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Dune establishment drivers on the beach: narrowing down the window of opportunity

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Abstract.

Coastal dune development is typically initiated by the interaction between recently established dune-building vegetation and sediment transport processes. Narrowing down biotic and environmental conditions needed for vegetation establishment could improve predictions of dune initiation, yet obtaining such data on a meaningful spatial scale has proven to be challenging.

We investigated grass establishment and dune initiation across a range in environmental conditions at four beach sections in the Netherlands. To understand spatial patterns of spontaneous establishment, we mapped grass seedling occurrence in July 2021 in 1899 plots. To explore the role of environmental drivers on grass establishment and ensuing dune initiation, we conducted an establishment experiment using 750 plots. We introduced seeds and rhizome pieces of *Elytrigia juncea* and *Ammophila arenaria* and monitored establishment success (shoot emergence, survival and shoot density), dune initiation and environmental conditions (soil moisture, salinity and beach bed level change) between February 2022 and March 2023.

Field observations in 2021 showed that 69 – 84 % of seedlings occurred close to adult dune-building grasses, suggesting limited dispersal of diaspores, or alternatively, strong positive biotic feedback during the seedling stage. Establishment of introduced seeds and rhizomes peaked at locations with high soil moisture (at 15 – 20 %), low salinity (< 340 mS/m) and low sediment dynamics (–2 - +5 cm bed level change). Here, the highest dune initiation probabilities were found, with the highest probability being associated with substantial shoot emergence (330 shoots/m^2). Moreover, dune initiation was associated with the middle section of the beach, characterised by moderate slopes and elevation and sufficient beach width.

Our findings indicate that the window of opportunity for dune initiation is smaller than for plant establishment, as it not only depends on the arrival of plant material but also favorable environmental growing conditions. Our results can be applied to better predict dune initiation and development on the beach.

1 Introduction

Climate change is projected to impact sandy shorelines worldwide, which cover approximately 31 % of the ice-free globe (Luijendijk et al., 2018; Ranasinghe, 2016). Indeed, about 24 % of sandy beaches worldwide have been showing a receding trend over the last 30 years (1984–2016) (Luijendijk et al., 2018), likely partly due to increased storm frequencies. For anthro-

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pogenic beaches, where space for coastal retreat is limited, beach nourishments are often used (Arens et al., 2013; Keijsers et al., 2015b) to create a positive sediment budget, enabling beach recovery, stimulating new dune development and improving the climate-resilience of dunes. While re-establishment of vegetation may be a decisive factor for dune initiation and beach recovery (Castelle et al., 2017; Hesp, 1989, 2002; P. A. Hesp, 1981; Hilton and Konlechner, 2011; Houser et al., 2015; Snyder and Boss, 2002), much less is known about the environmental conditions necessary to support vegetation establishment and dune initiation.

As coastal vegetation establishes and grows over time, dunes may develop as a result of interactions between plant attributes (e.g., cover, density, height) and aeolian sediment transport (Hesp, 2002, 1989). Here, perennial dune-building grasses play an important role, as their shoots remain present during the winter season (Hesp, 2002). Dune-building grasses establish from seeds and rhizome fragments or through clonal expansion (Bonte et al., 2021; Davy and Figueroa, 1993). While the latter is a localized process (Keijsers et al., 2015a; Reijers et al., 2021), seeds and rhizome fragments can be important for re-colonization of the beach and recovery of the dune topography following severe storm disturbances (Harris and Davy, 1986; Snyder and Boss, 2002). In regions affected by storms, management efforts may be targeted at restoring dunes by planting dune-fixating species, while in other regions removal of vegetation is prioritized to recover sediment dynamics and restore original habitats (Martínez et al., 2013). European marram grass is an excellent example for it is both planted as a dune-stabilizing species on European coastlines (Provoost et al., 2011) yet also removed as an invasive species in countries like South Africa, or New Zealand (Martínez et al., 2008; Hilton and Konlechner, 2010; Thomas et al., 2018). Therefore, understanding the environmental conditions influencing vegetation establishment is necessary to help optimizing both of these management strategies.

In ecosystems prone to disturbance, propagules typically rely on windows of opportunity (i.e., periods without disturbances) for successful establishment (Balke et al., 2014). In dune ecosystems, changes to the bed level (i.e., erosion or accretion) are considered key drivers for plant success. Too much burial by sediments can limit shoot emergence and may cause plant mortality, especially under complete plant burial (Bonte et al., 2021; Harris and Davy, 1987; Ievinsh and Andersone-Ozola, 2020; Konlechner et al., 2013). Conversely, slight amounts of burial may be beneficial (Ievinsh and Andersone-Ozola, 2020; Lammers et al., 2024; Maun, 1994). While the impact of burial appears to be well established, much less is known about erosion, soil moisture and salinity. Erosion is thought to strongly limit the survival of seedlings (Maun, 1994; Huiskes, 1977), though some tolerance for it may exist in adult plants (Konlechner et al., 2019). Lack of soil moisture or rainfall is often mentioned as another important limiting factor for establishment (Abdelhak et al., 2013; Konlechner et al., 2013; Maun, 1994); similarly, salinity appears to especially influence germination or shoot emergence from rhizome fragments (Abdelhak et al., 2013; Konlechner et al., 2013; Walmsley and Davy, 1997).

While the importance of initial plant establishment for dune initiation is widely recognized, there is still a limited amount of studies that investigate both simultaneously (van Puijenbroek et al., 2017a; Costas et al., 2024). Even less is known about vegetation establishment during the earliest phase of dune formation, which difficult to observe on a large spatial scale. Yet, the strong spatial dependencies of abiotic conditions along a beach topography are important. Salinity decreases with distance from the ocean and might not be a limiting factor for plant performance unless certain levels are reached (van Puijenbroek et al., 2017b). During periods without considerable wave action, changes to the bed level typically result from wind transport,

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with most of the sediments being picked up close to the high tide line (Strypsteen et al., 2024) and deposited at the dune toes (Hesp, 2002; Keijsers et al., 2015a). At lower beach elevations, groundwater can form a stable source of moisture as opposed to rainfall dependent locations (Homberger et al., 2024). This may contribute to seedling recruitment (Huiskes, 1977). Identifying the best conditions for plant establishment and their occurrence on the beach will help translate results to guidelines for management.

In this study, we aimed to narrow down windows of opportunity for plant establishment and dune initiation by focusing on three major abiotic factors: salinity, soil moisture and changes to the bed level. We expected that 1) establishment is dispersal limited, 2) shoot emergence, survival and growth are driven by environmental conditions, primarily bed level change and 3) dune initiation is a function of the number of emerged shoots depending on both dispersal patterns and environment. To test these hypotheses, we combined field mapping of spontaneous seedlings with a field establishment experiment to separate the impacts of dispersal and environment on the establishment of dune-building grasses on a landscape scale. In the establishment experiment, we introduced seeds and rhizome fragments of two common dune-building grasses: *Ammophila arenaria (L.) Link* (European marram grass) and *Elytrigia juncea (L.) Nevski* (sand couch).

2 Materials and Methods

2.1 Study areas

The research was conducted at four beach sections, three located on the Dutch island of Terschelling (52° 24'19.4" N, 5°16'10.9" E) and one located on the Sand Engine (52°02'51.0" N, 4° 10'59.0" E) (Fig. 1) . All study areas share limited management interventions (e.g., none of the beaches are mechanically cleaned), a beach width that supports vegetation and dune development and a wide range in expected environmental conditions.

Terschelling is a barrier island on the northern coast of the Netherlands. The northern coastline of Terschelling has comparably wide beaches, with widths ranging from 200 to 300 m for the studied beach sections. The predominant wind direction is southwest (Galiforni-Silva et al., 2020). Embryo dunes in the investigated areas are dominated by *Elytrigia*, but occasionally *Ammophila* is found closer to the foredunes.

The Sand Engine is a mega-nourishment constructed in 2011 by supplying the foreshore with a volume of 21.5 Mm3 (Stive et al., 2013). Since the Sand Engine is artificially wide (up to approx. 600 m) and high (up to approx. 7 m.a.m.s.l [meters above sea level] in 2021), it provides a wide accommodation space for dune development (Nolet and Riksen, 2019). The dominant wind direction is south-to-southwest (Hoonhout and de Vries, 2017). Prominent landscape features on the Sand Engine include a dune lake and an extensive embryo dune field, with the most frequently occurring grass species being *Ammophila* (Huisman et al., 2021).

Precipitation and temperature conditions during the experimental setup were comparable between the two study areas and there were no storm occurrences (Table 1).

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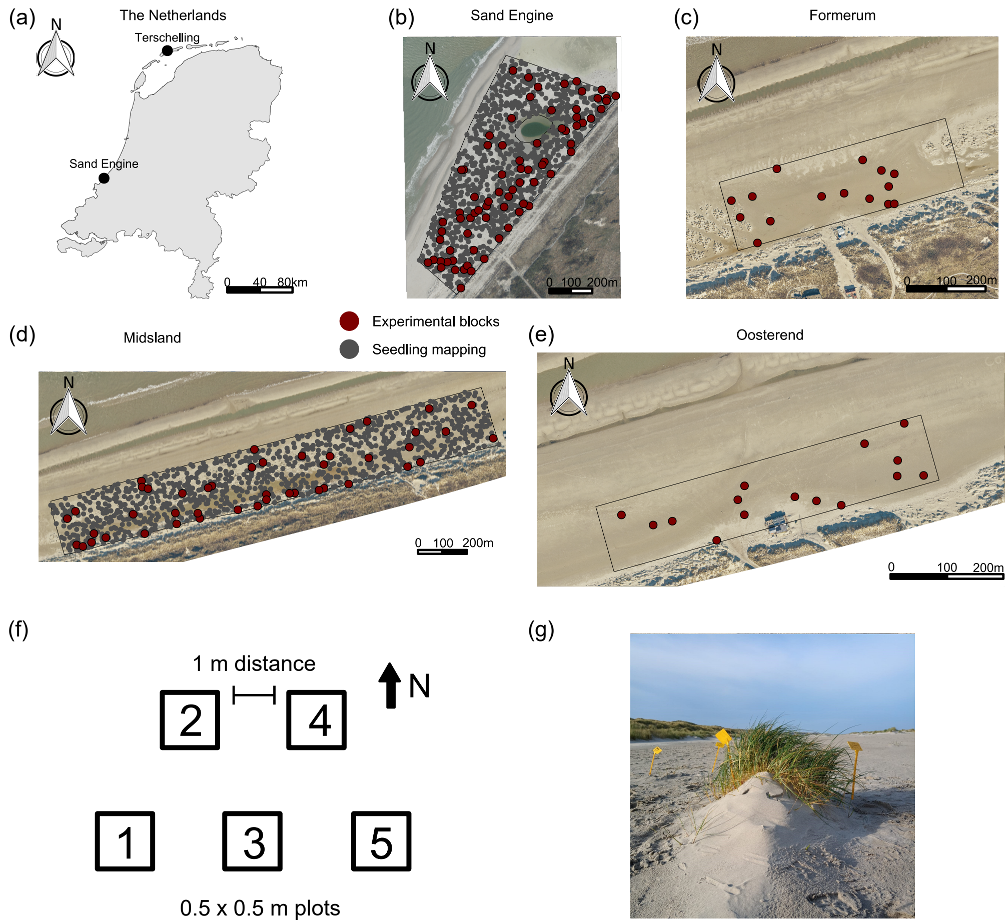

Figure 1. Study areas and experimental setup. (a) Map of the Netherlands with study areas (satellite imagery from www.beeldmateriaal.nl; licensed under CC BY 4.0). (b) Sand Engine beach section. (c - e) Beach sections on Terschelling. *Note:* The beach sections were delineated to encompass adult vegetation on the beach. As a landward limit, we used the foredune toe and as a seaward limit we used a buffer from existing vegetation extending up to 100 meters (Sand Engine) and 40 meters seaward (Terschelling). (f) Block with plot arrangement. (g) Plot with a small (embryo) dune (Photo by Myrthe Bouma).

2.2 Study design

We combined field mapping of seedlings with a field establishment experiment across environmental gradients to separate the impacts of dispersal and environment on the establishment of dune-building grasses on a landscape scale.

2.2.1 Seedling mapping: spontaneous establishment

To investigate patterns in spontaneous grass seedling establishment, we mapped seedling occurrence in 920 plots at the Sand Engine and 979 at Midsland. Plots were allocated using a random number generator, covering about 1.5 % of the area of each

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Table 1. Mean precipitation (mm), mean temperature (°C) and maximum recorded hourly wind speed (m/s) during the monitoring period.

Study area	**Meteorological variable**	**Yearly average** (1996-2022)	**Exp. period average** (March – January, 1996–2022)	**Experimental setup** (March 2022 – January 2023)	**Seedling mapping** (2021)
Sand Engine	Precipitation	878	817	741	932
	Temperature	11	12	13	11
	Max hourly windspeed			20 m/s (March 2022)	
Terschelling	Precipitation	810	703	752	852
	Temperature	10	11	12	10
	Max hourly windspeed			18m/s (January 2023)	

Note: retrieved from KNMI weather stations 'Hoek van Holland' (WMO code 06330, about 7 km from the Sand Engine) and 'Terschelling Hoorn' (WMO code 06251, about 4 to 5 km from the Beach sections).

beach section. The minimum distance between plots was set to 10 m. All plots were visited in July 2021 and their location was recorded with a real-time kinematic positioning system (RTK, Topcon Positioning Systems, Inc.) with reference to NAP (Normaal Amsterdams Peil, located around mean sea level). Within a radius of 2.5 m from the recorded point, the occurrence of grass seedlings and adult grasses was recorded. Grass seedlings were defined as grass plants shorter than approximately 15 cm with slender, green leaves growing isolated from adults and not growing in a line as do shoots from clonal expansion (Fig. S1).

2.2.2 Establishment experiment

We collected inflorescences with seeds of *Elytrigia* and *Ammophila* at the Sand Engine in August 2021 and stored them at ambient outside temperatures and humidity. To mimic the natural dispersal process the seeds-in-husks were removed from the inflorescence of *Ammophila* as described by (Huiskes, 1979) using mechanical threshing and manual sieving. For *Elytrigia*, the rachis was removed, leaving only spikelets attached to the pedicels. Rhizomes of both species were collected locally during the experimental setup and cut into smaller pieces, leaving two nodes per piece. We assumed that each rhizome node and each seed could potentially turn into a shoot (Table 2).

Table 2. Overview over species and introduced plant material per plot. To determine the potential number of emerging shoots from seeds we repeatedly counted the number of seeds in 1 g of seeds for *Ammophila* and 10 g for *Elytrigia*.

Species	**Common name**	**Seed material [g/plot]**	**Shoot emergence potential**	
			Seeds	Rhizome nodes
Ammophila arenaria	(European) Marram grass	5.00 ± 0.05	1055	40
Elytrigia juncea	Sand couch grass	9.00 ± 0.05	214	40

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We selected block locations from areas with similar environmental conditions (see Fig. S2). Within each area, we allocated blocks using the doubly spaced sampling algorithm (Table 3; detailed methods in Supplementary Material S2). Block locations were moved away minimally 1m from existing vegetation and pathways to further ensure similar conditions within each block. At each block, we created five plots (50 x 50 cm) at a minimum distance of 1 meter. The treatments (Table 2) and a control were assigned randomly to the plots. The control plot was left untreated to account for spontaneous establishment. Rhizomes and seeds were covered by 2 cm of sand to ensure good contact between sediment and plant material. To avoid human disturbance, the plots were not marked, but their positions were recorded with the RTK.

Table 3. Allocation of blocks and plots at different beach sections.

Beach section	Number of similar areas	Blocks	Plots
Sand Engine	5	75	375
Midsland	3	45	225
Formerum	1	15	75
Oosterend	1	15	75

2.3 Measurements

2.3.1 Shoot emergence and dune initiation

Shoot emergence was monitored during the growing season of 2022 in May/June, August and October. A fourth monitoring round was carried out at the end of January and beginning of February 2023 (hereinafter referred to as the onset of winter) to assess long-term survival. Here, only blocks for which shoots had been recorded previously were re-visited. During each monitoring round, the number of emerged shoots per plot was counted. We then corrected this number for spontaneous shoot emergence in the control plots. Dune initiation was assessed visually by observing the sand surface level within the plot relative to the surroundings. Given a visual confirmation, we measured the highest point inside the plot with the RTK (on average 7.4 cm). We defined plant survival as shoot presence at the last monitoring moment. We expressed plant establishment success as the corrected number of shoots present in a plot at the last monitoring round relative to the amount of introduced plant material in March 2022.

2.3.2 Bed level change, moisture and salinity

Abiotic conditions were measured during each field monitoring visit. Using the RTK, we recorded the height of two plot corners. We defined the change in bed level as the difference between the average plot height between two consecutive monitoring moments. Soil moisture and salinity were measured by carefully inserting a WET2 sensor into the soil of the plot and recording with a HH2 moisture meter (DELTA-T Devices LTD). The WET-2 sensor measures the first 6.8 cm of the soil at a volume of 500 mL and 3 % accuracy (Delta-T Devices Ltd., 2019).

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2.4 Data analysis

2.4.1 Seedling mapping

To explore arrival limitations, we visualized the number of seedlings and adults on the study area scale. For this, we interpolated our spatial data (coordinates x and y and seedling/adult occurrence) using bilinear interpolation for irregularly spaced data points. For better visualization, we converted the resulting rasters into polygons using the criterion of an interpolated seedling occurrence of more than 50 %. To explore if the seedling density was higher near adult vegetation, we also calculated the number of plots that contained both seedlings and adult grass species and divided it by the total number of plots per study area. To compare the seedling mapping approach with our establishment experiment, we also interpolated the occurrence of shoots from the seeds of *Ammophila* and *Elytrigia* per block recorded in August 2022.

2.4.2 Establishment experiment

To investigate how dune-building grass establishment is influenced by key abiotic drivers, we used two different approaches. First, we explored whether shoot presence or absence after one growing season was affected by the maximum change in bed level, maximum salinity and minimum soil moisture. Second, we explored whether the plant establishment success could be explained by average environmental conditions that occurred during the study period.

2.4.3 Dune initiation

To investigate the response of dune initiation to biotic and abiotic conditions, we first explored the relationship between end-of-season shoot number, average environmental conditions and dune presence or absence. To highlight interactions between conditions leading to plant establishment and dune formation, we combined predictions from two generalized additive models (GAM). First, we predicted the number of shoots over a range in bed level changes and two moisture levels. Second, we predicted the probability of dune occurrence from predicted shoot numbers under the same conditions. We identified plant establishment and dune-building promoting landscape features using the k-means algorithm. Variables included plant establishment success, maximum dune height, height above sea level, slope, and distance to the coastline at average high tide (all measured at the onset of winter). The distance between plots and the coastline was determined from satellite imagery. Slopes were calculated as the difference in height between two plot corner points divided by their distance.

2.4.4 Statistical analysis

Considering the previously observed non-linearity in dune-building grass growth responses (Nolet et al., 2018), we fitted GAMs to each response variable. Random effects for blocks and study areas were included to address spatial autocorrelation and site-specific effects. For model parameter selection, we used the double penalty approach (Marra and Wood, 2011) and smoothness was determined from restricted maximum likelihood (REML) (Wood, 2011). Further details on statistical models and assumptions can be found in Supplementary Materials S3 – S6 .

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Statistical analysis and data processing were conducted in R version 4.2.3 (R Core Team, 2023). The experimental sampling design was created with BalancedSampling (Grafström et al., 2024). GAMs were fitted using the mgcv package (Wood, 2017). Model assumption adequacy was evaluated using simulated residual diagnostics with the DHARMa package (Hartig, 2022). Post-hoc Wald tests for differences between plant material treatments were performed using the itsadug package (van Rij et al., 2022). Figures and maps were generated using ggplot2 and sf (Pebesma, 2018; Wickham, 2016). Spatial interpolations of plant presence/absence and shoot numbers utilized the akima package (Akima and Gebhardt, 2022).

3 Results

3.1 Arrival limitations

Mapped spontaneous seedling occurrences showed distinct spatial patterns for both beach sections (Fig. 2). The majority of seedlings occurred near adult grasses, with 69 % (Sand Engine) and 84 % (Midsland) observed within a 2.5 meter radius of adults. Seedling occurrences were generally lower near the sea. On the Sand Engine, occurrence was also concentrated around the dune lake, with significant seedling presence even at considerable distances from existing adult vegetation.

Shoot and seedling emergence patterns in the establishment experiment showed less spatial variation than the natural seedling occurrences. Shoot emergence was also observed in areas with only a few naturally occurring seedlings , suggesting dispersal of plant material is likely a limiting factor under natural conditions.

3.2 Establishment success

During the course of the establishment experiment, grass shoots were observed in 36 % of plots, out of which 100 shoots/m^2 occurred on average. Shoot numbers over time increased with precipitation but decreased with high burial rates. They generally increased in summer but decreased during periods of low precipitation and at the last monitoring moment (see Supplementary Material S7).

Dune-building grass establishment success was explained by the average abiotic conditions recorded during the monitoring period. It was constrained by the average change in bed level over the monitoring period (Fig. 3). Establishment success was notably higher at locations below 2.4 m elevation, reaching an average of 10 % compared to 5.6 % at higher elevations (Fig. 3). These low elevations coincided with high average soil moisture and limited changes to the bed level.

The statistical analysis confirmed a significant effect of the average change in bed level on establishment success, with success being highest between 2 cm of erosion and 5 cm of burial, irrespective of species (Fig. 3 b). We also found a significant generalized effect of average salinity on establishment success, with success being negatively affected by salinity above 340 mS/m (Table 4 and Fig. 3 c).

We did not find a significant generalized effect for moisture, but significant interactions with bed level and treatment (Table 4). Yet, the nature of these interactions was not always clear, likely due to limited amounts of data in specific ranges. Neverthe-

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Figure 2. Spatial patterns in dune-building grass occurrence (not vegetation cover) at the Sand Engine (upper) and Midsland (lower). The line marks the approximate coastline at average high tide. Left panel: natural occurrence from seedling mapping (July 2021) right panel: presence shoots from seeds or rhizomes from the establishment experiment (August 2022). The black points show the location of the experimental blocks.

less, it might be interesting to note that both the seeds of *Elytrigia* and the rhizomes of *Ammophila* showed a positive response, with a suggested optimum within the range of 15 % - 20 % of average moisture.

The establishment success also differed between the plant species and diaspore. In our establishment experiment, seeds of *Elytrigia* showed the highest establishment success, followed by rhizome pieces of *Ammophila* and then rhizomes of *Elytrigia*, though none of them was significantly different from the other (W(2) = 0 – 0.471, $p > 0.1$). In contrast, seeds of *Ammophila* had a significantly lower establishment success than any of the other treatments (W(2) = 102–158.6, $p<0.001$).

Finally, we also tested if extreme conditions that occurred during the study period could explain the survival of dune-building grass shoots at the onset of winter. Here, we found that extreme bed level change was the only factor significantly explaining survival ($p < 0.001$, $\chi^2 = 85.7$) (see Table S6 and S8, Fig. S14).

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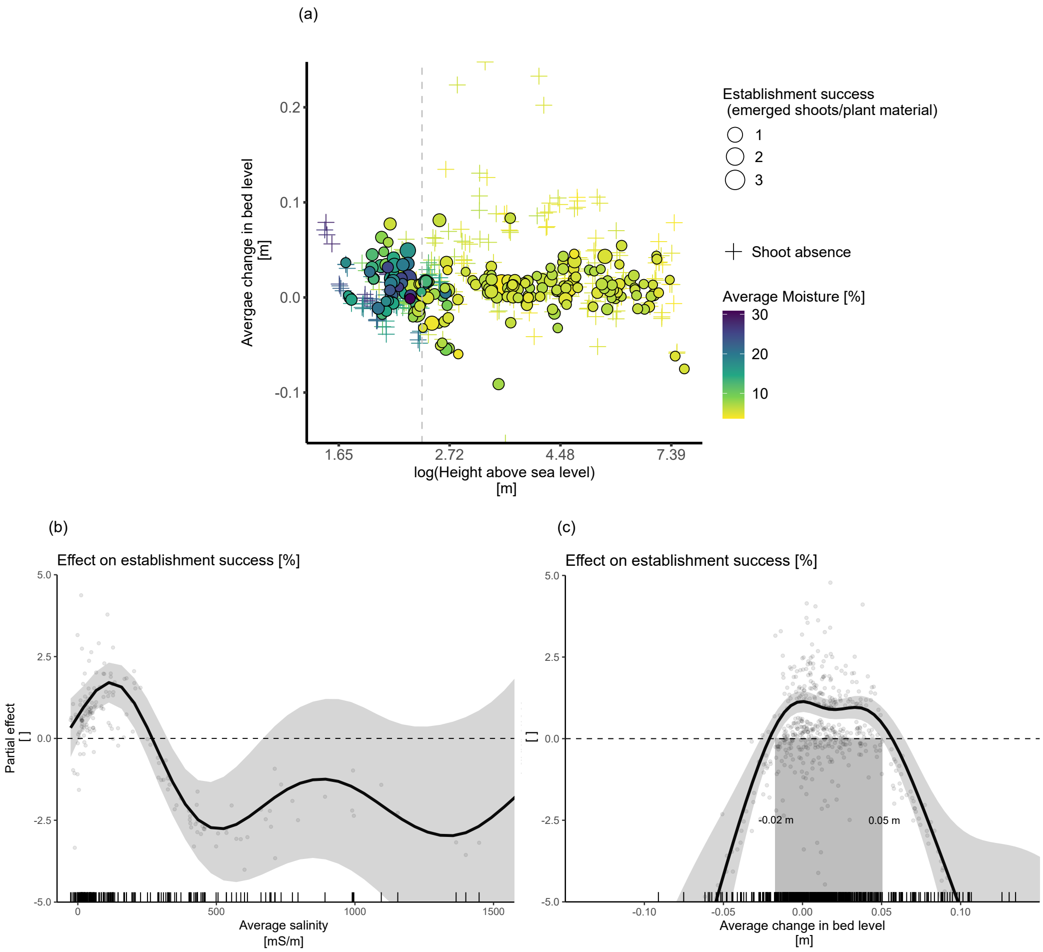

Figure 3. The effect of abiotic conditions on plant establishment success at the onset of winter 2023. (a) Establishment success across an elevation gradient in relation to average soil moisture and bed level change. The dashed gray line marks a change from dry to wet conditions which occurs at 2.4m approximately. (b) The model-predicted average partial effect of the change in bed level on plant establishment success. (c) The model-predicted average partial effect of average salinity on plant establishment success. *Note:* The salinity effect was modelled for a conditional dataset with fewer observations (N=173).

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Table 4. Statistical model results of the relationship between establishment success (shoot number/introduced plant material), biotic and average abiotic predictors.

	Full model		**Salinity model**	
Approximate significance of smooth terms	Ref.df	Chisq	Ref.df	Chisq
Moisture	9	5.36	9	447.82***
Change in Bed Level	9	1,370.03***	9	0
Salinity		*N/A*	9	534.88**
Salinity x Moisture		*N/A*	16	333.65*
Moisture × Change in Bed Level	16	20,123.41***	16	12,410.13***
Moisture × Rhizomes Aa	9	1,137.77***		*N/A*
Moisture × Seeds Aa	9	305.31***		*N/A*
Moisture × Rhizomes Ej	9	0		*N/A*
Moisture × Seeds Ej	9	3,372.35***		*N/A*
Change in Bed Level × Rhizomes Aa	9	0		*N/A*
Change in Bed Level × Seeds Aa	9	240.29***		*N/A*
Change in Bed Level × Rhizomes Ej	9	965.18***		*N/A*
Change in Bed Level × Seeds Ej	9	16.95		*N/A*
Random smooth terms				
Study area	3	1307.17	3	0
Block	126	2,244.01***	47	523.3***
Deviance explained: 0.903 (Full model), 0.962 (Salinity model)				
REML: 1344.15 (Full model), 402.433 (Salinity model)				
N: 508 (Full model), 173 (Salinity model)				

Note: We used the average bed level change and average recorded moisture per plot recorded during the monitoring period (March 2022 - January 2023). The complexity of the model which includes average salinity was reduced as less salinity data was available.
***p < 0.001 significant level. **p < 0.01 significant level. *p < 0.05 significant level.

3.3 Dune initiation

Dune formation was first observed during the second monitoring campaign in August 2023 on all four beach sections. In subsequent campaigns, dune formation was recorded in 11 - 12 % of all plots, during which the newly developed dunes showed an average accreting trend.

We found dune initiation significantly explained by the number of emerged shoots ($p < 0.001$, $\chi^2 = 77.8$), with the probability of dune formation increasing almost exponentially with the shoot number and reaching the highest probability at 330 shoots/m^2. Furthermore, the interaction between shoot number and bed level change was significant ($p < 0.01$, $\chi^2 = 17.46$), with higher shoot numbers and accretion leading to the highest probability of dune formation.

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Neither moisture (p = 0.06, χ^2 = 30.61) nor the interactions with the moisture term were found to be statistically significant (details see Table S10). However, when looking at the combined model predictions of establishment success and dune formation probabilities, we found that the probability of dune formation is highest when soil moisture is high and bed level change is within the tolerance level of dune-building plants (Fig. 4b).

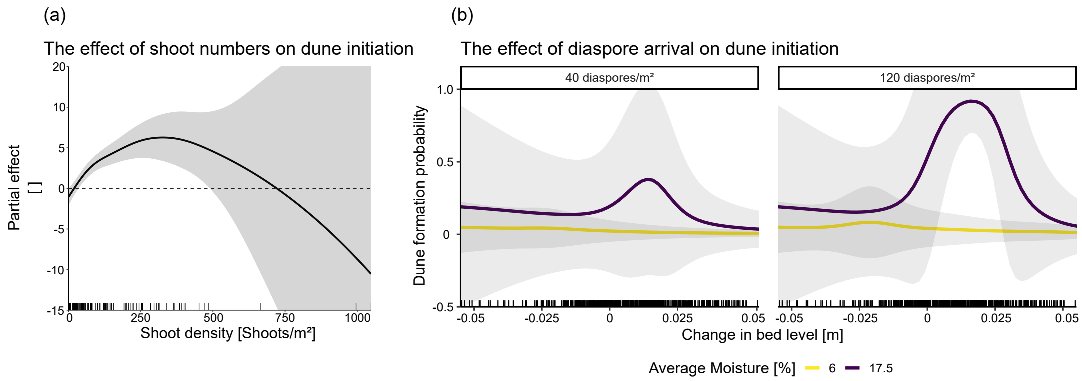

Figure 4. Dune initiation probability in relation with abiotic and biotic conditions. (a) The effect of shoot numbers on the dune initiation probability. (b) bed level change and moisture effects on dune initiation. *Note:* For the predictions shoot numbers were averaged over all treatment combinations. For the moisture levels, we used 6 % (average moisture at locations higher than 2.4 m) and conditions at 17.5 % moisture for which the statistical model and the raw data suggest optimal conditions.

3.4 Hot spots for dune development on the beach

Dunes that persisted until the onset of winter 2023, tended to occur at locations where a lot of shoots also persisted (Fig. 5). Spatial patterns of dune formation further showed, that on Midsland and Formerum, more dunes tended to persist closer towards the land side, though such a trend was not visible on the Sand Engine and Oosterend. While patterns of dune formation until the onset of winter largely coincided with high shoot numbers, some of the observed dunes occurred as remnants of earlier dune formation where the shoots had already died off.

Dune development and high shoot numbers coincided with an average distance from the coastline of 279 m (SD±100 m), moderate heights above sea level (avg. 2.92 m, SD±1.05 m) and moderate slopes (avg. 6 %, SD ± 6.4 %).

4 Discussion

In this study, we aimed to narrow down the window of opportunity for establishment and subsequent dune initiation from two major dune-building grasses (*Ammophila* and *Elytrigia*).

Dispersal to new locations appears to be a first important barrier, limiting spontaneous establishment to locations downwind from the sea near existing vegetation. In turn, plant establishment success is restricted to locations with average bed-level changes between –2 cm and 5 cm over the study period (c. -9.3 - +23.25 cm per year), while moisture may play a key role

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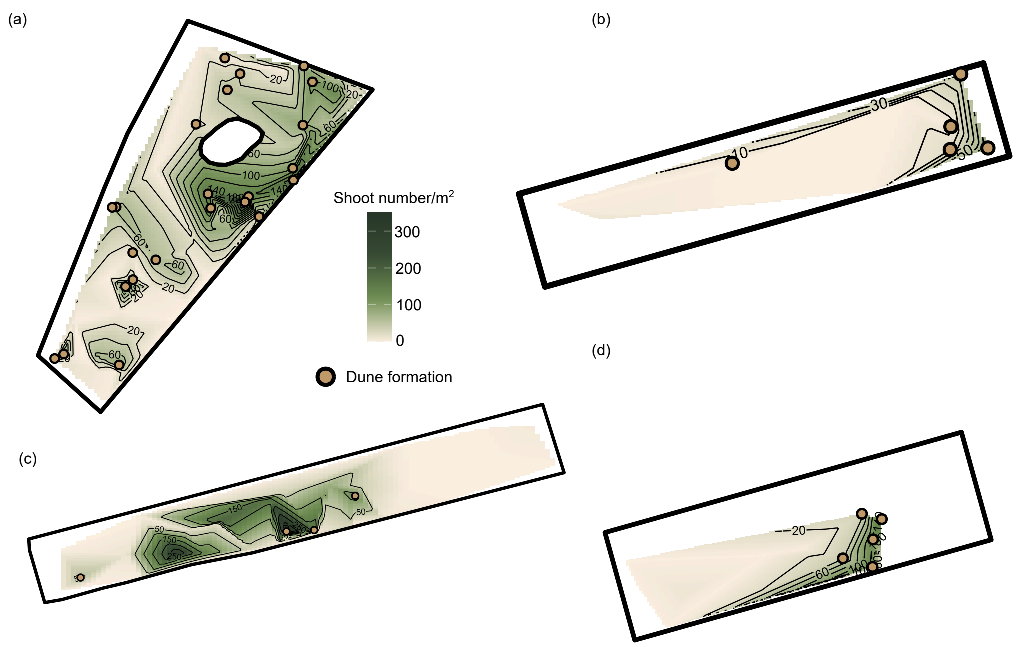

Figure 5. Patterns of dune development and shoot numbers at the onset of winter 2023 on four beach sections. (a) Sand Engine. (b) Oosterend. (c) Midsland. (d) Formerum. *Note:* for the interpolation, shoot numbers were summed up per block location. Orange points show locations with observed dune development; darker green colors indicate higher shoot numbers.

for subsequent shoot growth. Finally, initiation of a new dune was most probable when shoot densities reached 330 shoots/m^2, suggesting the window of opportunity for dune initiation is smaller than that for plant establishment. The optimal locations for dune initiation were typically constrained to the middle of the beach, with high establishment success being associated with an average distance to the sea of 279 m. Our results provide valuable insights for coastal management strategies. In the following, we discuss our results in more detail.

4.1 Arrival of plant material

Our results indicate that the arrival of plant material to new locations can be an important limiting factor for seedling establishment. 69 – 84 % of the spontaneous seedlings occurred in close proximity to existing adult vegetation. These limitations may also exist for rhizome pieces since we did not observe any rhizome fragments or adult vegetation at certain sections of both beaches. Another reason for finding many seedlings close to adults could be positive biotic feedbacks. However, grass adults may inhibit seedling recruitment through habitat modifications (Lammers et al., 2024), which contrasts with biotic facilitation.

It is important to differentiate dispersal mechanisms for both types of diaspores. Wind, capable of carrying seeds over long distances, offers high colonization potential in new areas. At the Sand Engine, we observed considerable colonization near the dune lake, even at bigger distances from adult plants (Fig. 2), likely due to prevailing southwest winds. Yet, unfavorable wind directions may limit seed arrival, dispersing them landward instead of onto the beach (Hilton et al., 2019; Lammers et al., 2024). While wind dispersal is important for seeds (Huiskes, 1979), for rhizome pieces, storms are crucial detaching rhizome fragments from adult plants. Both seeds and rhizome pieces may then be dispersed by sea water to new areas over large distances, and especially deposited along wreck lines, facilitating plant establishment and dune formation within areas of accumulated wreck material (Aptekar and Rejmánek, 2000; de la Peña et al., 2011; Davy and Figueroa, 1993; Hesp, 1989; Costas et al., 2024). Moreover, dispersal potential may vary between species. *Ammophila* has smaller, lighter seeds but larger rhizome pieces compared to *Elytrigia*, potentially affecting their transport by wind and water. However, the extent to which diaspore size influences arrival limitations requires further research.

4.2 Response to key environmental drivers

We demonstrated that key environmental drivers considerably influence shoot emergence, growth and survival. We found burial to be an important limiting factor, starting to limit establishment when exceeding 5 cm. In contrast, our results suggest that erosion is a stronger limiting factor for establishing dune-building grasses since a negative effect occurs already at 2 cm of erosion. While our findings on burial are in line with previous studies (Bonte et al., 2021; Konlechner et al., 2013), the limited tolerance of dune-building grasses to erosion has not been previously described.

We also found a positive impact of soil moisture on establishment success in the range of 10–20 % moisture, mostly at lower locations where dune-building grasses may be able to access fresh groundwater. As has been previously hypothesized (Homberger et al., 2024; Huiskes, 1977) lower locations may be subjected to a lesser extent to precipitation deficits and consequently favor establishment. Another advantage of these locations may be the interaction between sediment transport and surface moisture, with soil moisture limiting the amount of aeolian-caused bed level change (Hallin et al., 2023). Indeed, our findings suggest that wet conditions lead to a smaller range in bed level change, resulting in higher establishment success (see Fig. 3). However, in lower lying areas close to the sea, the benefits of wet conditions may be outweighed by increased salinity from the sea, negatively impacting shoot emergence.

Finally, we also found clear differences in overall establishment success between treatments. While rhizome pieces of both species showed similarly high establishment success, the seeds of *Elytrigia* were much more successful compared to the seeds of *Ammophila*.

4.3 Conditions for rapid dune initiation

In our research, we were able to demonstrate that vegetation establishment and initial dune formation following a major dispersal event can be quick and may occur within one growing season. Our establishment experiment therefore mimics the natural process of storm recovery, which tends to start with the recolonization of vegetation in the first growing season (Houser et al., 2015; Snyder and Boss, 2002). While previous studies acknowledge the role dune vegetation establishment plays for dune and beach recovery (Castelle et al., 2017; Houser et al., 2015; Snyder and Boss, 2002) much less attention has been paid to the environmental conditions that determine dune formation in the context of successful plant establishment.

We demonstrated that plant-environment interactions are crucial in the initial phase of dune formation, influencing the number of emerged shoots. Additionally, we found that shoot numbers must be sufficient to trap sediments and promote

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dune formation (Fig. 4). Thus, conditions leading to peaks in dune-building grass shoot growth should be important for dune formation and recovery post-storms. Favorable climatic conditions, such as wet summers following storms, may expedite vegetation colonization and dune recovery. Conversely, recovery may be prolonged under unfavorable climatic conditions.

5 Implications for coastal management

The management of coastlines in many parts of the world relies on sandy beaches and their coastal dunes to protect coastal communities against flooding. To be an effective nature-based solution, coastal dunes should recover after storm disturbances. Our results show that dune initiation and thus recovery depends on specific plant-environment interactions promoting peaks in establishment. These insights into arrival limitations and spontaneous establishment patterns can potentially be integrated into beach restoration and management strategies.

Currently, beach nourishment interventions are frequently used (Arens et al., 2013; Keijsers et al., 2015b), which create sufficient sediment supply for natural dune development. This management strategy can promote dune development, since nourishments may lead to wide beaches with plenty of accommodation space for dunes (Nolet and Riksen, 2019). In order to further promote dune development and recovery, coastal managers could refine their strategies while focusing on designing landscape features that facilitate establishment and dune formation. Such a design may include creating suitable conditions at the middle section of a wide beach with limited slopes and heights above mean sea level. Wet landscape features such as the dune lake on the Sand Engine can similarly contribute to dune development, as this provides a stable source of moisture with a lower susceptibility to fluctuations in weather. Dune-building grass growth at higher elevations is susceptible to hydrological extremes (Homberger et al., 2024), which may slow down dune and vegetation recovery after storms. Yet, lower laying wet areas could still contribute to dune recovery.

Following large storm disturbances, dunes and their entire vegetation communities can be removed (Harris and Davy, 1986). In these cases, recovery may take longer, especially if the dominant wind direction limits seed arrival on the beach. Hence, dune-building grasses may have to grow back from the foredunes by clonal expansion, which is a localized process (Keijsers et al., 2015a; Reijers et al., 2021), during which dune-building vegetation may remain vulnerable to new storm disturbances (Castelle et al., 2017). To help with the recovery and restoration of dunes, vegetation is often planted, though typically focusing on the foredunes and using only one key species (in Europe, typically *Ammophila*). Since our results showed that *Elytrigia* is not only equally well suited to establish from rhizomes but also is superior in establishing from seeds, it might be worthwhile considering including it for restoration projects, especially if the aim is to speed up dune formation after storms.

Finally, while in our study we discuss implications for dune recovery, our results may also inform management interventions with other purposes, such as embryo dune habitat development or limiting the establishment of dune stabilizers. The latter may be especially interesting for efforts to recover sediment dynamics by creating blowouts or international invasive species eradication programs.

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Data availability. The experimental data that supports the main findings of this study can be found under via the Data Archiving and Networked Services (DANS) EASY (https://doi.org/10.17026/PT/EEZGNY).

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Competing interests. The authors declare that they have no conflict of interest.

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