within the foredune (zone III) died from sand burial, similar to that on the natural coast on Texel. At the dune foot (zone II), where the storm waves were reduced and rate of sand burial was moderate, plant survival was highest.

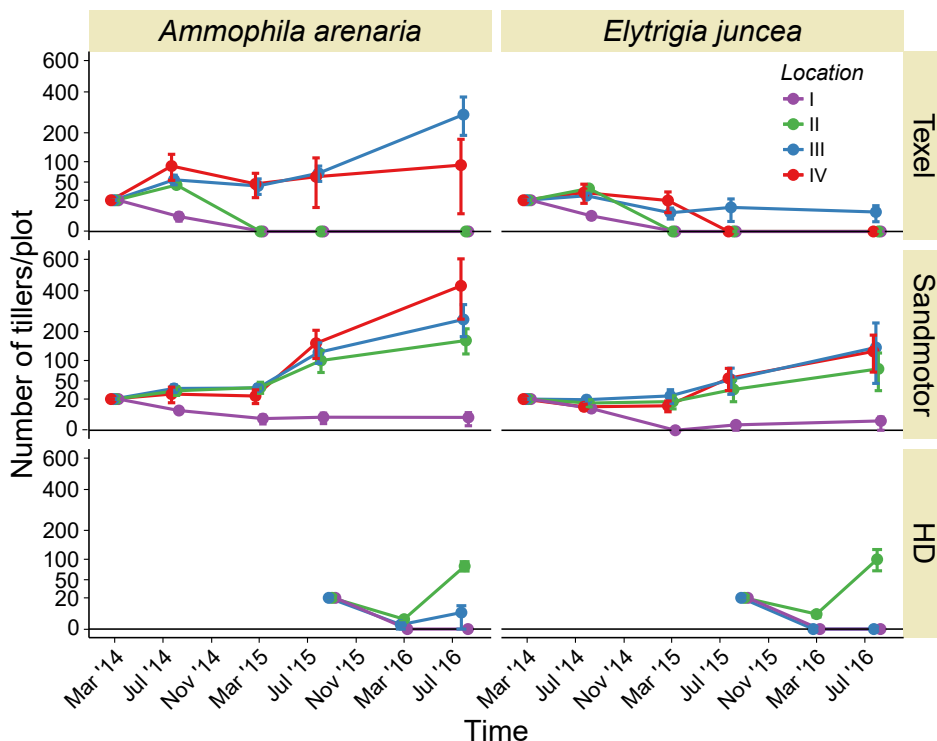


Figure 6.7. Growth expressed as the number of living tillers per plot of dune building grasses *A. arenaria* (left) and *E. juncea* (right) transplanted a different distances (locations) from the sea on a natural coast (Texel) and on two mega-nourishments: Sandmotor and Hondsbossche Duinen (HD). Location I is closed to the sea and location IV the furthest from the sea, for the Hondsbossche Duinen only three locations were planted. Field experiment on the Hondsbossche Duinen started in September 2015 was monitored for one year. For more method detail see Box 6.1.2.

Green beach vegetation often contains species that are rare in the Netherlands and Europe (European Commission 2007). These species mainly establish on accreting beaches behind the shelter of dunes, where there is no sand burial and storm erosion. Since the number of accreting beaches in the Netherlands is limited, the development of green beach vegetation, and especially dune-slack vegetation, has been incorporated as a goal for some mega-nourishments. In the Netherlands, potential dune slack habitats have been constructed in two areas: Spanjaardsduin near Hoek van Holland, constructed in 2008 – 2009 and the Hondsbossche Duinen, constructed in 2013. The potential dune-slack area has been developed as a low-lying area between the newly constructed foredune and the secondary dunes. Dune-slack species depend on low habitats with high soil moisture content, fresh water supply and no sand burial (chapter 5). So far, no dune-slack vegetation has developed in these two areas. The area at Spanjaardsduin might have a too high elevation with too low soil moisture content, whereas the area at the Hondsbossche Duinen is now a brackish lake. In Spanjaardsduin the expectation is that sand erosion will lower the elevation of the area, which might result in

higher soil moisture levels. The higher soil moisture might be beneficial for the development of dune-slack vegetation. At the Hondsbossche Duinen the expectation is that the water level will decrease and the brackish lake will become fresh, which would result in abiotic conditions beneficial for dune-slack vegetation. For now it is too early to tell whether dune-slack vegetation will develop at the Hondsbossche Duinen. The Spanjaardsduin is already 8 years old and so far no dune slack vegetation has established, which indicates that it is difficult to construct a coastal area that also has the right abiotic conditions for the development of dune-slack vegetation. The window of opportunity where the right abiotic conditions are present for the establishment of dune slack species can be rather short, which results in a high dispersal limitation of these dune-slack species.

Table 6.1. Overview of the consequences of different design options for embryo dune development.

Design option	Embryo dune development	Green beach development
Beach width	From a upper beach width of 300 m the development of large embryo dune complexes is possible.	+ 300 m upper beach and presences of dunes that give shelter against sand burial and storm erosion
Beach elevation	+ 4 m NAP = no storm erosion* + 2 m NAP low soil salinity Affects groundwater depth, which affects the dependency of vegetation on precipitation	High diversity at a maximum elevation of 2.5 m NAP
Sand transport	Sand deposition positive for embryo dune development	Sand deposition above 2.5 cm/year reduces green beach diversity
Presence of vegetation	Can act as a seed source for further vegetation development	
Recreation: public access, vehicle driving on the beach	High recreation pressure could reduce vegetation establishment and result in vegetation mortality. Recreation pressure can be decreased by reducing beach access roads and fencing the area with vegetation.	

Note: * this value depends on the tidal range of the area and the storm intensity. This value has been based on the Sandmotor and a storm intensity that occurs once every 50 years.

6.3.3 Design options for mega-nourishments

The results discussed above allow us to identify the effects of the design of a mega-nourishments on embryo dune development and biodiversity. Design parameters that affect dune development are beach width, beach elevation, the presence of vegetation and public access and vehicle driving on the beach (Table 6.1). The results from chapter 3 indicate that a wide beach is necessary for the development of large embryo dune complexes on natural beaches. We assume that a similar width is needed on mega-nourishments. For the development of green beach vegetation, the beach may need to be even wider, since green beach species require shelter by either the presence of embryo dunes or a very large beach width (chapter 5). Beach elevation influences the storm frequency, soil salinity and soil moisture. A high ele-

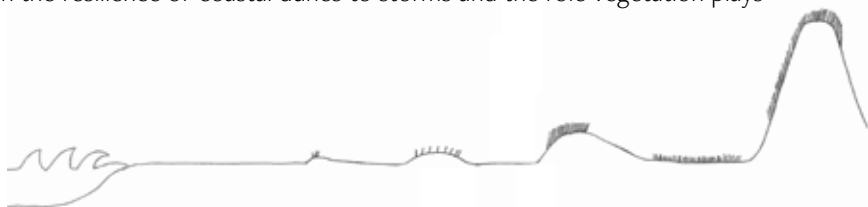
vation promotes embryo dune development due to the absence of storms and the low soil salinity on high elevations. A higher elevation would result in an increased groundwater depth, which would make the vegetation more dependent on precipitation. Green beach vegetation depends on high soil moisture and occurs on lower elevated areas. Sand transport is essential for the development of embryo dunes, and therefore sand transport needs to be high. However sand burial is detrimental for green beach vegetation and reduces green beach diversity. The presence of vegetation could act as a seedbank for further vegetation development. A large foredune is often constructed at a mega-nourishment, which will be a source of seeds that facilitates embryo dune development. Green beach species depend on colonisation from nearby sites, which means the distance to these sites could have important effects (Bossuyt et al., 2003; Shahrudin, 2014). Lastly, the recreation pressure can result in plant mortality and reduce vegetation establishment at both embryo dunes and green beaches. Recreation pressure can be decreased by reducing beach access, prohibit vehicle driving on the beach, avoiding mechanical cleaning and fencing off areas with vegetation. The design of a mega-nourishment does depend on its goal. If the goal is coastal safety, a mega-nourishment with high beach elevation might be appropriate. At such a mega-nourishment, embryo dunes will develop and storm erosion will be low. However, if the goal is to increase biodiversity, a wide beach with a lower elevation might be more suitable. As these green beach species can be limited in dispersal, introducing propagules of green beach target species might be an effective method to establish a green beach vegetation. If recreation is the goal, the high pressure and management will limit vegetation development.

TAKE HOME MESSAGE

The design of a mega-nourishment determines the potential for the development of embryo dunes and/or green beach vegetation. On wide beaches with high elevation large area of embryo dunes can develop, whereas green beach vegetation needs a low elevated beach with shelter.

6.4 Future challenges in dune research

The expected sea-level rise of 18 – 59 cm within the next century (IPCC, 2014; KMNI and PBL, 2015), will have large effects on dune development. Sea-level rise reduces the sediment budget of beaches potentially setting in motion a vicious cycle of beach erosion, decreasing beach width, and further beach and dune erosion, (McGranahan et al., 2007; FitzGerald et al., 2008; Watkinson, 200; de Winter, 2014; Keijsers et al., 2014a; Hsiang et al., 2017). To mitigate erosion by sea-level rise, the frequency and volume of sand-nourishment may need to be increased. Consequently, it is to be expected that mega-nourishments will be used more frequently in the future (MinV&W, 2015). Even though this study has filled a number of important research gaps, we still lack knowledge to accurately predict the consequences of a changing climate for coastal dune development on natural coasts and mega-nourishments. More in particular we lack knowledge on the resilience of coastal dunes to storms and the role vegetation plays in this resilience.



Future dune research should be mainly related to 1) how vegetation may help to resist storm erosion, and how this resistance depends on vegetation characteristics and/or plant traits, 2) how the recovery of dunes after storm erosion is affected by the changing climate and whether this recovery depends on the vegetation growth, and 3) the (better) incorporation of embryo dune development in existing models on dune development.

The sea-level rise will lead to more intense storms (McInnes et al., 2003; von Storch and Woth, 2008), which have a large effect on the survival of embryo dunes. In chapter 4 we found that dune erosion depended on the plant species covering the dune, suggesting that the resistance of a dune to storm partly depends on plant species. This resistance may be a function of aboveground vegetation characteristics that are involved in dissipating wave energy, or belowground characteristics that may stabilise the sediment or facilitate plant survival. Most research on how vegetation interacts with sediment erosion has been conducted in salt-marsh ecosystems. However, dunes have much coarser and granular sand compared to salt-marshes, which makes the comparison less straightforward (Feagin et al., 2015). Predicting how and to what extent vegetation may mitigate storm erosion is difficult but necessary. For future research, more experimental flume studies where we can assess the effects of high water inundation are needed (Bouma et al., 2009; Blackmar et al., 2014; Silva et al., 2016). Using this method, we can assess to what extent plant and vegetation traits, such as vegetation density, height and leaf flexibility mitigate the erosion of sandy, coarse materials. Root architecture is much harder to study experimentally, since it is difficult to artificially create a root system. A better approach might be to monitor dune erosion and plant survival in the field and relate it to different root traits, such as rooting depth, root thickness and root density. In our study, only a low intensity storm occurred during the measurement period (chapter 4). Since a more intensive storm may have a much larger effect on sediment erosion, continuous monitoring and experiments with different storm intensities are necessary to better understand embryo dune development with respect to sea level rise.

Storm erosion can either partly or completely erode dunes. Recovery of embryo dunes therefore depends on the ability of the dune to trap sediment and vegetation growth to rebuild the eroded dunes. We found that large embryo dunes increased more in volume than small embryo dunes over one summer season (chapter 4). For future research, it would be interesting to extend the time-period of monitoring dune volume and vegetation response and relate the changes over different time-periods to aeolian transport (or to a proxy such as wind speed) and weather conditions. Although we did not find any effect of vegetation on dune growth over summer (chapter 4), vegetation may still affect dune growth under different conditions, such as an extreme summer drought (Tsoar et al., 2009; Yizhaq et al., 2009). In our study only two grasses were compared, perhaps reducing effect sizes. Repeating the same study for plant species contrasting more in morphology, such as grasses and shrubs would be worthwhile. UAV-imaging is an excellent method to determine dune growth (chapter 4; Hugenholtz et al., 2013), and longer monitoring of a dune field may clarify the relationship between dune growth, vegetation and sand supply. In chapter 2 we found a positive effect of precipitation on vegetation growth. However, this relationship probably depends on the rooting depth. If the dune building species can access and use the groundwater, they are less dependent on precipitation. Dune building species grow with the sand deposition and can therefore have a deep rooting depth, but we do not know whether these roots are still functioning within a foredune. Especially in countries which are expected to become drier by climate change, the effect of

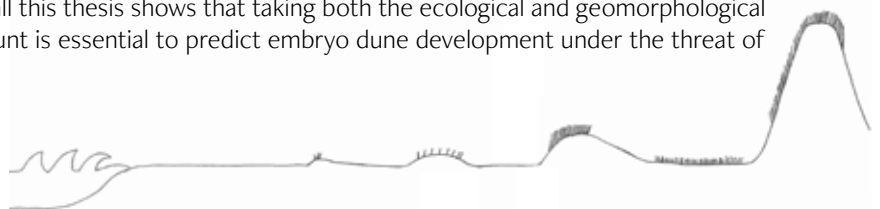
precipitation on dune growth would be a worthwhile avenue for future research.

At present most dune models focus on foredune development, one of the exceptions being a model by Baas (2007a; 2007b) who simulated the development of nebkha dunes consisting of different species. This model does not include storm erosion. Since storm erosion has such a large effect on embryo dune development, including storm erosion would certainly make the model more realistic for coastal dune development. As the amount of storm erosion depends on the species, this should be included as well.

Currently, there are only two models that include the beach, dunes with vegetation, sand deposition and storm erosion: the model by Durán and Moore (2015) and the DUBEVEG (Dune-Beach-VEgetation) model by Keijsers et al. (2016), although these two models focus on foredunes. Nevertheless, the results of my thesis could still improve these models, not only by including a zone for embryo dune development. Durán Vinent & Moore (2015) modelled barrier island dynamics, and included a limit for vegetation on the beach in their model, which they relate to soil salinity. Their model might be more realistic if a more dynamic vegetation limit were included, as suggested by our results in chapter 2. Keijsers et al. (2016) expressed vegetation cover as a function of sedimentation and erosion, which results in more dynamic vegetation limit that depends on the storm intensity and sand supply. Furthermore, Keijsers et al. (2016) modelled the effect of vegetation growth on foredune development, and found that vegetation growth especially affected the recovery time of the foredune after a severe storm. The vegetation growth in his model could be linked to precipitation. By including the effect of precipitation on vegetation growth we can predict what the effect will be of changing precipitation patterns on dune development and dune recovery.

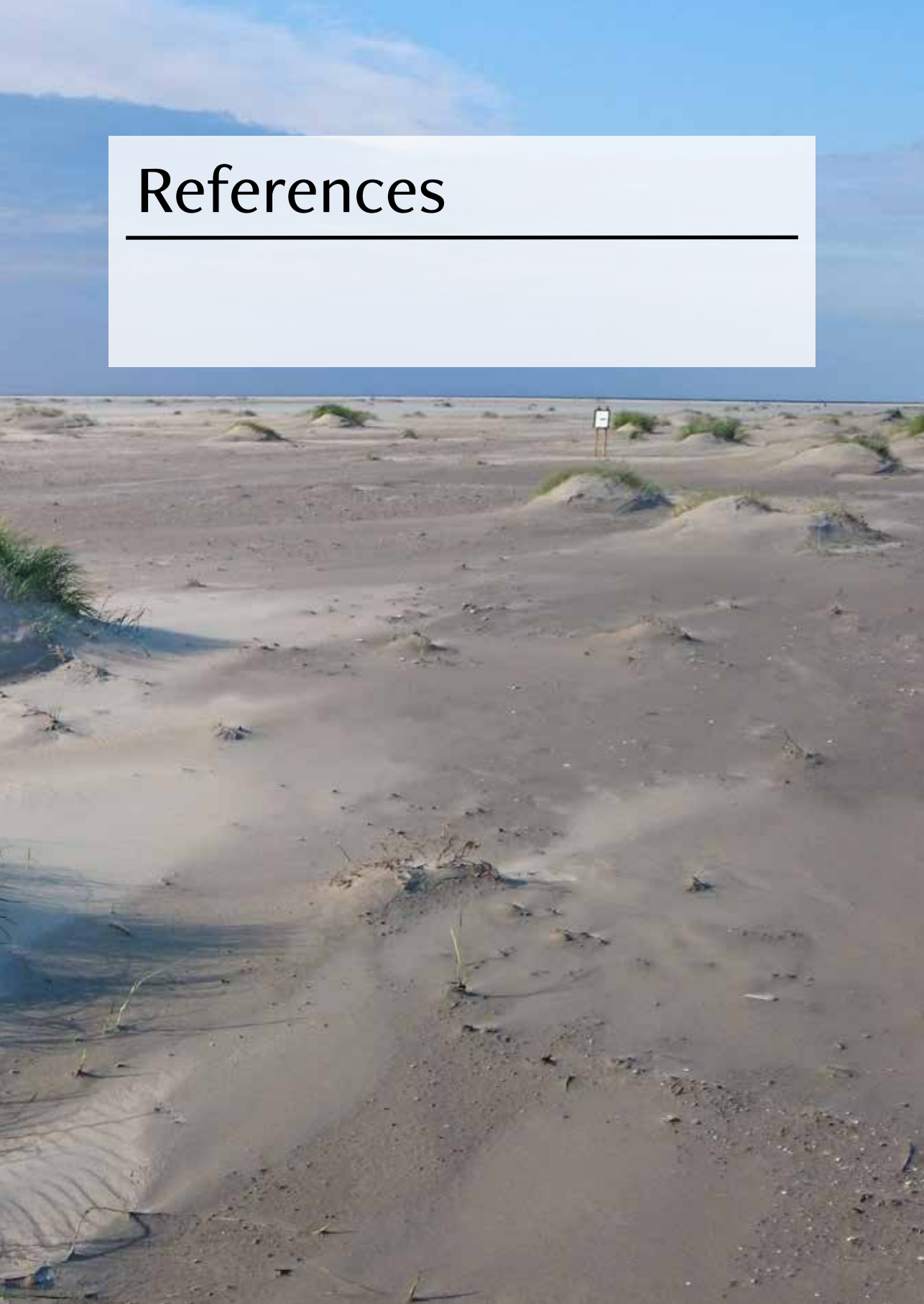
6.5 Conclusion

The aim of this thesis was to understand the interactions between the ecological and geomorphological processes that determine early embryo dune development. The key findings of this thesis are 1) the potential for embryo dune development depends on the beach width, as on wider beaches more embryo dunes can develop, and on the vegetation limit of dune building species which is mainly related to storm intensity. 2) Embryo dune growth over summer is mainly determined by dune size and sand supply rather than by vegetation height, density or species composition. 3) High-intensive storms limit embryo dune development, but dune erosion can be mitigated by vegetation composition. *E. juncea* has more dune erosion and lower plant survival compared with *A. arenaria*, which had higher vegetation density and plant height. 4) Embryo dunes can be a source of shelter for green beach vegetation, but can also compete for space thus reducing the area suitable for green beach vegetation. On accreting beaches which continuously provide area for the development of new embryo dunes green beach vegetation can develop. 5) The design of a mega-nourishment determines the potential for the development of embryo dunes and green beach vegetation. On beaches with high elevation large embryo dune area can develop, since these dunes are protected from storm erosion. However, green beach vegetation needs a low elevation and shelter by embryo dunes or a foredune. Overall this thesis shows that taking both the ecological and geomorphological processes into account is essential to predict embryo dune development under the threat of sea-level rise.





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Summary

Coastal dunes occur along the sandy shores of most continents where they serve as coastal defence against flooding, provide areas for recreation, store drinking water and harbour unique biodiversity. Coastal dunes and the services they provide are threatened by climate-induced sea-level rise. This threat may be mitigated by the spontaneous formation of new dunes, for example in combination with mega-nourishments aimed at increasing beach width. Coastal dunes form by the interaction between vegetation, wind and wave action. Persistent dune development begins with the establishment of vegetation on the beach: the vegetation traps the wind-blown sand, forming an embryo dune. Over time an embryo dune can develop into a bigger foredune, increasing coastal safety. The formation and development of embryo dunes into foredunes depend on the vegetation establishment on the beach, dune growth over summer and dune erosion during winter. Although vegetation succession and geomorphological processes are each well described, the interaction between ecological and geomorphological processes during embryo dune development are not well known. The thesis aimed at further exploring these interactions, using a combination of experiments and high-resolution dune monitoring to study the mechanisms underlying early dune development and their implications for mega-nourishment design.

To explore whether soil salinity, salt spray or storms determine the vegetation limit of dune building plant species on the beach, we performed a field transplantation experiment and a glasshouse experiment with two dune building grasses *Ammophila arenaria* and *Elytrigia juncea*. In the field growth of grasses transplanted into four vegetation zones from sea to dune was monitored for over a year and the response of these species to salt spray and soil salinity was tested in a glasshouse experiment. In the field, the vegetation zones were associated with differences in summer soil salinity: zones with both species present were significantly less saline than zones with only *E. juncea* or the zones without any vegetation. However, in our experiments the transplanted *A. arenaria* performed equal or better than *E. juncea* in all vegetation zones, suggesting soil salinity did not limit species performance at the studied site. Both species showed severe winter mortality. In the glasshouse experiment, *A. arenaria* biomass decreased linearly with soil salinity, presumably as a result of osmotic stress. *Elytrigia juncea* showed a nonlinear response to soil salinity with an optimum at 0.75% soil salinity and a decrease in biomass at higher salt concentrations. Our findings suggest that soil salinity stress either takes place in winter during storm inundation, or that development of vegetated dunes is less sensitive to soil salinity than hitherto expected.

To understand the boundary conditions for embryo dune development over a longer time period we explored the effects of beach morphology, meteorological conditions and sand nourishment on early dune development using a 30 year time series of aerial photographs and beach profile monitoring data. We concluded that 1) beach morphology is highly influential in determining the potential for new dune development, with wide beaches enabling development of larger embryo dune fields, 2) sand nourishments stimulate early dune development by increasing beach width, and 3) weather conditions and non-interrupted sequences of years without high-intensity storms determine whether progressive dune development will take place.

Dune development is the result of the interaction between vegetation development and sedimentation and erosion processes. To disentangle the effects of vegetation characteristics and that of dune size we monitored a natural dune field of 8 hectares for one year using an Unmanned Aerial Vehicle (UAV) with a camera. By constructing a digital surface model and a geometrical corrected image (an orthomosaic) for each flight campaign we calculated changes in dune volume over summer and winter and related these changes to vegetation, dune size and degree of shelter. The dune growth over summer was mainly determined by dune size, whereas dune growth over winter was determined by vegetation characteristics. Degree of shelter determined whether dune growth was limited by storm erosion (exposed dunes) or sand supply (sheltered dunes). These results suggest that vegetation characteristic may be particularly important for resisting storm erosion and speeding up recovery after erosion.

Embryo dunes have been hypothesised to facilitate development of species rich green beach vegetation in the sheltered location between the embryo dunes and the primary foredunes. To test this hypothesis we explored the relative impacts of abiotic soil conditions as affected by the geomorphological setting on the species richness and species turn-over of green beach vegetation. To this end we characterised the geomorphology and measured abiotic conditions and species composition of green beach vegetation along transects from beach to foredune. We found that the geomorphological setting influenced plant species composition indirectly by affecting soil salinity and rate of sand burial. We found that plant species richness declined less at sheltered conditions, where there was a build-up of organic matter and no sand burial. Our results further suggest a non-linear relationship between embryo dune volume and number of green beach species: embryo dunes can be a source of shelter, thus stimulating green beach development, but can also compete for space, reducing green beach development. The net effect of embryo dunes most likely depends on the sediment budget of the beach and storm intensity.

Mega-nourishments are single large sand nourishments that are applied locally, and are expected to exist for about 20 years, providing opportunities for the development of embryo dunes and rare pioneer plant communities (green beach vegetation). We explored this potential by comparing growth and development of dune building species on natural beaches with the results of plant transplantation and monitoring data of two mega-nourishments: the low-elevated Hondsbossche Duinen and the high-elevated Sandmotor. Our results suggest that establishment of dune building species on high-elevated mega-nourishment proceed slower than on natural beaches due to dispersal limitation. Once vegetation has established however, embryo dune development on high-elevated mega-nourishments may proceed faster than natural beaches due to low salinity and protection against storm erosion. Development of dune-building vegetation on the low-elevated mega-nourishment Hondsbossche Duinen showed the same rate and pattern as that on a natural beach. The potential for embryo dune development on mega-nourishments is far bigger than the potential for green beach development, since green beach vegetation develops under a narrower range of abiotic conditions. Such abiotic conditions can develop behind the shelter of embryo dunes or foredunes at low beach elevations.

In conclusion this thesis shows that, 1) the potential of embryo dune development depends on a large beach width and low storm erosion which determines the vegetation limit. 2) Embryo dune growth over summer is mainly determined by existing dune volume and sand supply. 3) Heavy storms limit embryo dune development during winter, although dune erosion can

be mitigated by vegetation composition. 4) On accreting beaches which continuously provide area for the development of new embryo dunes green beach vegetation can develop. 5) The design of a mega-nourishment determines the potential for the development of embryo dunes and green beach vegetation. Our findings provide insights in the interaction between ecological and geomorphological processes that determine embryo dune development. This knowledge can help to obtain better predictions of embryo dune development under the threat of sea-level rise.



Samenvatting

Kustduinen zijn wijdverspreid langs de zandige kusten van de meeste continenten, waar ze een breed scala aan functies vervullen. Kustduinen beschermen het achterland tegen hoogwater, bieden ruimte voor recreatie, vormen een bron van schoon drinkwater en herbergen een hoge biodiversiteit. Kustduinen, en de daarmee de functies die zij vervullen, worden in toenemende mate bedreigd door de stijgende zeespiegel. Stimulering van spontane duinvorming, bijvoorbeeld door megasuppleties van zand, kan mogelijk tegenwicht bieden tegen deze ontwikkeling. We weten echter op het moment nog te weinig van de sturende factoren achter spontane duinontwikkeling om hierover conclusies te kunnen trekken. Kustduinen ontstaan door het samenspel tussen vegetatie, wind en golfslag. Blijvende duinontwikkeling begint met de vestiging de eerste planten op het strand: de vegetatie vangt het stuivende zand in en vormt een embryoduin. Na verloop van tijd kan een embryoduin zich verder ontwikkelen tot een groter, vaak aaneengesloten voorduin: dit type duin biedt de beste bescherming tegen de zee. Het ontstaan van embryoduinen en de ontwikkeling van embryoduinen naar voorduinen zijn afhankelijk van de vestiging van vegetatie op het strand en van de balans tussen duingroei in de zomer en duinerosie in de winter. Hoewel de vegetatiesuccessie en de geomorfologische ontwikkeling goed beschreven zijn, geldt dit voor de causale relaties tussen deze processen veel minder. Dit proefschrift richt zich op deze kennislacune met als doelen 1) de sturende factoren van duinontwikkeling beter te begrijpen en 2) vanuit dit begrip een handuitreiking te geven voor het ontwerp van toekomstige megasuppleties.

Om te onderzoeken welke factoren (zoutgehalte in bodem, zoutsproei of stormen) bepalend zijn voor het voorkomen van duinvormende grassen op het strand hebben we een veld transplantatie experiment en een kasexperiment opgezet met helm (*Ammophila arenaria*) en biestarwegras (*Elytrigia juncea*). Op de Hors in Texel hebben we in de zomer het zoutgehalte op het strand gemeten langs een transect van zee naar duin. De keuze van de meetlocaties was gebaseerd op de vegetatiezonering: we selecteerden locaties waar beide grassen niet, alleen, of samen voorkwamen. In dezelfde zones hebben we ook beide soorten getransplanteerd en hun groei een jaar lang gevolgd. In de kas hebben we de grassen drie maanden lang blootgesteld aan verschillende concentraties bodemzout met en zonder zoutsproei. Uit onze metingen op het strand bleek dat vegetatiezones verschilden in het bodemzoutgehalte: de zone zonder vegetatie en de zone met enkel *E.juncea* waren zouter dan de zones met zowel *E. juncea* als *A. arenaria*. In het transplantatie experiment groeide *A. arenaria* even hard of harder dan *E. juncea* in alle vegetatie zones, wat suggereert dat zoutstress niet de groei van de planten limiteerde in ons onderzoeksgebied. Beide soorten vertoonden hoge winter mortaliteit. In het kasexperiment, nam de biomassa van *A. arenaria* af met toenemend zoutgehalte in de bodem, waarschijnlijk door osmotische stress. De biomassa van *E. juncea* nam toe tot 0.75% bodemzoutgehalte en nam vervolgens af bij hogere zoutgehaltes. De zoutgehaltes waarbij planten stressverschijnselen vertoonden lagen veel hoger dan die wij op het strand hadden gemeten. Zoutsproei had geen effect. Onze resultaten suggereren dat het voorkomen van duinvormende grassen op het strand, en daarmee de potentie voor duinvorming, waarschijnlijk bepaald wordt door de condities in de winter: hetzij door zoutstress na storminundatie of door stormerosie.

Om beter te begrijpen welke factoren de ontwikkeling van embryoduin en over een langere tijdsperiode bepalen, hebben we de effecten van strandmorfologie, meteorologische condities en zandsuppleties op jonge duinontwikkeling over een periode van 30 jaar onderzocht met behulp van luchtfoto's en strandprofiel monitoring data. We concludeerden dat 1) strandmorfologie, met name strandbreedte, de potentie voor de ontwikkeling van nieuwe duinen bepaalt, 2) zandsuppleties de ontwikkeling van embryoduin en stimuleren door het strand te verbreden en 3) weeromstandigheden en het aantal opeenvolgende stormvrije jaren bepalen of ontwikkeling van embryoduin en wel of niet kan plaats vinden.

Duinontwikkeling is het gevolg van de interactie tussen vegetatie ontwikkeling en sedimentatie- en erosieprocessen. Om de invloed van vegetatiekenmerken en duingrootte op duinontwikkeling te bepalen hebben we een natuurlijk duincomplex van 8 hectare op de Hors (Texel) een jaar lang gevolgd door middel van een drone met een camera. Door een digitaal hoogte model en een geometrisch correcte foto (een orthomosaïek) te creëren voor elke vliegdag konden we de veranderingen in duinvolume over een zomer- en winterperiode berekenen. We hebben vervolgens onderzocht wat de relatie was tussen eigenschappen van de vegetatie (plantensoort, vegetatiedichtheid en vegetatiehoogte), initieel duinvolume en de mate van beschutting. De toename in duinvolume (groei) tijdens de zomerperiode werd voornamelijk bepaald door het initiële duinvolume en niet door verschillen in vegetatiekenmerken. In tegenstelling tot de zomer, was duingroei tijdens de winter wel deels gerelateerd aan vegetatiekenmerken waarbij de duinen begroeid door een soort met een lagere vegetatiedichtheid meer erosie door stormen hadden te verduren. De mate van beschutting bepaalde in hoeverre duingroei werd beperkt door stormerosie (onbeschutte duinen) of door zandtoevoer (beschutte duinen). Deze resultaten suggereren dat de eigenschappen van de vegetatie sterk bepalend zijn voor de mate van wintererosie en het herstel na winterschade.

Er wordt aangenomen dat beschutting door embryoduin en de ontwikkeling van soortenrijke zilte pionier gemeenschappen (groene strand) tussen embryo duinen en voorduin en kan stimuleren. Om deze hypothese te verkennen onderzochten we de relaties tussen vegetatiesamenstelling en -ontwikkeling met strand- en duinmorfologie langs 11 permanente transecten op Schiermonnikoog voor een periode van 10 jaar. We vonden dat strand- en duinmorfologie de vegetatiesamenstelling indirect beïnvloedde via het zoutgehalte van de bodem en de mate van zanddepositie. Het aantal groene strandsoorten nam af, maar handhaafde zich het langste op beschutte plekken, waar een organische laag werd opgebouwd en de planten niet onder het stuivende zand werden bedolven. Onze resultaten suggereren dat embryoduin en inderdaad de ontwikkeling van groene stranden kunnen stimuleren door beschutting te geven, maar ook kunnen concurreren om de ruimte en het strandoppervlak verminderen dat potentieel geschikt is voor de begroeiing van groene stranden. Het netto-effect van embryoduin en op de ontwikkeling van groene stranden wordt waarschijnlijk bepaald door het sedimentbudget van het strand en de stormintensiteit, waarbij een positief sediment budget van het strand en een lage stormintensiteit de kans verhogen dat een groen strand zich kan ontwikkelen.

Mega-suppleties zijn grote zandsuppleties die lokaal worden aangelegd en waarvan verwacht wordt dat ze minimaal 20 jaar blijven bestaan. Hiermee bieden mega-suppleties kansen voor de ontwikkeling van zeldzame natuurlijke habitats zoals duinvalleien en groene stranden. We hebben de potentie van mega-suppleties voor vegetatieontwikkeling verkend door de groei van duinvormende soorten op een natuurlijk strand (de Hors, Texel) te vergelijken met die op

twee mega-suppleties: het lage strand van de Hondsbossche Duinen en het hoge strand van de Zandmotor. Onze resultaten laten zien dat de strandhoogte de vegetatieontwikkeling sterk bepaalt. Op het hoge strand van de Zandmotor verliep de vestiging van duinvormende soorten langzamer dan op de Hors, waarschijnlijk door een beperkte verspreiding van zaden of plantenresten. Na vestiging van duinvormende soorten, verliep de embryoduinontwikkeling op het hoge strand van de Zandmotor sneller dan op de Hors, waarschijnlijk door het lage zoutgehalte van de bodem en de afwezigheid van stormerosie. Op het lage strand van de mega-suppletie Hondsbossche Duinen lieten ontwikkeling en groei van duinvormende soorten dezelfde snelheid en patronen zien als op een natuurlijke kust. De potentie voor de ontwikkeling van embryoduin op een mega-suppletie is veel groter dan de potentie voor de ontwikkeling van groene strandvegetaties, omdat groene strand vegetaties zich alleen ontwikkelen onder specifieke abiotische omstandigheden. Deze specifieke abiotische omstandigheden kunnen voorkomen op lage stranden onder de beschutting van embryo duinen of voorduin.

Samenvattend laat dit proefschrift zien dat, 1) brede stranden en lage stormintensiteit de mogelijkheden voor embryoduinontwikkeling vergroten, door de vegetatielimiet op het strand zeewaarts te verschuiven. 2) In de zomer wordt de groei van embryoduin voornamelijk bepaald door het initiële duinvolume en de mate van zandtoevoer vanaf het strand. 3) In de winter wordt groei van embryoduin gelimiteerd door (zware) stormen. De soortensamenstelling van de vegetatie bepaald mee hoe gevoelig het duin is voor erosie. 4) Zeldzame zilte pioniersvegetaties (groene stranden) kunnen zich optimaal ontwikkelen op aangroeiende stranden onder de beschutting van embryoduin. Op eroderende stranden krijgen zilte pioniergemeenschappen of geen kans zich te ontwikkelen of ze worden op termijn – tijdens stormen – begraven door eroderende embryoduin. 5) Het ontwerp van een mega-suppletie bepaalt de potentie voor de ontwikkeling van embryoduin en groene strandvegetatie. Op hoge, brede stranden kunnen embryoduin zich optimaal ontwikkelen, terwijl voor de ontwikkeling van zilte pioniervegetatie lage stranden met beschutting nodig zijn.

Deze resultaten verlenen inzicht in de interacties tussen de ecologische en geomorfologische processen die de embryoduinontwikkeling bepalen. Deze kennis kan worden gebruikt voor betere voorspellingen van kustontwikkeling onder de dreiging van een stijgende zeespiegel.



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About the author

Marinka van Puijenbroek was born on the 27th of January 1988 in Utrecht, the Netherlands. She grew up in Biltoven, where she loved to run, hop, and fall through the grasses in her parents' garden. After her secondary school (Herman Jordan Lyceum in Zeist), Marinka went to Groningen to study Biology. During her study in Groningen she often went to the Dutch West-Frisian island Schiermonnikoog, which sparked her interest in the coastal system. For her Master in Ecology and Evolution at the University of Groningen Marinka did two master theses. Her first was about the effect of nutrient mineralization on plant-soil feedback (supervised by Esther Chang and Han Olff) and her second master thesis was on the effect of macrodetritivores on plant competition under stress (supervised by Ruth Howison and Chris Smit). Afterwards she started her PhD study at Wageningen University where she researched the dynamics of the coastal region by studying the development of new dunes on a bare beach under supervision of Frank Berendse and Juul Limpens. This PhD position was part of the STW project Nature-Coast. To do fieldwork for her PhD Marinka also obtained an official drone pilot license. After four years she finished her PhD thesis: "Dunes, above and beyond: Interactions between ecological and geomorphological processes during early dune development". Marinka will continue her career as a postdoc on the effect of sand nourishment on embryo dune development at Utrecht University.

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- o *Embryo dune development: Role of beach morphology and climate*. Netherlands Centre for Coastal Research Days (NCK), 17-18 March 2016, Schouwen, The Netherlands
- o *Vegetation development on the Sand motor*. The Sand-motor Conference: Five years of building with nature, 14-15 September 2016, Scheveningen, The Netherlands
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