



Build back better

On the resilience of *Ammophila arenaria* along the
bio-geomorphological dune gradient

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Abstract

Coastal dune ecosystems offer a plethora of ecosystem services, but in order to endure the environmental changes as a result of climate change these ecosystems require a certain degree of resilience. To determine the resilience of these ecosystems, we tracked the resistance and recovery of beach grass *Ammophila arenaria* along the bio-geomorphological dune gradient after disturbance (clipping of aboveground biomass) early in the growing season. As a measure of resilience, we investigated both the resistance, indicated by the capacity for the number and the diameter of the shoots to not decrease following disturbance, and the recovery, indicated by the capacity for the leaves to grow to pre-disturbance levels. We found the resilience of *A. arenaria* to be dependent on its location along the bio-geomorphological dune gradient, where the beach showed the highest degree of resilience, followed by intermediate resilience at the white dunes and the worst resilience at the grey dunes. Nonetheless, disturbance of *A. arenaria* early in the growing season generally did not impact the capacity for growth by the end of the season. In addition, we found that the resilience of *A. arenaria* along the dune gradient varied between the four studied locations, and was dependent on its height above sea-level and distance from the waterline, as well as the salinity, acidity and organic matter content of the soil, and the amount of surrounding vegetation. Combining these findings, we think that the resilience of *A. arenaria* and consequently that of coastal dune ecosystems, while influenced by various (a)biotic properties, is predominantly dependent on the availability of nutrients along the bio-geomorphological gradient.

Layman's summary

To ensure that coastal dune ecosystems can act as protection against coastal disturbances that will occur more often due to climate change, we studied how resilient these ecosystems are to sudden changes. We studied this by looking at *A. arenaria* or Marram grass, which is a common beach grass found along the bio-geomorphological dune gradient and aids in the formation of dunes. The bio-geomorphological dune gradient is the range of a dune throughout its lifetime, from its formation on the beach to its stabilization in more landward areas, while constantly being influenced by different (a)biotic factors. The dune gradient starts at the beach, where dynamics of sea and wind result in an abundance of nutrients, but also cause physical stress for *A. arenaria*. Using its sand trapping abilities, *A. arenaria* is elevated, which decreases both the amount of nutrients and the degree of physical stress, and forms the first ridge of the area known as the white dunes. Where the dynamics of sea and wind are mostly absent, in the grey dunes, *A. arenaria* is outcompeted by plants better suited to the conditions of this nutrient-poor area. To determine resilience, we clipped away the aboveground shoots of *A. arenaria* plants along the dune gradient early in the growing season. We then tracked the ability for the shoots to not decrease in number or thickness, and for the leaves to be able to grow to the same length as they were before they were clipped. We found that the resilience of *A. arenaria* was dependent on where on the dune gradient it was located. *A. arenaria* was most resilient at the beach, intermediate at the white dunes and least at the grey dunes. Nonetheless, disturbed *A. arenaria* tended to resemble their undisturbed counterparts by the end of the growing season for all of areas of the dune gradient, showing that disturbance is compensated for within one growing season. The resilience along the dune gradient did however vary between the studied locations, which we thought to be due to the bio-geomorphological differences between these locations. We found the height above sea-level and distance from the waterline, as well as the salinity, acidity and organic matter content of the soil, and the amount of vegetation surrounding it to all influence the resilience of *A. arenaria*. From our findings we conclude that resilience of *A. arenaria*, and as a result the resilience of coastal dunes, is mainly dependent on the amount of available nutrients, more than the presence of physical stressors and competing plants.

Keywords *Ammophila arenaria* · Bio-geomorphology · Coastal dunes · Disturbance · Resilience

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Introduction

Coastal dune ecosystems offer a plethora of ecosystem services, among which the filtration of water, habitat formation for various organisms and protection from coastal disturbances, such as extreme weather events (EWE, Barbier et al., 2011; Everard et al., 2010). It is the latter service that will become more relevant in the coming years, with sea levels rising and EWEs becoming more prevalent as a result of climate change (He & Silliman, 2019). Since approximately 40% of the global population lives within 100km of the coast and the majority of natural capital is generated within coastal regions, ensuring that they remain able to fulfil their protective functions is of utmost importance (Costanza et al., 1997; The United Nations, 2017).

In order for coastal ecosystems to endure these changing conditions, a certain degree of resilience is required. Resilience can be divided into two aspects; resistance and recovery (van Belzen, 2020; van Belzen et al., 2017). The first aspect, resistance, indicates how the system can be influenced without reverting to an alternate state. The second aspect, recovery, describes how the system is able to revert back to a stable state, which can be further described by the time span over which the transition occurs and the degree to which the recovered state resembles the original state. It is these two factors that influence the capacity of a coastal ecosystem to cope with external influences and can therefore be an indicator of its protective value against the aforementioned coastal disturbances (Bonte et al., 2021; De Battisti, 2021).

To study the resilience of coastal dune ecosystems, we focused on *Ammophila arenaria* or Marram grass, a prevalent dune grass native to the European coast. *A. arenaria* is an ecosystem engineer, as it is able to alter the surrounding physical environment as a result of its sand-trapping capabilities (Crooks, 2002; van der Putten, 1989). *A. arenaria* aids in the formation of characteristic tall dunes along the bio-geomorphological gradient from the sea inland (Fig. 1A). It is due to these tall dunes that *A. arenaria* has been introduced to coastal areas outside of Europe as well, leading to widespread coverage of the dune grass (Reijers et al., 2020; Seabloom et al., 2013). The bio-geomorphological gradient follows the natural growth and succession of a dune under the influences of both the biological and geological environment, from its inception in the embryonic dunes on the beach, to the established white dune

ridges and ending in the leeward stabilized grey dunes (Huiskes, 1979; Olff et al., 1993).

Plant growth along the dune gradient is influenced by three parallel stress axes, being the availability of nutrients, the direct coastal and aeolian dynamics, and the competition with other plants (Figure 1B, Bonte et al., 2021; Reijers et al., 2020). The beach is where nutrients are most abundant, as they are continuously replenished by sea and wind through sediment deposition, yet it is also where the dynamics of the sea and wind are felt most strongly (Ciccarelli, 2015; Darke et al., 2016). Vegetation in this area is somewhat sparse, so competition is of lesser influence here (Martínez & García-Franco, 2008). The higher one is from the sea, as at the white dunes, the more attenuated the physical stress and nutrient replenishment by coastal and aeolian influences become (Gao et al., 2020; Keijsers, 2015). The absence of these influences results in a stabilised nutrient-poor, acidic environment at the grey dunes, which facilitates the growth of plant species better suited to these conditions, consequently increasing the amount of plant competition (Gao et al., 2020; Martínez & García-Franco, 2008; Miyanishi & Johnson, 2007).

The dune forming process of *A. arenaria* is continuously influenced by these three parallel axes. The process starts at the beach, where the forces of sea and wind limit its growth, but it has an abundance of nutrients (Fischman et al., 2019; van der Putten, 1989). An embryo dune is then formed, often in conjunction with dune grass *Elytrigia juncea*, which can be considered an ecosystem pioneer due to its capabilities to colonize lower, more saline areas compared to *A. arenaria* (Reijers et al., 2020; van Puijenbroek, Limpens, et al., 2017). Once *E. juncea* initiates dune formation, *A. arenaria* can trap sediment washed up onto the shore and transported landward through aeolian forces with its shoots and root system, further fastening itself within the sand (Zarnetske et al., 2012). The ability of *A. arenaria* to cope relatively well with burial through vertical outgrowth facilitates the formation of steep dunes (Brown & Zinnert, 2018; Ievinsh & Anderson-Ozola, 2020).

Once the dune has reached a certain height, the direct influence of the sea on *A. arenaria* is absent and aeolian transport is diminished, resulting in a decrease in nutrient availability (Hart et al., 2012; Reijers et al., 2020). At this point on the bio-geomorphological gradient *A. arenaria* is outcompeted by plant species that are better adapted to the environmental conditions, in which

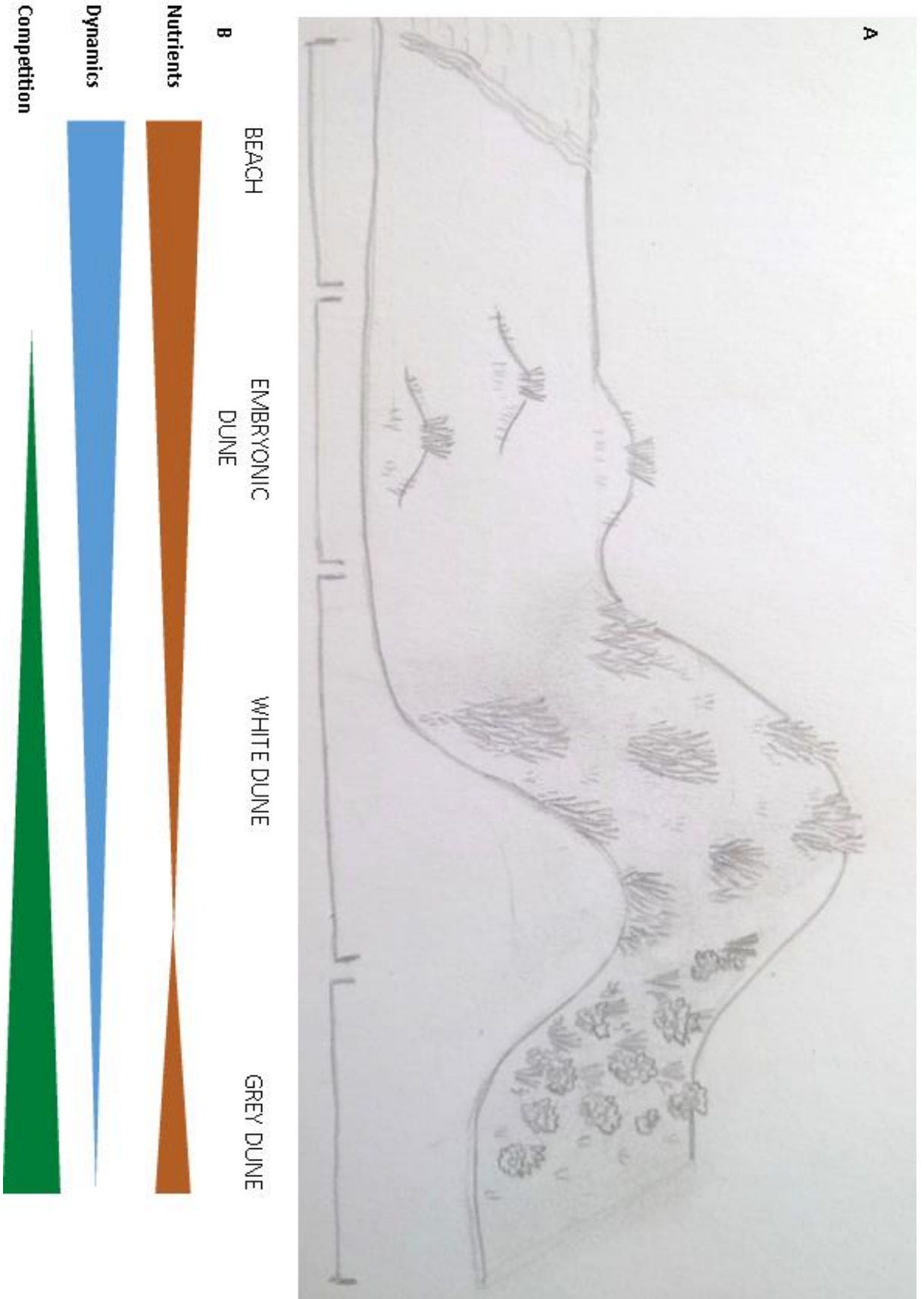


Figure 1. Sketch indicating (A) the coastal dune bio-geomorphological gradient with beach and embryonic dunes, white dunes and grey dunes and (B) influences on *A. arenaria* growth: nutrient availability (orange), coastal and aeolian dynamics (blue) and competition with other plants (green)

fungal pathogens and nematodes are additionally present, leading to its gradual disappearance in the grey dunes (Marshall, 1965; Van Der Putten & Troelstra, 1990).

In addition, morphological differences between landscapes may affect the resilience of *A. arenaria*. Previous studies have shown that the width and steepness of a beach can affect the dynamics of the sea and wind within a coastal area, and consequently influence the development of this area over time (Jarmalavičius et al., 2012; Keijsers et al., 2013; Silva et al., 2019).

Studying the ability of individual plants to recover after disturbance gives important insight into the capacity to which an ecosystem as a whole is able to bounce back after adversity. Comparing the growth capacity of disturbed with non-disturbed *A. arenaria* individuals over the growing season may give an indication of the possible advantages or disadvantages of interfering with *A. arenaria* early in the growing season. The findings of this study could be used in the development of new strategies for the management of coastal dune ecosystems. To optimize dune management strategies, it is of utmost importance to acknowledge the protective functions of these ecosystems against EWEs and rising sea levels.

For that reason, we aimed to elucidate the resilience of *A. arenaria* along the bio-geomorphological dune gradient. To do this, we formulated four questions and tried to answer them by investigating the resistance and recovery of several of its properties after disturbance early in the growing season. They are as follows: (I) How resilient is each area of the bio-geomorphological dune gradient? (II) How do disturbed plants compare to undisturbed plants for the studied properties? (III) Are the findings the same for all studied locations and (IV) In the case that the findings are not the same, which (a)biotic properties offer an explanation for this variation.

On the basis of the three parallel stress axes influencing plant growth across the dune gradient, as described before, we hypothesised that resistance and recovery of *A. arenaria* would be highest in the white dune area, as we expect an optimum to be there, with nutrients being somewhat abundant, physical stressors diminished and relatively little competition. For the embryonic and grey dune areas, we expected a lesser degree of resistance and recovery. For the former this is primarily due to the harsh conditions of the region, and for the latter due to the individuals having to

outcompete other species for the limited available nutrients. Due to the same reasons, we also expect disturbed *A. arenaria* to also be most similar to undisturbed individuals in the white dunes, before the beach and grey dunes. Furthermore, we expect the degree of resistance and recovery to differ between the studied locations, and think that this will be due to factors that influence nutrient abundance, the amount of physical stress and the amount of plant competition, as well as the morphological properties, such as the width of the beach and the height of the white and grey dunes.

Materials & Methods

Study location

The study was performed between early April and mid-September 2021 on the Wadden Sea island of Terschelling, the Netherlands (53° 24' N, 5° 21' E). Along the coastline of Terschelling, four distinct locations were selected using Google Earth Pro on the basis of three morphological properties; width of the beach, width of the foredune and height of the first foredune ridge (Figure 2). For each location a bin of approximately 150 m in width was used to accurately resemble the region. The bio-geomorphological dune gradient was divided into three distinct areas: the beach (either with or without clear embryonic dunes), the white dunes and the grey dunes.

The plant species of interest was the beach grass *Ammophila arenaria*, also known as Marram grass. This grass can be found along the bio-geomorphological gradient, but varies in its abundance for the distinct areas of the gradient. The distinction between the different areas of the gradient was based on plot height for the beach/white dune distinction (embryo dune = 3.5±1.2 m vs white dune = 11.7±6.4 m) and the presence of species besides *A. arenaria* and the other dominant beach grass *E. juncea* for the white dune/grey dune distinction.

Experimental setup

Following a paired design, we selected 10 pairs of *A. arenaria* in close proximity (approximately 5 m) for each of the bio-geomorphological areas at all four locations. Individuals similar in size and vitality were selected for each pair.

Control individuals were chosen first, as they also acted as controls for a parallel study. Individuals belonging to the experimental condition had all their aboveground biomass clipped. Rhizomal

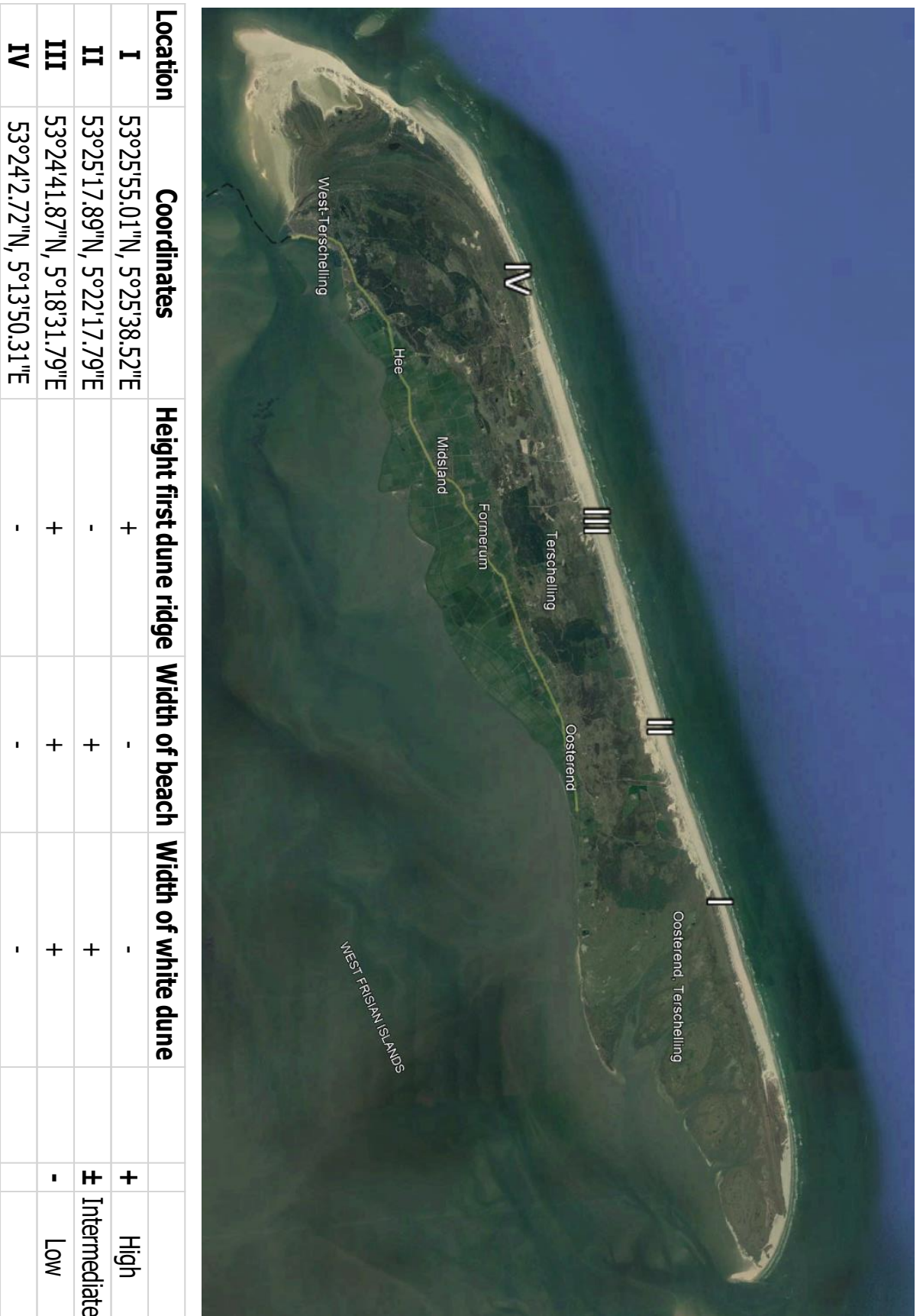


Figure 2. Satellite overview of the barrier island Terschelling with the studied locations (I-IV) with the noted coordinates and morphological properties (first dune ridge height, beach width and white dune width)

connections were severed for every control and experimental individual by digging a trench around the selected individual of 50 cm in radius and 30 cm in depth. In addition, the area within 50 cm of the individual was cleared from other vegetation by digging this trench.

As the presence of embryonic dunes is dependent on several external factors, such as the occurrence of EWEs, these dunes are not found everywhere. In the case of this study, embryonic dunes were only found for location II and III and *A. arenaria* individuals were selected from there. Where embryonic dunes were absent, as in location I and IV, *A. arenaria* individuals were selected from the front line of the white dune. At the white and grey dune areas, we selected the individuals haphazardly, though ensuring that they were not located on a steep slope, as erosion could affect survival.

Plant analyses

Shoot number, diameter, and length of the longest leaf

In order to determine recovery of the disturbed individuals, shoot number, shoot diameter, and length of the longest leaf were taken into account during the recovery period. We measured those variables prior to disturbance, and at multiple time points throughout the growing season from early April to mid-September. Alive shoots were counted manually. The diameter was determined by randomly measuring 4 shoots just above the base using a calliper and then calculating the average. The length of the longest leaf was measured using a carpenter's ruler to give an indication of photosynthetic capacity of the individual. This value was then corrected for the amount of sediment accretion/erosion for each plot to get an indication of the change in leaf length growth for each individual. We calculated the rate of change in shoot number, diameter and length of the longest leaf over the growing season using the following formula (1). When the rate of change significantly differs from 0, a change has occurred for the parameter over the growing season.

$$\text{Rate of change (\%)} = \frac{y_{t7} - y_{t0}}{y_{t0}} * 100 \quad (1)$$

To determine the disturbance ratio on the rate of change in shoot number, diameter and length of the longest leaf over the growing season, we divided the rate of change of the disturbed to that of the undisturbed individuals (2). When the disturbance ratio significantly differs from 1, the disturbance has resulted in a net change for that parameter over the growing season.

$$\text{Disturbance ratio} = \frac{\text{Growth rate}_{\text{disturbed}}}{\text{Growth rate}_{\text{undisturbed}}} \quad (2)$$

Biomass

To measure the initial differences in biomass for *A. arenaria* individuals of the different areas of the gradient, aboveground wet biomass weight was determined after disturbance (early April 2021). Biomass was cut off at the base of the shoots using a serrated knife for every individual of the experimental condition. They were then placed in a plastic bag and weighed using a digital Tefal scale.

Leaf C:N ratio

To investigate leaf C:N ratio of *A. arenaria*, we took a single shoot from the clipped aboveground biomass. We used this to determine whether the C:N ratio differs between the areas of the biogeomorphological dune gradient at the beginning of the growing season (early April 2021). Shoot samples were dried at 70 °C, after which they were cut into small pieces using scissors and pulverized using a bullet mill. 3 mg of each pulverized sample was then packaged in aluminium to form a small ball. These balls were then analysed for C:N ratio at NIOZ Yerseke.

Prior to drying and milling, these shoot samples were in addition used to determine differences in leaf number per shoot and leaf surface area between the areas of the geomorphological gradient.

Soil analyses

To determine how soil properties differ between the studied plots early in the growing season, soil samples were taken at the beginning of the growing season (early April 2021). For grain size analysis, we took surface soil samples from the top 2 cm between the shoots of three control individuals per area per location. For the other soil analyses, root soil was taken from a depth of approximately 10 cm directly below each control individual.

Grain size

In the case that surface soil samples contained a lot of organic material, such as lichens, twigs and grass, they were treated with 35% H₂O₂. To speed up this reaction, these samples were then boiled. Grain size analysis of the surface soil samples was then performed over the span of two days using the Laser Diffraction Analyser at NIOZ Texel.

pH and Salinity

To determine pH and salinity, as well as moisture and organic matter content of the soil samples, an adapted version of the “verwerking bodemonsters” protocol for of the ecology department of the University of Groningen was used (Supplementary materials: Protocols).

15 g of each soil sample was placed in a glass vial together with 60 mL of distilled water for both pH and salinity determination. Vials were shaken overnight using an automatic shaker. For pH determination, pH probes were first calibrated with pH 4 and pH 7 buffer solutions and verified using distilled water. For salinity determination, we used a conductivity meter at a frequency of 200 c/s. Vials were shaken prior to usage and the suspension was measured directly afterward using the probes at about 2-2,5 cm depth, ensuring not to touch the suspended material. Salinity findings were corrected for the amount of dilution to get a right indication of soil salinity percentage.

Moisture content and Organic Matter

Ceramic cups were weighed (C). A standardised amount of each soil sample was placed in one of these cups and weighed again (A). These cups were then incubated overnight in a stove at 110 °C and weighed again (B). Moisture content was determined using the following formula (3):

$$\begin{aligned} \text{Moisture content (\%)} &= \frac{(A - C) - (B - C)}{A - C} * 100 \\ &= \frac{A - B}{A - C} * 100 \end{aligned} \quad (3)$$

After moisture content was determined, cups were incubated for four hours in the stove at 550°C. Once cooled to workable temperatures, cups were cooled even further in a desiccator and weighed again (D). Organic matter content was determined using the following formula (4):

$$\begin{aligned} \text{Organic matter content (\%)} &= \frac{(B - C) - (D - C)}{B - C} * 100 \\ &= \frac{B - D}{B - C} * 100 \end{aligned} \quad (4)$$

Sediment accretion/erosion

To determine the sediment transport along the geomorphological gradient, sediment accretion/erosion was measured. This was done by inserting a glass fibre stick (approximately 100 cm in length, 3 mm in diameter) into the soil in the middle of the *A. arenaria* plot so that 50cm sticks out of the soil. The aboveground part of the stick was later reduced to 40 cm to decrease visibility for external influences. Changes in sediment were measured at every time point until the end of the growing season.

Satellite image computations

To combine the field work data with satellite imaging, we used dGPS localisation to pinpoint the exact location of each *A. arenaria* pair as well as the height at each location. We then imported the dGPS locations into the Google Earth Engine Code Editor for further analysis concerning the morphological differences, such as the height of the plot and the distance of plot to sea.

In addition, we used satellite images derived from the Planet Explorer with a resolution of 3.7 m. The computer software qGIS version 3.18.2 was used for the determination of the amount and distribution of vegetation between the studied areas by using the Soil Adjusted Vegetation Index (SAVI) as a proxy. The SAVI is an adaption of the NDVI to compensate for the reflective nature of bare soil, as is the case with sand. The formula used to calculate the SAVI is noted below, where NIR is the value of the near infrared band, RED the value of the red band and L is a soil brightness correction value for which we used 0.5, which is a standardly used value (5):

$$\text{SAVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED} + L} * (1 + L) \quad (5)$$

Statistical analyses

Statistical analyses were performed in RStudio version 1.4.1106. Extreme outliers were determined and removed from the dataset. Shapiro-Wilk tests were performed to test for normality within and

Levene's tests to test for equal variances between the groups.

Two-way analyses of variances (ANOVA) were performed in order to compare the parameters between the three areas of the bio-geomorphological dune gradient. These parameters entail sediment grain size, soil pH, salinity, moisture and organic matter content, and plant C:N ratio, aboveground biomass weight, shoot number and diameter, the length of the longest leaf, and SAVI. In addition, differences in the change in shoot number, shoot diameter, and length of the longest leaf over the growing season and the change in relation to the control group between the areas were also analysed with two-way ANOVAs. In the case of a significant result from the ANOVAs, post-hoc testing was performed using pairwise t-tests to determine which areas differed from each other for the parameter in question, with a Bonferroni correction to compensate for multiple comparisons.

Linear models were applied to the various (a)biotic properties of the studied locations to test whether they correlate with each other. These properties are the height of the plot and its distance to the sea, the soil pH, salinity, moisture and organic matter content, the C:N ratio, and aboveground biomass weight of *A. arenaria*, and the SAVI for the plots and their surroundings. In addition, correlations between the (a)biotic properties of the studied locations and shoot number, shoot diameter, and length of the longest leaf were tested. We made use of the R^2 -value analysis of Cohen (1992) to determine the strength of the correlation between the properties.

For the shoot number, diameter, and length of the longest leaf, which were tracked over time, repeated measures ANOVAs were performed to compare the parameters between the groups over time. In the case of a significant result from the ANOVAs, post-hoc testing was again performed using Bonferroni-corrected pairwise t-tests.

One sample t-tests were used to determine whether the changes in shoot number, shoot diameter and length of the longest leaf were significant over the season and whether the disturbed and control individuals differed from one another for this parameter.

To identify variables that explain the variation in shoot number, shoot diameter and length of the longest leaf over time between the studied locations, linear models were built using the plot parameters and one by one removed the parameter with the highest P-value until all effects were significant to optimize its fit. The used parameters are sediment grain size, soil pH, salinity, moisture and organic matter content, plant C:N ratio, aboveground biomass weight, shoot number and diameter, the length of the longest leaf, and SAVI. These linear models were corrected for the area we assigned each individual to, as well as for the duration of the study. We then looked into each area separately, to test whether the variables explained the variation homogeneously over the bio-geomorphological gradient.

For the rate of change in leaf length over time, we applied various nonlinear regression models to the data to test which one fit best. We found that a Michaelis-Menten equation had the best fit (6). Using this equation on the data we estimated the maximum achievable value (V_{max}) and the value of the Michaelis constant (K), which is equal to the value of TIME at which the VALUE is half of V_{max} . In this manner K can be used as a proxy for the leaf growth rate.

$$VALUE = \frac{V_{max} * TIME}{K + TIME} \quad (6)$$

A significance level of 0.05 was used for all analyses.

Results

Grain size

Sediment grain size did not differ between the areas of the bio-geomorphological dune gradient ($F_{2,22} = 1.183$; $P = 0.325$, Figure 3A). Mean and SD are noted in Table S1A. We found no statistically significant differences in sediment grain size between the other areas of the four studied locations.

Soil pH

Soil pH did differ between the areas of the bio-geomorphological dune gradient ($F_{2,106} = 95.893$; $P < 0.001$, Figure 3B). Mean and SD, as well as T values from pairwise comparisons and associated P

values are noted in Table S1B. When comparing the beach and white dunes, we found that soil pH was higher at the beach of location IV. In addition, comparing the beach and grey dunes, we found that soil pH was higher at the beach of locations I, II, III, and IV. Lastly, comparing the white and grey dunes, we found that soil pH was higher at the white dunes of locations I, II, and III. We did not find any statistically significant differences in soil pH between the other areas of the four studied locations.

Soil salinity

Soil salinity also differed between the areas of the bio-geomorphological dune gradient ($F_{2,103} = 14.858$; $P < 0.001$, Figure 3C). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S1C. Soil salinity was higher at the beach in comparison to both the white and grey dunes of location IV. We did not find any statistically significant differences in soil salinity between the other areas of the four studied locations.

Soil moisture content

Soil moisture content again differed between the areas of the bio-geomorphological dune gradient ($F_{2,108} = 8.563$; $P < 0.001$, Figure 3D). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S1D. Comparing the beach and white dunes, we found that soil moisture content was higher at the beach of locations I and IV. In addition, comparing the beach and grey dunes, we found soil moisture content to be higher at the beach of location IV. Lastly, comparing the white and grey dunes, we found that soil moisture content was lower at the white dunes of location I, yet was higher for those of location IV. We did not find any statistically significant differences between the other areas of the four studied locations.

Soil organic matter content

Lastly, soil organic matter content differed between the areas of the bio-geomorphological dune gradient ($F_{2,107} = 73.413$; $P < 0.001$, Figure 3E). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S1E. Comparing the beach and white dunes, soil organic matter content was lower at the beach

of location II. In addition, comparing the beach and grey dunes, soil organic matter content was lower at the beach of locations I and III. Lastly, comparing the white and grey dunes, we found that organic matter content was higher at the grey dunes of locations I, III, and IV. We did not find any statistically significant differences between the other areas of the four studied locations.

SAVI

SAVI differed between the areas of the bio-geomorphological dune gradient ($F_{2,107} = 999.034$; $P < 0.001$, Figure 4A). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S2A. Comparing the beach and white dunes, SAVI was higher at the white dunes of locations I and IV. In addition, comparing the beach and grey dunes, SAVI was higher at the grey dunes of locations I, II, III, and IV. Lastly, comparing the white and grey dunes, we found SAVI was higher at the grey dunes of locations I, II, III, and IV. We did not find any statistically significant differences between the beach and white dunes of locations II and III. Figure 4B shows SAVI over time for the areas of the bio-geomorphological dune gradient.

Correlation of plot properties

To get a better understanding of the relationships within coastal dune ecosystems, we applied linear models to the various (a)biotic properties of all plots of the studied locations to test whether they correlate (Table 1). These properties were the height of the plot, its distance to sea, the pH, salinity, moisture and organic matter content of the soil, and the SAVI for the plots and their surroundings.

We found that the height of the plot was positively correlated strongly with the SAVI-value and moderately with soil organic matter content. Plot height was furthermore negatively correlated strongly with pH of the soil, and moderately with soil salinity. The SAVI-value of the plot was negatively correlated strongly with pH and moderately positively with organic matter content of the soil. Soil pH of the plot negatively correlated strongly with organic matter content of the plot. No other moderate or strong correlations were found between the rest of the plot properties.

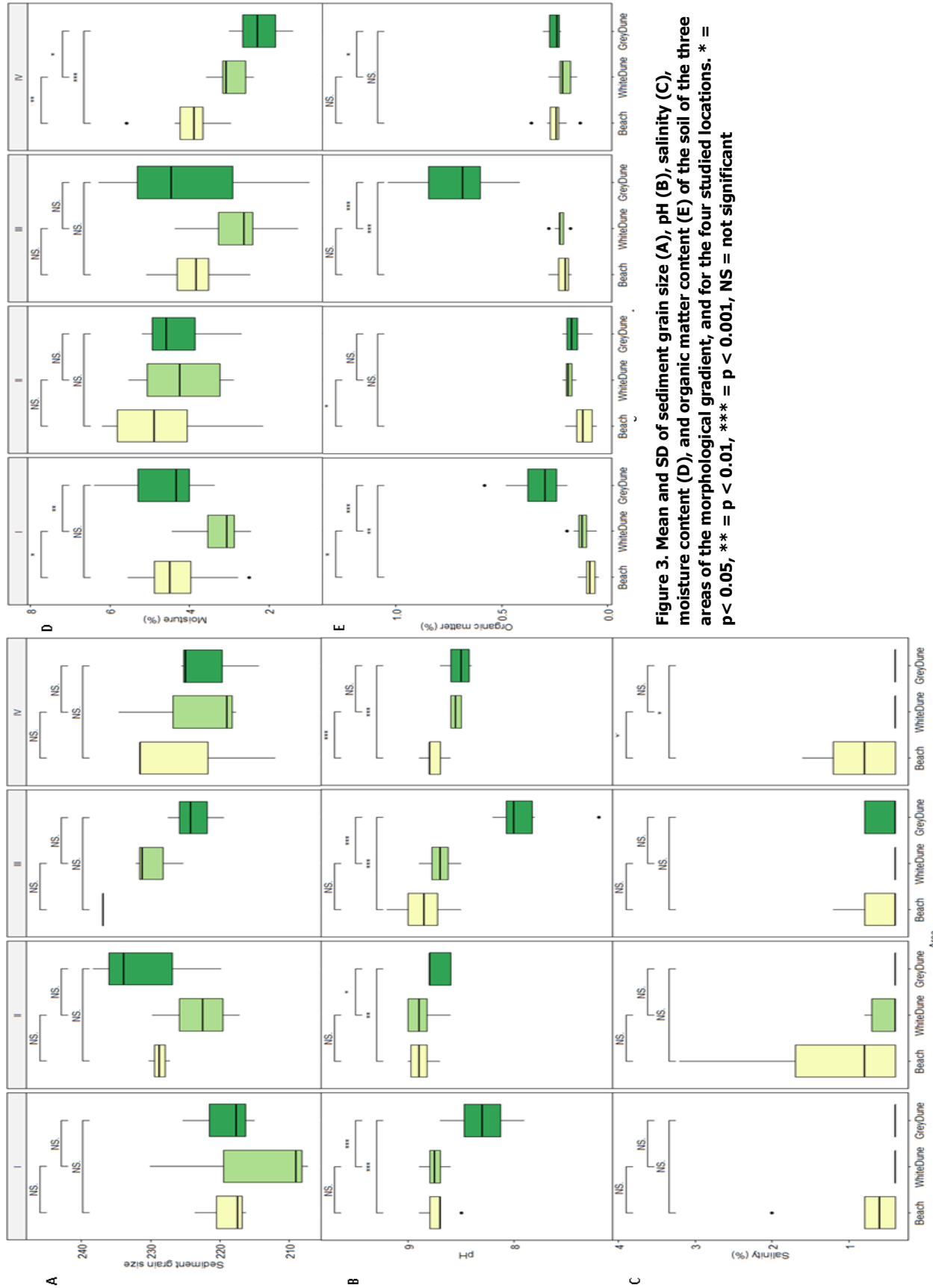


Figure 3. Mean and SD of sediment grain size (A), pH (B), salinity (C), moisture content (D), and organic matter content (E) of the soil of the three areas of the morphological gradient, and for the four studied locations. * = p < 0.05, ** = p < 0.01, * = p < 0.001, NS = not significant**

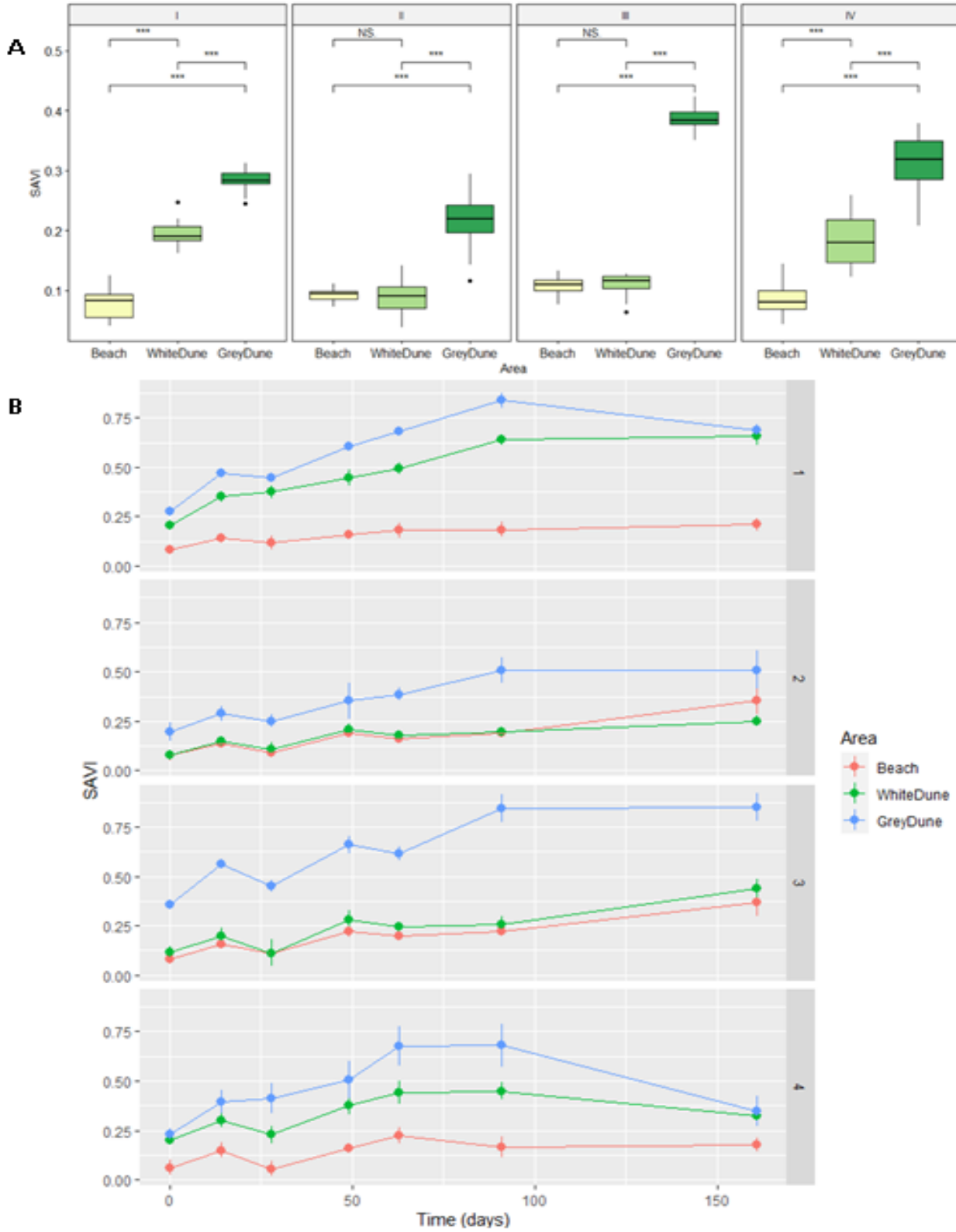


Figure 4. Mean and SD of SAVI of disturbed *A. arenaria* plots in the three areas of the morphological gradient for the four studied locations at the beginning of the growth season (A), the change in SAVI over the growing season (B). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

Table 1. R²-values of the plot properties for the four studied locations and three areas along the bio-geomorphological dune gradient

	HEIGHT	DISTANCE	GRAINSIZE	SAVI	pH	SALINITY	MOISTURE	ORGANIC
DISTANCE	0.002355	-	0.03739	0.001192	0.03157	-0.0007919	0.004063	0.05605
GRAINSIZE	-0.01015	0.03739	-	-0.02002	0.01357	-0.0227	-0.02789	-0.03
SAVI	0.4466	0.001192	-0.02002	-	0.3636	0.06548	0.00364	0.2306
pH	0.3224	0.03157	0.01357	0.3636	-	0.001295	-0.0001289	0.6507
SALINITY	0.1741	-0.0007919	-0.0227	0.06548	0.001295	-	0.01557	-0.001169
MOISTURE	0.07885	0.004063	-0.02789	0.00364	-0.0001289	0.01557	-	0.005376
ORGANIC	0.1314	0.05605	-0.03	0.2306	0.6507	-0.001169	0.005376	-

C:N ratio

Leaf C:N ratio differed between the areas of the bio-geomorphological dune gradient ($F_{2,42} = 30.967$; $P < 0.001$, Figure 5A). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S2B. When comparing the beach and the white dune, we found that the C:N ratio was lower at the beach of locations I and III. C:N ratio was also lower at the beach in comparison to the grey dunes of locations I and II. Lastly, comparing the white and grey dunes, we found the C:N ratio to be lower at the grey dunes of location III. We did not find any statistically significant differences between the other areas of the four studied locations.

Aboveground biomass

Aboveground biomass wet weight also differed between the areas of the bio-geomorphological dune gradient ($F_{2,105} = 12.408$; $P < 0.001$, Figure 5B). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S2C. When comparing the beach and white dunes, we found that wet biomass weight was higher at the white dunes of locations III and IV. In addition, wet biomass weight was higher at the white in comparison to grey dunes of locations I and III. No statistically significant differences were found between the other areas of the four studied locations.

Shoot number

The shoot number differed between the areas of the bio-geomorphological dune gradient ($F_{2,223} = 43.953$; $P < 0.001$, Figure 6A). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S3A. Comparing the beach and white dunes, we found the shoot number to be higher at the beach of location I. In addition, comparing the beach and grey dunes, the

shoot number was higher at the beach of locations I, II, and III. Lastly, comparing the white and grey dunes, we found the shoot number to be lower at the grey dunes of locations I, II, and III. We did not find any statistically significant differences between the beach and white dunes of locations II and III, or between the areas of location IV.

Furthermore, we found differences in the shoot number across all time points between the areas of the bio-geomorphological gradient ($F_{2,101} = 5.174$; $P = 0.007$, Figure 6B). In addition, we found differences across all time points between the different locations we studied ($F_{3,101} = 12.238$; $P < 0.001$). For the number of shoots over time the linear model with the best fit was as follows (7):

$$SHOOTS \sim AREA * TIME + SAVI + ORGANIC + (1|ID) \quad (7)$$

It shows that the number of shoots at each plot is positively correlated with the SAVI-value and negatively correlated with the organic matter content of the soil. T values from linear mixed model and associated P values are noted in Table 2. When looking specifically at the separate areas, we see that for the beach, white dunes and grey dunes the number of shoots is negatively correlated with organic matter content of the soil. For the SAVI-value, we see that is positively correlated with shoot number for the white and grey dunes.

To identify whether the number of shoots of the disturbed *A. arenaria* individuals had remained stable or changed over the growing season, we determined the rate of change in the shoot number (Figure 6C). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S3B. We found that the rate of change in the shoot number was higher than 0 for

the beach and grey dune areas of locations I and II. This was also the case for the white dune areas of locations I and IV. The shoot change ratio was lower than 0 for the grey dunes of location III. The shoot change ratio did not differ significantly from 0 for the other areas of the other studied locations.

In addition, we found that the rate at which new shoots are formed differed between the areas of the bio-geomorphological dune gradient ($F_{2,101} = 14.248$; $P < 0.001$, Figure 6C). T values from pairwise comparisons and associated P values are noted in Table S3B. The shoot number growth rate was higher for the white dunes compared to grey dunes for location III. No statistically significant differences were found between the other areas of the four studied locations.

To compare the change in shoot number of the disturbed in comparison to the undisturbed *A. arenaria* individuals, we then determined the disturbance ratio for the number of shoots (Figure 6D). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S3C. We found that the disturbance ratio was lower than 1 for the white dunes of location II. The disturbance ratio did not differ significantly from 1 for the other areas of the other studied locations.

We found that the disturbance ratio for shoot number change did not differ significantly between the areas of the bio-geomorphological gradient ($F_{2,96} = 2.125$; $P = 0.125$, Figure 6D). Therefore, no statistically significant differences were found between the areas of the four studied locations.

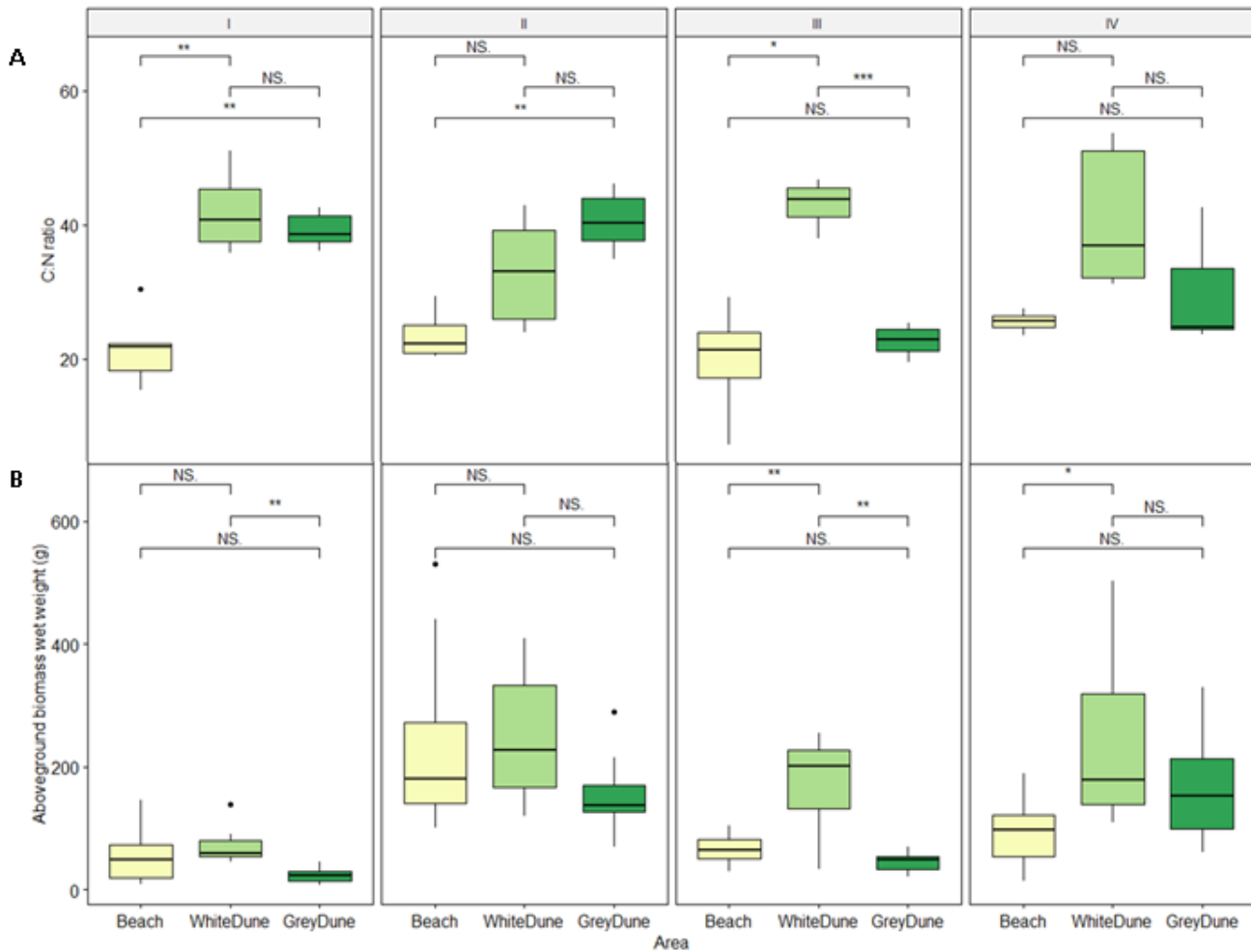


Figure 5. Mean and SD of aboveground biomass wet weight (A) and C:N ratio (B) of *A. arenaria* individuals of the three areas of the morphological gradient, and for the four studied locations. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

Table 2. Determination of explanatory variables for shoot number change over time for all areas together, and beach, white dunes, and grey dunes separately. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
AllAreas	AREA	6685.57342	3342.78671	2	199.4885153	0.412526181	0.662539265	
	TIME	600300.7189	600300.7189	1	781.3151229	74.08183185	4.09E-17	***
	SAVI	114980.0302	114980.0302	1	789.5316405	14.18944039	0.000177584	***
	ORGANIC	98379.64001	98379.64001	1	119.607699	12.14082162	0.000690162	***
	AREA:TIME	698131.089	349065.5445	2	697.107582	43.07743463	2.29E-18	***
Beach		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	1108293.707	1108293.707	1	236.1433563	60.74840775	2.06E-13	****
	SAVI	44220.18216	44220.18216	1	245.7040149	2.423821085	0.12079021	
	ORGANIC	124422.5944	124422.5944	1	36.4009903	6.819920072	0.013015174	*
WhiteDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	17309.69096	17309.69096	1	272.7736047	5.192115719	0.023462749	*
	SAVI	118953.5065	118953.5065	1	183.14192	35.68061222	1.18E-08	***
	ORGANIC	24396.92584	24396.92584	1	42.82132127	7.317962087	0.009758378	**
GreyDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	26189.46127	26189.46127	1	251.6419672	7.871371298	0.005414779	**
	SAVI	45479.99659	45479.99659	1	266.9008993	13.66923649	0.000264577	***
	ORGANIC	28173.42396	28173.42396	1	44.35382469	8.467661034	0.005633756	**

Shoot diameter

When looking at the shoot diameter, we found that it differed between the areas of the bio-geomorphological dune gradient ($F_{2,222} = 53.821$; $P < 0.001$, Figure 7A). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S4A. When comparing the beach and white dunes, we found the shoot diameter to be lower at the beach of locations I, II, and IV. In addition, comparing the beach and grey dunes, the shoot diameter was lower at the beach of locations I, II, and IV, but higher at the beach of location III. Lastly, comparing the white and grey dunes, we found the shoot diameter to be higher at the white dunes of location III. We did not find any statistically significant differences between beach and white dunes of location III, or between the white and grey dunes of locations I, II, and IV.

Furthermore, we found differences in the shoot diameter across all time points between the areas of the bio-geomorphological gradient ($F_{2,94} = 8.909$; $P < 0.001$, Figure 7B). In addition, we found differences across all time points between the different locations we studied ($F_{3,94} = 12.238$; $P < 0.001$). For the shoot diameter over time the linear model with the best fit was as follows (8):

$$DIAMETER \sim AREA * TIME + SAVI + pH + ORGANIC + (1|ID) \quad (8)$$

It shows that the shoot diameter for each individual is negatively correlated with the SAVI-value and the pH and organic matter content of the soil. T values from linear mixed model and associated P values are noted in Table 3. When looking specifically at the separate areas, we see that for the beach and white dunes the shoot diameter is negatively correlated significantly with organic matter content of the soil. The shoot diameter is also negatively correlated with soil pH for the beach. In addition, shoot diameter is negatively correlated with SAVI-value for the grey dunes.

To identify whether the thickness of the shoots of the disturbed *A. arenaria* individuals had remained stable or changed over the growing season, we determined the rate of change of the shoot diameter (Figure 7C). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S4. We found that the rate of change was significantly higher than 0 for the beach of locations I, II, and IV. In contrast, the rate of change was significantly lower than 0 for the white

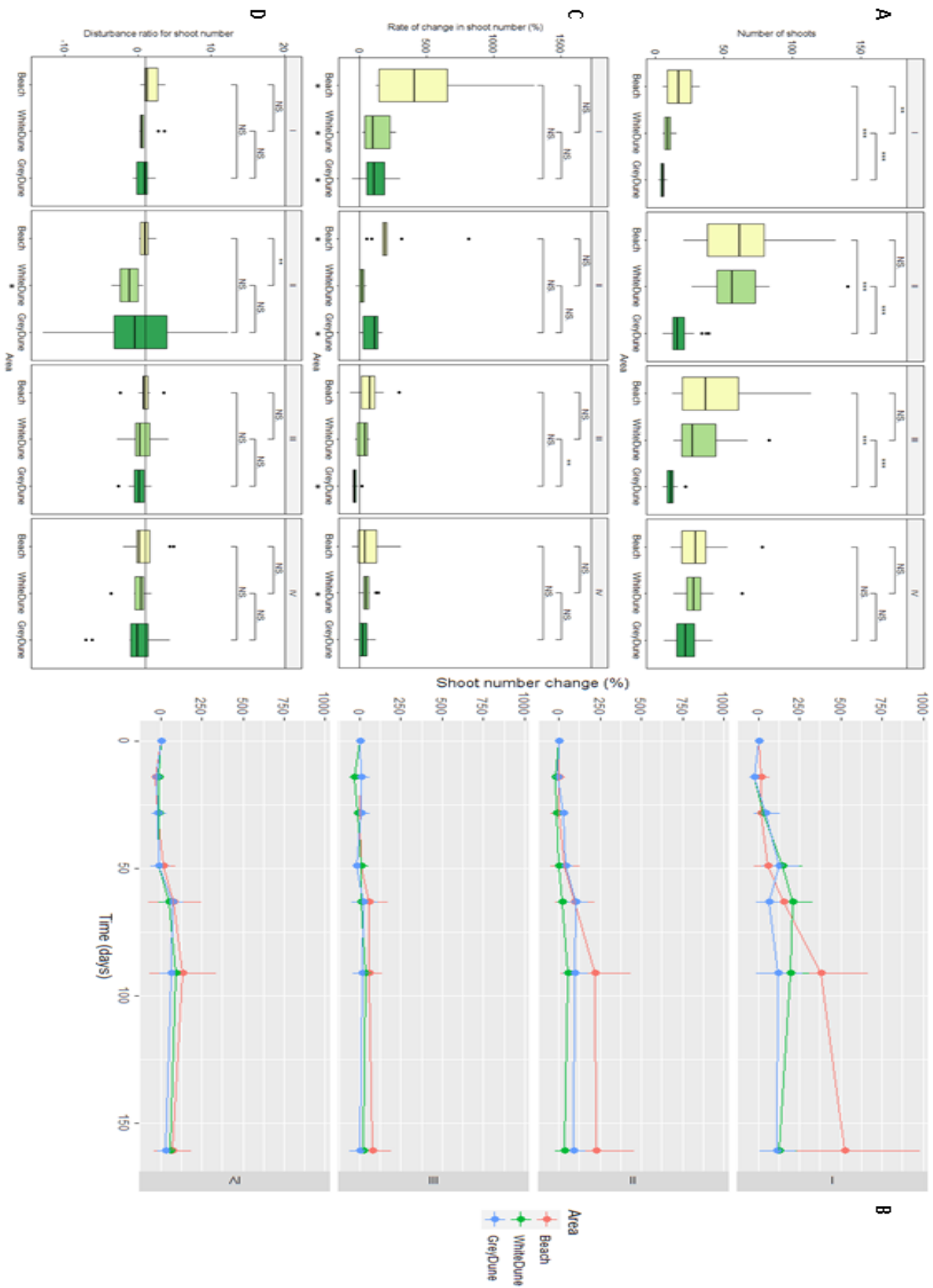


Figure 6. Mean and SD of shoot count of disturbed *A. arena/ria* individuals in the three areas of the morphological gradient for the four studied locations at the beginning of the growth season (A), the change in shoot count over the growing season (B & C) and this change relative to that control individuals (D). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

Table 3. Determination of explanatory variables for shoot diameter change over time for all areas together, and beach, white dunes, and grey dunes separately. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
AllAreas	AREA	8792.964664	4396.482332	2	173.1883805	6.251517491	0.002390713	**
	TIME	78115.46906	78115.46906	1	744.1497209	111.0752152	2.66E-24	***
	SAVI	6441.096644	6441.096644	1	772.6105259	9.158828648	0.002557377	**
	pH	10696.36813	10696.36813	1	111.5420445	15.20955332	0.000164802	***
	ORGANIC	5832.170376	5832.170376	1	106.6895803	8.292974329	0.004810475	**
	AREA:TIME	18595.48326	9297.74163	2	669.4807347	13.22079564	2.34E-06	***
Beach		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	49911.1163	49911.1163	1	218.0544856	42.39351877	5.07E-10	***
	SAVI	2266.916867	2266.916867	1	227.4022448	1.925474521	0.16661263	
	pH	17501.03964	17501.03964	1	32.05437823	14.86503824	0.000523597	***
	ORGANIC	18251.90535	18251.90535	1	30.97143214	15.50280878	0.000435163	***
WhiteDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	9687.128702	9687.128702	1	269.7034461	18.77734552	2.08E-05	***
	SAVI	7.138437814	7.138437814	1	164.3065607	0.013837012	0.90650385	
	pH	832.0037641	832.0037641	1	42.90117203	1.612740228	0.210952089	
ORGANIC	2427.34849	2427.34849	1	46.93494558	4.705126016	0.035171691	*	
GreyDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	14183.48367	14183.48367	1	240.3761959	28.85218799	1.84E-07	***
	SAVI	5224.439476	5224.439476	1	253.9220502	10.62760838	0.001266439	**
	pH	21.30357912	21.30357912	1	36.69483706	0.043335959	0.836245122	
ORGANIC	763.4693284	763.4693284	1	35.6166645	1.55305714	0.220819552		

and grey dunes of location IV. However, the rate of change did not differ significantly from 0 for the other areas of the other studied locations.

In addition, we found that the rate of change in shoot diameter differed between the areas of the bio-geomorphological dune gradient ($F_{2,103} = 26.655$; $P < 0.001$, Figure 7C). T values from pairwise comparisons and associated P values are noted in Table S4B. We found the rate of change to be higher for the beach compared to white dunes for location I, II and IV. In addition, the rate of change was higher for the beach compared to grey dunes for location I and IV. However, no statistically significant differences were found between the other areas of the four studied locations.

To compare the change in shoot thickness of the disturbed in comparison to the undisturbed *A. arenaria* individuals, we determined the disturbance ratio for the shoot diameter (Figure 7D). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S4C. We found that the disturbance ratio was lower than 1 for the grey dunes of location I and the white dunes of location II. The disturbance ratio did not differ

from 1 for the other areas of the other studied locations.

We found that the disturbance ratio for shoot diameter change did not differ between the areas of the bio-geomorphological gradient ($F_{2,96} = 0.189$; $P = 0.828$, Figure 7D). Therefore, no statistically significant differences were found between the areas of the four studied locations.

Longest leaf

As a proxy for photosynthetic capacity of *A. arenaria*, we measured the length of the longest leaf of each individual over the growing season. Leaf length also differed between the areas of the bio-geomorphological dune gradient ($F_{2,226} = 45.766$; $P < 0.001$, Figure 8A). Mean and SD, as well as T values from pairwise comparisons and associated P values are noted in Table S5A.

Comparing the length of the longest leaf between the individuals of the beach with those of the white dunes, we found them to be shorter at the beach of locations I, II, and IV. In addition, we compared the beach with the grey dunes and found the longest leaf to be shorter at the beach of location II. Lastly, when comparing the white and grey dunes, we

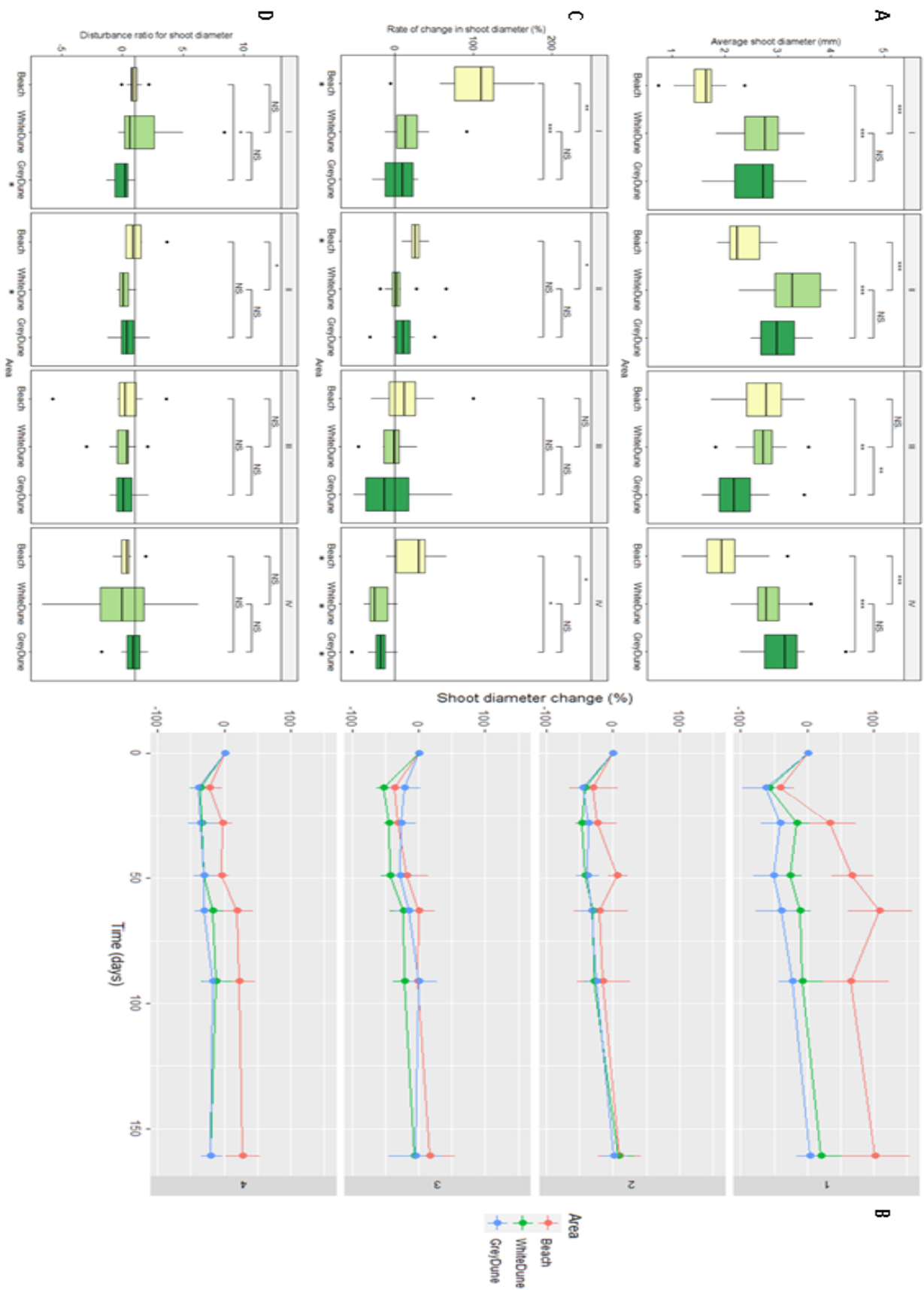


Figure 7. Mean and SD of shoot diameter of disturbed *A. arena/ria* individuals in the three areas of the morphological gradient for the four studied locations at the beginning of the growth season (A), the change in shoot diameter over the growing season (B & C) and this change relative to that control individuals (D). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

found the longest leaf to be shorter for the white dunes of location II, but longer for the white dunes of location IV. No statistically significant differences were found between the other areas of the four studied locations.

Furthermore, we found differences in the length of the longest leaf across all time points between the areas of the bio-geomorphological gradient ($F_{2,101} = 45.092$; $P < 0.001$, Figure 8B).

To identify the estimated maximum leaf length and leaf growth rate, we fitted a Michaelis-Menten equation on the longest leaf data. We found that V_{max} and K differed between the three areas of the bio-geomorphological gradient (Table 4).

K was highest at the beach, then the white dunes and then the grey dunes of locations I and II. However, the exact opposite order was found at location IV. In addition, K was highest for the white dunes, then the beach and then the grey dunes of location III.

V_{max} was highest at the white dunes, then the beach and then the grey dunes of locations I and IV. In addition, V_{max} was found to be highest at the beach of both locations II and III, but the white dunes were second highest and the grey dunes last at location II, and the opposite was found at location III.

In addition, we found differences across all time points between the different locations we studied ($F_{3,101} = 13.212$; $P < 0.001$). For the length of the longest leaf over time the linear model with the best fit was as follows (9):

$$\begin{aligned} \text{LONGEST} \sim & \text{AREA} * \text{TIME} + \text{HEIGHT} + \text{DISTANCE} \\ & + \text{SAVI} + \text{SALINITY} + \text{ORGANIC} \\ & + (1|ID) \end{aligned}$$

(9)

It shows that the leaf length is positively correlated with the SAVI-value and height of the plot, the distance of the plot to sea and the salinity of the soil and negatively correlated with the height of the plot and the organic matter content of the soil. T values from linear mixed model and associated P values are noted in Table 5. When looking specifically at the separate areas, we see that at all three areas, leaf length is positively correlated with the SAVI-value. In addition, at the beach leaf length is positively correlated with soil salinity, but negatively

correlated with organic matter content of the soil. Lastly, leaf length is negatively correlated with the height of the plot at the beach and white dunes, but positively correlated with the distance of plot to sea at the grey dunes.

To identify whether the disturbed *A. arenaria* individuals had returned to their pre-disturbed photosynthetic capacity over the growing season, we determined the rate of change in the longest leaf (Figure 8C). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S5B. When looking at the white dunes, we found that the rate of change was higher than 0 at the beach of locations I, II, and III. The rate of change was also found to be higher than 0 at the white dunes of locations I and II. However, the rate of change did not differ from 0 for the length at the other areas of the studied locations.

In addition, we found that the rate of change in the longest leaf differed between the areas of the bio-geomorphological dune gradient ($F_{2,105} = 34.397$; $P < 0.001$, Figure 8C). T values from pairwise comparisons and associated P values are noted in Table S5B. When comparing the beach with the white and grey dunes, we found that the individuals at the beach had a higher rate of change than those at the white and grey dunes of locations I and II. In addition, the rate of change at the white dune was higher at the white in comparison to grey dunes for location I. No statistically significant differences

Table 4. Half time rate (K) and maximum value (V_{max}) of the longest leaf for all areas of the bio-geomorphological gradients of the four studied locations, both absolute and sediment-corrected values

LOCATION	AREA	Longest		LongestCorrected	
		K	Vmax	K	Vmax
I	Beach	61.4	143.0	59.6	142.2
	WhiteDune	130.0	187.0	132.3	188.5
	GreyDune	132.8	129.7	154.6	141.3
II	Beach	47.2	145.4	31.9	125.7
	WhiteDune	61.1	133.2	59.5	133.8
	GreyDune	67.7	125.9	64.8	123.7
III	Beach	68.8	142.6	58.4	134.4
	WhiteDune	66.3	120.4	77.4	133.1
	GreyDune	122.6	130.7	129.8	133.8
IV	Beach	71.0	119.6	106.3	147.2
	WhiteDune	69.7	132.5	70.8	130.8
	GreyDune	50.0	108.2	53.1	108.7

Table 5. Determination of explanatory variables for leaf length change over time for all areas together, and beach, white dunes, and grey dunes separately. * = p < 0.05, ** = p < 0.01, * = p < 0.001, NS = not significant**

		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
AllAreas	AREA	990.4292493	495.2146247	2	162.0178151	2.929925171	0.056236775	***
	TIME	234469.9307	234469.9307	1	672.3206821	1387.235589	1.36E-165	**
	DISTANCE	1786.276273	1786.276273	1	105.1168987	10.56845972	0.001546056	***
	HEIGHT	2522.272303	2522.272303	1	128.1279773	14.92296217	0.000176925	***
	SAVI	12101.65454	12101.65454	1	693.627594	71.59914204	1.56E-16	*
	SALINITY	937.161709	937.161709	1	102.4003061	5.544694247	2.04E-02	**
	ORGANIC	1280.587183	1280.587183	1	98.35201372	7.576562637	0.007042404	***
	AREA:TIME	12819.18829	6409.594145	2	624.582944	37.92220643	2.86E-16	***
Beach		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	70969.92671	70969.92671	1	216.1534532	302.7184766	5.60E-43	***
	DISTANCE	508.4252368	508.4252368	1	33.91766923	2.168661013	0.150068625	
	HEIGHT	531.8654145	531.8654145	1	31.26170093	2.268643854	0.142054212	
	SAVI	1928.309478	1928.309478	1	213.1537762	8.225102302	0.00454653	**
	SALINITY	1700.511924	1700.511924	1	31.78971792	7.25344386	0.011199444	*
	ORGANIC	1048.830616	1048.830616	1	34.73328503	4.473731634	4.17E-02	*
WhiteDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	51478.35628	51478.35628	1	212.7479886	360.7668587	1.06E-47	***
	DISTANCE	227.7722782	227.7722782	1	37.18229932	1.596257054	0.214299174	
	HEIGHT	2614.741939	2614.741939	1	69.40315896	18.32444359	5.86E-05	***
	SAVI	5804.531213	5804.531213	1	217.0629696	40.67889194	1.07E-09	***
	SALINITY	0.050632901	0.050632901	1	27.27256855	0.000354842	9.85E-01	
	ORGANIC	19.34882609	19.34882609	1	34.31963321	0.135599031	0.714957632	
GreyDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	56597.27155	56597.27155	1	222.1545165	430.5648075	6.69E-54	***
	DISTANCE	1468.752524	1468.752524	1	37.24086451	11.17356245	0.001899467	**
	HEIGHT	69.34864061	69.34864061	1	31.81823057	0.527571087	0.472939606	
	SAVI	6668.77296	6668.77296	1	227.841132	50.73281568	1.37E-11	***
	SALINITY	74.4311071	74.4311071	1	31.35184426	0.566236047	0.457371478	
	ORGANIC	0.92459195	0.92459195	1	31.58445057	0.007033851	0.933690663	

were found between the other areas of the four studied locations.

To compare the change in photosynthetic capacity performance of the disturbed in comparison to the undisturbed *A. arenaria* individuals, we determined the disturbance ratio on leaf growth for each pair (Figure 8D). Mean and SD, as well as *T* values from one sample t-tests and associated *P* values are noted in Table S5C. When looking at the grey dunes, we found that the ratio was lower than 1 for those of locations I and IV. We did not find any significant differences from 1 for the other areas of the studied locations.

In addition, we found that the disturbance ratio differed between the areas of the bio geomorphological gradient ($F_{2,93} = 6.525$; $P = 0.002$, Figure 8D). *T* values from pairwise

comparisons and associated *P* values are noted in Table S5C. Comparing the grey dunes with the beach and white dunes, we found the ratio to be lower at the grey dunes in comparison to the beach and white dunes of location I. No statistically significant differences were found between the other areas of the four studied locations.

Longest leaf corrected for sediment accretion/erosion

To determine the actual growth rate of *A. arenaria*, we measured the length of the longest leaf of each individual over the growing season and corrected it for the sediment accretion/erosion that we registered. Corrected length of the longest leaf differed across all time points between the areas of

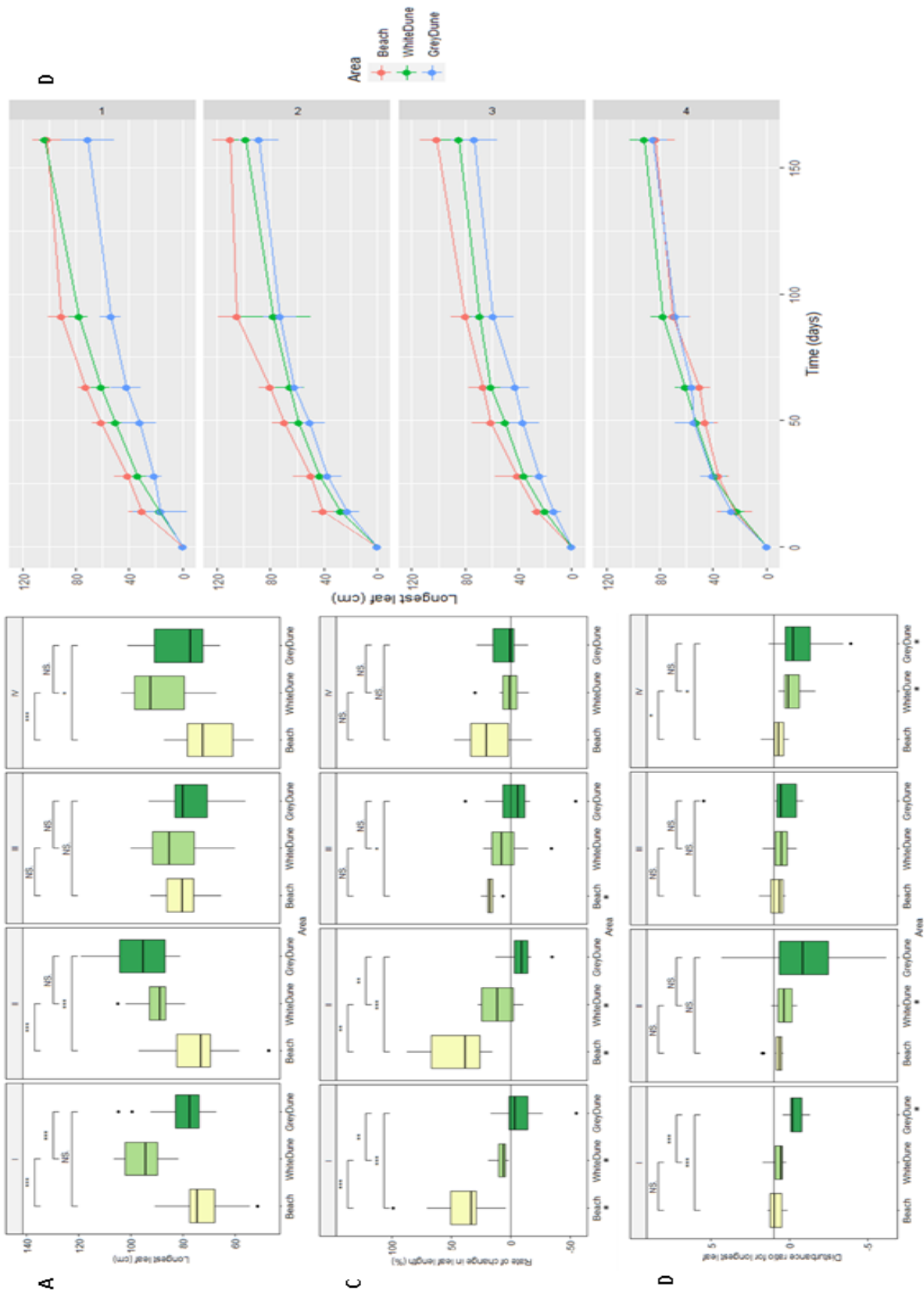


Figure 8. Mean and SD of longest leaf length of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations at the beginning of the growing season (A), the change in longest leaf length over the growing season (B & C) and this change relative to that control individuals (D). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

Table 6. Determination of explanatory variables for corrected leaf length change over time for all areas together, and beach, white dunes, and grey dunes separately. * = p < 0.05, ** = p < 0.01, * = p < 0.001, NS = not significant**

		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
AllAreas	AREA	1011.097793	505.5488964	2	167.9382678	2.822479465	0.062282179	.
	TIME	233881.3041	233881.3041	1	665.6971102	1305.75931	4.34E-159	***
	DISTANCE	1799.78446	1799.78446	1	103.6529342	10.04819656	0.00200526	**
	HEIGHT	3195.627457	3195.627457	1	128.0533599	17.84118795	4.52E-05	***
	SAVI	11075.84369	11075.84369	1	673.2274017	61.83643484	1.49E-14	***
	SALINITY	848.4995484	848.4995484	1	100.3680626	4.73717294	0.03186277	*
	ORGANIC	1740.662094	1740.662094	1	96.3753727	9.718116389	0.002405318	**
	AREA:TIME	10428.70897	5214.354484	2	615.0860935	29.11174085	8.32E-13	***
Beach		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	74352.60193	74352.60193	1	215	245.4098211	2.09E-37	***
	DISTANCE	610.9931558	610.9931558	1	215	2.016657348	0.157029734	
	HEIGHT	1818.715927	1818.715927	1	215	6.002893491	0.015081703	*
	SAVI	1185.842264	1185.842264	1	215	3.914016865	0.049161788	*
	SALINITY	1775.023737	1775.023737	1	215	5.858682097	0.016330977	*
	ORGANIC	2896.999918	2896.999918	1	215	9.561901171	0.002249749	**
WhiteDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	53243.4432	53243.4432	1	211.7718661	412.0546694	1.40E-51	***
	DISTANCE	228.8309616	228.8309616	1	35.47136505	1.770938553	0.191757573	
	HEIGHT	3458.811297	3458.811297	1	70.52066706	26.76797855	2.06E-06	***
	SAVI	5532.441797	5532.441797	1	216.1308454	42.81594763	4.29E-10	***
	SALINITY	15.95155168	15.95155168	1	24.87773319	0.123450156	0.72828058	
ORGANIC	12.90502027	12.90502027	1	31.52248732	0.09987284	0.754065388		
GreyDune		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
	TIME	57286.40832	57286.40832	1	215.2132389	516.3878131	4.24E-59	***
	DISTANCE	1551.988014	1551.988014	1	36.35920699	13.98984018	0.000632139	***
	HEIGHT	16.90179158	16.90179158	1	31.35703514	0.152355148	0.698933853	
	SAVI	6518.345807	6518.345807	1	220.5564237	58.75729401	5.62E-13	***
	SALINITY	71.36552075	71.36552075	1	30.53621607	0.64329893	0.428716729	
ORGANIC	0.091046141	0.091046141	1	30.84426767	0.000820703	0.977329961		

the bio- geomorphological gradient ($F_{2,80} = 40.683$; $P < 0.001$, Figure 9B).

To identify the estimated maximum leaf length and leaf growth rate, we again fitted a Michaelis-Menten equation on the longest leaf data. We found that V_{max} and K differed between the three areas of the bio-geomorphological gradient (Table 4). We found that K was highest for the beach, then the white dunes and then the grey dunes for locations I, II, and III, but found the opposite for location IV. V_{max} was highest for the white dunes, then the beach and then the grey dunes of locations I and II. However, V_{max} was highest for the beach of locations III and IV. For location III the grey dune was second and then the white dune, and for location IV the opposite was found. In addition, we found differences across all time points between the

different locations we studied ($F_{3,80} = 16.753$; $P < 0.001$). For the corrected leaf length over time the linear model with the best fit was as follows (10):

$$\begin{aligned}
 \text{LONGESTCORRECTED} \sim & \text{AREA} * \text{TIME} + \text{HEIGHT} \\
 & + \text{DISTANCE} + \text{SAVI} + \text{SALINITY} \\
 & + \text{ORGANIC} + (1|ID)
 \end{aligned}
 \tag{ 10 }$$

It shows that the corrected leaf length is positively correlated with the SAVI-value and height of the plot, the distance of the plot to sea and the salinity of the soil and negatively correlated with the height of the plot and the organic matter content of the soil. T values from linear mixed model and associated P values are noted in Table 6. These findings resemble those of the uncorrected leaf

lengths. When looking specifically at the separate areas, we see that at all three areas, corrected leaf length is positively correlated with the SAVI-value. In addition, at the beach corrected leaf length is positively correlated with soil salinity, but negatively correlated with height of the plot and organic matter content of the soil. Lastly, corrected leaf length is negatively correlated with the height of the plot at the white dunes, but positively correlated with the distance of plot to sea at the grey dunes.

To identify whether the disturbed *A. arenaria* individuals had grown back to their pre-disturbed height over the growing season, we determined the rate of change in the longest leaf corrected for sediment accretion/erosion (Figure 9C). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S6B. When looking at the beach, we found that the rate of change was higher than 0 at locations I and III. In addition, at the white dunes, the rate of change was higher than 0 at location I. Lastly, at the grey dunes, the rate of change was lower than 0 at location II. However, the rate of change did not differ from 0 for the corrected length at the other areas of the studied locations.

In addition, we found that the disturbance ratio differed between the areas of the bio geomorphological gradient ($F_{2,94} = 13.229$; $P < 0.001$, Figure 9C). T values from pairwise comparisons and associated P values are noted in Table S6B. Comparing the grey dunes with the beach and white dunes, we found the ratio to be lower at the grey dunes in comparison to the beach and white dunes of location I. No statistically significant differences were found between the other areas of the four studied locations.

To compare the change in growth performance of the disturbed in comparison to the undisturbed *A. arenaria* individuals, we determined the disturbance ratio on the corrected leaf growth for each pair

(Figure 9D). Mean and SD, as well as T values from one sample t-tests and associated P values are noted in Table S6C. When looking at the beach, we found that the ratio was lower than 1 at the beach of location IV. For the white dunes, we found the ratio to be lower than 1 at locations II and IV. And lastly, for the grey dunes, we found the ratio to be lower than 1 at locations I and IV.

However, the disturbance ratio did not differ from 1 at the other areas of the studied locations.

In addition, we found that the disturbance ratio differed between the areas of the bio geomorphological gradient ($F_{2,79} = 3.932$; $P = 0.024$, Figure 9D). T values from pairwise comparisons and associated P values are noted in Table S6C. Comparing the grey dunes with the beach and white dunes, we found the ratio to be lower at the grey dunes in comparison to the beach and white dunes of location I. No statistically significant differences were found between the other areas of the four studied locations.

Correlations of plant and plot properties

To get an additional better understanding of the relationships within coastal dune ecosystems, we applied linear models to the various (a)biotic properties of the studied locations and the shoot number, shoot diameter and length of the longest leaf of the studied *A. arenaria* individuals to test whether they correlate (Table 7). The (a)biotic properties again consist of height of the plot and its distance to sea, the soil pH, salinity, moisture and organic matter content and the SAVI for the plots and their surroundings.

We found that for the initial situation the number of shoots was positively correlated strongly with the height the plot and moderately with the SAVI and negatively correlated moderately with soil pH. No other moderate or strong correlations were found between the rest of the plant and plot properties.

Table 7. R²-values of the plot and plant properties for the 4 studied locations over the bio-geomorphological dune gradient

	HEIGHT	DISTANCE	GRAINSIZE	SAVI	pH	SALINITY	MOISTURE	ORGANIC
SHOOTS	0.2648	0.001983	0.03947	0.2015	0.2024	0.01922	-0.008474	0.04065
DIAMETER	0.02358	0.03695	-0.01515	0.01253	-0.0008798	0.0352	0.03496	-0.007256
LENGTH	0.08091	0.07608	-0.00923	0.01658	-0.007888	0.1279	-0.007441	-0.001551

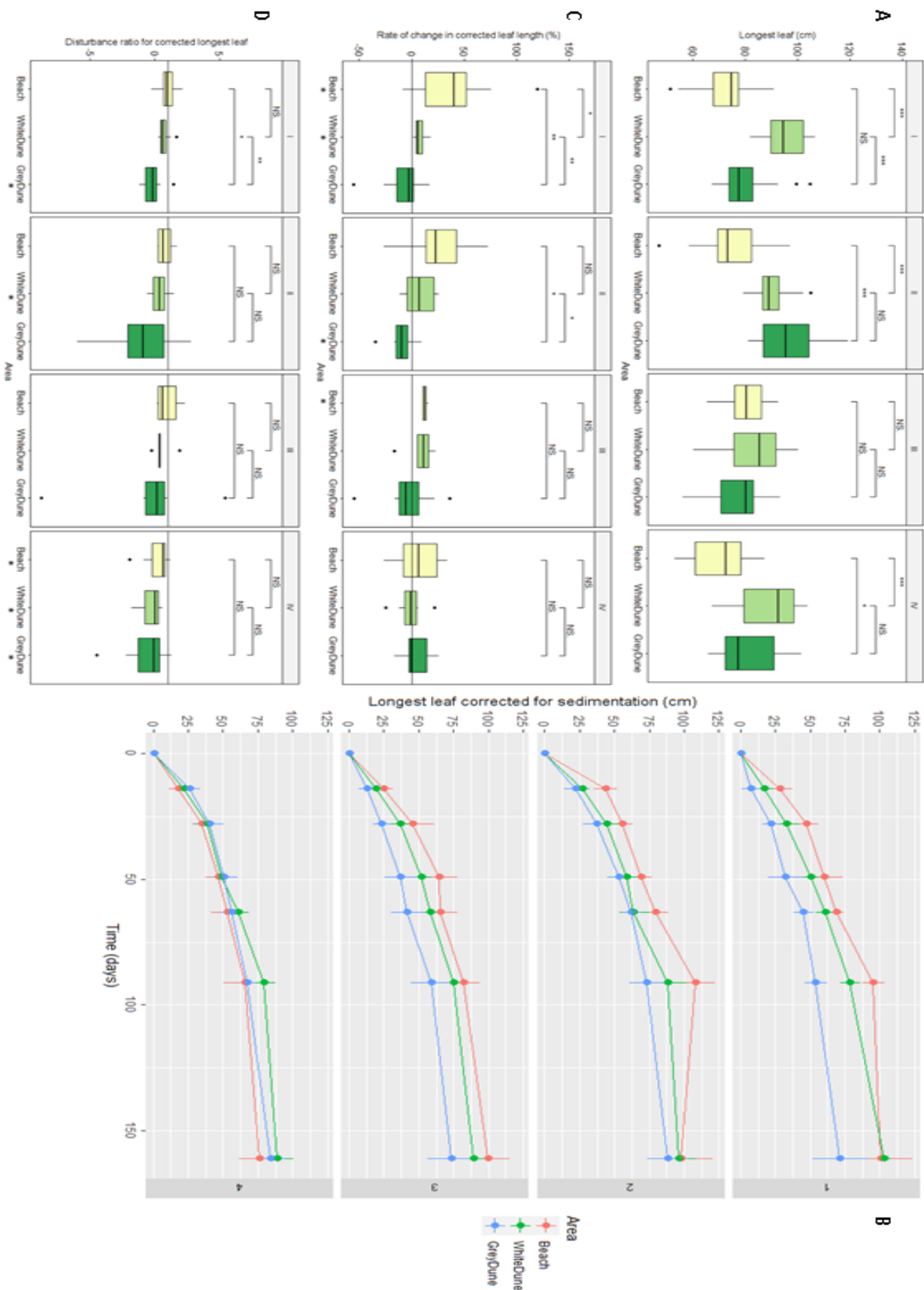


Figure 9. Mean and SD of longest leaf length corrected for sediment accretion/erosion of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations at the beginning of the growth season (A), the change in longest leaf corrected for sediment accretion/erosion length over the growing season (B & C) and this change relative to that control individuals (D). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = not significant

Discussion

In this study we aimed to elucidate how resilient the areas of the bio-geomorphological dune gradient are to disturbances early in the growing season. We found that the resistance and recovery of disturbed *A. arenaria* was highest at the beach, before the white and the grey dunes. Nonetheless, disturbed were comparable to undisturbed *A. arenaria* by the end of the growing season. The degree of recovery and resistance did however vary between the four studied locations. Subsequently, we found this variation to be due to the bio-geomorphological differences between these locations.

Resilience along the dune gradient

Firstly, to determine the resistance and recovery of *A. arenaria* individuals along the bio-geomorphological dune gradient, we investigated the differences in rate of change in shoot number, shoot diameter, leaf length, and photosynthetic capacity between the beach, white dunes, and grey dunes of the four studied locations. We found that the rate of change for these parameters was dependent on the position along the dune gradient.

In general, *A. arenaria* showed the most recovery at the beach, followed by the white dunes. This is not what we had expected on the basis of the three parallel stress axes of nutrient availability, physical stress due to coastal and aeolian dynamics, and competition with other plants (Bonte et al., 2021; van der Putten, 1989). This is because we thought the optimum of these axes to be at the white dunes, and would therefore have expected *A. arenaria* to show the most recovery in this area.

However, our findings are in agreement with those of Reijers et al. (2020), where *A. arenaria* individuals proved to be highly resilient in the embryonic dunes in comparison to the foredunes. These findings could be an indication that the axes are not equal in importance, and that for the beach the availability of nutrients is a stronger stimulator of *A. arenaria* growth than the physical stress of coastal and aeolian dynamics are a limiter of it.

The recovery of the studied individuals in the white dunes may have additionally been influenced by competition they would have had with other *A. arenaria* individuals, as judged by the SAVI as a proxy for the amount of vegetation in and surrounding the plots. This would be in line with the

conclusions of Martínez & García-Franco (2008), stating that plant-plant interactions occur along the entirety of the dune gradient.

The finding that the grey dunes showed the least recovery is in accordance with our expected results, as we assumed *A. arenaria* to fare less well here. This is due to the amount of nutrient competition with other *A. arenaria* individuals and other plant species being even higher than in the white dunes. This is also in agreement with our findings that organic matter content of the soil, as well as the SAVI is higher in the grey dunes.

Besides competition, the degree of recovery in the grey dunes may have been negatively influenced by the relatively acidic soil, as the growth of *A. arenaria* has been found to be more vigorous for more alkaline soils (Huiskes, 1979).

In addition to increased competition, *A. arenaria* is at greater risk of root damage in the grey dunes due to physical damage by nematodes and infection by fungal pathogens (Huiskes, 1979; Marshall, 1965). One way that the harmful effects of nematodes and fungi can be escaped is by sediment deposition, so that *A. arenaria* can outgrow them vertically (De Rooij-Van Der Goes et al., 1995). But as our findings on sediment accretion and erosion corroborate, there was little to no sediment deposition in the grey dunes, so vertical outgrowth was not a possibility for *A. arenaria*.

One possible explanation for the reduced recovery and resistance is therefore that the plants had to redirect their energy from their shoots to their root network to both be able to outcompete other plants for nutrients, as well as restore damage done by nematodes and fungal pathogens. This could be tested by comparing the belowground biomass of disturbed *A. arenaria* with that of their undisturbed counterparts, though this will only be possible at the end of the study.

Effect of disturbance

Secondly, to find out whether disturbed *A. arenaria* individuals fare differently in comparison to those left undisturbed, we compared the rate of change in shoot number, shoot diameter, leaf length, and photosynthetic capacity between the two conditions. We found that for the studied parameters, the change in comparison to its pre-disturbed state generally did not differ for the

disturbed *A. arenaria* individuals compared to their undisturbed counterparts after one growing season.

The matter that they are comparable could be an indication of the following three things. For one, it could be that the undisturbed plants have reached their maximum length and disturbed plants were able to reach the same length within the growing season (Huiskes, 1979). However, the reason that the undisturbed individuals did not show more growth can also be due to them having to divert energy to sick or dying shoots, which would otherwise reduce the overall fitness of the plant (Huot et al., 2014). This would not be the case for the disturbed individuals, as all less-than-fit shoots would have been clipped at the start of the growing season. Lastly, it could be due to the undisturbed plants redirecting more energy to their belowground biomass, since a strong and extensive root network would increase their chances of survival due to improved nutrient acquisition (van der Putten, 1989).

In addition, we found that the disturbance ratios for the studied parameters generally were similar between the areas of the bio-geomorphological dune gradient. In the cases that they did differ, predominantly in the white and grey dunes, *A. arenaria* showed a reduction in resistance and recovery. Presumably, this is again due to the amount of competition from other *A. arenaria* individuals and other plants that compete with the studied individuals for nutrients (Martínez & García-Franco, 2008). The increasing occurrence of nematodes and fungal pathogens in these areas may also play a role in the reduced resistance and recovery (Van Der Putten & Troelstra, 1990).

Another explanation could be the age of the *A. arenaria* individuals in the white and grey dunes in comparison to those of the beach. As the dune formation process of *A. arenaria* starts at the beach, individuals in the white and grey dunes are at successive stages of the process. Due to their age, they would have therefore had a larger number of long-leaved shoots at the start of the study. Once disturbed, it would therefore take a longer period of time for the length to be at pre-disturbed levels in these regions than it would be at the beach, where the leaves were relatively short at the start of the study. This may indicate that a single growing

season may not be enough time for *A. arenaria* in the white and grey dunes to recover completely.

Explanatory factors for resilience

Thirdly, to determine whether the findings on *A. arenaria* resistance and recovery can be generalised, we investigated the rates of change in and disturbance ratios for shoot number, shoot diameter, leaf length, and photosynthetic capacity of the areas of the bio-geomorphological dune gradient between the four studied locations. While showing a large degree of resistance and recovery overall, we did find some discrepancies between the studied locations. Since the four locations are all coastal ecosystems on the same island, and are at most 14 km apart, we would not assume large differences in the composition of these locations. We therefore think that these discrepancies are due to the specific bio-geomorphological makeup of each studied location.

Fourthly, to explain this variation in resilience, we accordingly looked into the (a)biotic factors in which the four locations differ. Using linear modelling, we found the height of the plot above sea level and its distance to the waterline, as well as the pH, salinity, and organic matter content of the soil, and the amount of vegetation in and surrounding the plot all to offer explanations for the variation. However, the extent to which each of these factors is explanatory, is dependent on the area of the bio-geomorphological dune gradient.

The explanatory effects of both the height above sea-level and its distance to the waterline emphasize our first discussed results that the resilience of *A. arenaria* is dependent on its location on the bio-geomorphological dune gradient.

We should acknowledge here that height above sea level only correlates with leaf length, and consequently photosynthetic capacity, but not shoot number and diameter. Furthermore, this is only the case at the beach and the white dunes. We therefore think that this is due to the deposition of nutrient-rich sediment, which mainly occurs in these areas and attenuates with increasing height above sea-level (Bonte et al., 2021). This is in agreement with the tendency of *A. arenaria* to increase leaf growth over new shoot formation in the case of large amounts of sediment deposition (Reijers et al., 2019).

As for the soil conditions, we found that more alkaline soils at the beach result in thicker shoots, as is in agreement with the increased vigour seen for *A. arenaria* grown in alkaline conditions (Huiskes, 1979). It is also at the beach that we find increases in leaf length and consequent photosynthetic capacity at a higher salinity. Previous studies have however not found *A. arenaria* to be constrained by salt stress (van Puijenbroek et al., 2017). One possible explanation is therefore salt spray, which is common at the beach and can provide additional nutrients to *A. arenaria* and stimulate its growth (Du & Hesp, 2020).

In addition, we note that the soil organic matter content and SAVI, both indicators of the presence of competing plants, together hamper resistance and recovery of *A. arenaria* along the whole dune gradient. This further emphasizes the conclusions of Martínez & García-Franco (2008), who state that plant–plant interactions occur throughout the different successional stages of dune formation.

Although soil organic matter content and the SAVI are both thought to give an indication of the amount of competition, they are contradictory for the number of shoots, leaf length, and photosynthetic capacity. For these parameters, we find that although soil organic matter content is negative correlated with resilience, the SAVI is positively correlated. One possible explanation for this contradiction is that the SAVI of each pixel is influenced by the total surface area of each plant, which is dependent on the number of shoots and the leaf length of a plant.

Furthermore, it seems to be the case that the influence of soil organic matter content seems to gradually decrease from the beach to the grey dunes, while we find the opposite for the SAVI. This can be explained by the abundance of vegetation in the grey dunes, resulting in competition for both nutrients and light (Martínez & Psuty, 2004). This is in opposition to the beach, where vegetation is sparser and light competition is not an issue. Competition will predominantly occur at the beach when plants are proximate and their root networks have to compete for nutrients (Huiskes, 1979).

These findings could therefore be indicative of aboveground competition becoming more

important in addition to belowground competition when moving from the beach to the grey dunes. This would force *A. arenaria* in the grey dunes to balance their energy between both belowground and aboveground biomass, even though nutrients are already sparse.

Taking all of these factors of influence into consideration, an explanation for the higher recovery speed found for the beach can be found in the replenishment of nutrient-rich sediment transported by aeolian forces and wrack that is continuously washed ashore (Bonte et al., 2021; Reijers et al., 2020). As this nutrient replenishment decreases the further and higher one is from the sea and competition concurrently increases, this would explain the reduced recovery and resistance for the white and grey dunes. Furthermore, this would strengthen the aforementioned hypothesis that the parallel stress axes of the bio-geomorphological dune gradient are not of equal importance, and that the availability of nutrients is a stronger stimulator than physical stress is a limiter of growth.

Conclusion

To elucidate the resilience of *A. arenaria* along the bio-geomorphological dune gradient, we tried to answer four questions during this study. We found that the resilience of *A. arenaria* is dependent on its location along the dune gradient, where the beach shows the highest degree of resilience, followed by intermediate resilience at the white dunes and the worst resilience at the grey dunes.

However, we found that disturbance of *A. arenaria* early in the growing season generally does not affect the capacity for growth by the end of the season. When it does, it is generally only the case for the older areas of the dune gradient. This shows that *A. arenaria* can overcome the effects of disturbance relatively rapidly.

Additionally, we found that the four studied locations showed some variation in how resilient *A. arenaria* is for each area of the dune gradient. Subsequently, we were able to assess that resilience for *A. arenaria* can be explained by its height above sea-level and distance from the waterline, as well as the salinity, acidity and organic matter content of the soil, and the amount of surrounding vegetation.

Combining these findings, we think that the resilience of *A. arenaria* and consequently that of coastal dune ecosystems, although influenced by various (a)biotic properties, is predominantly

dependent on the availability of nutrients along the bio-geomorphological gradient.

Elucidating the capacity for resilience of *A. arenaria* along the bio-geomorphological dune gradient, as well as the factors that mediate it, has given a clear insight into how coastal dune ecosystems will be able to enact their protective functions against coastal disturbances that will become more prevalent in the coming years as a result of climate change. This knowledge can be used to the advantage of nature managers, who can apply it to dune management strategies for the stimulation of new dune ridge formation and enhancement of overall dune health.

Limitations & future recommendations

Despite our best efforts, we must acknowledge four limitations to our study. Firstly, concerning the experimental setup, it must be noted that our study mainly took part in the field. While the goal was to pair *A. arenaria* individuals that resemble each other, we must note the natural differences between these individuals and their surrounding conditions. These natural differences would mean that, while seemingly similar, these paired individuals are not exactly comparable. However, we have attempted to alleviate this problem by taking a sample size of 10 pairs for each area of each studied location. In this way, we aimed to represent the natural variation of each studied location sufficiently within the study.

Secondly, the results of this study are in large part influenced by the groups we placed the *A. arenaria* individuals in at the beginning of the study. Since the differences between the beach, white dunes and grey dunes are gradual and harder to distinguish at the beginning of the growing season, the placement of the areas, especially for the grey dunes, may thus not be entirely accurate. Since we are dealing with a gradient, wrongly categorizing an area as another will not have too large of a detrimental effect. However, it may influence the effect size of the differences between the areas of the dune gradient.

This is to a certain extent also the case for the boundaries of the growing season as set for the study. Due to logistical reasons, we set the last visit to Terschelling in mid-September. Looking at the growth curves for the different locations however, the plants still seemed to be increasing in growth

instead of stabilizing, which ought to be expected at the end of the growing season.

Thirdly, accurately measuring the amount of sedimentation over time proved to be a difficult parameter to measure. This is in large part due to the flags, that we used to mark the plots and their height relative to the surface, being removed by passers-by. This mainly occurred at the beach, since that is where most people pass by and was predominantly the case for *A. arenaria* individuals that did not show much growth, because otherwise the flags would have been slightly masked by the shoots.

One way that future studies can avoid this is by placing the flags deeper into the soil, so that it is more difficult for passers-by to notice. For disturbed individuals, which are more visible at the start of the growing season, it may be helpful to place a label on the top, so that when it is spotted people know that it is for research purposes and do not mistake it for trash. It is furthermore also recommended to immediately log all of the points using a dGPS to be able to find the plots back once a flag has disappeared and furthermore be able to track the sedimentation over time by looking at the height that is registered.

Lastly, we only tracked a selection of plant parameters over the growing season and this may not give conclusive evidence of the overall vitality of *A. arenaria*. Future studies may therefore benefit from looking at additional parameters. One such a parameter may be the chlorophyll of the leaves, to give an additional insight into photosynthetic capacity. This would however require taking a biomass sample at each time point, the impact of which would be larger for individuals with a lower number of shoots.

An alternative option would be to take photosynthetic capacity as a measure for plant health. This can also be determined using satellite imaging, in the form of vegetation indices such as NDVI. In the current study, we used the SAVI as an alternative to compensate for differences in surface reflectance between the areas of the bio-geomorphological dune gradient. The satellite data that we used had a resolution of 3.7 m, which is of course much larger than the studied individual and therefore gives more of an indication about the plot surroundings than the individual itself. Being able to

use SAVI as a measure for plant vitality would therefore require images with an even higher resolution. One way to acquire this would be through drone photography instead of satellite imaging. In order to be able to calculate the SAVI, a 4-band drone is however necessary as both the red and near infrared bands are required.

Taking the aforementioned limitations into consideration, we are still able to give an indication of the vitality of *A. arenaria* using the properties we did study. However, we do recommend that this study be tracked over the winter and a second growing season. This will give a clearer understanding of the advantages and disadvantages of *A. arenaria* disturbance early in the growing season. If it is indeed beneficial for the vitality of *A. arenaria* and consequent dune formation, we will be able to advise nature managers on how to best take care of the dunes, to ensure that we can make use of their ecosystem services far into the future.

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Supplementary materials
Protocols

Verwerking bodemmonsters

Vanaf februari 2013 werkt iedereen (Ecologie, B-ware en Bargerveen) volgens dezelfde protocollen!!!!

Vermeng de bodem goed en verwijder zoveel mogelijk de aanwezige wortels.

Bepaling vochtgehalte:

Weeg een aluminiumbakje (C). Vul het aluminiumbakje met bodemmonster en weeg het bakje opnieuw (A). Zet het bakje met bodemmonster 2 dagen bij 70°C in een stoof (plant/bodem lab). Weeg het bakje met bodemmonster weer (B).

$$\text{vochtgehalte (\%)} = \frac{(A-C)-(B-C)}{(A-C)} \times 100 = \frac{A-B}{A-C} \times 100$$

Opm: wil je na drogen zowel gloeiverlies bepalen als bodem malen voor destructie/meting CN, weeg dan in duplo af. Dan heb je 1 bakje om te verassen en het andere om te malen voor verdere metingen.

Bepaling gloeiverlies (maat voor organisch stofgehalte, LOI):

Zet het aluminiumbakje met het gedroogde bodemmonster in de (koude) oven (plant/bodem lab). Laat het bodemmonster 4 uur uitgloeien bij 550°C (de oven heeft ongeveer 30 minuten nodig om op temperatuur te komen!). Laat het uitgloeide bodemmonster in de oven (of in een excicator) afkoelen. Weeg het bakje met het uitgloeide bodemmonster (D).

$$\text{gloeiverlies (\%)} = \frac{(B-C)-(D-C)}{(B-C)} \times 100 = \frac{B-D}{B-C} \times 100$$

Supplementary Tables

Table S1. Mean and SD of sediment grain size (A), pH (B), salinity (C), moisture content (D), and organic matter content (E) of the soil of the three areas of the morphological gradient for the four studied locations, with non-pairwise comparisons between these areas. * = p < 0.05, ** = p < 0.01, * = p < 0.001, NS = not significant**

variable	LOCATION	AREA	n	mean	sd								
A	GRAINSIZE	I	Beach	3	219,047	3,959							
			WhiteDune	3	215,45	12,639							
			GreyDune	3	219,307	5,399							
		II	Beach	2	228,715	2,171							
			WhiteDune	4	222,963	5,484							
			GreyDune	3	230,643	9,632							
		III	Beach	1	236,79	NA							
			WhiteDune	3	229,497	3,757							
			GreyDune	3	223,7	4,123							
		IV	Beach	3	224,973	11,287							
			WhiteDune	3	223,69	9,42							
			GreyDune	3	221,597	6,298							
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif		
B	pH	I	Beach	10	8.74	0.117	Beach	WhiteDune	-0,21821789	16,40166318	1	ns	
			WhiteDune	10	8.75	0.085	Beach	GreyDune	5,284229076	13,20535391	0,00042	***	
			GreyDune	10	8.3	0.236	WhiteDune	GreyDune	5,679492686	11,30111122	0,000387	***	
		II	Beach	10	8.89	0.099	Beach	WhiteDune	0	16,92437421	1	ns	
			WhiteDune	10	8.89	0.129	Beach	GreyDune	3,716237066	16,86742388	0,005	**	
			GreyDune	9	8.722	0.097	WhiteDune	GreyDune	3,225936085	16,54645037	0,015	*	
		III	Beach	10	8.86	0.222	Beach	WhiteDune	2,021164611	13,53369639	0,19	ns	
			WhiteDune	10	8.7	0.115	Beach	GreyDune	8,393250913	17,09687104	5,43E-07	****	
			GreyDune	10	7.91	0.281	WhiteDune	GreyDune	8,231350233	11,96170233	8,61E-06	****	
		IV	Beach	9	8.778	0.097	Beach	WhiteDune	6,252441384	12,04560261	0,000125	***	
			WhiteDune	10	8.55	0.053	Beach	GreyDune	5,603799345	16,9563393	9,57E-05	****	
			GreyDune	10	8.52	0.103	WhiteDune	GreyDune	0,818181818	13,38979778	1	ns	
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif		
C	SALINITY	I	Beach	10	0.72	0.492	Beach	WhiteDune	2,057983022	9	0,139	ns	
			WhiteDune	10	0.4	0	Beach	GreyDune	1,824855361	7	0,222	ns	
			GreyDune	8	0.4	0	WhiteDune	GreyDune	NA	NA	NA	NA	
		II	Beach	10	1.12	0.958	Beach	WhiteDune	1,893164229	9	0,273	ns	
			WhiteDune	10	0.52	0.193	Beach	GreyDune	2,377217447	9	0,124	ns	
			GreyDune	10	0.4	0	WhiteDune	GreyDune	1,963961012	9	0,243	ns	
		III	Beach	9	0.622	0.291	Beach	WhiteDune	1,870828693	7	0,312	ns	
			WhiteDune	8	0.4	0	Beach	GreyDune	0,609994281	8	1	ns	
			GreyDune	10	0.56	0.207	WhiteDune	GreyDune	-2,0493901537	9	0,239	ns	
		IV	Beach	10	0.84	0.44	Beach	WhiteDune	3,160826741	9	0,023	*	
			WhiteDune	10	0.4	0	Beach	GreyDune	3,160826741	9	0,023	*	
			GreyDune	10	0.4	0	WhiteDune	GreyDune	NA	9	NA	NA	
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif		
D	MOISTURE	I	Beach	10	4.244	0.973	Beach	WhiteDune	2,76527827	14,68187738	0,044	*	
			WhiteDune	10	3.253	0.58	Beach	GreyDune	-0,849592885	17,98884489	1	ns	
			GreyDune	10	4.609	0.949	WhiteDune	GreyDune	-3,854344983	14,90268007	0,005	**	
		II	Beach	10	4.7	1.359	Beach	WhiteDune	0,919843164	16,613963	1	ns	
			WhiteDune	10	4.208	1.009	Beach	GreyDune	0,720709055	15,16042209	1	ns	
			GreyDune	10	4.334	0.855	WhiteDune	GreyDune	-0,302373606	17,52567524	1	ns	
		III	Beach	10	3.885	0.807	Beach	WhiteDune	2,637979776	17,59584444	0,051	ns	
			WhiteDune	10	2.852	0.94	Beach	GreyDune	-0,277697712	12,83662075	1	ns	
			GreyDune	10	4.05	1.705	WhiteDune	GreyDune	-1,947172709	14,00613812	0,215	ns	
		IV	Beach	10	3.994	0.686	Beach	WhiteDune	4,10160149	14,96741107	0,003	***	
			WhiteDune	10	2.949	0.422	Beach	GreyDune	6,217129152	17,10980094	2,73E-05	****	
			GreyDune	10	2.273	0.544	WhiteDune	GreyDune	3,105080544	16,96156879	0,019	*	
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif		
E	ORGANIC	I	Beach	10	0.083	0.03	Beach	WhiteDune	-2,256262399	16,82161876	0,113	ns	
			WhiteDune	10	0.119	0.04	Beach	GreyDune	-5,988759802	10,06329617	0,000393	***	
			GreyDune	10	0.327	0.125	WhiteDune	GreyDune	-5,008606703	10,81628545	0,001	**	
		II	Beach	9	0.12	0.052	Beach	WhiteDune	-3,390890459	10,1956537	0,02	*	
			WhiteDune	10	0.183	0.021	Beach	GreyDune	-1,743057027	16,26732665	0,3	ns	
			GreyDune	10	0.16	0.047	WhiteDune	GreyDune	1,415334157	12,27743958	0,546	ns	
		III	Beach	10	0.21	0.034	Beach	WhiteDune	-1,000669113	16,93470232	0,993	ns	
			WhiteDune	10	0.223	0.026	Beach	GreyDune	-7,37377611	9,477053592	9,60E-05	****	
			GreyDune	10	0.702	0.208	WhiteDune	GreyDune	-7,207826669	9,28586606	0,000128	****	
		IV	Beach	10	0.246	0.061	Beach	WhiteDune	1,670032591	15,77712771	0,345	ns	
			WhiteDune	10	0.207	0.041	Beach	GreyDune	-0,216049192	13,25549274	1	ns	
			GreyDune	10	0.25	0.03	WhiteDune	GreyDune	-2,685334186	16,62603907	0,048	*	

Table S2. Mean and SD of SAVI (A), aboveground biomass wet weight (B), and C:N ratio (C) of *A. arenaria* individuals of the three areas of the morphological gradient for the four studied locations, with non-pairwise comparisons between these areas. * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif
A	I	Beach	20	0.078	0.024	Beach	WhiteDune	-16,26672104	37,22479255	5,01E-18	****
		WhiteDune	20	0.195	0.021	Beach	GreyDune	-28,61364844	37,16480582	1,93E-26	****
		GreyDune	20	0.283	0.021	WhiteDune	GreyDune	-13,31002942	37,99875498	2,09E-15	****
	II	Beach	20	0.092	0.011	Beach	WhiteDune	0,602555136	26,29557825	1	ns
		WhiteDune	20	0.089	0.025	Beach	GreyDune	-10,85523596	21,12589369	1,27E-09	****
		GreyDune	20	0.211	0.048	WhiteDune	GreyDune	-10,16520242	28,89982182	1,42E-10	****
	III	Beach	20	0.107	0.015	Beach	WhiteDune	-0,78906422	37,5086216	1	ns
		WhiteDune	20	0.111	0.017	Beach	GreyDune	-52,99947048	37,0973529	4,29E-36	****
		GreyDune	20	0.386	0.018	WhiteDune	GreyDune	-49,59404626	37,93217776	1,26E-35	****
	IV	Beach	20	0.085	0.027	Beach	WhiteDune	-9,245253958	32,74434527	3,60E-10	****
		WhiteDune	20	0.187	0.041	Beach	GreyDune	-15,92227851	27,14636763	8,10E-15	****
		GreyDune	20	0.309	0.057	WhiteDune	GreyDune	-7,777747573	34,66281903	1,25E-08	****
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif
B	I	Beach	10	56.1	45.155	Beach	WhiteDune	-0,880983595	15,02512852	1	ns
		WhiteDune	10	70.9	27.986	Beach	GreyDune	2,181805336	10,66634565	0,157	ns
		GreyDune	8	23.5	12.444	WhiteDune	GreyDune	4,796002466	12,97914013	0,001	**
	II	Beach	10	237.5	142.249	Beach	WhiteDune	-0,18973752	16,31412137	1	ns
		WhiteDune	10	248	101.931	Beach	GreyDune	1,674263745	12,22709058	0,357	ns
		GreyDune	10	155.5	61.258	WhiteDune	GreyDune	2,459680165	14,75082561	0,08	ns
	III	Beach	10	64.7	24.445	Beach	WhiteDune	-4,430820193	10,82695179	0,003	**
		WhiteDune	10	177	76.33	Beach	GreyDune	2,112773141	15,3119313	0,154	ns
		GreyDune	9	45.111	15.358	WhiteDune	GreyDune	5,345157908	9,805543935	0,001	**
	IV	Beach	10	96.8	56.682	Beach	WhiteDune	-3,097631327	12,40601097	0,027	*
		WhiteDune	10	233.8	127.858	Beach	GreyDune	-2,192611851	14,73464643	0,134	ns
		GreyDune	10	173.2	94.49	WhiteDune	GreyDune	1,205361471	16,57213559	0,735	ns
variable	LOCATION	AREA	n	mean	sd	group1	group2	t	df	p,adj	p,adj,signif
C	I	Beach	5	21.644	5.668	Beach	WhiteDune	-4,820768374	5,911792729	0,009	**
		WhiteDune	4	42.035	6.773	Beach	GreyDune	-6,26307416	5,72272416	0,003	**
		GreyDune	5	39.225	2.697	WhiteDune	GreyDune	0,781831148	3,763918899	1	ns
	II	Beach	4	23.569	4.118	Beach	WhiteDune	-2,245206432	6,127859723	0,195	ns
		WhiteDune	5	32.969	8.151	Beach	GreyDune	-5,882297372	6,82874102	0,002	**
		GreyDune	5	40.58	4.541	WhiteDune	GreyDune	-1,824018773	6,264433248	0,348	ns
	III	Beach	4	19.777	9.163	Beach	WhiteDune	-4,68579202	4,017323367	0,028	*
		WhiteDune	4	43.045	3.83	Beach	GreyDune	-0,609251842	3,45645178	1	ns
		GreyDune	4	22.673	2.535	WhiteDune	GreyDune	8,870953284	5,204767541	0,000738	****
	IV	Beach	4	25.564	1.682	Beach	WhiteDune	-3,195864399	4,249708625	0,091	ns
		WhiteDune	5	40.961	10.608	Beach	GreyDune	-1,112302215	4,410958111	0,969	ns
		GreyDune	5	29.771	8.245	WhiteDune	GreyDune	1,86248284	7,540807801	0,306	ns

Table S3. Mean and SD of shoot count of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations with non-pairwise comparisons between these areas at the beginning of the growth season (A), the change in shoot count over the growing season with comparisons to 0 and between areas (B), and this change relative to that control individuals, with comparisons to 1 and between areas (C). * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

variable	LOCATION	AREA	n	mean	sd	t	df	p	signi	group1	group2	t	df	p _{adj}	signi _{if}		
																statistic	df
A	I	Beach	20	17.15	9.01					Beach	WhiteDune	3,76590225	23	69998601	0,003	**	
		WhiteDune	20	9.1	3.194					Beach	GreyDune	5,952529367	20	33670683	2,25E-05	****	
		GreyDune	19	4.947	1.649					WhiteDune	GreyDune	5,138884411	28	76873177	5,28E-05	****	
		Beach	19	62.316	30.887					Beach	WhiteDune	0,300560581	34	53807786	1	ns	
		WhiteDune	18	59.5	26.001					Beach	GreyDune	5,923088353	21	12976891	2,06E-05	****	
		GreyDune	20	18.55	9.367					WhiteDune	GreyDune	6,322946412	20	94745647	8,70E-06	****	
	SHOOTS	III	Beach	20	43.7	29.704					Beach	WhiteDune	1,178588822	33	3712648	0,741	ns
			WhiteDune	20	34.25	20.086					Beach	GreyDune	4,871571	19	69101221	0,000289	***
		GreyDune	20	11.05	4.006					WhiteDune	GreyDune	5,065607678	20	50928358	0,000165	****	
		Beach	19	30.947	15.869					Beach	WhiteDune	0,584447398	32	55873243	1	ns	
	IV	WhiteDune	20	28.35	11.398					Beach	GreyDune	2,24094241	27	5912253	0,1	ns	
		GreyDune	20	21.7	8.688					WhiteDune	GreyDune	2,075047666	35	50600605	0,136	ns	
B	I	Beach	10	520,243	451,786	3,641442226	9	0,00539	**	Beach	WhiteDune	2,783499189	9	0,064	ns		
		WhiteDune	10	127,794	98,922	4,085234524	9	0,00274	**	Beach	GreyDune	2,806901707	9	0,062	ns		
		GreyDune	10	110,274	110,631	3,152064683	9	0,0117	*	WhiteDune	GreyDune	0,437607172	9	1	ns		
		Beach	9	245,287	225,515	3,263023416	8	0,0115	*	Beach	WhiteDune	2,432160345	5	0,178	ns		
		WhiteDune	7	13,901	27,428	1,340917532	6	0,228	ns	Beach	GreyDune	1,732822527	8	0,363	ns		
		GreyDune	10	87,46	68,541	4,03512777	9	0,00295	**	WhiteDune	GreyDune	-2,620796033	6	0,118	ns		
	SHOOTS	III	Beach	10	75,713	107,956	2,217810102	9	0,0538	ns	Beach	WhiteDune	1,412013474	9	0,576	ns	
			WhiteDune	10	23,434	41,982	1,765197082	9	0,111	ns	Beach	GreyDune	2,478812319	7	0,127	ns	
		GreyDune	8	-32,172	23,779	-3,826823828	7	0,00648	**	WhiteDune	GreyDune	4,938713108	7	0,005	**		
		Beach	9	71,335	113,389	1,887356024	8	0,0958	ns	Beach	WhiteDune	0,169953237	8	1	ns		
	IV	WhiteDune	10	56,934	44,806	4,018189963	9	0,00303	**	Beach	GreyDune	1,343654688	8	0,648	ns		
		GreyDune	10	28,732	50,217	1,809336687	9	0,104	ns	WhiteDune	GreyDune	1,189932785	9	0,795	ns		
C	I	Beach	10	1,748	1,154	2,047861434	9	0,0709	ns	Beach	WhiteDune	1,042662475	8	0,984	ns		
		WhiteDune	9	1,052	1,27	0,123120504	8	0,905	ns	Beach	GreyDune	2,26305222	8	0,16	ns		
		GreyDune	9	0,695	0,995	-0,918683507	8	0,385	ns	WhiteDune	GreyDune	0,645651986	7	1	ns		
		Beach	8	0,993	0,798	-0,023186467	7	0,982	ns	Beach	WhiteDune	2,912010491	5	0,1	ns		
		WhiteDune	7	-1,313	1,758	-3,482088335	6	0,0131	*	Beach	GreyDune	0,421884737	7	1	ns		
		GreyDune	10	-0,245	6,933	-0,567910966	9	0,584	ns	WhiteDune	GreyDune	-0,081178153	6	1	ns		
	SHOOTS	III	Beach	9	0,794	1,57	-0,393396629	8	0,704	ns	Beach	WhiteDune	0,892014275	8	1	ns	
			WhiteDune	10	0,325	2,063	-1,034397472	9	0,328	ns	Beach	GreyDune	0,484498496	7	1	ns	
		GreyDune	9	-0,022	1,365	-2,246761824	8	0,0548	ns	WhiteDune	GreyDune	0,453213462	8	1	ns		
		Beach	9	0,992	2,288	-0,10686849	8	0,992	ns	Beach	WhiteDune	0,786382023	6	1	ns		
	IV	WhiteDune	8	-0,027	1,647	-1,763992398	7	0,121	ns	Beach	GreyDune	1,203121098	8	0,789	ns		
		GreyDune	10	-0,706	3,496	-1,543360947	9	0,157	ns	WhiteDune	GreyDune	0,8988958	7	1	ns		

Table S4. Mean and SD of shoot diameter of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations, with non-pairwise comparisons between these areas at the beginning of the growth season (A), the change in shoot count over the growing season with comparisons to 0 and between areas (B), and this change relative to that control individuals, with comparisons to 0 and between areas (C). * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

variable	LOCATION	AREA	n	mean	sd	t	df	p	p _f signi	group1	group2	t	df	p _{adj}	p _{adj} signi	
A	I	Beach	20	1.587	0.377					Beach	WhiteDune	-8.089990314	36	50386454	3.51E-09	****
		WhiteDune	20	2.669	0.463					Beach	GreyDune	-6.99155944	34	7033415	1.23E-07	****
		GreyDune	20	2.591	0.519					WhiteDune	GreyDune	0.500759258	37	52254633	1	ns
		Beach	15	2.347	0.363					Beach	WhiteDune	-6.424881803	32	9476078	8.40E-07	****
		WhiteDune	20	3.292	0.508					Beach	GreyDune	-5.10954763	30	41307287	4.95E-05	****
		GreyDune	20	2.981	0.365					WhiteDune	GreyDune	2.225348819	34	48304935	0.098	ns
		Beach	20	2.701	0.508					Beach	WhiteDune	-0.044400683	34	84866721	1	ns
		WhiteDune	20	2.708	0.372					Beach	GreyDune	3.250377263	37	89747173	0.007	**
		GreyDune	20	2.192	0.482					WhiteDune	GreyDune	3.782255151	35	71988259	0.002	**
II	I	Beach	19	1.949	0.524					Beach	WhiteDune	-5.887237274	34	34497353	3.48E-06	****
		WhiteDune	20	2.844	0.416					Beach	GreyDune	-6.990878386	36	27871714	9.72E-08	****
		GreyDune	20	3.075	0.48					WhiteDune	GreyDune	-1.628784337	37	25908978	0.336	ns
		Beach	10	101.168	51.742	6.182974083	9	0.000162	***	Beach	WhiteDune	4.533980297	9	0.004	**	
		WhiteDune	10	20.034	30.204	2.097487489	9	0.0654	ns	Beach	GreyDune	5.637773875	9	0.000957	****	
		GreyDune	10	3.809	21.385	0.563187565	9	0.587	ns	WhiteDune	GreyDune	1.246893425	9	0.732	ns	
		Beach	6	25.675	11.605	5.419275184	5	0.0029	**	Beach	WhiteDune	3.767127067	5	0.039	*	
		WhiteDune	10	6.922	24.006	0.911811196	9	0.386	ns	Beach	GreyDune	3.282334955	5	0.066	ns	
		GreyDune	10	10.003	21.47	1.473362092	9	0.175	ns	WhiteDune	GreyDune	-0.601398458	9	1	ns	
III	I	Beach	10	16.201	37.277	1.374367299	9	0.203	ns	Beach	WhiteDune	1.991722801	9	0.233	ns	
		WhiteDune	10	-7.163	23.531	-0.962545033	9	0.361	ns	Beach	GreyDune	1.041117863	9	0.975	ns	
		GreyDune	10	-5.421	40.771	-0.420437635	9	0.684	ns	WhiteDune	GreyDune	-0.13183435	9	1	ns	
		Beach	9	26.274	26.376	2.988354726	8	0.0174	*	Beach	WhiteDune	3.96586799	8	0.012	*	
		WhiteDune	10	-21.47	14.784	-4.592390628	9	0.0013	***	Beach	GreyDune	3.93168576	8	0.013	*	
		GreyDune	10	-20.208	15.63	-4.088375693	9	0.00272	**	WhiteDune	GreyDune	-0.171870799	9	1	ns	
		Beach	10	0.912	0.623	-0.448505826	9	0.664	ns	group1	group2	statistic	df	p _{adj}	p _{adj} signi	
		WhiteDune	10	1.867	2.829	0.968725369	9	0.358	ns	Beach	WhiteDune	-0.987773461	9	1	ns	
		GreyDune	10	-0.051	0.804	-4.136813861	9	0.00253	**	Beach	GreyDune	2.694652879	9	0.074	ns	
II	I	Beach	6	1.226	1.321	0.420003168	5	0.692	ns	WhiteDune	GreyDune	1.955800996	9	0.247	ns	
		WhiteDune	10	0.155	0.498	-5.359059782	9	0.000457	****	Beach	WhiteDune	1.712088873	5	0.444	ns	
		GreyDune	10	0.478	1.012	-1.629947573	9	0.138	ns	Beach	GreyDune	1.285352353	5	0.765	ns	
		Beach	8	0.005	2.677	-1.051669276	7	0.328	ns	WhiteDune	GreyDune	-1.236794313	9	0.741	ns	
		WhiteDune	9	0.012	1.42	-2.087780227	8	0.0703	ns	Beach	WhiteDune	0.027333358	7	1	ns	
		GreyDune	8	0.246	1.112	-1.916911734	7	0.0968	ns	Beach	GreyDune	-0.677072826	5	1	ns	
		Beach	8	0.337	0.811	-2.312236516	7	0.054	ns	WhiteDune	GreyDune	-0.026926083	6	1	ns	
		WhiteDune	9	-0.168	3.957	-0.885348907	8	0.402	ns	Beach	WhiteDune	0.006069107	6	1	ns	
		GreyDune	10	0.725	1.078	-0.807681455	9	0.44	ns	Beach	GreyDune	-0.543652983	7	1	ns	
WhiteDune	10	0.725	1.078	-0.807681455	9	0.44	ns	WhiteDune	GreyDune	-0.613931136	8	1	ns			

Table S5. Mean and SD of the length of the longest leaf of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations with non-pairwise comparisons between these areas at the beginning of the growth season (A), the change in shoot count over the growing season with comparisons to 0 and between areas (B), and this change relative to that control individuals with comparisons to 0 and between areas (C). * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

variable	LOCATION	AREA	n	mean	sd	t	df	p	signif	group1	group2	t	df	p _{adj}	signif _{if}	
A	I	Beach	20	71.94	9.85					Beach	WhiteDune	-8.247474161	35	5.1417375	2.72E-09	****
		WhiteDune	20	94.785	7.512					Beach	GreyDune	-2.494444668	37	9.2791789	0.051	ns
		GreyDune	20	79.885	10.289					WhiteDune	GreyDune	5.230544065	34	7.7274166	2.44E-05	****
		Beach	20	73.695	11.525					Beach	WhiteDune	-5.381198762	31	3.5944343	2.09E-05	****
	II	WhiteDune	20	89.925	7.008					Beach	GreyDune	-6.376470869	37	9.1405599	5.25E-07	****
		GreyDune	20	96.4	10.989					WhiteDune	GreyDune	-2.221829479	32	2.6038588	0.1	ns
		Beach	19	80.758	7.301					Beach	WhiteDune	-0.851905514	33	2.5681576	1	ns
		WhiteDune	20	83.285	10.949					Beach	GreyDune	1.151056439	35	1.7750607	0.771	ns
	III	GreyDune	20	77.6	9.717					WhiteDune	GreyDune	1.736690208	37	4.7119463	0.272	ns
		Beach	19	70.042	10.968					Beach	WhiteDune	-5.360640514	36	9.9241865	1.38E-05	****
		WhiteDune	20	89.525	11.728					Beach	GreyDune	-3.038976225	36	9.4944139	0.013	*
		GreyDune	20	81.22	11.998					WhiteDune	GreyDune	2.21368106	37	9.8038285	0.099	ns
B	I	Beach	10	41.485	26.728	4.908328729	9	0.00038	***	Beach	WhiteDune	3.821909023	9	0.012	*	
		WhiteDune	10	8.133	6.182	4.160170174	9	0.00245	**	Beach	GreyDune	4.861696206	9	0.003	**	
		GreyDune	10	-9.26	19.907	-1.471052613	9	0.175	ns	WhiteDune	GreyDune	3.158747262	9	0.035	*	
		Beach	10	45.165	26.024	5.488140523	9	0.000386	***	Beach	WhiteDune	3.454389805	9	0.022	*	
	II	WhiteDune	10	10.899	14.719	2.341603096	9	0.0439	*	Beach	GreyDune	5.167576968	9	0.002	**	
		GreyDune	10	-8.826	13.029	-2.142134809	9	0.0608	ns	WhiteDune	GreyDune	2.539677446	9	0.095	ns	
		Beach	8	16.904	5.534	8.639312067	7	5.56E-05	****	Beach	WhiteDune	2.894564158	7	0.07	ns	
		WhiteDune	10	4.287	18.035	0.751738639	9	0.471	ns	Beach	GreyDune	2.059054819	7	0.236	ns	
	III	GreyDune	10	-3.494	24.711	-0.447138184	9	0.665	ns	WhiteDune	GreyDune	1.217810387	9	0.762	ns	
		Beach	9	16.888	22.827	2.21947323	8	0.0572	ns	Beach	WhiteDune	1.605786178	8	0.441	ns	
		WhiteDune	10	1.429	12.665	0.356766019	9	0.729	ns	Beach	GreyDune	1.111244018	8	0.897	ns	
		GreyDune	10	4.916	13.412	1.159182364	9	0.276	ns	WhiteDune	GreyDune	-0.604373055	9	1	ns	
C	I	Beach	10	0.863	0.456	-0.95252129	9	0.366	ns	Beach	WhiteDune	0.423196732	8	1	ns	
		WhiteDune	9	0.717	0.482	-1.759207228	8	0.117	ns	Beach	GreyDune	4.982204301	7	0.005	**	
		GreyDune	8	-0.389	0.572	-6.864597903	7	0.000239	***	WhiteDune	GreyDune	3.917864941	7	0.017	*	
		Beach	10	0.797	0.496	-1.294033488	9	0.228	ns	Beach	WhiteDune	1.828845596	8	0.315	ns	
	II	WhiteDune	9	0.31	0.598	-3.465232197	8	0.0085	**	Beach	GreyDune	1.356910556	7	0.651	ns	
		GreyDune	8	-0.806	3.171	-1.610725339	7	0.151	ns	WhiteDune	GreyDune	0.901210278	6	1	ns	
		Beach	9	0.859	0.653	-0.649649054	8	0.534	ns	Beach	WhiteDune	2.268892082	6	0.191	ns	
		WhiteDune	8	0.504	0.692	-2.024776535	7	0.0825	ns	Beach	GreyDune	0.184508887	6	1	ns	
	III	GreyDune	7	0.831	2.153	-0.208226859	6	0.842	ns	WhiteDune	GreyDune	0.790677935	5	1	ns	
		Beach	7	0.732	0.612	-1.158124081	6	0.291	ns	WhiteDune	WhiteDune	2.937698821	6	0.078	ns	
		WhiteDune	10	-0.194	0.737	-5.11805805	9	0.00063	***	Beach	GreyDune	1.710218939	6	0.414	ns	
		GreyDune	10	-0.826	1.689	-3.418008234	9	0.00765	**	WhiteDune	GreyDune	1.154782785	9	0.834	ns	

Table S6. Mean and SD of the length of the longest leaf corrected for sediment accretion/sedimentation of disturbed *A. arenaria* individuals in the three areas of the morphological gradient for the four studied locations with non-pairwise comparisons between these areas at the beginning of the growth season (A), of the change in leaf length corrected for sediment accretion/sedimentation over the growing season (B), and this change relative to that of control individuals (C). * = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$, NS = not significant**

variable	LOCATION	AREA	n	mean	sd	t	df	p	signif	group1	group2	t	df	p _{adj}	p _{adj} signif
A	I	Beach	20	71.94	9.85					Beach	WhiteDune	-8,247474161	35,51417375	2,72E-09	****
		WhiteDune	20	94.785	7.512					Beach	GreyDune	-2,494444668	37,92791789	0,051	ns
		GreyDune	20	79.885	10.289					WhiteDune	GreyDune	5,230544065	34,77274166	2,44E-05	****
		Beach	20	73.695	11.525					Beach	WhiteDune	-5,381198762	31,35944343	2,09E-05	****
	II	WhiteDune	20	89.925	7.008					Beach	GreyDune	-6,376470869	37,91405599	5,25E-07	****
		GreyDune	20	96.4	10.989					WhiteDune	GreyDune	-2,221829479	32,26038588	0,1	ns
		Beach	19	80.758	7.301					Beach	WhiteDune	-0,851905514	33,25681576	1	ns
		WhiteDune	20	83.285	10.949					Beach	GreyDune	1,151056439	35,17750607	0,771	ns
	III	GreyDune	20	77.6	9.717					WhiteDune	GreyDune	1,736690208	37,47119463	0,272	ns
		Beach	19	70.042	10.968					Beach	WhiteDune	-5,360640514	36,99241865	1,38E-05	****
		WhiteDune	20	89.525	11.728					Beach	GreyDune	-3,038976225	36,94944139	0,013	*
		GreyDune	20	81.22	11.998					WhiteDune	GreyDune	2,21368106	37,98038285	0,099	ns
B	I	Beach	10	40,975	37,739	-0,360328451	8	0,728	ns	Beach	WhiteDune	2,710361278	9	0,072	ns
		WhiteDune	10	7,915	5,823	-1,809596507	8	0,108	ns	Beach	GreyDune	3,68050483	9	0,015	*
		GreyDune	10	-9,237	19,894	-4,386556231	8	0,00233	**	WhiteDune	GreyDune	3,136113799	9	0,036	*
		Beach	6	24,898	33,719	-0,929758005	5	0,395	ns	Beach	WhiteDune	1,260115531	5	0,789	ns
	II	WhiteDune	10	8,028	14,227	-3,203701652	9	0,0108	*	Beach	GreyDune	1,916773799	5	0,339	ns
		GreyDune	10	-9,55	12,277	-2,027025314	7	0,0823	ns	WhiteDune	GreyDune	2,368834339	9	0,126	ns
		Beach	5	12,294	2,171	-0,149215813	5	0,887	ns	Beach	WhiteDune	-9,692489656	1	0,196	ns
		WhiteDune	6	7,912	13,716	-1,293912471	4	0,265	ns	Beach	GreyDune	1,442524204	4	0,669	ns
	III	GreyDune	10	-3,79	24,317	-1,003015915	7	0,349	ns	WhiteDune	GreyDune	0,528333442	5	1	ns
		Beach	9	5,831	21,563	-2,71806867	8	0,0263	*	Beach	WhiteDune	0,829886579	8	1	ns
		WhiteDune	10	-1,776	12,221	-5,224086186	9	0,000546	***	Beach	GreyDune	0,142397711	8	1	ns
		GreyDune	10	3,754	13,028	-2,827419602	9	0,0198	*	WhiteDune	GreyDune	-0,921709397	9	1	ns
C	I	Beach	9	0,911	0,737	-0,360328451	8	0,728	ns	Beach	WhiteDune	-0,018690272	7	1	ns
		WhiteDune	9	0,726	0,454	-1,809596507	8	0,108	ns	Beach	GreyDune	3,325191308	7	0,038	*
		GreyDune	9	-0,165	0,797	-4,386556231	8	0,00233	**	WhiteDune	GreyDune	3,904772921	8	0,014	*
		Beach	6	0,765	0,618	-0,929758005	5	0,395	ns	Beach	WhiteDune	0,613712635	5	1	ns
	II	WhiteDune	10	0,33	0,661	-3,203701652	9	0,0108	*	Beach	GreyDune	2,748268825	4	0,154	ns
		GreyDune	8	-0,962	2,737	-2,027025314	7	0,0823	ns	WhiteDune	GreyDune	1,262827176	7	0,741	ns
		Beach	6	0,943	0,933	-0,149215813	5	0,887	ns	Beach	WhiteDune	1,470797963	1	1	ns
		WhiteDune	5	0,529	0,814	-1,293912471	4	0,265	ns	Beach	GreyDune	0,745381698	5	1	ns
	III	GreyDune	8	-0,392	3,926	-1,003015915	7	0,349	ns	WhiteDune	GreyDune	0,824487122	2	1	ns
		Beach	9	0,089	1,006	-2,71806867	8	0,0263	*	Beach	WhiteDune	0,953434878	8	1	ns
		WhiteDune	10	-0,329	0,805	-5,224086186	9	0,000546	***	Beach	GreyDune	1,246787215	8	0,744	ns
		GreyDune	10	-0,578	1,765	-2,827419602	9	0,0198	*	WhiteDune	GreyDune	0,448631182	9	1	ns