

UNDERSTANDING THE EFFECT OF MICROCLIMATE ON MARRAM GRASS GROWTH

DEVELOPING A CAUSAL AND PREDICTIVE CLIMATE MODEL IN COASTAL DUNES
USING STRUCTURAL EQUATION MODELLING

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DISCLAIMER: During this master's dissertation, ChatGPT was used to generate and problem-solve R codes to obtain the desired dataframe structures and assist with data-exploration. It was also used for the original layout of the introduction, although this structure has been heavily modified in the final version. AI was also used to structure the final summary of the dissertation, although this summary was entirely based on original text.

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1. INTRODUCTION

1.1. Coastal dunes: ecology, functionality and formation

Coastal dunes form the transition zone between land and sea where wind- or water-driven sand has accumulated in large mounds, ridges and hills (Barbier et al., 2011; Davidson-Arnott et al., 2018; Martínez & Psuty, 2004a). Due to their unique location, they function as a barrier, protecting us from several climatic threats (Barbier et al., 2011; Martínez & Psuty, 2004b; Provoost et al., 2014). This functionality is amplified by their ability to absorb waves and minimize erosion (Strypsteen, de Vries, et al., 2024a). The importance of dunes manifests itself further through providing invaluable regulating, provisioning and cultural ecosystem services (Everard et al., 2010). In example, they play a role in carbon cycling, sequestering carbon both above- and belowground in their vegetation and soil respectively (Drius et al., 2016; Hu et al., 2015; Jay et al., 2025; Vecchio et al., 2022). Their sand particles also function as a natural filter and house purifying bacteria, contributing to water purification services (Nelissen, 2013). Additionally, dunes provide raw materials and have a massive cultural importance for tourism, recreation and spirituality (Barbier et al., 2011; Everard et al., 2010). Coastal dunes have not only proven to be of critical importance for humans but for nature as well (Barbier et al., 2011). Despite their barren façade, coastal dunes house an abundance of plants, fungi and animals on account of the diversity of ecological niches found within them (Provoost & Bonte, 2004). Their complex topography and concomitant vegetations create a range of microhabitats, each associated with their own fauna and flora (Everard et al., 2010).

Globally, arenaceous beaches and dunes cover approximately 34% of all ice-free coastlines (Hardisty, 1994). The Western-European coastal dunes as we know them today arose roughly 7000 years ago, after the sea had risen to about its current level (Mörner, 1995). Since then, interchangeable phases of dune building and stability have occurred, driven by climatic and sea level changes. Coastal landscapes are therefore inherently unstable (Provoost et al., 2011). They are dynamic, continuously shifting and can be completely built up or broken down over the course of a single century (Pye & Neal, 1994). Regular flooding of the coastline leads to an accumulation of marine sediment, forming the perfect reservoir for transport by coastal wind dynamics (Provoost et al., 2011). Not all dune sediment is derived from the offshore seabed as inland rivers provide an important additional source of sand (Ruz & Hesp, 2014). At the delta, where the river meets the sea, this sediment is deposited due to the decreased water velocity, eventually allowing waves and currents to redistribute it onto adjacent beaches where it can be transported inland to contribute to the formation of dunes.

Dune formation is a successive process at the hands of several ecosystem engineers (Emery & Rudgers, 2014). Such species play a disproportionate role in establishing ecosystems by initiating and sustaining necessary ecological processes. These include modifying the local environment, establishing new habitats, increasing biodiversity and modulating pre-existing processes (Losapio et al., 2024). Marram grass (*Ammophila arenaria* (L.) Link), for example, is a perennial, drought-resistant dune engineer that plays a key role in European dune systems (Huiskes, 1979). It partakes in an interaction of multiple feedback mechanisms involving biotic and abiotic factors (Bonte et al., 2021; Jebali et al., 2018). Initially, sand accumulates at the upper beach through onshore winds generating embryonal dunes. Here, the sand volumes depend on wind speed, soil moisture and the morphology of the surrounding landscape (de Vries et al., 2012; Delgado-Fernandez, 2010; Strypsteen et al., 2019). Marram grass can effectively capture this sand flux, allowing for the development of foredunes. Simultaneously, sand accretion and dune growth also affects marram performance, creating an intricate feedback system (Bonte et al., 2021). This innate sand-capturing ability is caused by their extensive root network and the clonal expansion strategy of this species, consisting of multiple dense shoot patches to maximize sand trapping efficiency (Reijers et al., 2019). As a result, marram can fixate the soil and facilitate settlement of other plant species. As sand accumulation diminishes the habitat slowly shifts away from dynamic white dunes. When diverging from the sea, the soil

begins to develop a freshwater lens, and a humus layer is formed due to increased decay of plant matter. The additional nutrients and water-content allows mosses and small shrubs to grow, fixing the dunes in the process and generating what is known as grey dunes. In further stages of the succession, more stable landscapes are formed and can be characterized by larger plants, and trees and unique aquatic habitats due to the formation of dune slacks (Cosyns et al., 2019).

1.2. Challenges to coastal dunes

Despite their wide array of ecosystem services, coastal dunes have faced severe deterioration at the hands of mankind, both directly and indirectly. Cattle grazing and marram grass cutting have drastically changed aeolian sand dynamics (Gilbertson et al., 1999; Sommerville et al., 2007). Reducing the local vegetation is followed by increased sand mobility and dune instability. However, over the last century an opposing trend has occurred. These traditional dune activities have been replaced by artificial marram planting to ensure coastal protection (van der Maarel et al., 1985). As a result, dune stability has been enhanced passed the natural boundary, leading to a loss of mobile dune habitat and preventing the formation of new dunes (Provoost et al., 2011, 2014). This lack of dynamicity implies a gradual loss of characteristic young habitats and their associated species, as can be seen on the Belgian coast. Here, mobile dunes have shockingly decreased by over 60% in the last century (Cosyns et al., 2019).

In addition, urbanization has further disturbed dune connectivity and its associated aeolian sand dynamics. Not only has the presence of urban and agricultural areas increased the need for coastal protection and fixation measures (Provoost et al., 2011), it has also led to major habitat loss and fragmentation, interfering with important geomorphological processes needed to maintain these precious habitats (Provoost et al., 2014). In addition, urbanization is often associated with the introduction of non-native invasive plant species. It comes to no surprise that the booming development of the Belgian coast has thus increased the proportion of alien species by 15% over the last 50 years (Provoost et al., 2011).

Finally, indirect impact on coastal ecosystems is mostly mediated through anthropogenically-induced climate change. Weather pattern shifts change the intensity and course of storms. In addition to the rise in sea level, this creates high magnitude waves which can reach further inland, eroding sand dunes on their path (Almar et al., 2021; Dangendorf et al., 2017; de Winter & Ruessink, 2017). This remobilizes the sand and increases dune instability. Moreover, these saltwater intrusions affect the mineral content of the dunes and increase groundwater levels, placing a strain on the vegetation (Vandenbohede et al., 2008). Weather changes also affect wind patterns which in turn alter sand deposition and dune migration. Severe pattern-shifts due to climate change can thus create even more instability and may potentially cause serious harm to human assets (Derijckere et al., 2023; Gabarrou et al., 2018; Panario & Pineiro, 1997). Furthermore, global temperature increase influences mobility by inducing drought, although the effects on sand drift susceptibility vary (Bogle et al., 2015; J. Gao et al., 2020; Siegal et al., 2013). It also facilitates the settlement of foreign, invasive species introduced through urbanization. These continue to destabilize dune ecosystems as they outcompete important dune-building grasses and shrubs (Seabloom et al., 2013). For example, marram grass and sea buckthorn, two common Belgian dune species, are often threatened by invasion of exotic shrubs such as mahonia, Japanese rose and black cherry (Cosyns et al., 2019).

1.3. The role of *Ammophila* performance in coastal dune restoration and management

Considering their protective role as the physical barriers of the shoreline, coastal dune management and restoration is more important than ever. In the last few decades, the concept of dunes as nature-based solutions has gained popularity (Wittebrood et al., 2018). This entails enhancing natural dune systems and establishing novel artificial ones, which may potentially provide even greater protection when thoughtfully designed and maintained (Strypsteen et al., 2023). Such dynamic barriers provide additional benefits to

static ones, like the capacity to track the rising sea level based on interactions between vegetation growth and aeolian sediment supply (Bonte et al., 2021; de Vries et al., 2012; Duarte et al., 2013a; Strypsteen et al., 2019). On the Belgian coast, traditionally reliant on immovable structures for erosion mitigation, this more dynamic approach has been favoured in recent years (Houthuys, 2012; Lebbe et al., 2008; Strypsteen et al., 2019). This method grants us the ability to utilize natural elements and processes to improve coastal resilience, allowing us to counteract the consequences of climate change while simultaneously restoring crucial habitats (Strypsteen, Bonte, et al., 2024).

Marram planting has been a longstanding practice for the development of (artificial) dune systems (Bonte et al., 2021). It has likely existed since the 14th century and has been used extensively ever since (Bridges et al., 2015; Hobbs et al., 1983). More recently, this technique has become part of the dune-in-front-of-a-dike principle, a typical example of a Hybrid Nature-based Solution where conventional hard infrastructure is merged with dynamic ecological processes (Strypsteen, Bonte, et al., 2024; Strypsteen, de Vries, et al., 2024b). Optimizing the functionality of the dune-dike hybrid approach necessitates improved knowledge on processes that drive dune morphodynamics, including factors driving the growth of important ecosystem engineers such as *Ammophila*. Understanding the intricate feedback systems between *Ammophila* and its environment can provide crucial information for further implementation of these solutions, especially considering the variability in microclimates occurring within coastal dunes.

1.4. How do microclimatological parameters influence marram grass growth

Although the consequences of macroclimatic changes are decently understood in dune ecosystems, the same cannot be said for their microclimates. Defined as having their own unique climatic conditions on a small scale, microclimates can affect plant growth significantly due to their variety (Wartena, Vanboxel, et al., 1991).

The variability in microclimates in coastal dunes is the result of multiple processes that interact with one another in ecological feedback loops (Wartena, Vanboxel, et al., 1991) (Fig X.). The interaction between the sloping surfaces and the specific macroclimate tied to the unique location of coastal dunes between land and sea is the primary driver for this small-scale variability (Wartena, Vanboxel, et al., 1991). On the one hand, the heterogeneous geomorphology of dunes is mainly derived from larger-scale weather patterns, which control the sand flux and are themselves a culmination of solar radiation, precipitation and wind profiles. On the other hand, geomorphological processes and soil properties influence microclimatological parameters directly and indirectly through modification of the atmosphere. As a result, temperature, moisture and sediment transport are the outcome of an interaction between surface and weather properties, mediated by energy, momentum and matter exchange processes. In addition, differing sand accumulations lead to peaks and valleys with slopes varying in steepness, their orientation going into every direction. The latter determines radiation load and the associated temperature, in turn affecting evaporation of soil moisture alongside wind flux. Permeability of the soil also determines moisture and is usually high in dunes. Consequently, most of the precipitation is lost to ground water with some exceptions in topographical depressions. Here, the ground water table is high enough to be reached by plant roots (Wartena, Vanboxel, et al., 1991). Finally, wind and grain movement is affected by drag forces occurring at the surface causing a gradual decrease in wind speed and sediment transport further inland. Additional obstacles such as vegetation and dune crests create complex patterns at a small scale (Wartena, Van Boxel, et al., 1991)

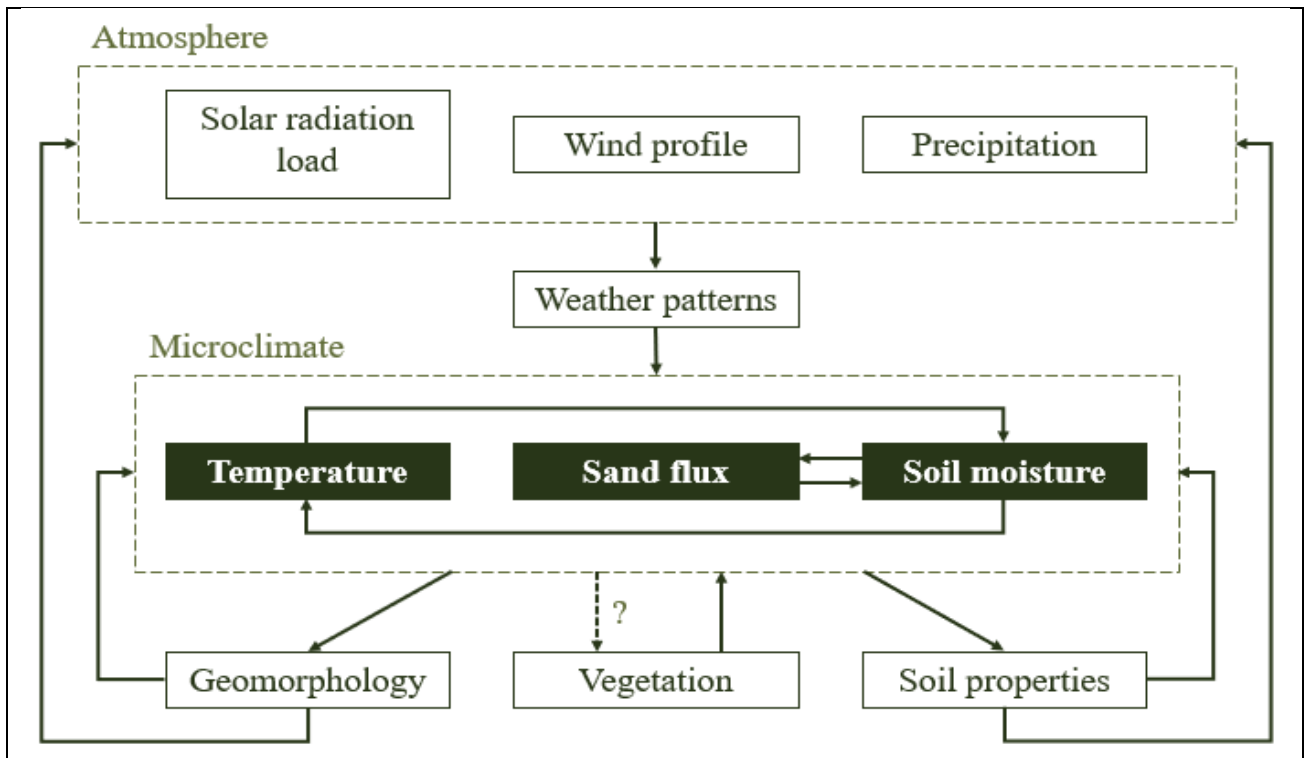


Fig 1. Feedback mechanisms influencing the microclimate in coastal dunes. The arrows illustrate the relationships between the different elements within coastal dune systems. The dotted arrow represents the main question of this thesis: “How does the microclimate influence the vegetation, specifically marram grass, in coastal dune ecosystems?”. The filled in text boxes are the microclimatological parameters which will be considered during this study.

Differences in **temperature**, **moisture** and **sand flux** at a small scale, are reflected in vegetation cover, fitness and composition as each species responds differently to these environmental parameters (Fig 1.). In turn, this affects how ecosystem engineers such as marram grass can stabilize blown surfaces and build up dune environments. Hence the extent to which marram is able to stabilize dune ecosystems should be profoundly influenced by the local microclimate according to Wartena, Vanboxel, et al. (1991).

Temperature, for one, plays an important role in marram performance. Seed germination occurs in a wide range of temperatures, between 15°C to 30°C, and is strongly influenced by diurnal fluctuations, becoming optimal at 20°C nighttime and 30°C daytime (Chergui et al., 2013; Huiskes, 1977; Van Der Putten et al., 1990). The effect on growth after germination has not yet been studied extensively. According to its distribution range, *Ammophila arenaria* is heat-tolerant as it is able to survive and grow in regions up to 50°C (Huiskes, 1979). Biel & Hacker (2021) confirmed this tolerance and showed a neutral or positive response to warming in both biomass and tiller production. However, these experiments were conducted in a controlled environment, lacking the heterogeneity of a natural dune system. Global analysis of vegetation cover in natural coastal dunes has for example shown a greening effect in multiple areas, coinciding with the global temperature increase and other climatic changes (X. Gao et al., 2021; Jackson et al., 2019). Contrarily, Curreli et al. (2013) and Lammers, Berghuis, et al. (2024) suggest a dryer global climate may drastically impact dune vegetations. Therefore, how temperature affects vegetation, and specifically marram, in a natural environment remains unclear on a macroclimatic scale and understudied on a microclimatic scale.

Another crucial factor for marram growth is soil moisture, determined by precipitation, soil permeability and slope directionality (Homberger et al., 2024; Wartena, Vanboxel, et al., 1991). Establishment of marram seeds and rhizome fragments is more successful in high soil moisture locations (Homberger et al., 2025).

The same study found these areas coincided with low elevations, suggesting groundwater determines marram growth rather than precipitation variations and is in line with earlier findings by Wartena et al. (1991). Another study by Homberger et al. (2024) additionally showed that, in controlled pot experiments, soil moisture significantly increased plant growth of *Ammophila* in attributes associated with dune building. *Ammophila* seeds and rhizome fragments show differential responses to hydric stress with the former being sensitive while the latter are more drought-resistant (Chergui et al., 2013; Konlechner et al., 2013). Older and mature individuals on the other hand are overall tolerant to drought, only exhibiting mortality after prolonged periods below a critical moisture threshold (Dixon et al., 2004; Homberger et al., 2024; Lammers, Berghuis, et al., 2024).

Furthermore, local burial strongly affects marram seed germination and growth in dunes (Lim, 2011; McLachlan, 2014; Nolet et al., 2018; Van Der Putten et al., 1990). Sand burial is a direct consequence of aeolian dynamics, dune topography and vegetation as these determine sediment transport to any given location (Derijckere et al., 2023; P. A. Hesp, 1989; P. Hesp & Smyth, 2019; Wartena, Vanboxel, et al., 1991). Although the potential for germination is high in marram due to a voluminous and persistent seed bank, field conditions seem to limit its establishment (Hilton et al., 2019; Huiskes, 1977; Salisbury, 1953, Taelman, 2024 (unpublished data)). This can partially be explained by the results of Bonte et al. (2021) and Lim (2011), whom showed a burial depth of 3 cm already results in a 60% reduction of germination. Contrarily, marram growth shows a positive response to sand burial, although parabolic rather than linear with vertical growth increasing to an optimum when partially buried but decreasing past this point (Levinsh & Andersone-Ozola, 2020; Konlechner et al., 2013; Maun, 1998). Using UAV-imaging, Nolet et al. (2018) were able to monitor the *Ammophila* growth response to sand burial, indicating an optimal burial rate of 0.31m and a maximum tolerance of 0.78 to 0.96m per growing season. Due to this resistance limit, marram grass eventually leads to its own downfall as its sand-capturing ability promotes the growth of the dune and the instalment of less tolerant, yet more competitive, species (Bonte et al., 2021; P. Hesp, 2002, 2002; Lammers, Schmidt, et al., 2024; Psuty & Martinez, 2008). Stimulating the growth of other individuals increases further stabilizes the surrounding area resulting in what Marshall (1965) coined as “The *Ammophila* problem”. Here, vigour and abundance of marram grass decreases due to increased organic matter, lack of nutrient import from mobile sand, poor aeration, competition from other plants and increasing soil acidity as the soil continues to stabilize (Marshall, 1965). On the other hand, negligible sand deposition can also negatively affect sand burial as marram fails to outgrow the herbivory of its roots from accumulating nematodes in the soil, eventually resulting in its decay (Maxwell et al., 2017; Schwarz et al., 2018; Van Der Putten et al., 1990).

Temperature, soil moisture and sand burial can thus contribute to marram grass growth in diverse ways, although it is important to note they are not even across the landscape. The heterogeneity of dune ecosystems creates a range of microclimatological gradients (Larkin et al., 2006; Ott & van Aarde, 2014; Wartena, Vanboxel, et al., 1991). The intensity of these gradients is, at a local scale, mostly mediated through elevation, surrounding vegetation cover and distance to sea (Ott & van Aarde, 2014; Wartena, Vanboxel, et al., 1991). Elevation, as mentioned prior, determines access to the groundwater table in addition to exposure to sediment transport and solar radiation, respectively dictating local soil moisture, sand burial and temperature (P. A. Hesp, 1989; Homberger et al., 2024; Ott & van Aarde, 2014; Wartena, Vanboxel, et al., 1991). Vegetation cover can influence the climate at a microscale by creating shade and reflecting solar radiation, hence lowering the local surface temperature while also regulating evaporation of soil moisture and increasing sand entrapment efficiency (Howe & Smith, 2021; Reijers et al., 2019; Wartena, Vanboxel, et al., 1991). Finally, the distance to the ocean affects the water-holding capacity of the soil and the vegetation cover, where both increase with larger distances to the sea (Cosyns et al., 2019; Wartena, Van Boxel, et al., 1991). Aeolian dynamics also become more subdued further inland due to the shifting drag forces from sea to land, influencing local sand deposition (Wartena, Van Boxel, et al., 1991). Exposure to salt spray forms and additional factor when considering sea-distance and directly influences

salt concentrations in the soil (Acosta et al., 2007; Du & Hesp, 2020). Consequently, salt spray can induce water stress, tissue necrosis and leaf loss, directly affecting the growth of dune plants (Du & Hesp, 2020). For *Ammophila* specifically, Konlechner et al. (2013) could not find an effect of salt spray although sea-water immersion, representative of one high tide event, did significantly reduce survival.

The way in which the abiotic environment affects *Ammophila arenaria* survival and growth has thus been the subject of multiple studies. Most of them focus on a single parameter or are performed in a controlled environment (Biel & Hacker, 2021; Chergui et al., 2013; Dixon et al., 2004; Homberger et al., 2024; levinsh & Andersone-Ozola, 2020; Konlechner et al., 2013; Van Der Putten et al., 1990). These experiments fail to consider the natural environment of marram grass, where multiple abiotic variables influence plant growth at once. A more integrated approach, considering multiple factors, could thus give more insight into how the (micro)climate in its entirety acts on *Ammophila*.

2. RESEARCH RATIONALE AND OBJECTIVES

The objective of this master's dissertation is to obtain a better comprehension of the microclimatic variations in dune ecosystems and determine how these different abiotic parameters affect marram grass growth. Rather than studying marram growth in a heavily controlled environment, the set-up of this experiment will consist of tracking temperature, soil moisture and sand burial as well as observing the growth of *Ammophila* in high-detail in different microclimates within a natural dune system. Each local environment will vary in elevation, distance to sea and vegetation cover, consequently determining the microclimate for each individual. By measuring the plant response to the environment multiple times over the course of the experiment while simultaneously keeping a detailed record of temperature, soil moisture and sand burial, on top of their environmental determinants, I hope to assess how abiotic factors vary across the dune habitat and how they influence the growth of marram during its growth season.

In accordance with prior research, I suggest the following sub-hypotheses (Fig 2.); I hypothesize that small variations in temperature do not affect marram performance as it is a quite heat-tolerant species and no temperature effect has yet been observed on growth in controlled conditions (Biel & Hacker, 2021; Huiskes, 1977). Soil moisture may have a larger impact as Homberger et al. (2024, 2025) showed significantly more successful establishment in wetter dune patches and a positive growth in response to higher soil moisture. On the other hand, *Ammophila* is still considered highly resistant to drought and likely will not be affected by microvariations in moisture levels (Dixon et al., 2004; Lammers, Berghuis, et al., 2024). At last, marram growth has been shown to respond drastically to sand burial in natural and controlled environments (levinsh & Andersone-Ozola, 2020; Konlechner et al., 2013; Maun, 1998; Nolet et al., 2018). Plants should show improved growth in microclimates where sand burial is moderate and a growth decline only if sand accumulates in massive amounts over the growing season, over 78 centimetres based on Nolet et al. (2018), which is unlikely to occur during the rather short timing of the experiment.

As previously illustrated, these microclimatic parameters depend on elevation, surrounding vegetation and distance to sea. Overall, I expect plant performance will be negatively affected in bare, elevated patches closer to the ocean as they experience more wind dynamics while not being able to reach the groundwater table. Contrarily, areas with a denser vegetation, low elevation and further from the sea border should maintain moderate sand burial as well as higher soil moisture, thus promoting marram grass growth.

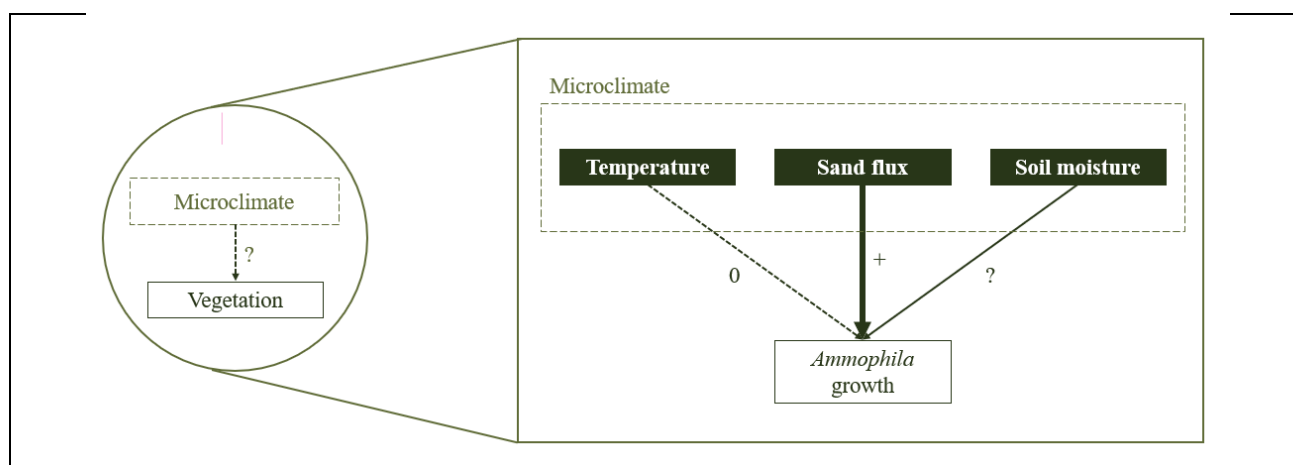


Fig 2. Illustration of the sub-hypotheses for this thesis. Micro-scale temperature variations are not expected to affect *Ammophila* growth (dotted arrow). Sand burial affects marram growth drastically and will thus likely have a strong positive influence (thick arrow) as burial rates are expected to remain below the lethal threshold. The effect of soil moisture is difficult to anticipate as marram has exhibited both increased growth to higher soil moisture as well as a high tolerance for drought (thin arrow).

3. MATERIALS AND METHODS

3.1. Location

The fieldwork was conducted in De Slufter (51.09352 °N, 2.559839 °E) (Fig 3. & Fig 4.), part of nature reserve De Westhoek which is situated in De Panne on the Belgian west-coast. The area contains a heterogenous topography, vegetation cover and exposure to the elements. Several dune succession stadia occur in close range from one another, varying from open patches of mobile white dunes with little vegetation to densely covered stabilized grey dunes.



Fig 3. Aerial photo of the experimental site within De Slufter | Photo belonging to the Flemish Government, map made in QGIS (QGIS Development Team, 2024)

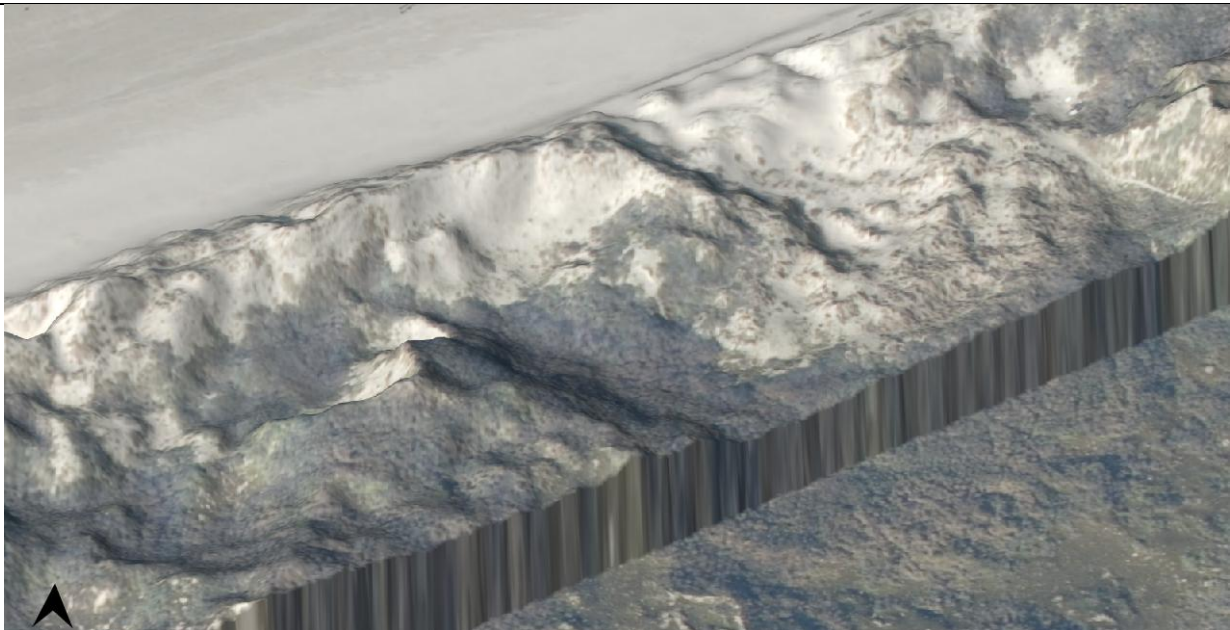


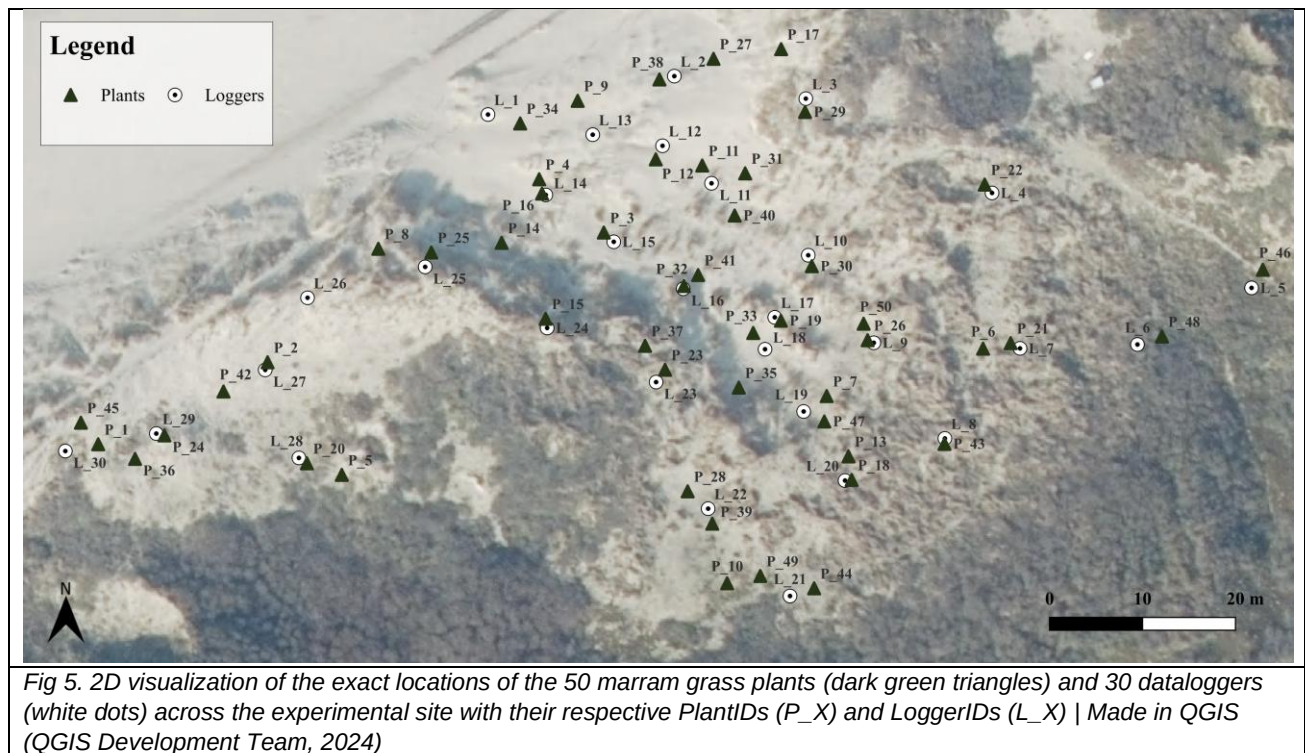
Fig 4. 3D visualization of the experimental site. The black arrow in the left corner represents the Northern direction. The 'wall' represents the edge of the elevation map used to make this model | Made in QGIS using the Qgis2threejs plugin (Akagi, 2024; QGIS Development Team, 2024)

3.2. Timing and duration

The experiment started on the 3rd of July 2024 and lasted until the 7th of October 2024, spanning a period of roughly 3 months. This timeframe was intentionally chosen as it matches the growing season of marram grass which is commonly used when assessing establishment and resilience in high-disturbance coastal environments (Reijers et al., 2019; Van Der Putten et al., 1990). During the extent of the experiment temperatures were on the warmer side, although it was also quite a wet summer.

3.3. Field work

On the 3rd of July 2024, 50 marram grass plants which were grown in the lab for 10 weeks until considered robust enough, were sparsely spread and planted in the site of the experiment, which is a heterogenous foredune. Plants were set out along a pre-existing transect of 30 partially buried TMS-4 Standard dataloggers (Tomst®) (Wild et al., 2019), that had already been placed in a winding path across the entire site for prior research (Taelman et al.). The plant location was chosen on a visual basis, ensuring that each logger had 2 to 3 individuals surrounding it (Fig 5. and 6.). The location of each marram grass was marked with a stick, carrying a unique PlantID. Northing (N), Easting (E) and elevation (Z) coordinates for each plant and datalogger were mapped in the Lambert72 coordinate-system (EPSG: 31370) using an RTK Carlson Brx7 unit which allowed for high-precision, real-time positioning data. The experimental set-up was concluded by taking up-close location photos for each plant by placing a 1x1 meter quadrant, maintaining the plant in the centre, and taking a picture from above (Fig 7.).



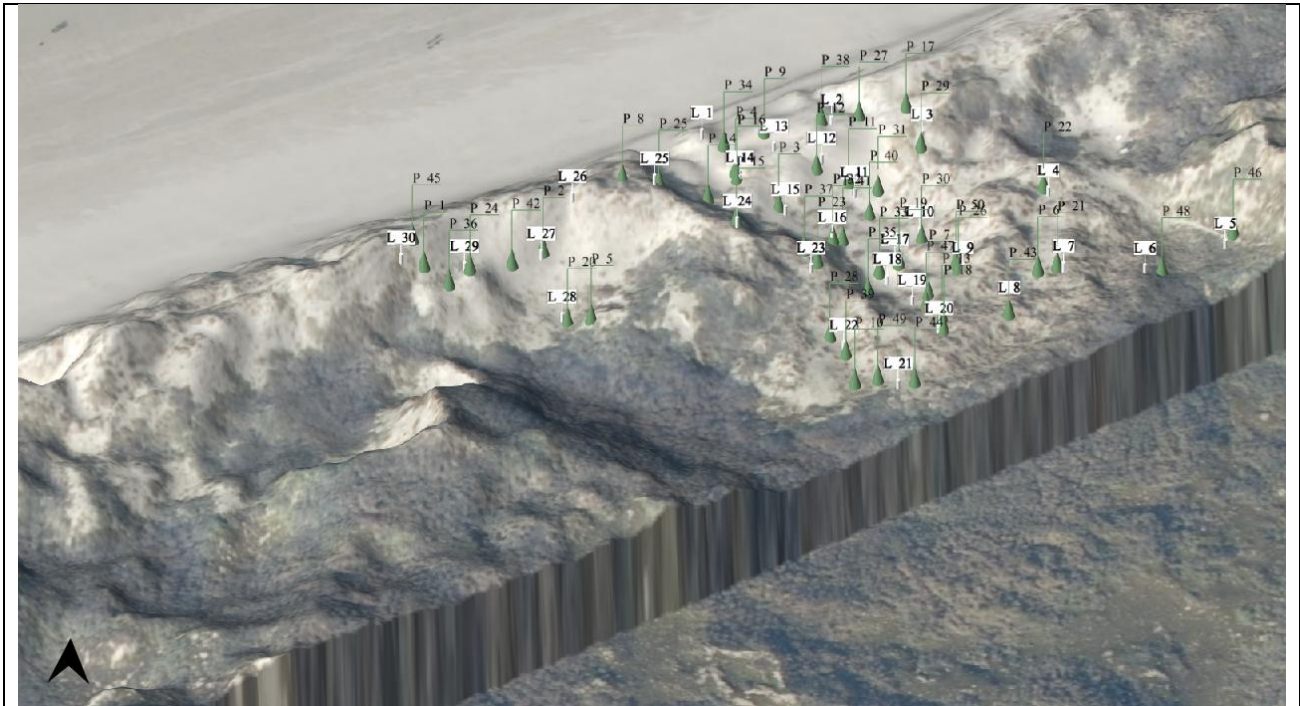


Fig 6. 3D visualization of the exact locations of the 50 marram grass plants (green cones) and 30 dataloggers (white cylinders) across the experimental site with their respective PlantIDs (P_X) and LoggerIDs (L_X) | Made in QGIS, 3D visualization made with the Qgis2threejs plugin (Akagi, 2024; QGIS Development Team, 2024)



Fig 7. Examples of the up-close location photos taken for PlantID 1 at the start (left; 3rd of July 2024) and the end of the experiment (right; 7th of October 2024) | Photos taken by TEREK-group

Throughout the experiment, for 14 weeks, 6 abiotic variables and 4 plant growth proxies were tracked. The abiotic variables consisted of:

- Soil temperature (T1)
- Surface temperature (T2)
- Atmospheric temperature (T3)
- Soil moisture
- Elevation
- Sand height

The proxies to track plant growth entailed:

- Shoot number
- Lateral density
- Leaf height
- Leaf width

Temperature was measured at roughly -6, +2 and +15 centimetres relative to the surface for T1, T2 and T3 respectively by the TMS-4 Standard dataloggers (Tomst®) (Fig 8.). All temperatures and soil moisture levels were measured every 15 minutes for the entire duration of the experiment. The climate data was extracted from each datalogger using a laptop with the TMD adapter and associated Lolly software (Tomst®) every two weeks. The Z coordinate of each plant, mapped once at the start of the experiment by the RTK unit, was used to equate its elevation. The marking sticks also served the purpose of measuring sand height during the experiment. An initial marking (T0) was made on the stick at the sand surface on the first day of the experiment and further markings with welder's tape were made to track sand dynamics.

Shoots were counted and drawn once at the beginning of the experiment (3rd of July 2024) and once at the end (3rd of October 2024), using shoot maps (Fig 9.) representing the circumference of the plant. Shoot-position was marked within the circle with a cross and all crosses were then summed to obtain the total number of shoots per individual.

Per plant, 5 leaves were selected to measure height using a ruler. The height was measured from the sand surface to the tip of the leaf, and the width was measured at the widest section of the blade at a precision of 0.1 centimeters. Each measurement was noted on paper alongside remarks such as signs of herbivory. To determine the lateral density, a head-on photo was taken of each plant using a white screen as a background to reduce visual noise (Fig 10.). The orientation in which the photo was taken varied, considering the position of the sun and surrounding vegetation to minimize shadows and intruding plants in every picture. A scale stick was included in every photo for calibration.

All fieldwork took place on an approximately weekly basis with an average of 9 days between measurements, and was usually done in the afternoon, from 12AM till 5PM. A detailed overview of the measurements taken for each day of fieldwork can be found in the Appendix (Appendix 1.)

Fieldwork was concluded, for the most part, on the 3rd of October 2024. In addition to the typical leaf height, width and sand height measurements, shoots were counted again in the exact same way as during the experimental set-up to obtain a final shoot count per plant and final location photos were taken with a quadrant. Lateral density photos were taken a week later due to time constraints, thus finalizing the experiment on the 7th of October (with the exception of logger data, which was collected a final time on the 27th of October). The marking sticks holding the sand height measurements were collected after completion of the experiment.

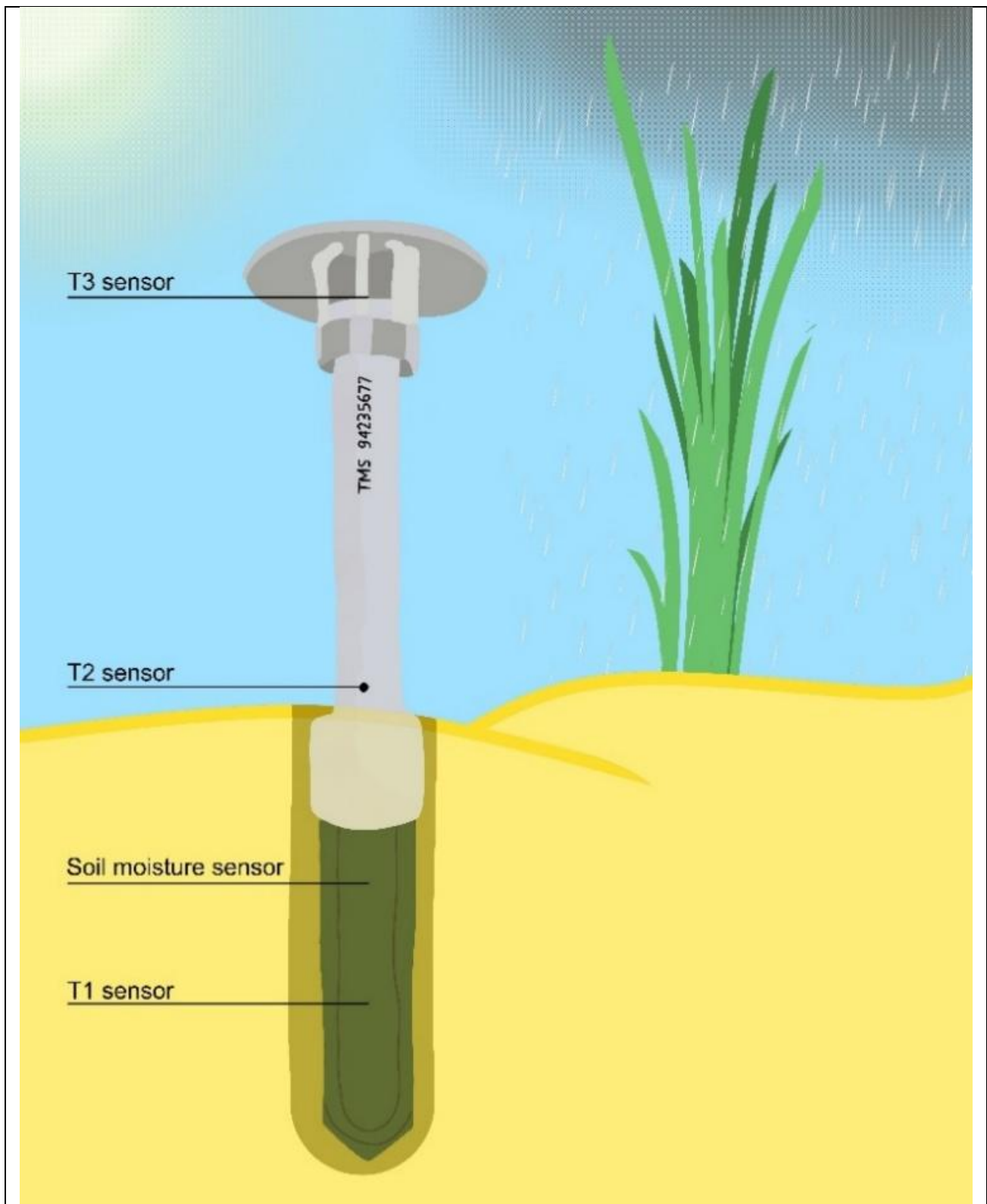


Fig 8. TMS-4 Standard datalogger (Tomst®) with the different sensors of the logger indicated by the black lines. The T1 sensor measures the soil temperature at a depth of ~6 cm, the T2 sensor measures the surface temperature at ~2 cm and the T3 sensor measures the atmospheric temperature at ~15 cm relative to the soil surface. | Illustrated by Charlotte Taelman & Samantha De Gottal

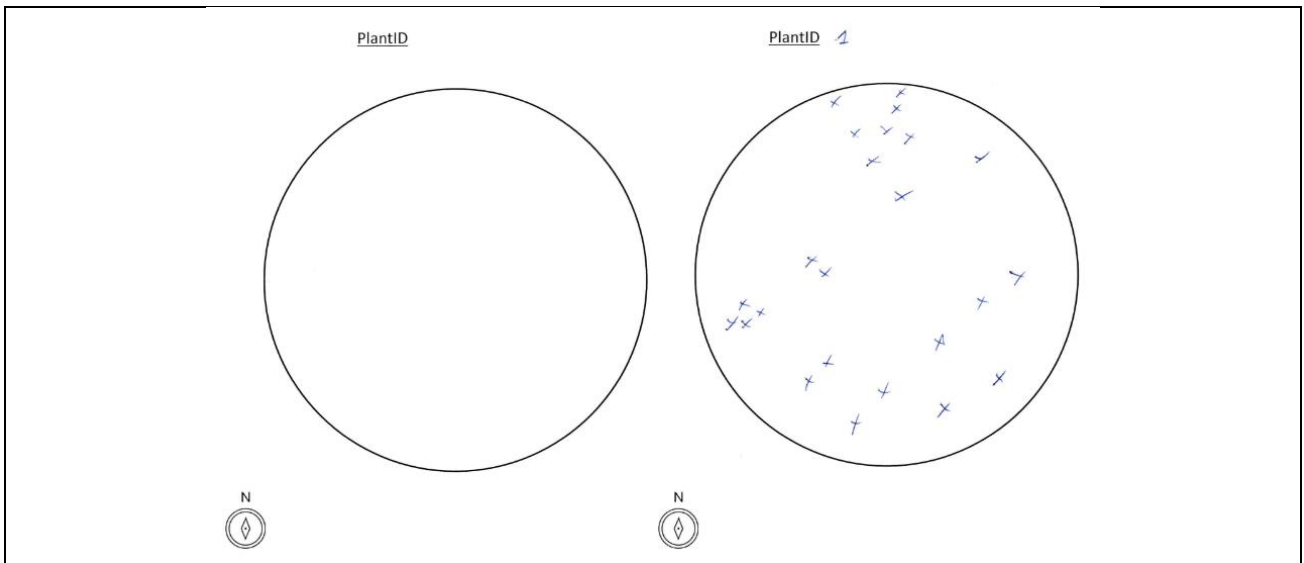


Fig 9. Shoot map template (left) used to count the number of shoots per plant and a completed shoot map of PlantID 1 (right). Shoots were marked as small crosses, indicating their relative position. The circle represents the circumference of the plant base, and the geographic direction is given by the compass. | Made by Charlotte Taelman



Fig 10. Examples of lateral density photos taken throughout the experiment for PlantID 28 at the start (left; 3rd of July 2024) and the end of the experiment (right; 7th of October 2024) | Photos taken by TEREK-group

3.4. Lab work

The collected marking sticks were brought back to the lab to measure the sand heights for each plant. Each stick was laid out on graph paper (mm), and the exact position of the tapes and markings on the stick, were transferred to the paper, thereby holding both the paper and stick in place. The T0 (3rd of July 2024) was carefully highlighted on the graph paper. Sand height on the sticks that were indicated by loosened tapes or lacking a T0 marking, were removed from the dataset.

The distance between each marking on the graph paper and T0 was measured for each stick, to assess an increase or decrease in sand height. These measurements represent the change in sand height compared to T0 for each fieldwork day.

3.5. Desktop work

To obtain lateral density measurements, all photos were processed using ImageJ. The scale of the photograph was set using the scale stick (10 cm). A selection around the marram grass individual was then made within the picture, clearing the outside to remove as much of the background as possible. Colours of the photo were adjusted to obtain a binary image of the photo (marram grass, and non-marram grass). Finally, a brush tool was used to clean up mistakes. The result is a full extraction of the marram grass plant and all its leaves. The area of these leaves could then be measured in ImageJ to assess the lateral density in m².

For each plant in the site the distance to the sea border, the closest logger as well the surrounding vegetation cover was calculated in QGIS (QGIS Development Team, 2024). For all QGIS work, the Belgian Lambert 72 coordinate reference system was used (EPSG: 31370). The sea border was drawn manually based on the global OpenStreetMap and converted to points using the SAGA Next Gen plug-in (North Road, 2023). Base QGIS was used to calculate the distance in meters between each plant and the sea border (Fig 11.). Identifying the closest logger was also done using base QGIS (Fig 12.). Vegetation cover was calculated using a binary vegetation classification map provided by the TEREK-group (Taelman, 2025) (Fig 13a. & 13b.). Buffers with a radius of 2 meters were drawn around each plant for which vegetation and non-vegetation pixels were counted. Distance to sea, closest loggers and vegetation cover were exported from QGIS as CSV files and imported in R for further processing. Lastly, the vegetation cover percentage (%) was calculated in R using the two raster classes.

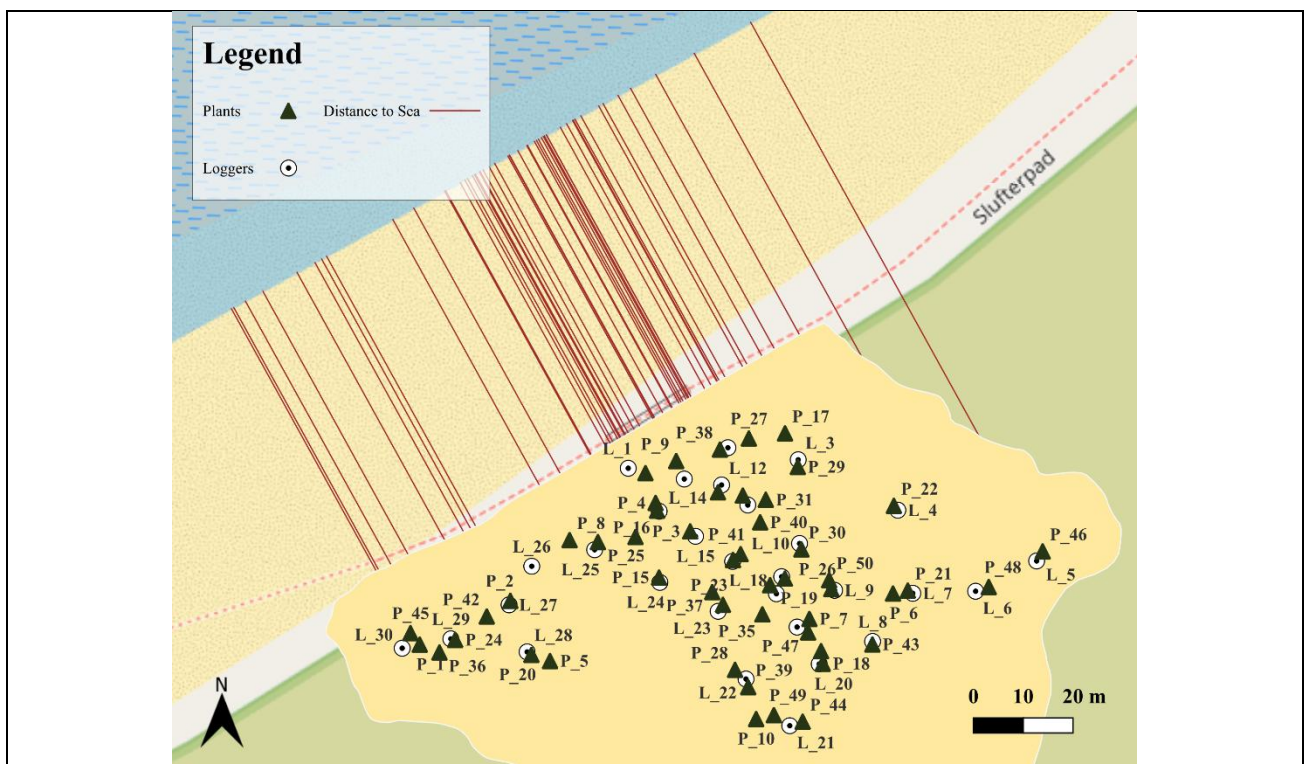


Fig 11. Visualization of the data-collection process in QGIS with plants (green triangles), loggers (white dots) and distance to sea shown for each plant (red lines) | Made in QGIS (QGIS Development Team, 2024)



Fig 12. Visualization of the data-collection process in QGIS with plants (green triangles), loggers (white dots) and the closest logger shown for each plant (red lines) | Made in QGIS (QGIS Development Team, 2024)

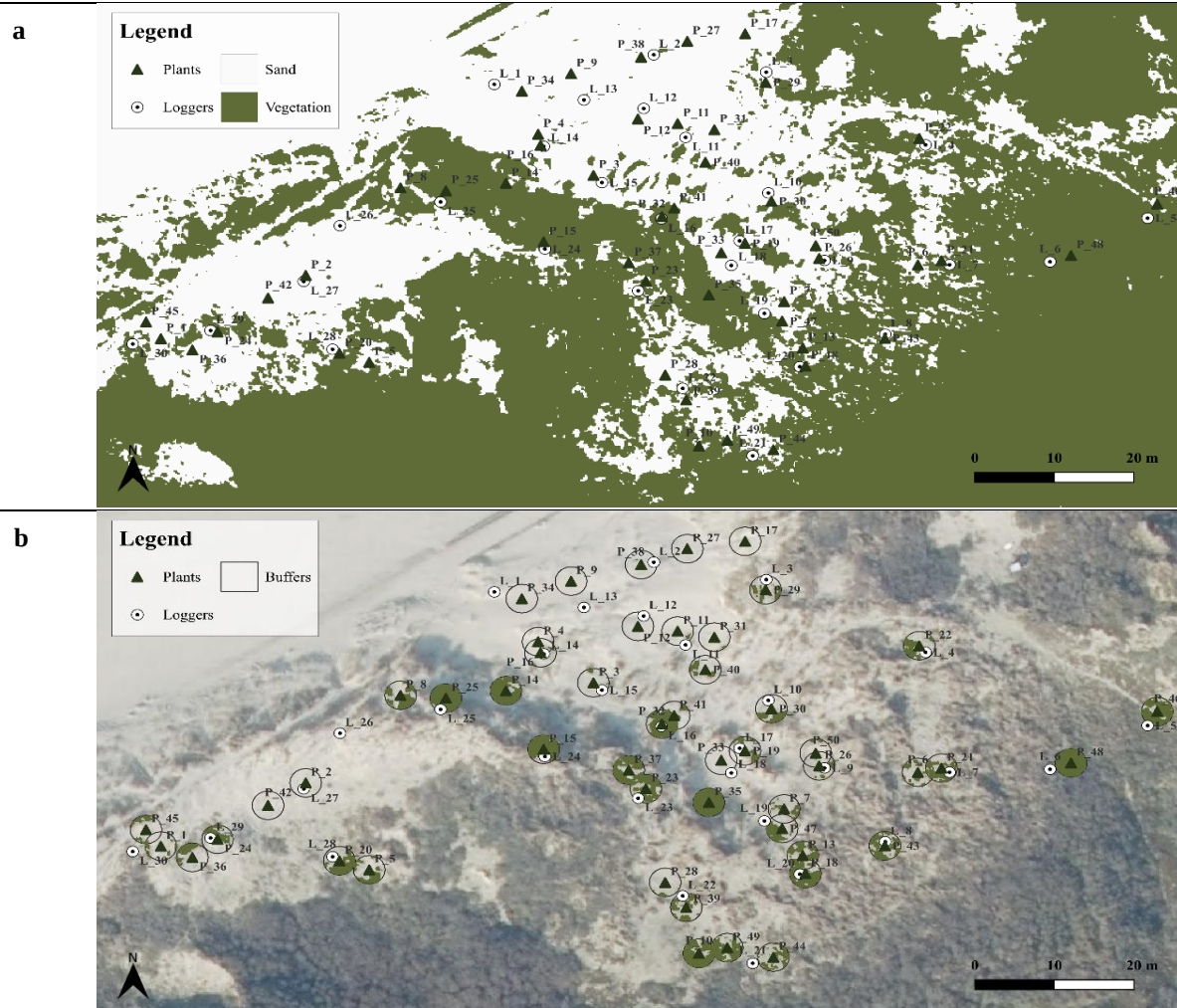


Fig 13. Visualization of data-collection process in QGIS, plants and loggers are always represented as dark green triangles and white dots, respectively; a) Closest logger for each plant (red lines); b) Binary vegetation classification map (top) and extracted vegetation within the 2 meter buffers (bottom) | Made in QGIS (QGIS Development Team, 2024)

The habitat for each plant and logger was roughly estimated based on field observations (Appendix 2. & 3.), aerial photos, a broad-scale habitat overview of the region and detailed descriptions of dune habitats (Cosyns et al., 2019; Herrier et al., 2020) (Fig 14.).

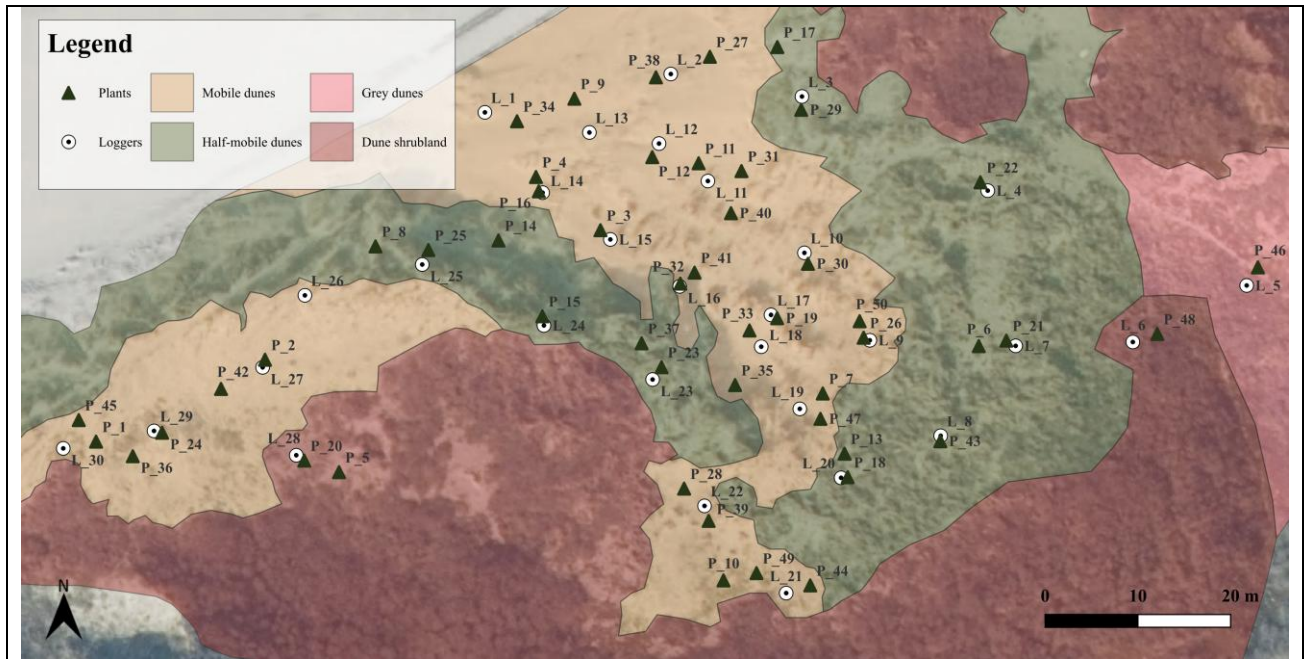


Fig 14. Dune habitats present in the experimental site, plants and loggers are always represented as dark green triangles and white dots, respectively | Made in QGIS (QGIS Development Team, 2024)

Data processing was conducted in R. Datasets were processed using the *tidyverse*, *dplyr*, *tidyr* and *lubridate* packages (Grolemund & Wickham, 2011; Hadley et al., 2023; Wickham et al., 2019, 2024).

Initial data exploration was done to obtain an overview of the structure of each dataset and general patterns within the data. These explorative plots and remarks made during the initial data exploration can be found in the Appendix (Appendix 4. & 5.). Based on the initial exploration, faulty measurements became apparent for T3 (atmospheric temperature) of Logger 4. A lower limit of -20°C was established and all values below were changed to NAs to correct this.

Several data frames were generated based on the initial datasets. Since there were 5 height and width measurements per plant per day of fieldwork, these were summarized by calculating the mean and standard deviation as to obtain one average height and one average width per fieldwork day per plant. Similarly, the sand height data from the sticks was summarized by taking the mean over all measurements per plant, to obtain a mean change in sand height over the course of the experiment. Herbivory was tracked in a separate dataframe by denoting the initial date a plant was marked as “chewed” as well as all subsequent dates. Two data frames were created from the abiotic parameters measured by the loggers: 1) a continuous dataset from start (3rd of July, 00:00AM) to finish (7th of October, 23:59PM) of the experiment and 2) a filtered dataset containing data 7 days prior to and including each fieldwork day. For the latter, a summarized dataset was created where maximum, minimum, mean, median and coefficient of variation (standard deviation/ mean) were calculated for each abiotic variable. This second dataset was only used for data exploration.

To further optimize the results of this thesis, Inverse Distance Weighted (IDW) interpolation was performed on the logger data in QGIS using the “IDW interpolation” tool. This method predicts values for unmeasured

locations based on their proximity to measured points (Shepard, 1968). Data used for IDW consisted of the X,Y coordinates, minimum, maximum, mean, median and coefficient of covariance for all temperatures and soil moisture levels per plant over the entire duration of the experiment¹. IDW was executed for all calculated values of the atmospheric, surface and soil temperature as well as the soil moisture. Predicted values for the exact coordinates of each individual plant were then extracted and exported for further use in R.

3.6. Statistical model

Multivariate analysis was conducted in R using the *FactoMineR* and *factoextra* packages (Kassambra & Mundt, 2020; Lê et al., 2008). Two data frames were generated: one focussing on plant growth during the experiment, as such containing the slope of the mean leaf height, width, their standard deviations and lateral density over time, as well as the difference in shoot number between the start and finish of the experiment. The second one contains all the interpolated abiotic logger data from the IDW calculation. Principal Component Analysis (PCA) was performed on both datasets for different reasons. The plant growth PCA on the one hand should show similarities in growth proxy measurements between individual plants over the course of the experiment, revealing potential clusters. Cluster-analysis was performed by including factors such as habitat or the closest logger for each plant and calculating 95% confidence ellipses in an attempt to identify the driver behind cluster formation. The abiotic data PCA was more used to summarize the different temperature and soil moisture calculations in Principal Components (PCs). A Scree plot of the eigenvalues was used to determine the contribution of each PC to explaining the variation in the data. The PC-scores of each plant for the most important PCs could then be used in the statistical model (see further) as approximations for the abiotic conditions.

To uncover the underlying mechanisms of the microclimate-plant growth relationships, I used **Structural Equation Modelling (SEM)**. SEM relies on a set of pre-determined causal relationships between variables in a given system (Lefcheck, 2016). Relationships are represented as additive linear equations, which are used to calculate the magnitude of the effect one variable has on another.

A base model was constructed consisting of four levels of measured variables: (1) experimental design (elevation, distance to sea and vegetation cover), (2) drivers of plant growth (contains the most important axes of the abiotic PCA-analysis and sand burial), (3) plant growth proxies (shoot difference, change in leaf height and change in leaf width) and finally, (4) the emerging plant property, which was measured as the lateral density of each individual (Fig 15.). The relationships between these variables were based on existing literature and critical evaluations.

First of all, the experimental design layer (1), which is expected to influence the plant growth drivers (2), i.e. the microclimate, contains the distance of each plant to the sea, as it dictates sediment transport dynamics, local temperature gradients and soil moisture levels (Cosyns et al., 2019; Wartena, Van Boxel, et al., 1991). Furthermore, elevation creates complex wind patterns, in turn changing sand burial patterns (P. A. Hesp, 1989; Wartena, Van Boxel, et al., 1991). It also determines access to the groundwater table and creates more exposure to solar radiation and evaporation, all influencing the local temperature and moisture (Homburger et al., 2024; Ott & van Aarde, 2014; Wartena, Van Boxel, et al., 1991). Lastly, vegetation cover creates micro-variations in temperature and soil moisture by reducing exposure, reflecting solar radiation and limiting soil moisture evaporation (Wartena, Van Boxel, et al., 1991). Vegetation structure and species-composition also determines sand entrapment at a local scale (Reijers et al., 2019).

¹ This is not to be confused with *summarized_abiotic_data*, which contains these values calculated over a 7-day period before each fieldwork day

Furthermore, I expect the drivers of plant growth (2) to affect the plant growth proxies (3). Previous studies have shown sand burial drives a growth response in *Ammophila* (Ivinskis & Andersone-Ozola, 2020; Konlechner et al., 2013; Maun, 1998; Nolet et al., 2018). Moreover, biomass and tiller production in marram shows a neutral to positive response to temperature in a controlled environment according to Biel & Hacker (2021). Finally, several indicators imply an effect of soil moisture on marram growth as both plant establishment and mortality is defined by soil moisture levels (Dixon et al., 2004; Homberger et al., 2024, 2025; Lammers, Berghuis, et al., 2024).

The final level contains the emerging plant property (4), in this case the lateral density as it should represent the approximate sum of the number of shoots, leaf lengths and leaf widths for each plant. Although these relationships are based on existing literature, which often concludes a directed response for each variable, I do not necessarily expect a similar response as my studies takes place at a much smaller scale.

Multiple additional SEM-models were built and compared to the base model as well as each another to find the best fitting structure for the data. The Akaike Information Criterion (AIC) was used to determine best fit as it is an estimator of prediction error which rewards goodness-of-fit while penalizing overfitting (Stoica & Selen, 2004). Therefore, the model with the lowest AIC should simultaneously explain the greatest amount of variation with the fewest possible variables.

The SEM-models were constructed in R using the *piecewiseSEM* package and a compiled SEM dataset (Lefcheck, 2016). This dataset contained the slopes and difference in growth proxies over time, broadened by the abiotic PC-scores derived from the multivariate analysis, the mean sand height difference, the elevation, vegetation cover and distance to sea per plant. Since each relationship represents a linear model, assumptions for independence, normality, linearity, variance and multicollinearity were checked for all of them.

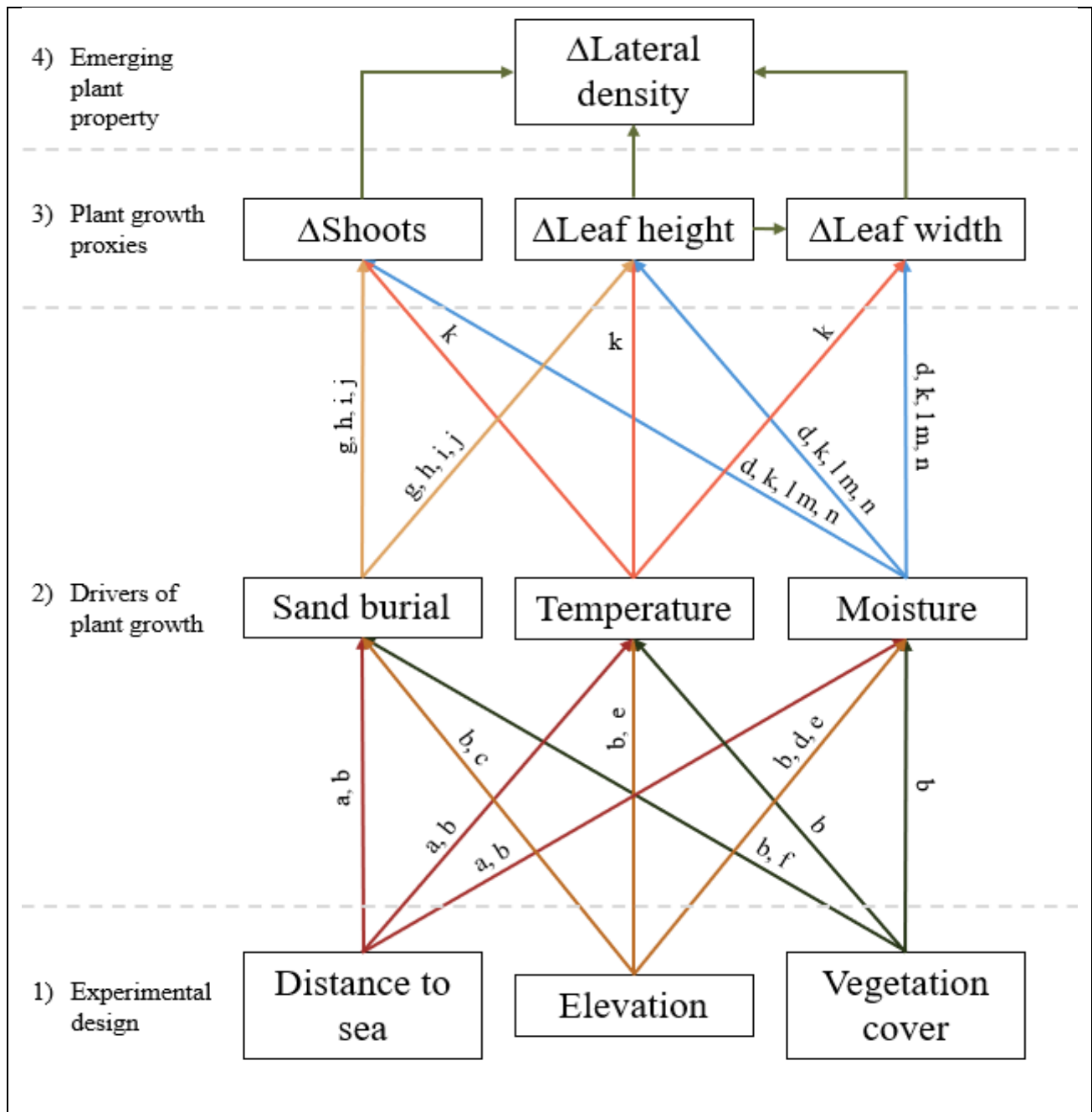


Fig 15. SEM-model of how microclimatic parameters affect plant growth and are themselves affected by elevation, distance to sea and vegetation cover. The model is divided in 4 levels, each containing measured variables: (1) experimental design (elevation, distance to sea and vegetation cover), (2) drivers of plant growth (contains the most important axes of the abiotic PCA-analysis and sand burial), (3) plant growth proxies (shoot difference, change in leaf height and change in leaf width) and finally, (4) the emerging plant property, which was measured as the lateral density of each individual. The arrows represent the relationships between the variables, and their colour shows from which variable each relationship emerges.

a) Cosyns et al., (2019); b) Wartena, Van Boxel, et al. (1991); c) P. A. Hesp. (1989); d) Homberger et al. (2024); e) Ott & van Aarde (2014); f) Reijers et al. (2019); g) Levinsh & Andersone-Ozola (2020); h) Konlechner et al. (2013); i) Maun (1998); j) Nolet et al. (2018); k) Biel & Hacker (2021); l) Dixon et al. (2004); m) Homberger (2025); n) Lammers, Berghuis, et al. (2024)

4. RESULTS

4.1. General patterns

The field data revealed certain patterns within the plant growth proxies (Fig 16.). Firstly, most experimental individuals showed a slight decrease in growth response over the duration of the experiment (Fig 16a., b. and c.). Especially the lateral density diminished drastically right after the initial set-up (Fig 16a.). The decrease in mean leaf height was more moderate across the measured plants, although some individuals exhibited stronger declines such as P_9, 20, 24 and 44 (Fig 16b.). Leaf width did not show a steady increase or decrease but rather an optimum around early September after which the width measurements dwindled for most plants (Fig 16c.). This reduced growth seen in the aforementioned proxies was not reflected in the final proxy, the number of shoots (Fig 16d.). Here, most experimental marram grasses improved their shoot count across the growth season, with individuals like P_5, 12 and 16 experiencing an increase of 25 shoots or more. A few of them did show a minimal to moderate decrease in shoots, in example plants 2, 29, 41, 47 and 50, with some even maintaining the exact same number of shoots over the whole experiment, being P_28, 35 and 44. The second observable pattern was that certain individuals performed poorly across the entire experiment. Notably, PlantID 47 had a much lower average leaf height and lateral density measure compared to others on every fieldwork day. Furthermore, P_47 started with the lowest shoot number at the start of the experiment and ended with an even lower count. Individuals such as 47, but also 7 and 17, revealed a third pattern where plants who started with low measurements usually continued this trend until the end. The opposite scenario is not as pronounced, initially superior performers like plant 15, 28 and 45, did not maintain high measurements throughout the experiment. There are some exceptions with individuals 32 and 37 performing equally or better towards the end, however this trend was not reflected in all growth proxies.

Herbivory which was tracked for each plant on each field day as the number of 'chewed' plants per field day (Fig 16e.), showed an increase that can be seen until the beginning of August, eventually plateauing. Out of all 50 plants, 33 showed signs of herbivory by the end of the experiment, characterized by variation in severity.

As for the abiotic data, there seemed to be less variability in soil temperatures (T1) than for surface (T2) and atmospheric (T3) temperatures across loggers (Fig 17a.). Minimum soil temperatures varied between 6°C and 13°C during which maxima ranged from 24°C to 34°C. Loggers 6, 9, 13, 16, 23 and 24 overall had a slightly cooler microclimate as soil temperatures remained below 27°C. Other loggers such as 3, 5, 10, 11, 12, 21 and 30 showed warmer soil temperature ranges, exceeding 32°C. The (type of) temperature range also varied as some dataloggers, for example logger 11, 12, 19 and 21, had broader, spread-out soil temperatures, stretching over 24°C from minimum to maximum temperature. On the other hand, loggers 6, 9, 23 and 27 had a narrower distribution, only ranging roughly 16°C. A similar pattern occurred in T2 and T3 temperatures although at higher extremes. The smallest distribution ranges, found for loggers 2, 10 and 24, already exceeded 26°C, with the largest spanning up to 46°C, seen in L_5. Minima of almost -2°C atmospheric temperature could be found for several loggers, including L_5, 20 and 28, as well as maxima of 45°C, found in L_14. Surface temperatures showed slightly higher minimum temperatures with only one logger, L_21, going below zero. However, surface temperatures reached 49°C, as seen in logger 30, considerably exceeding atmospheric and soil temperature maxima. Although distribution-variation was much higher for T2 and T3 than for T1, their means all varied similarly between 17°C and 21,5°C. They also indicated similar, though not identical, cooler and warmer microclimates to soil temperature with L_9, 13, 16 and 24 being on the colder side and L_5 and 30 being warmer. Other loggers had different microclimate interpretations based on surface and atmospheric temperature such as logger 2, 6, 10 and 27 having a colder range, while 8, 14 and 26 had warmer T2 and T3 microclimates.

Soil moisture showed a high degree of variation as well (Fig 17b.). Loggers ranged from lower limits of 742 to 1171 millimetres of soil moisture while the upper limits lied between 1339 and nearly 3000 millimetres. The moisture distribution was irregular across loggers with some, like L_4, 8, 14 and 18, showing small ranges of around 400 millimetres and others, such as L_20 and L_23, covering over 1900 millimetres from minimum to maximum. Drier soils could be found around loggers 2, 4, 8, 13, 14, 15 and 18, with some such as L_8 and L_14 being part of warmer microclimates and L_2 and L_13 ranging cooler temperatures. High moisture areas occurred around several loggers including logger 5, 20, 21, 22, 23 and 30 but again there did not appear to be a strict relationship between soil moisture and temperature as some loggers (e.g. 20 and 23) experienced colder temperatures while others (e.g. 5 and 30) had a hotter environment. Overall, the mean soil moisture approximately ranged between 1000 and 1410 mm over the entire site and duration of the experiment.

Finally, the sand height change over time, measured near each plant (Fig 17c.). For certain marram grass individuals, such as P_1, P_18, P_24 and P_32, a strong sand increase was measured from start to finish. Most other individuals showed either an overall decline in sand height, such as plant 3, 6 and 9, or fluctuated between sand accumulation and sand depletion, seen in P_24, 38 and strikingly in P_42. The latter showed a relatively disproportionate sand height increase which eventually diminished to levels more in line with all other measurements. Lastly, nearly half of all plants maintained a stable sand height during the whole experiment, where weekly field measurements showed little to no change compared to T0.

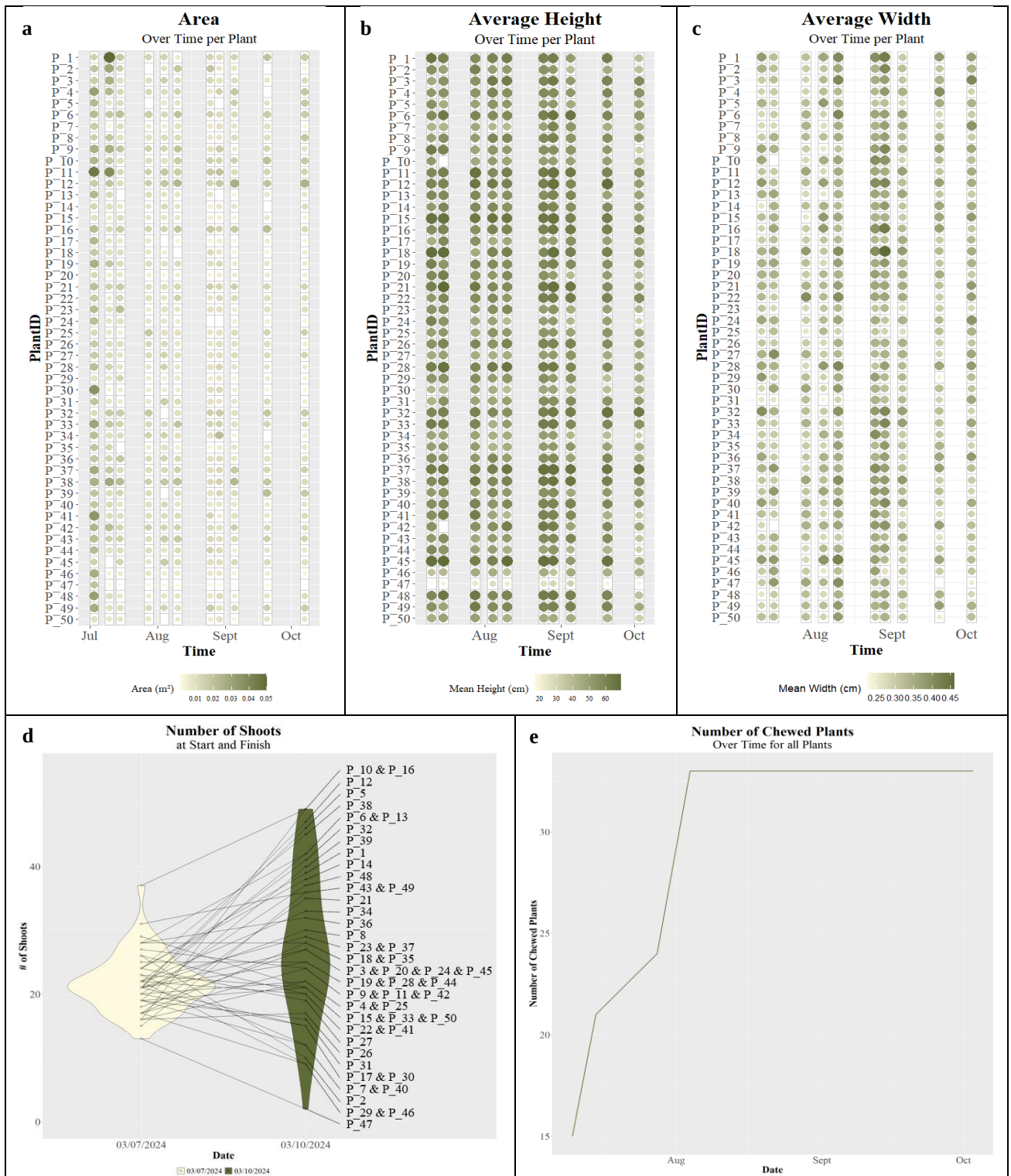
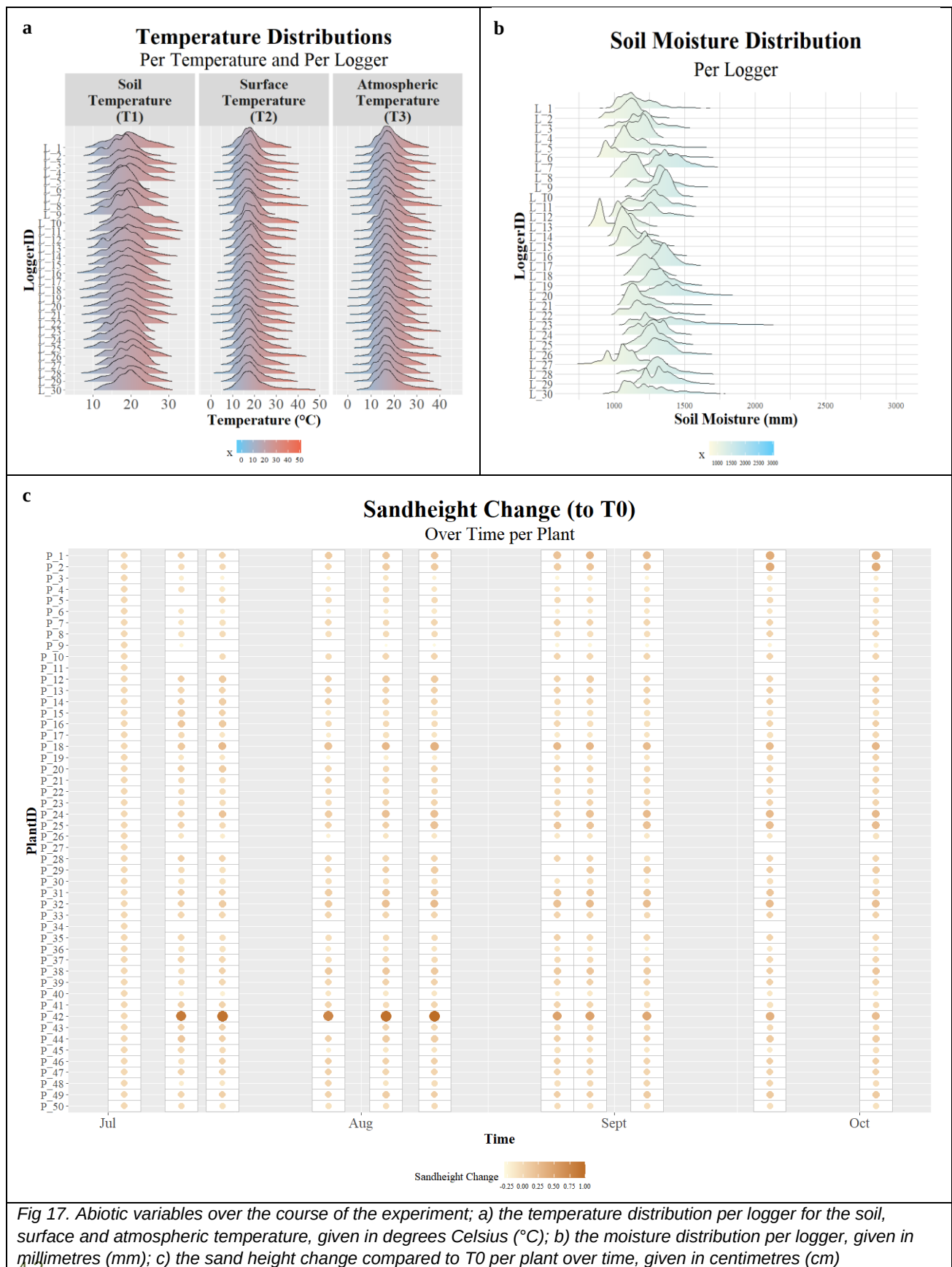


Fig 16. Growth proxy measurements over the course of the experiment, NA's are represented by empty tiles; a) lateral density over time per plant, measured as the area in squared meters (m²); b) the average leaf height over time per plant, measured in centimetres (cm); c) the average leaf width over time per plant, measured in centimetres (cm); d) the number of shoots at the start (3rd of July 2024) and finish (3rd of October 2024) of the experiment with lines connecting measurements from the same individual; e) number of chewed plants over time for all plants.



4.2. Correlograms

Derived interpolated measures such as minimum, maximum, mean, median and coefficient of covariance of abiotic logger data (T1, T2, T3 and soil moisture) over the whole duration of the experiment, showed correlations with one another. First and foremost, all measures derived from the atmospheric, surface and soil temperatures were tightly correlated with one another (Fig 18.). Hence, all temperatures measured by the different datalogger sensors were interlinked. Soil moisture was also tied to temperature, although correlations were overall weaker and on the negative side (Fig 18.). In addition, there were two remarkable correlations: a positive one between soil moisture and maximum surface temperature (T2 Max) and a strong positive relation between the moisture coefficient of covariance (Moisture CoV) and all derived temperature measures. Lastly, the derived moisture measures showed more variable correlations with each other compared to temperature measures, ranging from moderately negative to strongly positive.

Correlograms for sand burial and aspects of the experimental design, being the surrounding vegetation cover, distance to sea and elevation of every plant, can be found in Fig 19. The correlograms for derived soil (T1), surface (T2) and atmospheric (T3) temperatures implied a positive relationship with elevation and a negative one with the distance to the sea border (Fig 19a., b. and c.). On the other hand, the association with vegetation cover was rather weak or even non-existent for multiple derived temperature measures. Soil moisture maintains weaker correlations with all three experimental design parameters (Fig 19d.); it is slightly positive for surrounding vegetation and sea distance while rather negative for elevation. Here, the moisture coefficient of covariance also formed the exception, upholding similar relationships with these experimental parameters to temperatures. Ultimately, sand burial had a faintly positive relationship with the local vegetation and elevation while showing almost no link with distance to sea (Fig 19e.).

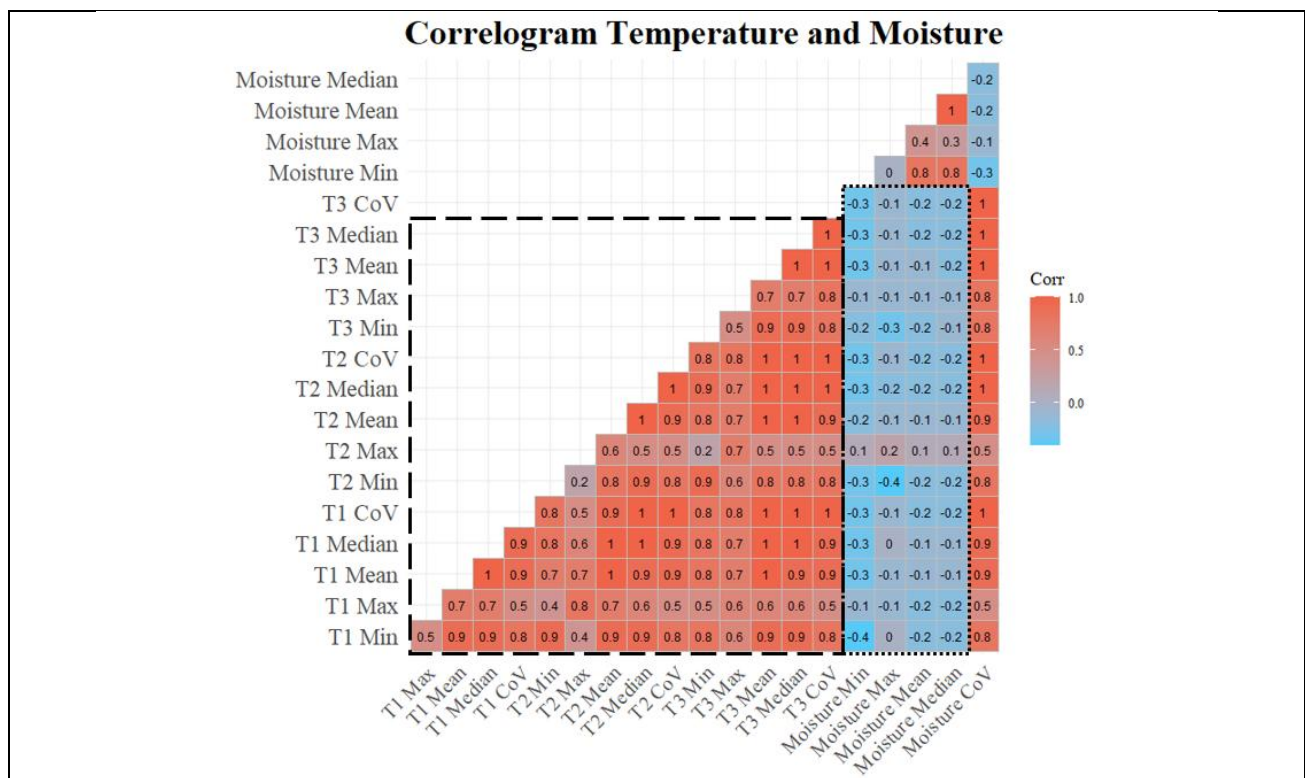


Fig 18. Correlogram of all interpolated derived measures for soil (T1), surface (T2) and atmospheric (T3) temperature as well as soil moisture. Positive correlations between the derived measures for all temperature variables are indicated by the dashed lines. Negative correlations between the derived temperature and soil moisture measures are indicated by the dotted lines. Red and blue represent positive and negative correlations, respectively

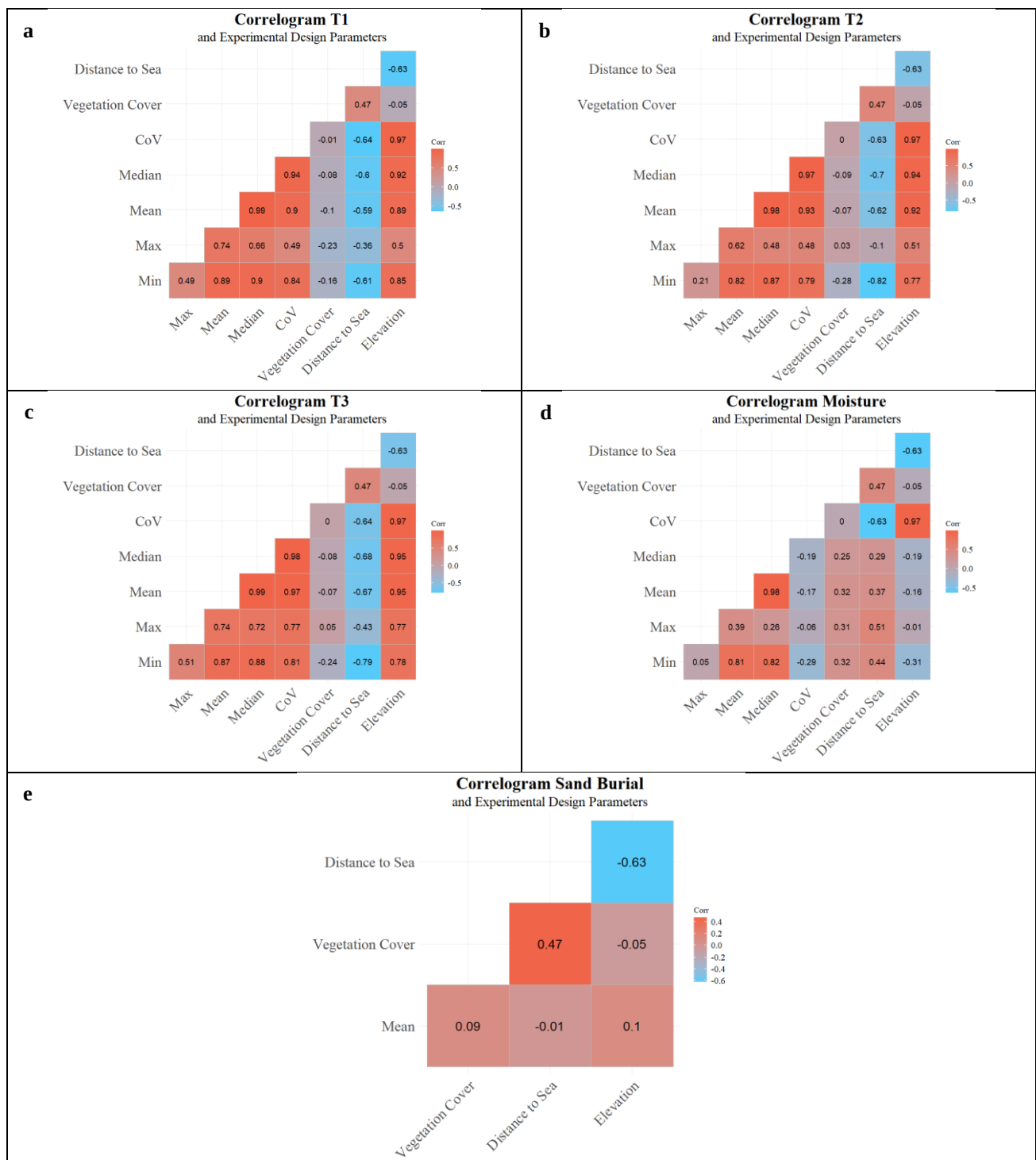


Fig 19. Correlograms of all interpolated abiotic variables and their derived measures alongside the experimental design parameters of vegetation cover, distance to sea and elevation of each plant. Positive correlations are indicated by red; negative correlations by blue; a) Correlogram for soil (T1) temperature measures and experimental design parameters; b) Correlogram for surface (T2) temperature measures and experimental design parameters; c) Correlogram for atmospheric (T3) temperature measures and experimental design parameters; d) Correlogram for soil moisture measures and experimental design parameters; e) Correlogram for mean sand burial and experimental design parameters.

4.3. Multivariate analyses

I performed 3 kinds of PCA: one on the plant proxy data, and two on the abiotic logger data. The multivariate analysis for plant growth proxies showed four total PCs with PC1, 2 and 3 describing 88.47% of the variance in the data (Appendix 6.). The first principal component (PC1) accounted for 37.35% of the total variance of the dataset. It is strongly positively correlated with lateral density (*Area_slope*), shoot difference (*Shoots_Difference*) and mean leaf height (*Mean_Height_slope*). PC2 explains 26.90% of the variation in the data and is strongly positively correlated with the mean leaf width (*Mean_Width_slope*). Furthermore, lateral density and leaf height are subsequently negatively and positively correlated with PC2. At last, PC3 explains an additional 24.22% of variance and is itself defined by a positive relation with differences in shoots and a negative relation with leaf height change. The complete output for all principal components can be found in the appendix (Appendix 6.).

The PCA-analysis provides additional insights in the relationships between the plant proxies. First, it suggests a positive correlation between the change in mean height and mean width of the leaves. A stronger positive correlation can additionally be found between shoot difference and the slopes of leaf height with lateral density, respectively. On the other hand, changes in leaf width show little to no correlation with shoot difference and lateral density. Second, clustering occurs almost near the centre of the biplot, with a slight bias towards the left of PC2, indicating that most samples show a homogenous response across the different growth proxies.

To identify the underlying driver behind this cluster, a cluster-analysis was executed for plant habitat, representing the broad scale climate (Fig 20a.). This analysis did not reveal any clear clustering explanations. Plants located in mobile dune habitats show a wide range of responses along both the first and second principal component, thus for all plant growth proxies. In contrast, plants in more stabilized half-mobile dune habitats are biased towards PC1 indicating their differential growth responses can mostly be explained by changes in leaf height, lateral density and shoot numbers while their leaf width change remains similar. There were not enough individuals planted in grey dunes (only 1 plant) or dune shrubland habitats to obtain confidence ellipses. Even so, points are again spread out along the first principal component for dune shrublands.

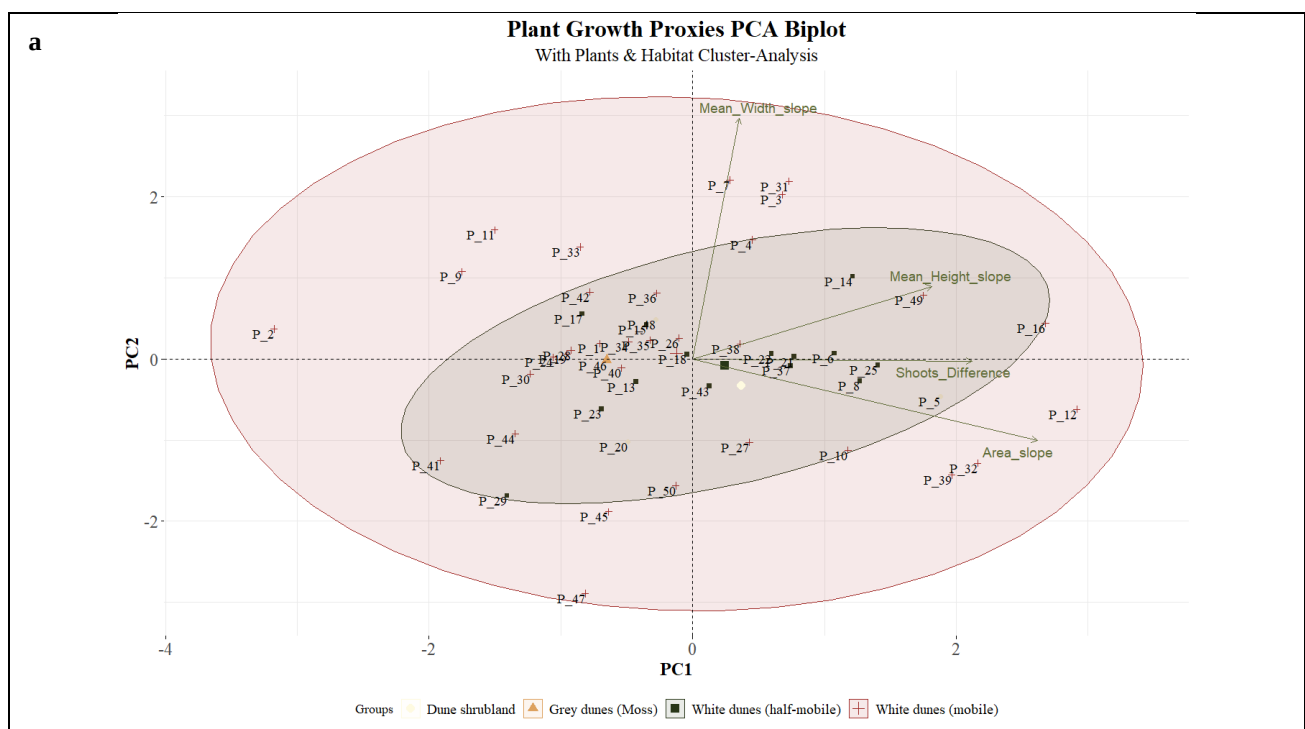
A first abiotic principal component analysis was conducted on the moisture and temperature measurements for each logger. This PCA described 20 dimensions, with PC1, 2, 3 and 4 having a cumulative variance of 82.79% (Appendix 7.). The first PC explained a large chunk of this variance, contributing 34.60%. It was exclusively positively correlated with temperature variables with soil, surface and atmospheric temperature contributing similar amounts. PC2, 3 and 4 respectively explained 22.26, 14.00 and 11.93% of variance in the data, all being defined by a mixture of derived soil and temperature measures. For most of these axes, soil moisture calculations showed the highest correlations, especially in PC3 and PC4. Nevertheless, several T1, T2 and T3 measures had a decent contribution as well.

The biplot of the first abiotic PCA was used to assess patterns of similarity in abiotic measurements between loggers and, by making use of cluster-analysis, different habitats (Fig 20b.). Most loggers were dispersed along the second PC, suggesting they differed in soil moisture and certain temperature measures, including among others all minimum temperatures (*T1_min*, *T2_min* and *T3_min*), all temperature coefficients of covariance (*T1_CoV*, *T2_CoV* and *T3_CoV*) and the maximum surface temperature (*T2_max*). Some smaller clusters were spread along PC1 as well, comprising L_6, 9, 16 and 24 whose differences were thus exclusively temperature based. Overlaying the habitat of the different loggers showed that in both mobile and half-mobile dune habitats loggers exhibited a wide array of temperature and moisture responses and were spread out across both PCs. Here, the number of loggers in

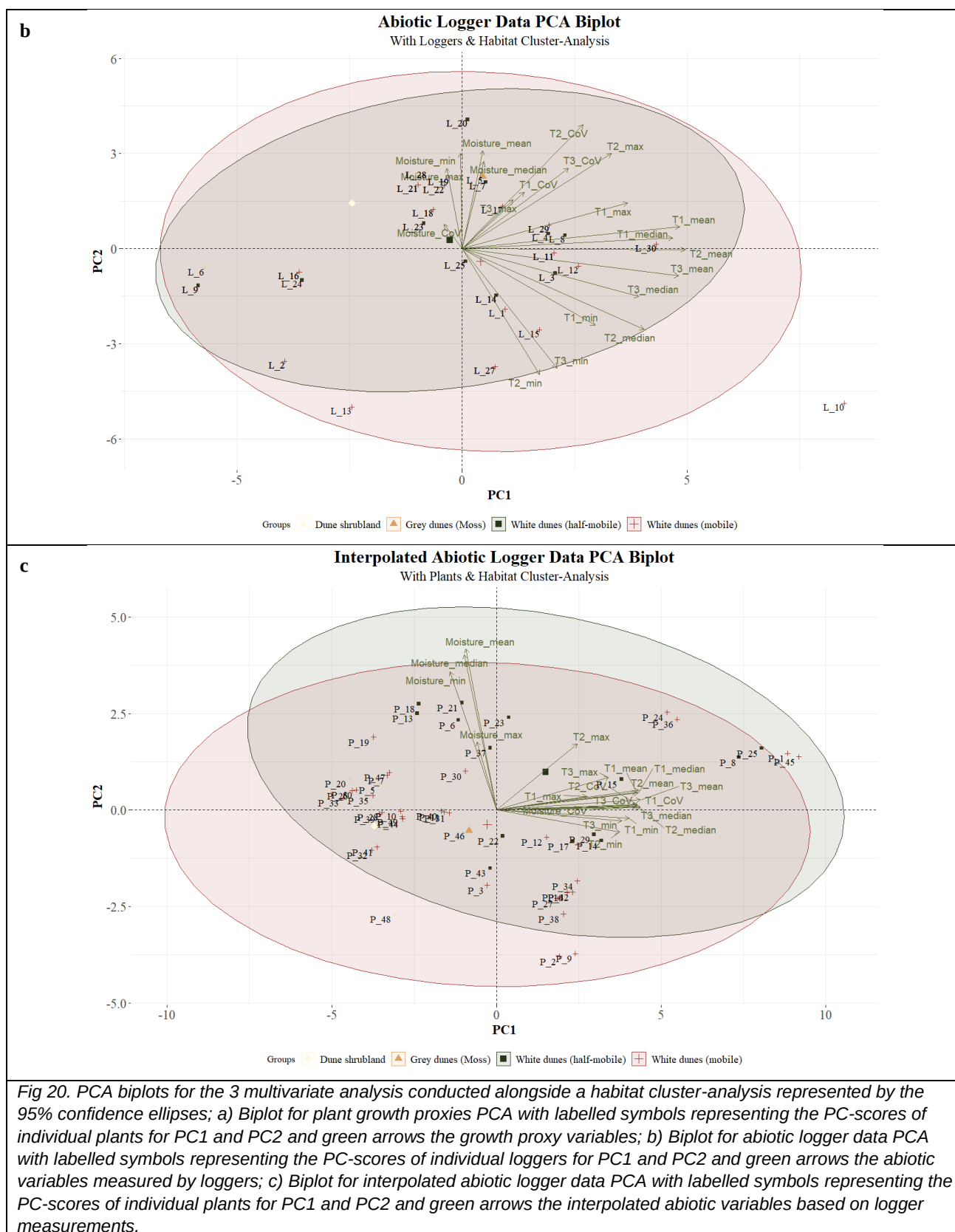
grey dunes and dune shrublands was again too small to calculate confidence ellipses but overall, there does not seem to be a clear relationship between habitat and the abiotic variables measured by loggers.

The second abiotic multivariate analysis, done for all interpolated abiotic logger data² also described 20 dimensions in total with PC1 and PC2 having a cumulative variance of 80.83% (Appendix 8.). Principal component 1 described most of this variance, contributing 66.76%, and was almost exclusively positively correlated with temperature variables. One exception was the positive correlation with the coefficient of covariance for soil moisture measurements, a relationship already highlighted previously by correlation-calculations. The mean atmospheric temperature had the highest correlation, although soil, surface and atmospheric temperature contributed to the PC1 axis in about equal amounts. PC2 had a much lower total variance of 14.07% and showed a strong positive correlation with minimum, mean and median soil moisture. Maximum moisture (*Moisture_max*) and surface temperature (*T2_max*) had far less correlation with PC2, although they were still notable contributors. In conclusion, PC1 and PC2 could thus be defined as the temperature and the soil moisture aspect of the microclimate. Consequently, the PC-scores of each plant for PC1 and PC2 were used as approximations for their microclimatic temperature and soil moisture, respectively, in the final SEM-model.

Visualisation of the second abiotic PCA allowed for a comparison with the biplot for plant growth proxies to see if any patterns in plant-clusters arose (Fig 20a. and 20c.). This was not the case with plants showing a similar growth response not necessarily existing in the same (temperature and soil moisture) microclimates, and vice versa. Some examples include P_3, 7 and 31 clustering on the plant growth biplot while being spread out across PC2 on the interpolated abiotic data biplot; Another cluster includes plants 1, 8, 25 and 45 all displaying temperatures and soil moisture much alike despite having different growth proxy responses. Habitat cluster-analysis showed once more there is no immediate relationship between a plants habitat and predicted abiotic environment.



² For clarification, the second abiotic PCA differed from the first in that it used the interpolated estimates of the logger data for each plant and not the raw data measured by each datalogger.



4.4. SEM-model

A total of three SEM-model structures were fitted and compared to one another (Appendix 9.):

- The base model or Model 0,
- Model 1 containing additional links from distance to sea of each plant to the plant growth proxies
- Model 2 which maintained the structure of Model 1 but has removed the change in mean leaf width and all its relationships.

The reasoning behind Model 2 was the fact that leaf height and width are inherently correlated as they contribute to the same plant structure. Moreover, the multivariate analysis also showed a positive correlation between these variables. Thus, removing leaf width could simplify the model without losing much information. Models 1 and 2 both held the same AIC value of -4046.184 and remarkable goodness-of-fit statistics, namely a Chi-Squared of 9.611 ($p = 0.975$) and a FisherC of 22.259 ($p = 0.956$) indicating the hypothetical model structure did not differ significantly from the relationships implied by the data. However, the base model had an even better fit with significance levels of 0.986 and 0.978 for the Chi-Squared- and FisherC-test, respectively. Moreover, the lowest AIC value belonged to the base model, subsequently defining it as the final SEM-model for further analysis (Appendix 9.).

Assumptions were checked for every linear equation within the final model (Table 1). These were overall met, apart from the following: skewed residual distribution in Δ Lateral density and Δ Leaf height, heteroscedasticity in Δ Shoots, non-linearity in Δ Leaf height and Moisture and slight multicollinearity ($VIF < 5$) in Temperature and Moisture. Due to negative values in most datasets, simple log- or squareroot-transformations were not possible to correct for normality and homoscedasticity deviations. More complex transformations were not considered as they complicate model interpretation. Non-linear relationships were addressed by squaring the appropriate predictive variable, this entailed the PC2 predictor in the Δ Leaf height linear equation and the Elevation predictor in the Moisture equation. After implementing the necessary transformations, a final SEM-model was established (Table 1. and Fig 21.). Its global goodness-of-fit was indicated with a Fisher's C statistic value of 65.317 ($p = 0.636$) and the lowest AIC-score out of all the tested models ($AIC = -4056.370$), implying it excels at describing the most data-variation using the least number of variables.

The model output (Appendix 10.) could be expressed in a hierarchical manner, starting with the bottom level, the "Experimental design", which contained the distance to sea, elevation and vegetation cover in the vicinity of each plant. The distance between the sea border and the individual, seemed to significantly impact both temperature and soil moisture, although in opposing directions with standardized estimates of respectively -0.1484 and 0.4875 (both $p < 0.05$). Sand burial was positively influenced by inland distance with a standardized estimate of 0.0375, although not significant. The same pattern arose for elevation, significantly affecting the local temperature and soil moisture with standardized predictions of respectively 0.8576 and 0.3767 ($p \lll 0.05$ and $p < 0.05$), and non-significantly improving sand burial with 0.1299 centimetres per metre of increased elevation. It should be noted that in the case of soil moisture, this estimate was calculated using the squared elevation. Finally, despite not having any significant relationships, vegetation cover did increase sand burial and soil moisture (Std. Est. = 0.076 and 0.1223, respectively) while having a very slight negative effect on temperature (Std. Est. = $-8.00 \cdot 10^{-4}$).

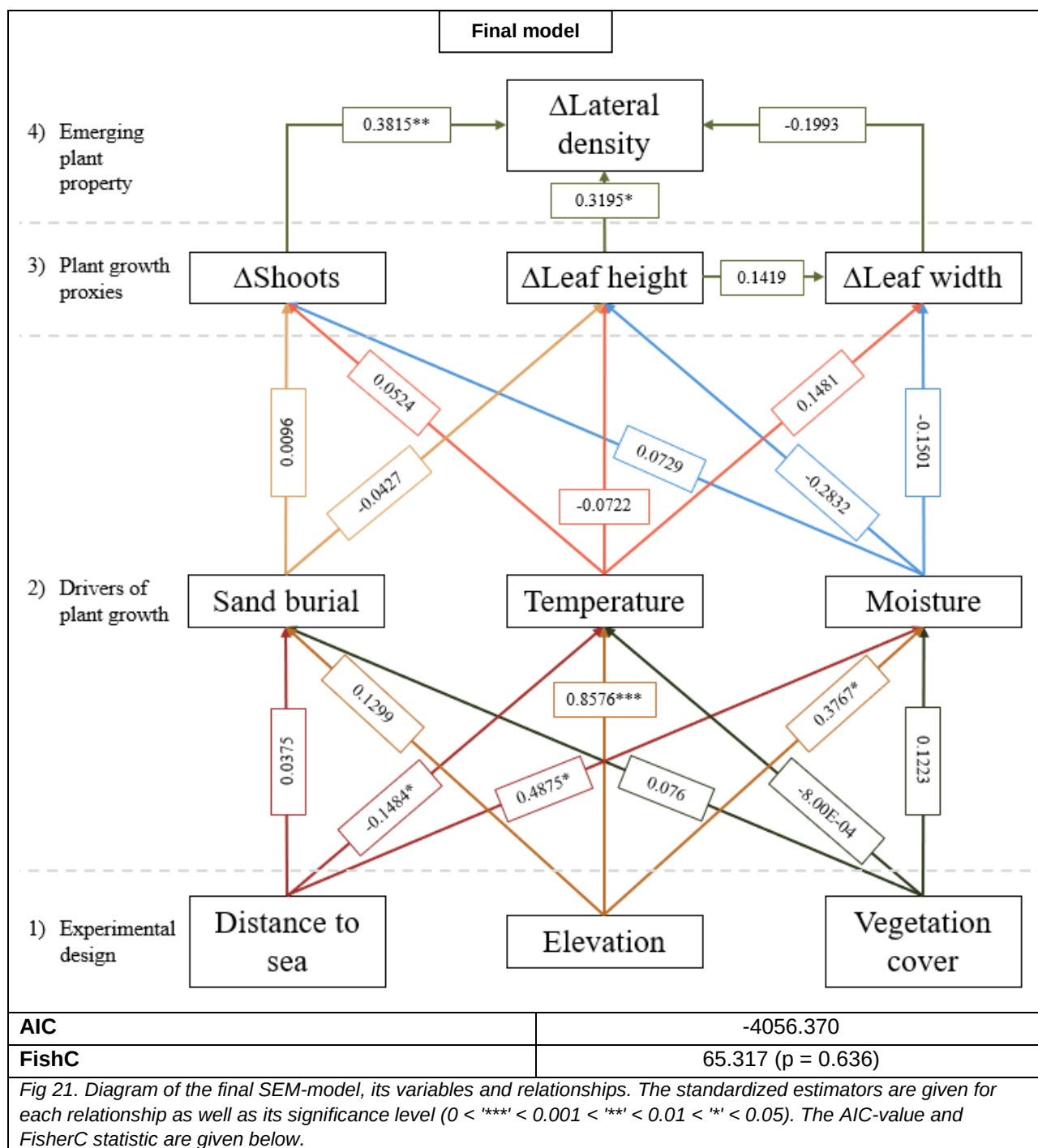
On the second level of the model, the drivers of plant growth, such as sand burial, temperature and soil moisture, did not appear to drive the plant growth response to a significant extent for any of the proxies. Regardless, the model implies sand burial does marginally drive shoot difference (Std. Est. = 0.0096) and inhibit mean leaf height change (Std. Est. = -0.0427). Temperature appeared to increase shoot number and mean leaf width, whilst simultaneously decreasing mean leaf height change with corresponding estimates of 0.0524, 0.1481 and -0.0722. At last, soil moisture had predicted effects equating to 0.0729 on the number of shoots, -0.2832 on the change in mean leaf height and -0.1501 on width change, implying a

stronger negative effect on leaf characteristics and a faintly positive one on shoot number. It should be pointed out that the relationship between mean leaf height and the squared soil moisture is approaching significance ($p = 0.056$). P-values near the threshold should be interpreted with care since the final model fails to meet certain assumptions.

Concluding with the third level, consisting of the plant growth proxies being shoot difference and change in mean leaf height and width. Within this level, one relationship was defined between the change in mean leaf height and width. The model predicted an increase of 0.1419 centimetres in leaf width change with every centimetre of change in leaf height, although this relation was notably not significant. All variables except mean leaf width significantly acted on the uppermost level, the emerging plant property which was described as the lateral density change of the plants. For change in mean height, an effect with magnitude 0.3195 ($p < 0.05$) was found, while the shoot difference had a standardized estimate of 0.3815 ($p < 0.05$). The relationship between mean leaf width change and lateral density, though not significant, was negative with an estimate of -0.1993.

Altogether, the results of the final SEM-model pointed out a clear effect of the experimental design on the suspected growth drivers. In turn, these microclimatic abiotic parameters did influence the growth proxies of the marram plants, although not significantly, which overall affected lateral density. Essentially what the model shows is that there were significant differences in abiotic parameters, in other words microclimates, within our experiment that were driven by distance to sea and elevation. These abiotic parameters, being sand burial, temperature and soil moisture, did not appear to have significant relationships with the growth of the individual plants but their effects did still differ from zero, suggesting an influence on growth nonetheless.

Variable	Linear equation
Δ Lateral density	<i>Area_slope</i> ~ Shoots_Difference + Mean_Height_slope + Mean_Width_slope
Δ Shoots	<i>Shoots_Difference</i> ~ PC1 + PC2 + Mean_Sandheight_Change
Δ Leaf height	<i>Mean_Height_slope</i> ~ PC1 + PC2_sq + Mean_Sandheight_Change
Δ Leaf width	<i>Mean_Width_slope</i> ~ Mean_Height_slope + PC1 + PC2
Sand burial	<i>Mean_Sandheight_Change</i> ~ Elevation + Sea_Distance_Plant + Cover_2M
Temperature	<i>PC1</i> ~ Elevation + Sea_Distance_Plant + Cover_2M
Moisture	<i>PC2</i> ~ Sea_Distance_Plant + Elevation_sq + Cover_2M
<i>Table 1. Linear equations for the final model after data transformations, the dependent variable is italicized. The squared predictors are indicated by '_sq' behind their name.</i>	



5. DISCUSSION

5.1. General patterns of plant responses within and among experimental plants

This field study of the timeseries of marram grass provided some early insights into how these plants responded to their environment. What became immediately apparent is that overall, the plants showed a severe decrease in lateral density, where most individuals had a moderate to strong decline in total leaf area a week after the start of the experiment. Several factors may have contributed to this pattern. Firstly, the plants were originally grown in a controlled lab environment and were only transplanted to the experimental site after becoming more robust. In consequence, the plants spent most of their early development before the experiment in optimal conditions, thereby minimizing all stressors on their growth. The sudden shift to a dynamic natural environment may thus have been paired with changes in growth and vigour, caused by variations in resource-availability, competition with other species and root-parasitism commonly found in the field as illustrated in Cosyns et al. (2019), Lammers, Reijers, et al. (2024), Reijers et al. (2021) and Van Der Putten et al. (1990). A second potential cause is herbivory, which may have contributed further to this data pattern as well as induced additional stress. The area where the experiment was conducted, is known to contain a fluctuating rabbit population, who seemed to prefer chewing on the fresh, young leaves belonging to our experimental plants rather than those of well-established, naturally occurring marram plants (Cosyns et al., 2019; Provoost et al., 2011, personal observations). Despite these potential causes, the other growth proxies, being the length of the plants and their shoot organisation, do not reflect this pattern to the same extent. However, herbivory may only be largely expressed in the lateral density data due to the data collection methods, thus explaining the dissimilarity with other proxies. For instance, chewed shoots were still considered to calculate shoot counts therefore not influencing these measurements. As for leaf heights and widths, although eaten leaves were not necessarily ignored, they may have been selected less for measurements purely by chance. Since only 5 leaves were measured per plant, this could skew the means for each plant significantly. Moreover, multiple people conducted the leaf measurements throughout the experiment, leading to inconsistencies in terms of leaf selection. If herbivory is considered the main cause for the initial reduction in lateral density, this would also explain why the area measurements show a far more moderate decline later in the experiment. That is to say, the herbivory data shows an increase until the beginning of August followed by a plateau, likely caused by plants settling and slowly withering making them less appetizing. This insinuates a decrease in herbivory as the experiment progressed, explaining why area measurements stabilized from then on.

Aside from this initial decrease in area, the experimental plants did show a mild, overall decline in vigour across most individuals. Although less obvious for leaf width, the mean leaf height and lateral density does generally go down towards the end of the experiment. Plants thus showed little signs of recovery after the initial set-up, except for shoot counts which did expand for most experimental grasses. Combined with the decline of the other proxies, this suggests the plants have obtained a 'stringier' appearance with shorter leaves and less overall aboveground biomass as the experiment continued. From these results it can thus be inferred the planted *Ammophila* favours extra shoot production over increasing leaf height and width. This may be an adaptation of marram to increase sand-trapping efficiency in a natural environment in hopes of acquiring more blown-in nutrients and promoting its own growth, which would be in line with the finding of Levinsh & Andersone-Ozola (2020), Nolet et al. (2018), Reijers et al. (2019) and Willis (1965).

The overall growth-decline was somewhat unexpected considering the experiment carried on throughout the growth season of marram grass. In addition, a recent study by Höfer et al. (2025) utilized a similar experimental design where marram plants were grown in the lab and transplanted as 4 month old juveniles, yet leaf height, width and shoot count all increased here. The marram grasses planted for this thesis were only lab-grown for 2.5 months. Hence, they may not have been robust enough to properly establish themselves in the natural dune environment, explaining their overall loss of vigour.

Finally, plant growth proxies showed expected signs of interrelatedness based on their multivariate analysis. Mainly changes in leaf height, shoot count and lateral density were closely associated to one another. On the other hand, width changes seemed more disconnected, except for their correlation with leaf height. Based on these associations and critical thinking, the lateral density change was considered as the emerging plant property within the SEM-model since it can be logically assumed leaf height, width and number of shoots all contribute to the total area of each marram plant. As predicted, the SEM-model indicated an increase in shoots and leaf height significantly promoted the lateral density. Contrarily, increased leaf width had an unexpected negative contribution to the plant's area which does not make sense and is likely the result of inaccuracy during width measurements. Namely, leaf heights and widths were measured using the same folding ruler with an accuracy of 1 millimetre. However, the height of marram leaves was, as anticipated, much larger than their width, causing the relative differences in heights across leaves to be much smaller. Since the measurement accuracy remained consistent for both, the smaller width measurements thus exhibited proportionally larger relative differences. This can also be seen in Appendix 4a., where leaf widths are distributed in distinct 'categories', while heights cover a broad range of values. The lack of width variation plausibly resulted in incorrect model predictions and may have further contributed to the lack of significant relation with leaf width within the SEM-model. Despite predicting larger height changes to co-occur with larger width-changes as expected, the magnitude of the estimated effect should be interpreted with consideration for width measurement errors.

5.2. A mosaic of abiotic gradients within the experimental dune site

The data collected by the climate loggers accentuated the intricate network of spatial gradients for abiotic parameters in coastal dunes. In the first place, surface and atmospheric temperature differences were rather pronounced, while soil temperature had a more stable distribution-variability across plants. The stability of soil temperature could be related to the fact that soil thermal properties are largely related to soil density and texture, as mentioned by Al-Kaisi et al. (2017), which should be relatively consistent across all logger sites. Nevertheless, the soils moisture also plays a major role in its temperature as this determines thermal conductivity (Wartena, Van Boxel, et al., 1991). Consequently, the highly variable soil moisture across loggers contributes to the slight variations seen among soil temperature distributions, in addition to those of the surface and atmospheric temperatures as a result of heat flux from the soil to the surrounding air. Despite their variations, this heat flux entailed all temperatures did have similar means over all loggers and showed high degrees of correlation with each other as shown in both the correlograms and the multivariate analysis for interpolated abiotic logger data. This insinuates soil, surface and atmospheric temperature are tightly interlinked at the microscale and thus will likely influence plant growth similarly.

Secondly, soil moisture also showed a considerable range of distributions with distinct dryer and wetter microclimates. For most derived measures, the soil moisture maintained a negative relationship with all temperature variables throughout the experiment. Higher temperatures are known to increase evaporation of soil moisture, explaining these correlations (Wartena, Van Boxel, et al., 1991). Nevertheless, some dryer areas within the experimental site had a lower soil temperature range and wetter soils were not necessarily colder, meaning other factors are also at play.

Elevation, for one, is indicated to have a considerable correlation with temperature by the correlograms and was additionally proven to be a strong and significant temperature-determinant by the SEM-model, with higher surfaces experiencing higher temperatures. This aligns well with the notion that more elevated areas experience more exposure to solar radiation, as explained by Wartena et al. (1991). Soil moisture exhibits a more nuanced picture where the correlograms imply a faintly negative correlation for most derived measures whilst the SEM-model predicts higher elevations are characterized by wetter soils. The difference in these results can be explained by the complexity of both calculations. Correlations simply consider a one-on-one relation between two variables, while the regressions within a SEM-model not only

review multiple variables but also assume directionality within the relationship. Taking this into account, the correlation represents the outcome of all processes between elevation and soil moisture, including how soil moisture affects elevation. For example, wetter soils may be less prone to erosion as the sand sticks together thus maintaining higher elevations (Dong et al., 2002). The sum of all these opposing feedback mechanisms explains why the correlation differs from the predictions made by the SEM-model. Nonetheless, the fact that the SEM-model predicts an increased soil moisture at higher points in the dune is difficult to explain. Due to the dune substrate, precipitation tends to trickle deep into the soil reaching the groundwater table as the sand fails to capture water (Wartena, Van Boxel, et al., 1991). Additionally, precipitation is fairly constant across coastal dunes (Homburger et al., 2024). Together, this should mean soil moisture decreases with elevation as the ground water table becomes further out of reach (Wartena, Van Boxel, et al., 1991). It is possible this relationship is actually mediated by other factors as SEM-models tend to show a simplified version of reality. As such, relations which are not explicitly modelled can manifest themselves through other links. In this case, the influence of vegetation cover on elevation may be the underlying cause. A higher cover increases sediment trapping and thus elevates the local area while simultaneously reflecting solar radiation and obstructing wind patterns, together reducing local evaporation of soil moisture (Ashkenazy & Shilo, 2018; Wartena, Van Boxel, et al., 1991). This association between elevation and vegetation cover is not immediately reflected in the correlograms, which almost indicate a lack of relationship among these parameters, yet again these calculations represent the outcome of all involved processes between these two parameters. Additionally, such unforeseen parameter-relationships may be caused by underlying aspects of the environment which were not measured during this thesis. Slope directionality and steepness, for example, can vary with dune elevation and influence local temperature, soil moisture and vegetation cover as south and west oriented dune sides experience higher loads of solar radiation, increasing both temperature and potential evaporation compared to north and east oriented slopes. Wartena, Van Boxel, et al. (1991) describe how this leads to north oriented slopes usually having a more well-developed vegetation due to an a beneficial water balance. Such underlying relationships further highlight the complexity found in dune ecosystems as determinants of abiotic parameters continually influence one another.

Distance to sea and the vegetation cover of each plant were also taken into account during this study. Temperatures measured by the loggers were usually lower when further from the sea and also lower in locations characterized by dense vegetation patches. On the contrary, soil moisture was differently impacted by plant cover and distance to the sea; soils were wetter when located more inland, and when covered by vegetation. Here, the SEM did mirror the correlogram results with distance to sea significantly impacting temperature and, even more so, soil moisture while the surrounding vegetation only maintained non-significant relationships with other variables. Temperature decreasing further inland can be explained by the vegetation cover, which becomes denser due to increased proximity to the groundwater table, caused by lower elevations and the soil developing a freshwater lens as it stabilizes (Wartena, Van Boxel, et al., 1991). Despite lacking from the SEM-model to limit over-parametrization, this relationship between vegetation and inland distance is reflected in the correlograms. In addition to this, a humus layer is formed from the increased decay of plant matter, allowing for additional hold on soil moisture (Cosyns et al., 2019). More vegetation creates shade and reflects solar radiation, explaining the decrease in temperatures (Howe & Smith, 2021; Wartena, Van Boxel, et al., 1991). On top of that, these processes, further mediated by lower wind dynamics and consequent evaporation, explain the results for soil moisture as well (Derijckere et al., 2023; van Westen et al., 2024; Wartena, Van Boxel, et al., 1991). Marram, which was the prominent species in the natural vegetation of the experimental site, has also been suggested to specifically alter its environment (Bonte et al., 2021; Strypsteen, Bonte, et al., 2024). For instance, Lammers, Schmidt, et al. (2024) hypothesized that, through environmental modification, dune grasses increase soil moisture levels. Although they could not find significant differences in moisture between modified and unmodified habitats, other studies have also suggested marram exhibits phenotypic plasticity in response to resource availability to optimize its environment (Reijers et al., 2021). Resultantly, marram grass may exhibit a similar strategy

concerning soil moisture, where it adapts its morphology and/ or expansion to stabilize the soil and indirectly increase local moisture levels.

Ultimately, elevation, distance to sea and vegetation cover have all contributed to sand burial as well. All three environmental parameters showed positive impacts on sand accumulation in the SEM-model. Despite not being significant, the geographical height of the plants showed the largest effect on sediment transport, insinuating higher elevations were more exposed to wind dynamics and the consequent sand level fluctuations. This is in line with Wartena, Van Boxel, et al. (1991) as well as the so-called speed-up effect, where airflows converge towards the dune crest creating higher wind speeds (Bo & Zheng, 2013). Areas further from the sea are normally expected to experience lower changes in sand burial due to reduced aeolian dynamics and a denser vegetation cover. However, this sediment transport gradient mostly varies across dune successional stages as it, along vegetation cover, is the driving factor for the succession from mobile dunes to stabilized ones. Since most of the experimental site consists of only 2 habitats, mobile and half-mobile dunes, sand burial rates may be similar across the field and thus do not significantly differ among plants. Although this explains the lack of significance for this relationship, temperature still shows a slight increase further inland according to the SEM rather than a neutral response. This can partially be explained by the fact multiple plants belonging to the mobile habitat can be found at the furthest inland points in the dataset. In the case of this experimental area, the mobile succession stage seems to reach deep into the site and, as it contains less vegetation, may thus be more exposed to wind dynamics. Moreover, the sand height dataset did show a significant outlier, namely PlantID 42, which may have skewed the predicted relationship. This outlier was located on a steep dune side (see Fig 6.), right beneath the pathway which had to be traversed to reach other individuals. It is possible movement along the path resulted in downward sand displacement, creating artificial sand height fluctuations. Contrarily, nearby plants did not experience dramatic sand height changes despite being on the same dune side. Since the exact cause of these extreme measurements is inconclusive, the outlier was kept in the dataset for all further analysis but may steer the SEM-predictions, nonetheless. Finally, the positive effect of vegetation cover on sand entrapment has been covered time and time again in previous literature (Bonte et al., 2021; Reijers et al., 2019; Strypsteen, Bonte, et al., 2024)

Even though many of the correlogram and SEM-results align with existing expectations and literature, they still hold some contradictions which may have been caused by the lack of information for other important components of dune systems. The direction of the dune slope (i.e. aspect), for instance, largely impacts solar radiation load across the dune. Another component is wind speed and patterns. In spite of being partially captured in sand burial measurements, the full extent of complex local aeolian dynamics was not measured. Wind can create cooling and drive evaporation by interacting with the soil surface, therefore impacting soil moisture and local temperature (Wartena, Van Boxel, et al., 1991). Such factors interplay with elevation, distance to sea, vegetation cover and each other, further increasing the number of abiotic gradients present in these ecosystems and adding to the intricate mosaic of microclimates found in coastal dunes.

5.3. Larger scale abiotic variation likely does not explain plant growth response

Cluster-analysis of the climatic variables implied, on the one hand, that the surrounding abiotic environment varied substantially in temperature and soil moisture across the different parts of the landscape where the loggers were installed. On the other hand, there does not appear to be a clear link between the logger's habitat, expressed as the different successional stages in dune development, and their microclimatologic parameter measurements. These results should be nuanced by adding that plants and loggers were not equally divided among habitats. The reason for this is that ensuring an equal spread along broad-scale habitats was not a priority during the experimental set-up.

The cluster-analyses on the plant's measurements allowed for a broader scale exploration of the relationship between the individuals' growth response and their local environment. Although the plants did show some homogenous responses, plant habitats could not explain this clustering, meaning that marram grass could grow similarly in a moss dune as in a mobile white dune. Regardless of the uneven distribution among habitats, the mobile and half-mobile dune niches contained multiple experimental plants each and yet did not show large differences in growth between them, aside from differences in leaf width, giving a first indication that the environment does not significantly seem to affect growth response of *Ammophila*. These results are also in-line with the recent findings of Höfer et al. (2025), who found transplanted juvenile marram grasses grew similarly well across the dune habitat gradient. However, both the current experiment and the one by Höfer et al. (2025) only consider aboveground growth proxies, ignoring potential changes in belowground biomass. In contradiction, other studies have shown a substantial influence of the dune succession stage on marram growth (Fischman et al., 2019; Levinsh & Andersone-Ozola, 2020; Reijers et al., 2019). Thus, the effect of the broader-scale climate on marram growth remains unclear in this experiment due to a lack of growth data in grey dunes and dune shrublands.

Cluster analyses which were performed on both the plants' growth response, as well as the (interpolated) climate they experienced, differed strongly. There was no apparently obvious similarity in clustering between these analyses as plants with comparable abiotic environments often had diverging growth responses, and vice versa. These results provide a second indication that even at a smaller scale, the abiotic surroundings of marram do not significantly influence its growth. Yet, these findings should again be nuanced by the fact they only represent the temperature and soil moisture variables of the abiotic environment. On top of that, these conclusions are based on interpolated predictions of these variables. IDW interpolation was originally used as plants were often located several meters away from their nearest loggers. Despite being small distances, in a highly variable dune ecosystem these can include large microclimatic variations, as illustrated above. However, inverse distance weighing only considers the distance and the elevation-difference to the nearest measured data-point, thus excluding other important factors such as exposure, local vegetation, orientation of the dune, etc. In consequence, although interpolation should give a more accurate representation of the microclimate of each individual plant, it fails to consider many other determinants of said climate. As such all results based on interpolated abiotic parameters, including this multivariate analysis but also the SEM-model and the correlation-calculations, should be interpreted with care. Lastly, the comparison of clusters in growth response and interpolated abiotic environment was done on a visual basis. A better approach would be to determine the amount of spatial autocorrelation for each of these datasets using metrics such as Moran's I (Moran, 1950). This method can determine whether the growth and abiotic metrics of plants located near each other are more alike, allowing for inferences on the relationship between proximity of plants and their associated measurements.

5.4. Specific abiotic microclimatic parameters do not significantly drive plant growth in dune ecosystems

At the smallest scale, a SEM-model was used to explore the relations between the plant growth and its microclimate. Despite none of these being significant, they do express how the microclimate drives different aspects of marram grass growth. Temperature for example, mildly increased the shoot difference during the growing season, as well as the width of the marram leaves, but opposingly decreased the vertical growth of the plants. These smaller opposing effects, alongside a stronger improved leaf width change, may explain why Biel & Hacker (2021) merely found a neutral to slightly positive temperature-response for marram biomass and tiller production. The lack of significance in the SEM-model further supports these results and corresponds with earlier findings, describing marram as a drought-tolerant species whose growth is not affected much in response to heat (Biel & Hacker, 2021; X. Gao et al., 2021; Huiskes, 1977).

Interestingly, the SEM-model demonstrated that increased soil moisture did not very strongly improve the number of shoots and was even negatively impacting the growth of the leaves, both in height and in width. Only the moisture-leaf height relationship, almost surpasses the significance threshold with a p-value of 0.0568. Since the model does fail to meet certain assumptions, p-values near the significance threshold are difficult to interpret and require additional testing to obtain conclusive results. Regardless of significance, all negative standardized estimates for the effect of moisture are unexpected as typically marram establishment benefits from a higher moisture level in the soil. For instance, Homberger et al. (2024) conducted pot experiments where they observed marram shoot and leaf count was significantly increased by soil moisture. In addition, their scenario analysis predicted a 23% reduction in marram growth for extremely dry years and a vast increase for wet periods. I would like to remark this study did not find an influence of soil moisture on maximum leaf height which, despite differing slightly from the leaf height measured for this experiment, does at least imply soil moisture does not increase leaf height. Another study by Homberger et al. (2025) also found higher establishment of *Ammophila* in dune patches with a higher soil moisture content, although this was only tested for seeds and rhizome fragments in beach segments, not foredunes. If anything, *Ammophila* is considered a drought-tolerant species and thus should not experience a growth decline unless it is exposed to prolonged periods of critically low soil moisture (Dixon et al., 2004; Homberger et al., 2024; Konlechner et al., 2013; Lammers, Berghuis, et al., 2024). Negative marram productivity in response to soil moisture is not completely unheard of, since during their pilot experiments Van der Putten & Peters (1997) actually found a decrease in biomass at higher soil moisture contents. It is possible that the growth response of the leaves, in particular an increased width in dryer conditions may be part of an adaptation to reduce evapotranspiration. Marram leaves are known to roll up in response to drought to limit water loss (Chergui et al., 2017). The plant may invest in increasing leaf width to roll up its leaves entirely, completely covering the stomata in the process.

At last, within the model sand burial is expected to increase shoot numbers and decrease leaf height over time, although both of these relationships together are almost negligible. The lack of significant sand burial effect can be justified by the limited variation in sand height at the microscale. Although burial is known to strongly drive and eventually inhibit marram growth, this concerns burial rates of over 10 centimetres per growing season (Levinsh & Andersone-Ozola, 2020; Nolet et al., 2018). These are nowhere near the sand height changes found during this experiment, which had a maximum of around 6.5 centimetres, including outlier P_42. Besides, the recent study by Höfer et al. (2025) suggest that growth stimulation by sediment deposition is not essential for juvenile transplants across the dune gradient in their first growing season. Consequently, a lack of significant growth response makes sense and denotes microclimatic changes in sand burial during its growth season do not affect marram grass growth significantly. I would like to clarify this conclusion may not apply outside the growth season, that is the winter season, as the winter months usually exhibit increased wind and sediment transport dynamics (Cosyns et al., 2019; Ludwig et al., 2017)

Taking the SEM-model, multivariate analyses and overall patterns in marram growth and abiotic environment into consideration, the microclimate's does influence several aspects of plant growth in *Ammophila*, although this impact does not seem significant.

5.5. Potential for dune restoration

As mentioned earlier, marram grass planting is a commonly used technique to establish artificial dunes and restore natural ones in the context of increasing coastal resilience and management (Bridges et al., 2015; Derijckere et al., 2023). In more recent years, the concept of dunes as nature-based solutions has gained popularity, specifically in implementations such as the so-called "dune-for-dike hybrid systems". This method for coastal protection relies on the properties of resilient vegetation, such as marram grass, since it is indispensable in developing stable and effective dune ecosystems (Bonte et al., 2021; Derijckere et al.,

2023; Duarte et al., 2013b). Improving our understanding of marram growth in relation to dune environment processes could thus have crucial implications for shielding our coast. As an ecosystem engineer, *Ammophila* modifies its biophysical and biochemical environment (Losapio et al., 2024). It not only traps sand with its fast-growing root system, but additionally uses its foliage to extract momentum from the air flow right above the soil surface, resulting in sand particle retainment (Derijckere et al., 2023; Wolfe & Nickling, 1993). Consequently, the growth of these plant-organs directly mediates the effectiveness of marrams sand capture and dune building ability. Considering our improved understanding of how dune microclimates influence this growth we can conclude it does not matter much where marram is planted along the different abiotic gradients within the foredune. *Ammophila* growth does not seem to be significantly impacted by its micro-environment, thus the outcome of coastal restoration and management plans utilizing marram planting for artificial dune formation should, at least during the growth season, not be affected by the location where marram is planted.

5.6. Future perspectives

The results of this study indicate a limited effect of the microclimate on marram grass growth. Nevertheless, these findings can be further improved and elaborated. On the one hand, improving certain aspects of the experiment such as habitat estimation and herbivory tracking could confirm or deny the results of this thesis to a greater extent. A more accurate identification of the successional dune phases in which the loggers and marram individuals were planted, could have been done using the overhead location photos taken at the start and finish of this experiment. Moreover, if the goal of the study is to compare growth across dune succession stadia, a more even distribution across these habitats would be more suited, as was executed by Höfer et al. (2025). Closely monitoring herbivory for individual plants, for example in terms of percentage of chewed leaves, allows for a better representation of the severity of herbivory and its concurrent effect on *Ammophila* growth.

On the other hand, it is also important to mention that temperature, soil moisture and sand burial do not encompass the full microclimate in dune ecosystems. Belowground factors such as nutrient content, pH, salinity and the presence and diversity of root nematode communities have all proven to, at least partially, determine the micro-environment in coastal dunes, and potentially affect marram growth (Du & Hesp, 2020; Gerlach, 1993; Mateille et al., 2011; Ott & van Aarde, 2014; van Puijenbroek et al., 2017). In example, salinity has been shown to create osmotic stress in *Ammophila*, ensuring a decline in growth (Konlechner et al., 2013; van Puijenbroek et al., 2017). Furthermore, Van Der Putten et al. (1990) have demonstrated how several soil pathogens, including plant parasitic nematodes, can lead to marram degeneration while Willis (1965) illustrated the importance of nutrients such as nitrogen, phosphorus and potassium to marram vigour. Additionally, not just the vegetation cover, but the composition of the surrounding vegetation can play an important role in the growth and development of *Ammophila* as it is often characterized by competitive interactions with other species (Cosyns et al., 2019; Van der Putten & Peters, 1997). Here, the location photos may again prove useful as they show all plant-species within a 1x1 metre quadrant for each marram individual, although in-field assessments would likely be better. Considering these additional factors may further illuminate the role of the microclimate in marram vigour.

Adding on to this, the data-analysis throughout this thesis was for the most part based on summaries of variables over the whole duration of the experiment, failing to capture the temporal variation. Analysing this temporal aspect could further highlight the complexity of growth patterns and abiotic variations seen during the data exploration. Furthermore, this experiment took place over one growth season of marram. Extending this research to cover multiple seasons may further elucidate how *Ammophila* responds to its microclimate both outside of its growth season and on the longer term as the variability in temperature, soil moisture, sand burial and other abiotic and biotic microclimatological parameters likely vary seasonally.

6. CONCLUSION

Overall, the results of this study indicated significant variation in microclimatological parameters such as soil, surface and atmospheric temperature as well as soil moisture and sand burial across the experimental foredune. Moreover, these gradients were clearly influenced by several aspects of the environment including the distance to sea, elevation and local vegetation cover of plants. Nevertheless, these abiotic measures did not impact the growth of marram grass extensively concerning its shoot expansion, change in leaf height and width, and finally its lateral density.

The hypothesis that small temperature-changes do not significantly affect marram as it is a drought-tolerant species is largely supported by the results. Temperature had minor opposing effects on different growth aspects of marram ultimately bringing about a neutral to slightly positive overall growth response, which is in line with the earlier findings of Biel & Hacker (2021).

Contrary to the initial hypothesis and prior research, soil moisture unexpectedly had a negative impact on several growth parameters regarding leaf growth. This suggests that while *Ammophila* is drought-tolerant, as indicated by Lammers, Berghuis, et al. (2024), its growth response to subtle changes in soil moisture levels might be more complex than previously thought. The changes in leaf morphology that were observed during this study may contribute to marrams tolerance against drought as they are potentially involved in adaptive measures to limit evapotranspiration when soil moisture levels are lower.

Finally, sand burial had unexpectedly negligible effects on all aspects of marram vigour, as the observed burial rates were well below the thresholds known to stimulate or inhibit growth, indicating its limited influence at the microscale and over the short term of the experiment.

To conclude the findings of this thesis, the measured microclimatological variations did not significantly impact different growth aspects of marram grass. These results should be nuanced by adding the measured abiotic factors do not encompass the full microclimate of marram grass. Furthermore, several important determinants of abiotic gradients were not taken into account, and the study was only executed over one growth season. Additional research with a deeper focus on temporal and seasonal variations of an even more diverse set of environmental factors and their determinants may provide further insight into the effect of the microclimate on marram grass growth.

7. SUMMARY

7.1. English summary

Coastal dunes are dynamic interfaces between land and sea, crucial for protecting shorelines from climatic threats and providing essential supporting, provisioning and cultural ecosystem services alongside supporting a large biodiversity. These naturally unstable landscapes are shaped by the interplay of sediment transport from multiple sources and coastal wind dynamics. Marram grass (*Ammophila arenaria*) acts as a key ecosystem engineer in European dune systems, actively trapping sand and stabilizing soil, thereby facilitating dune development and ecological succession. However, human activities, including excessive artificial marram planting and urbanization, have led to habitat loss and fragmentation, while climate change intensifies storms, alters sand dynamics, and promotes invasive species, all threatening the integrity of coastal dunes.

Given their protective role, effective dune management and restoration are vital. Nature-based solutions, which enhance natural dune systems, are increasingly favoured for improving coastal resilience. Optimizing these solutions requires a deeper understanding of the factors influencing dune morpho-dynamics, particularly the growth of ecosystem engineers like *Ammophila*. While macroclimatic effects on dunes and their vegetation are decently understood, the impact of microclimates remains less clear. Microclimates, defined by small-scale variations in abiotic factors such as temperature, soil moisture, and sand burial, result from complex interactions between dune geomorphology, weather patterns, and soil properties. These local conditions profoundly influence vegetation, directly affecting marram grass's ability to stabilize dunes.

The objective of this master's dissertation was to better understand microclimatic variations in natural dune ecosystems and determine how these abiotic parameters affect marram grass growth. This experiment tracked soil, surface and atmospheric temperature, soil moisture, and sand burial, alongside detailed observations of marram growth, across diverse microclimates within a natural foredune system. Each study location varied in elevation, distance to sea, and vegetation cover, determining a unique microclimate for individual plants. By repeatedly measuring plant responses and environmental parameters throughout the growing season, this research aimed to assess how abiotic factors varied across the dune habitat and how they influenced marram growth. Based on prior research, it was hypothesized that small temperature variations would not significantly affect marram, given its heat tolerance. Soil moisture was expected to have a larger impact, though not immediately clear as marram is both considered drought-tolerant and experiences growth-stimulation at higher soil moisture. Finally, marram growth was anticipated to improve with moderate sand burial, with decline only occurring from massive accumulation unlikely within the experimental timeframe.

Fieldwork for this study occurred in De Slufter, a diverse foredune on the Belgian coast in nature reserve De Westhoek, from July to October 2024, aligning with the marram grass growing season. 50 lab-grown *Ammophila* plants were transplanted across the site, positioned near 30 pre-existing dataloggers. Throughout the experiment, 6 abiotic variables (soil, surface, and atmospheric temperature, soil moisture, elevation, and sand height) and 4 plant growth proxies (shoot number, lateral density, leaf height, and leaf width) were tracked. Temperatures and soil moisture were continuously measured by dataloggers, while plant growth and sand height changes were monitored weekly. Data processing involved ImageJ for lateral density and QGIS for calculating plant-to-sea distance, nearest logger, and surrounding vegetation cover. Inverse Distance Weighted (IDW) interpolation estimated abiotic conditions for all plants based on the logger measurements. Statistical analysis in R included Principal Component Analysis (PCA) to summarize growth and abiotic data, followed by Structural Equation Modelling (SEM) to explore hierarchical relationships between experimental design (elevation, distance to sea, vegetation cover), microclimatic drivers (abiotic PCs, sand burial), plant growth proxies, and overall lateral density. Several models were

tested and evaluated based on their goodness-of-fit statistics. The base model was eventually selected as it was able to describe the most data variance with the least amount of variables.

Initial observations revealed that most transplanted marram grass individuals experienced a slight decrease in overall vigour, particularly in lateral density, immediately following transplant. This decline, despite the experiment occurring during the species' growing season, was likely due to transplant shock from a controlled lab environment to the dynamic natural dune system, in addition to significant rabbit herbivory. Interestingly, shoot numbers generally increased across the plants, suggesting *Ammophila* might prioritize new shoot production as an adaptive strategy to enhance sand-trapping efficiency in challenging environments. Abiotic data indicated substantial microclimatic variability in temperature, soil moisture, and sand burial across the foredune. Soil temperatures were less variable than surface and atmospheric temperatures, while soil moisture varied greatly and was negatively linked to temperature. Sand height also showed considerable localized fluctuations.

Microclimatic conditions were notably influenced by the surrounding environment. Higher temperatures tended to be found at greater elevations and closer to the sea. Moreover, soil moisture was generally higher at higher elevations, and slightly increased with more nearby vegetation and greater distance from the sea. Despite these clear differences in local conditions, a crucial finding was that the measured factors, being sand burial, temperature, and soil moisture, did not significantly alter how the marram grass grew, whether in terms of new shoots, leaf length, or leaf width, over the study's duration. This outcome was somewhat different from what earlier studies might suggest. While *Ammophila* is recognized for its tolerance to heat, its response to subtle shifts in soil moisture seemed more intricate than expected. Drier conditions were found to positively impact leaf growth, which could be part of an adaptive way for the plant to conserve water. As for sand burial, its effect was minimal, as the amount of sand accumulating was too low to either stimulate or hinder the plant's growth.

These findings highlight the complex nature of microclimate-plant interactions in dynamic dune systems. While environmental factors clearly shape the microclimate, their direct, short-term impact on *Ammophila* growth at the microscale was not statistically significant. Future research should consider longer experimental durations and a broader range of environmental factors, including their temporal and seasonal variations, to fully elucidate the intricate effects of microclimates on marram grass growth. Such insights may be crucial for optimizing nature-based coastal protection solutions, particularly in the context of ongoing climate change and the need for resilient dune management.

Kustduinen zijn dynamische grensvlakken tussen land en zee, die van cruciaal belang zijn voor de bescherming van kustlijnen tegen klimatologische bedreigingen en die essentiële ondersteunende, bevoorradende en culturele ecosysteemdiensten leveren naast de ondersteuning van een hoge biodiversiteit. Deze van nature instabiele landschappen worden gevormd door een samenspel van sedimenttransport uit verschillende bronnen en kustwinddynamiek. In Europese duinsystemen fungeert helmgras (*Ammophila arenaria*) als een belangrijke ecosysteemverbeteraar door actief zand vast te houden en de bodem te stabiliseren, waardoor duinontwikkeling en ecologische successie worden bevorderd. Menselijke activiteiten, waaronder de overmatige kunstmatige aanplanting van helm en verstedelijking, hebben echter geleid tot habitatverlies en versnippering. Daarbovenop speelt klimaatverandering een belangrijke rol. Zij versterkt stormen, verandert zanddynamieken en bevordert invasieve soorten, wat bedreigingen vormt voor de integriteit van kustduinen.

Gezien hun beschermende rol zijn effectief duinbeheer en -herstel van vitaal belang. Zogenaamde nature-based solutions, die natuurlijke duinsystemen versterken, krijgen steeds meer de voorkeur om de veerkracht van de kust te verbeteren. Om deze oplossingen te optimaliseren is een beter begrip nodig van de factoren die de ontwikkeling van duinen beïnvloeden, met name de groei van ecosysteemingenieurs zoals *Ammophila*. Terwijl de macro-klimatologische effecten op duinen en hun vegetatie redelijk goed bekend zijn, is de invloed van microklimaten minder duidelijk. Microklimaten, worden gedefinieerd door kleinschalige variaties in abiotische factoren zoals temperatuur, bodemvochtigheid en zandophoping, en zijn het resultaat van complexe interacties tussen duingeomorfologie, weerpatronen en bodemeigenschappen. Deze lokale omstandigheden hebben een grote invloed op de vegetatie, wat direct van invloed is op het vermogen van helmgras om duinen te stabiliseren.

Het doel van deze thesis was om micro-klimatologische variaties in natuurlijke duinecosystemen beter te begrijpen en te bepalen hoe deze abiotische parameters de groei van helmgras beïnvloeden. Dit experiment volgde bodem-, oppervlakte- en luchttemperatuur, bodemvochtigheid en zandophoping, naast gedetailleerde observaties van de groei van helm, in verschillende microklimaten binnen een natuurlijk duinsysteem. Elk plantlocatie varieerde in hoogte, afstand tot de zee en vegetatiebedekking, waardoor een uniek microklimaat voor individuele planten werd bepaald. Door gedurende het groeiseizoen herhaaldelijk de groeirespons van planten en omgevingsparameters te meten, wilde ik met dit onderzoek nagaan hoe abiotische factoren in de duinhabitat varieerden en hoe ze de groei van helm beïnvloedden. Op basis van eerder onderzoek werd verondersteld dat kleine temperatuurvariaties geen significante invloed zouden hebben op helm, gezien zijn tolerantie voor hoge temperaturen. Er werd ook verwacht dat de bodemvochtigheid een grotere invloed zou hebben, hoewel de richting van deze invloed niet meteen duidelijk was aangezien helm zowel droogtetolerant is als een gestimuleerde groei ondervindt bij een hogere bodemvochtigheid. Tot slot werd verwacht dat de groei van helm zou verbeteren bij een matige bestuiving met zand, waarbij een negatief effect enkel zou optreden bij massale ophoping, wat onwaarschijnlijk was binnen het experimentele tijdsbestek.

Het veldwerk voor deze studie vond plaats in De Slufter, een diverse voorduin aan de Belgische kust in natuurreservaat De Westhoek, van juli tot oktober 2024, in lijn met het groeiseizoen van helmgras. 50 lab-gegroeiende *Ammophila* planten werden over het terrein getransplanteerd, gepositioneerd in de buurt van 30 reeds geplaatste dataloggers. Gedurende het experiment werden 6 abiotische variabelen (bodem-, oppervlakte- en luchttemperatuur, bodemvochtigheid, hoogte en zandhoogte) en 4 plantengroei proxies (aantal scheuten, laterale dichtheid, bladhoogte en bladbreedte) opgevolgd. Temperaturen en bodemvocht werden continu gemeten door de dataloggers, terwijl de veranderingen in plantengroei en zandhoogte wekelijks werden bijgehouden. De gegevens werden verwerkt met ImageJ voor de laterale dichtheid en QGIS voor het berekenen van de afstand tot de zee, de dichtstbijzijnde logger en de omringende

vegetatiebedekking per plant. Inverse Distance Weighted-interpolatie werd gebruikt om de abiotische omstandigheden voor alle planten te schatten op basis van de loggermetingen. Statistische analyse in R omvatte PCA-analyse om clustering van groei- en abiotische gegevens te bekijken, gevolgd door Structural Equation Modelling (SEM) om hiërarchische relaties te onderzoeken tussen proefopzet (hoogte, afstand tot de zee, vegetatiebedekking), micro-klimatologische factoren (abiotische PC's, zandophoping), proxies voor plantengroei en totale laterale densiteit. Verschillende modellen werden getest en geëvalueerd op basis van hun goodness-of-fit statistieken. Het basismodel, Model , werd uiteindelijk geselecteerd omdat het de meeste gegevensvariantie kon beschrijven met het minste aantal variabelen.

De eerste observaties toonden aan dat de meeste getransplanteerde helmplanten een lichte afname in groeikracht vertoonden, vooral in laterale densiteit, onmiddellijk na de experimentele opzet. Deze afname, ondanks het feit dat het experiment plaatsvond tijdens het groeiseizoen van de soort, was waarschijnlijk te wijten aan de stress die gepaard gaat met een transplantatie vanuit een gecontroleerde lab-omgeving naar een dynamisch natuurlijke duinsysteem, naast aanzienlijke herbivorie door konijnen. Interessant genoeg nam het aantal scheuten over het algemeen toe bij alle planten, wat suggereert dat helm prioriteit geeft aan de productie van nieuwe scheuten, mogelijks als adaptatie om de zandvangefficiëntie in uitdagende omgevingen te verbeteren. Abiotische gegevens wezen op een aanzienlijke micro-klimatologische variabiliteit in temperatuur, bodemvochtigheid en zandophoping in de voorduin. De bodemtemperatuur was minder variabel dan de oppervlakte- en luchttemperatuur, terwijl de bodemvochtigheid sterk varieerde en negatief gekoppeld was aan de temperatuur. De zandhoogte vertoonde ook aanzienlijke lokale schommelingen.

De micro-klimatologische omstandigheden werden, zoals verwacht, vooral beïnvloed door de omgeving. Hogere temperaturen werden aangetroffen op hogere plekken en dichterbij de zee. Bovendien was de bodemvochtigheid over het algemeen hoger op verhoogde plaatsen en nam deze licht toe naarmate er meer vegetatie in de buurt was en de afstand tot de zee groter werd. Ondanks deze duidelijke verschillen in lokale omstandigheden, was een cruciale bevinding voor deze thesis dat de gemeten factoren, namelijk zandophoping, temperatuur en bodemvochtigheid, de groei van helmgras niet significant beïnvloedden, of het nu ging om nieuwe scheuten, bladlengte of bladbreedte. Dit resultaat week enigszins af van wat eerdere studies hadden ondervonden. Hoewel *Ammophila* bekend staat om zijn tolerantie voor hitte, leek zijn reactie op subtiele veranderingen in de bodemvochtigheid ingewikkelder dan verwacht. Drogere omstandigheden bleken een positieve invloed te hebben op de bladgroei, wat onderdeel zou kunnen zijn van een adaptieve manier voor de plant om evapotranspiratie te beperken. Het effect van zandophoping was minimaal, omdat de hoeveelheid zand verstuiving te klein was om de groei van de plant te stimuleren of te belemmeren.

Deze bevindingen benadrukken de complexe aard van interacties tussen microklimaat en planten in dynamische duinsystemen. Hoewel milieufactoren duidelijk het microklimaat bepalen, was hun directe korte-termijneffect op de groei van helmgras op microschaal statistisch niet significant. Verder zou toekomstig onderzoek rekening moeten houden met langere experimentele perioden en een breder scala aan omgevingsfactoren, net als hun temporele en seizoensgebonden variaties, om de complexe effecten van microklimaten op de groei van helmgras volledig op te helderen. Dergelijke inzichten kunnen cruciaal zijn voor het optimaliseren van nature-based solutions voor kustbescherming, vooral in de context van de voortdurende klimaatverandering en de behoefte aan een veerkrachtig duinbeheer.

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10. APPENDIX

Date	Days since last measurements	Data collected?	Remarks
3 rd of July 2024	/	• Sand heights • Shoots • Plant and logger coordinates • Location photos	
10 th of July 2024	7	• Leaf heights and widths • Sand heights • Lateral density photos • Logger data	
15 th of July 2024	5	• Leaf heights and widths • Sand heights • Lateral density photos • Logger data	
28 th of July 2024	13	• Leaf heights and widths • Sand heights • Lateral density photos • Logger data	
4 th of August 2024	7	• Leaf heights and widths • Sand heights • Lateral density photos • Logger data	
10 th of August 2024	6	• Leaf heights and widths • Sand heights • Lateral density photos • Logger data	
20 th of August 2024	/	/	Failed attempt due to unforeseen weather
25 th of August 2024	15	• Leaf heights and widths • Sand heights • Lateral density photos	
29 th of August 2024	4	• Leaf heights	

		- and widths • Sand heights • Lateral density photos	
5 th of September 2024	7	• Leaf heights and widths • Sand heights • Lateral density photos	
20 th of September 2024	15	• Leaf heights and widths • Sand heights • Lateral density photos	
3 rd of October 2024	13	• Leaf heights and widths • Sand heights • Shoots	
7 th of October 2024	7	• Lateral density photos	Only lateral density photos were taken due to lack of time on the previous fieldwork day
27 th of October 2024	17	• Logger data	Only logger data was collected to obtain the final climatological data for the experiment
<i>Appendix 1. Table which illustrates all fieldwork days. For each date the number of days since the last fieldwork day where data was collected is given as well as which data was collected on that day and remarks.</i>			

LoggerID	Habitat_Logger	Why?
L_1	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_2	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_3	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_4	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_5	Grey dunes (Moss)	Fixed dune covered by Star Moss
L_6	Dune shrubland	Surrounded by Sea Buckthorn
L_7	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_8	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_9	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_10	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_11	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_12	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_13	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_14	White dunes (half-mobile)	Hidden inbetween dense Marram Grass patch
L_15	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_16	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_17	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_18	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_19	White dunes (mobile)	Bare patch surrounded by Marram Grass
L_20	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_21	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
L_22	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
L_23	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_24	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_25	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
L_26	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
L_27	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
L_28	Dune shrubland	Surrounded by Sea Buckthorn
L_29	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
L_30	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hilltop

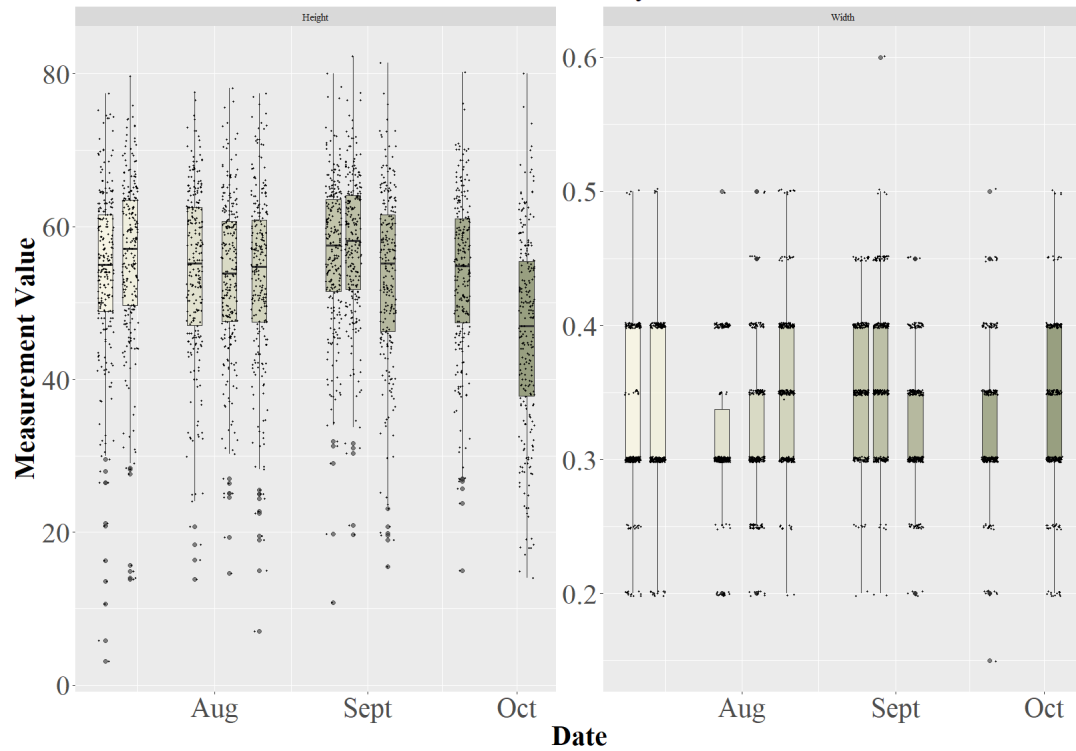
Appendix 2. Reasoning for the rough habitat estimation per logger. This does not include the additional use of the dune habitat map of the entire Westhoek (Herrier et al., 2020).

PlantID	Habitat_Plant	Why?
P_1	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
P_2	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
P_3	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_4	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_5	Thickets	Surrounded by Sea Buckthorn
P_6	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_7	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_8	White dunes (half-mobile)	More fixed but surrounded by Marram Grass and Sea Holly, hilltop
P_9	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_10	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
P_11	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_12	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_13	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_14	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_15	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_16	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_17	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_18	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_19	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_20	Thickets	Surrounded by Sea Buckthorn
P_21	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_22	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_23	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_24	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
P_25	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_26	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_27	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_28	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_29	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_30	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_31	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_32	White dunes (mobile)	Bare patch surrounded by Marram Grass

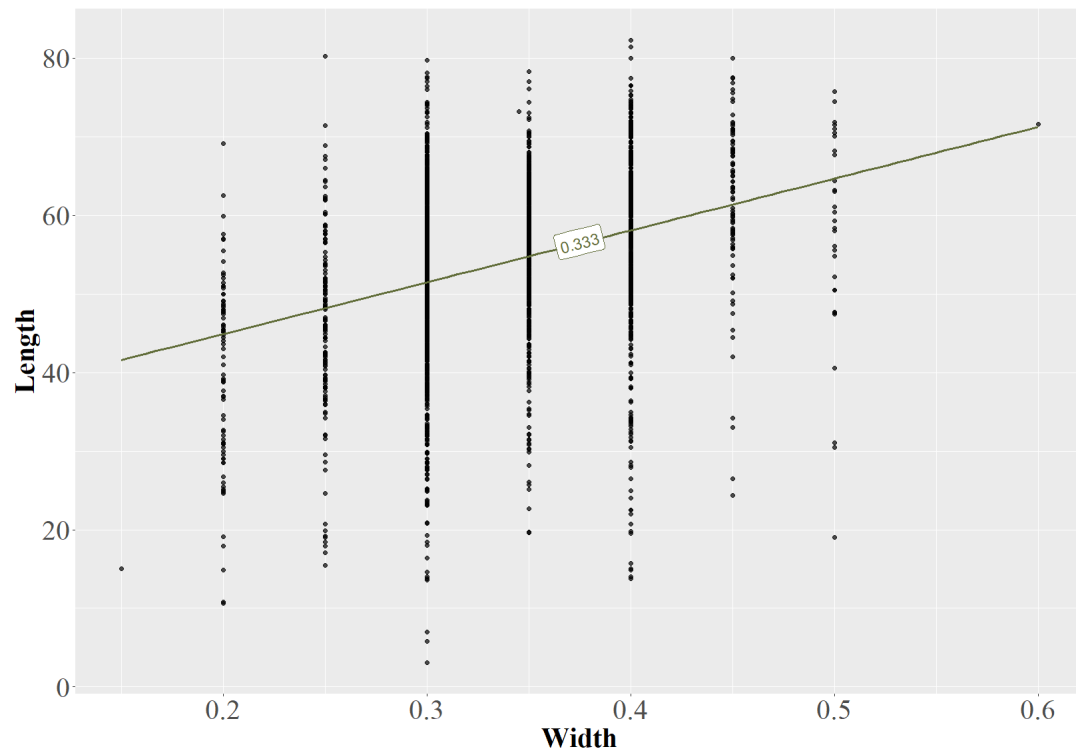
P_33	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_34	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_35	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_36	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
P_37	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_38	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_39	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
P_40	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_41	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_42	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hillside
P_43	White dunes (half-mobile)	More fixed but surrounded by Marram Grass
P_44	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
P_45	White dunes (mobile)	Bare patch surrounded by Marram Grass and Sea Holly, hilltop
P_46	Grey dunes (Moss)	Fixed dune covered by Star Moss
P_47	White dunes (mobile)	Bare patch surrounded by Marram Grass
P_48	Thickets	Surrounded by Sea Buckthorn
P_49	White dunes (mobile)	Bare patch surrounded by Marram Grass but close to Sea Buckthorn thickets
P_50	White dunes (mobile)	Bare patch surrounded by Marram Grass
<i>Appendix 3. Reasoning for the rough habitat estimation per plant. This does not include the additional use of the dune habitat map of the entire Westhoek (Herrier et al., 2020)</i>		

a

Distribution of Leaf Measurements For all Plants by Date

**b**

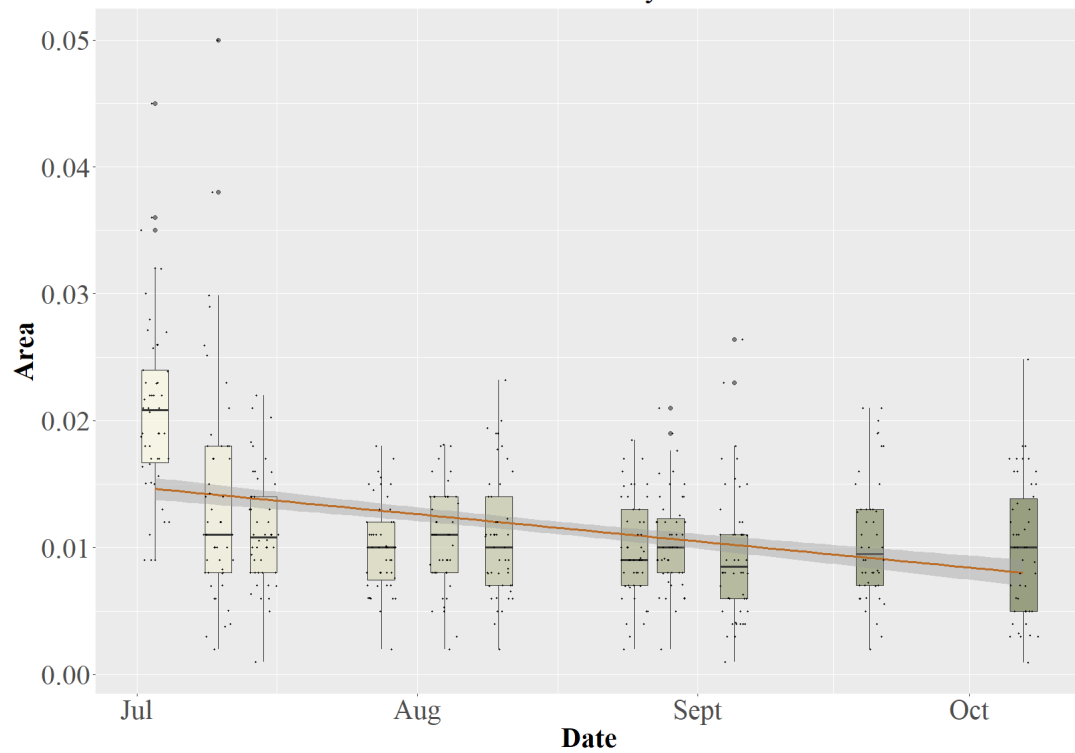
Correlation Width and Length For All Plants Over All Dates



c

Distribution of Area Measurements

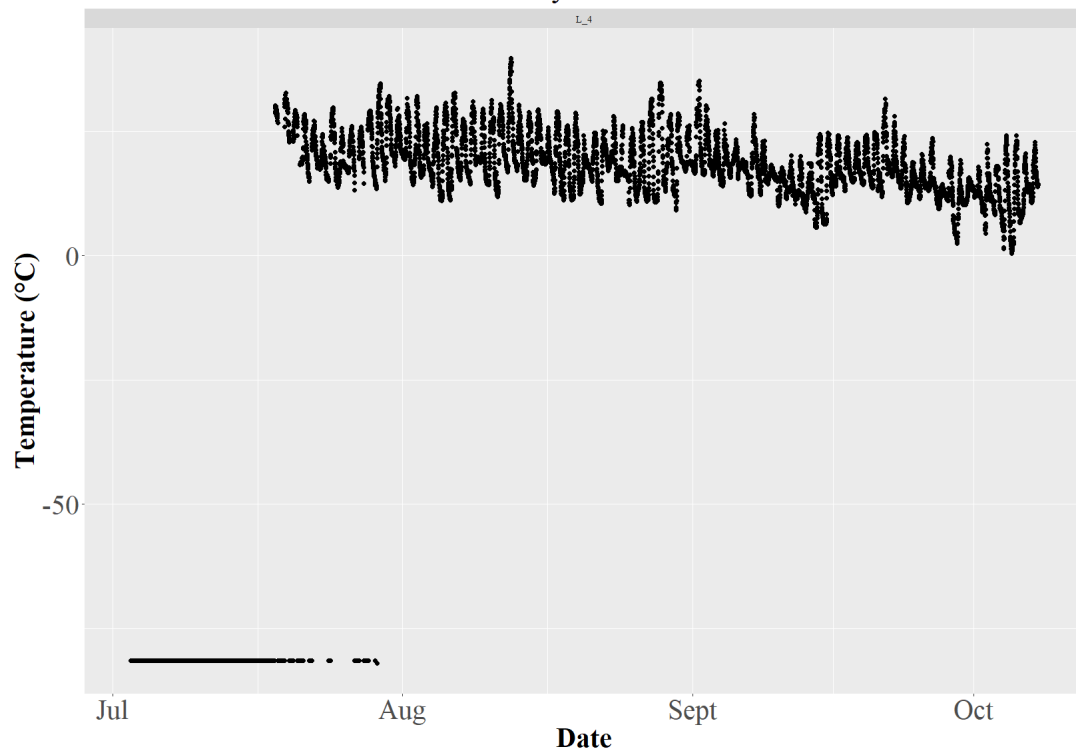
For all Plants by Date

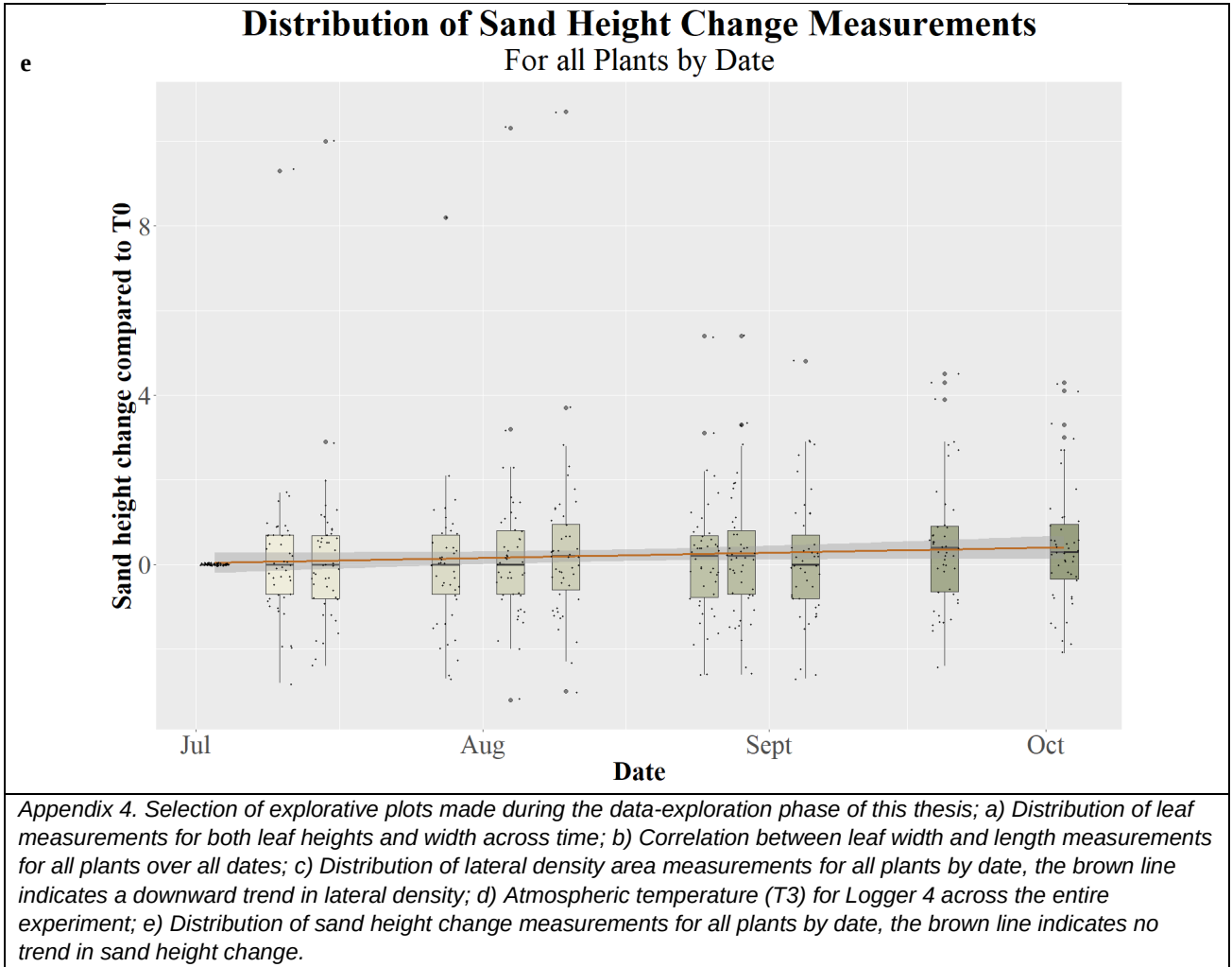


d

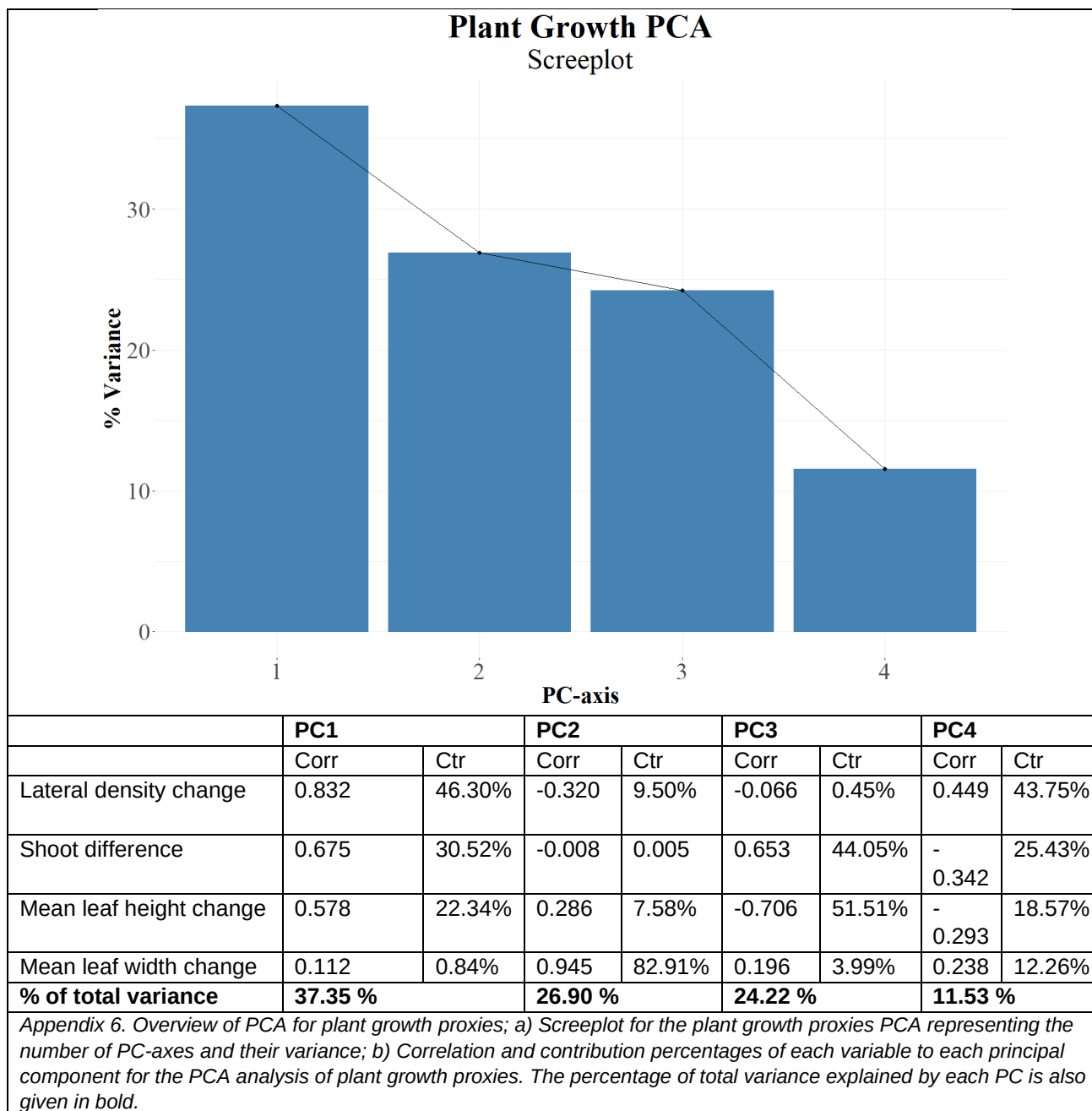
Atmospheric Temperature (T3) For Logger 4

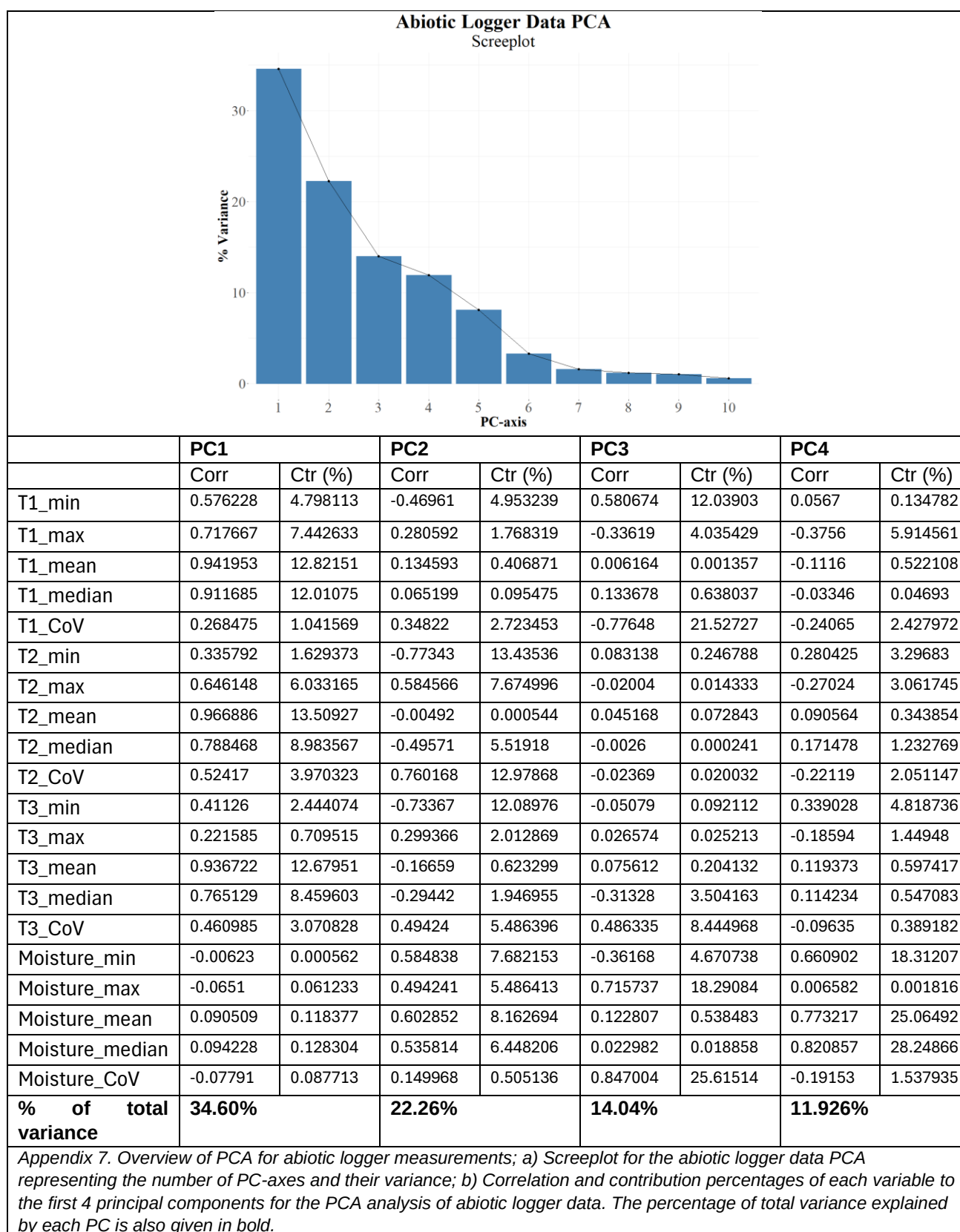
By Date

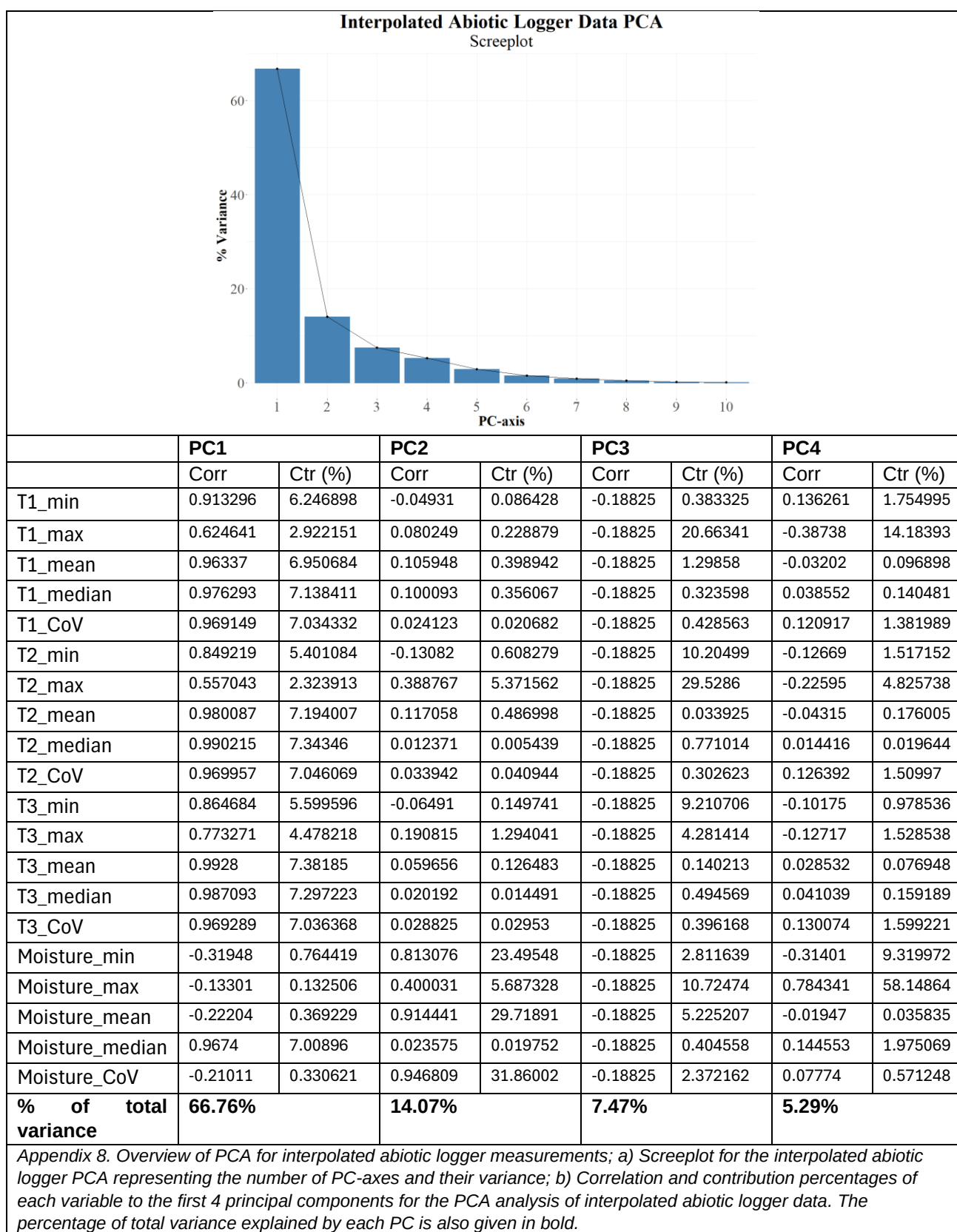




Dataset	Remark	Course of action
<i>abiotic_data</i>	Faulty measurements of -86°C were found for T3 in Logger 4.	A threshold of -20°C was set based on the explorative graph for T3 in logger 4 and to avoid removing correct measurements. All values below it were changed to Nas.
<i>closest_logger</i>	Logger 26 turned out not to be the closest logger for any of the plants.	/
<i>Appendix 5. Remarks on datasets made during data-exploration and digital data-collection.</i>		







Model 0 Emerging plant property Plant growth proxies Drivers of plant growth Experimental design		Model 1 Emerging plant property Plant growth proxies Drivers of plant growth Experimental design																
AIC	-4051.137	AIC	4046.184															
X²	10.727 (p = 0.986)	X²	9.611 (p = 0.975)															
FishC	25.674 (p = 0.978)	FishC	22.259 (p = 0.956)															
Model 2 Emerging plant property Plant growth proxies Drivers of plant growth Experimental design		<table><tr><th>Variable</th><th>Linear equation</th></tr><tr><td>ΔLateral density</td><td>Area_slope ~ Shoots_Difference + Mean_Height_slope + Mean_Width_slope</td></tr><tr><td>ΔShoots</td><td>Shoots_Difference ~ PC1 + PC2 + Mean_Sandheight_Change</td></tr><tr><td>ΔLeaf height</td><td>Mean_Height_slope ~ PC1 + PC2_sq + Mean_Sandheight_Change</td></tr><tr><td>ΔLeaf width</td><td>Mean_Width_slope ~ Mean_Height_slope + PC1 + PC2</td></tr><tr><td>Sand burial</td><td>Mean_Sandheight_Change ~ Elevation + Sea_Distance_Plant + Cover_2M</td></tr><tr><td>Temperature</td><td>PC1 ~ Elevation + Sea_Distance_Plant + Cover_2M</td></tr><tr><td>Moisture</td><td>PC2 ~ Sea_Distance_Plant + Elevation + Cover_2M</td></tr></table>	Variable	Linear equation	Δ Lateral density	Area_slope ~ Shoots_Difference + Mean_Height_slope + Mean_Width_slope	Δ Shoots	Shoots_Difference ~ PC1 + PC2 + Mean_Sandheight_Change	Δ Leaf height	Mean_Height_slope ~ PC1 + PC2_sq + Mean_Sandheight_Change	Δ Leaf width	Mean_Width_slope ~ Mean_Height_slope + PC1 + PC2	Sand burial	Mean_Sandheight_Change ~ Elevation + Sea_Distance_Plant + Cover_2M	Temperature	PC1 ~ Elevation + Sea_Distance_Plant + Cover_2M	Moisture	PC2 ~ Sea_Distance_Plant + Elevation + Cover_2M
Variable	Linear equation																	
Δ Lateral density	Area_slope ~ Shoots_Difference + Mean_Height_slope + Mean_Width_slope																	
Δ Shoots	Shoots_Difference ~ PC1 + PC2 + Mean_Sandheight_Change																	
Δ Leaf height	Mean_Height_slope ~ PC1 + PC2_sq + Mean_Sandheight_Change																	
Δ Leaf width	Mean_Width_slope ~ Mean_Height_slope + PC1 + PC2																	
Sand burial	Mean_Sandheight_Change ~ Elevation + Sea_Distance_Plant + Cover_2M																	
Temperature	PC1 ~ Elevation + Sea_Distance_Plant + Cover_2M																	
Moisture	PC2 ~ Sea_Distance_Plant + Elevation + Cover_2M																	
AIC	4046.184	AIC	-4056.370															
X²	9.611 (p = 0.975)	X²	38.06 (p = 0.421)															
FishC	22.259 (p = 0.956)	FishC	65.317 (p = 0.636)															

Appendix 9. The 3 fitted model structures and the final SEM-model with their respective AIC-scores and goodness-of-fit statistics; a) the base model, Model 0, prior to transformations with all measured variables and relationships in accordance with literature; b) Model 1 with additional relations between Sea_Distance_Plant and all variables of the Plant growth proxies layer; c) Model 2 which is based on Model 1 but lacks the Mean_Width_slope variable and all its relationships; d) Overview of all linear equations encompassed in the final model after transformations and the associated goodness-of-fit statistics

Response	Predictor	Estimate	Std.Error	Df	Crit.Val	P.val	Std.Est
Area_slope	Shoots_Difference	0	0	46	2.9875	0.0045	0.3815
Area_slope	Mean_Height_slope	2.00E-04	1.00E-04	46	2.4986	0.0161	0.3195
Area_slope	Mean_Width_slope	-0.0285	0.0184	46	-1.5487	0.1283	-0.1993
Shoots_Difference	PC1	0.1586	0.4467	46	0.3551	0.7241	0.0524
Shoots_Difference	PC2	0.4805	0.968	46	0.4964	0.622	0.0729
Shoots_Difference	Mean_Sandheight_Change	0.0795	1.2251	46	0.0649	0.9485	0.0096
Mean_Height_slope	PC1	0	0	46	-0.4955	0.6226	-0.0722
Mean_Height_slope	PC2_sq	0	0	46	-1.9538	0.0568	-0.2832
Mean_Height_slope	Mean_Sandheight_Change	0	0	46	-0.3032	0.7631	-0.0427
Mean_Width_slope	Mean_Height_slope	7.00E-04	7.00E-04	46	0.9807	0.3319	0.1419
Mean_Width_slope	PC1	0	0	46	1.0242	0.3111	0.1481
Mean_Width_slope	PC2	0	0	46	-1.0489	0.2997	-0.1501
PC1	Elevation	2.0855	0.1417	46	14.7167	0	0.8576
PC1	Sea_Distance_Plant	-0.0306	0.0136	46	-2.2564	0.0288	-0.1484
PC1	Cover_2M	-0.0094	0.5702	46	-0.0164	0.9869	-8.00E-04
PC2	Sea_Distance_Plant	0.0462	0.0188	46	2.457	0.0178	0.4875
PC2	Elevation_sq	0.0244	0.0114	46	2.1438	0.0374	0.3767
PC2	Cover_2M	0.6237	0.8008	46	0.7788	0.4401	0.1223
Mean_Sandheight_Change	Elevation	0.1152	0.1779	46	0.6475	0.5206	0.1299
Mean_Sandheight_Change	Sea_Distance_Plant	0.0028	0.0171	46	0.1655	0.8693	0.0375
Mean_Sandheight_Change	Cover_2M	0.3081	0.7159	46	0.4304	0.6689	0.076
Appendix 10. Coefficient output of the final SEM-model after data transformations.							