Author response on "Exploring the contributions of vegetation and dune size to early dune building using unmanned aerial vehicle (UAV)-imaging" *by* Marinka E. B. van Puijenbroek et al.

Marinka E.B. van Puijenbroek

I would like to thank both reviewers for their comments and the helpful feedback, which will help us improve both clarity and impact of the MS. Below we provide a point-by-point response to the comments, including their consequences for the MS.

Reviewer comments are indicated with open bullet points, whereas our response is indicated with a dash. Text that will be changed in the manuscript is italicized. After the point-by-point responses to the comments the manuscript with track changes is attached.

Kind regards, also on behalf of all co-authors

Marinka van Puijenbroek

Reviewer 1

Summary: This is a very interesting piece of work that assesses the relationships between vegetation and dune morphology based on UAV surveys. The authors successfully follow the contributions of vegetation and dune morphology to dune development on a large beach in the Netherlands. A truly interesting part of this study is the fact the dune growth is determined in summer and winter by dune size and vegetation respectively. I believe the paper is a valuable contribution, and I think it should be published after the authors have clarified/reviewed a few points. I have no issues with the work per sein terms of the statistical analyses applied to relate dune volume with both vegetation species and characteristics. However, I have some moderate comments regarding the analysis of the UAV acquisition and processing.

Moderate comments

- o There are only 5 ground control points used which are not homogenously located in the investigated study site (e.g. not in each corner and middle of the site). Thus, my concern is that the sum of error from data acquisition to DTM generation is likely to be above 5cm. Also the error of the DSM for each survey is likely to be different due to difference of weather conditions and survey acquisition. I would suggest the authors to report the error of the DSM of each survey.
  - Thank you for calling attention to this aspect. We set out to calculate three potential sources of error: 1) the vertical error associated with the use of photogrammetry, 2) the error involved in performing multiple campaigns and 3) the relationship between NDVI and vegetation biomass. Concerning 1) The vertical error of the DTM ranged between 0 – 20 cm. This value did depend on the distance to the ground control marker, further from the marker the higher the vertical error. This vertical error means for the dune volume that there will be an error in dune volume between 5 – 12 % depending on the vertical error. Concerning 2), the repeatability of the photogrammetric reconstruction was on average 3 cm. We do not expect the vertical error to affect our results however, since the measurement error is random in nature and not systematic making explanatory variables less significant rather than more significant. The third point is discussed in the comments below.
  - We added information on the accuracy of the photogrammetry reconstruction to the results (lines 426 – 439) and discussed the implications of the accuracy of the photogrammetric reconstruction for our results in our discussion (lines 557 – 575).
  - We included in the supplementary data 1) graphs of the frequency distribution of the vertical error, 2) the relationship between distance of the ground control marker and the vertical error, and 3) a graph on the repeatability of the photogrammetric reconstruction. In the supplementary data we also included two tables of the deviation of the dune volume for different vertical errors and information about the dense point cloud for the different mapping campaigns.
- o Unfortunately no field vegetation height surveys are reported to be carried out during the UAV flight. Could the authors report the error of vegetation height extracted by the difference between DSM and DTM? I would expect a difference between summer and winter since the vegetation binding is likely to be higher for the latter.
  - Unfortunately we did not measure the vegetation height during our mapping campaigns and can therefore not report the error of the vegetation height. The maximum vegetation height calculated in our study is most likely an under-estimation, because the during photogrammetric reconstructions outliers are removed. During winter the maximum

vegetation height will most probably be lower, partly because in the field the vegetation height is lower. The NDVI signal is also lower and this will also result in a lower maximum vegetation height, especially for the dunes covered with *Elytrigia juncea*, since their NDVI signal is very weak in winter.

- We did relate the summed NDVI per dune with the biomass of the vegetation per dune (see response earlier comment). We did not find a significant relationship between the NDVI and the biomass on a dune, but this was partly due to the low sample size. Biomass also includes vegetation parts such as stems and litter, and these parts do not contribute (much) to the NDVI signal, which could explain the absence of a correlation. We added this result to our manuscript at lines 440 - 443.

o I would suggest the authors to be critical about the limitations of their technique.

- We agree that is it important to be critical about the limitation of the UAV monitoring, and therefore we added a paragraph to the discussion, which discusses how the accuracy of the DTM could affect our results.

o I think that it would be nice if the authors present the DTM, DEM and orthomosaics for each survey in a Figure. This could help further to support the analysis.

- We agree, and included a graph with the DTM, DSM and orthomosaic for each mapping campaign in a figure in the supplementary material.

Minor comments:

o In the abstract, some result values should be added to support the interpretation of the findings. I would not suggest to have biogeomorphology as a keyword because it is not mentioned in the text of the manuscript.

- We added some result values in the abstract and remove biogeomorphology as a keyword.

o I would suggest to modify Figure 1 by: adding a ground picture where dunes, and vegetation could be visualized and locating the foredune.

- We added a ground picture of the area, unfortunately there is no photograph from which we can clearly indicate the foredune.

o The methodology section is quite long. I would suggest to have a separate study site section. Also I think that it would be easier for the reader to have a figure of theworkflow of the methodology.

- We added a title above the study site section. We added a figure with the workflow of our methodology.

o Could the authors justify the thresholds used to define the dunes in lines 184-185.

- We added this sentence to justify the thresholds used to define dunes at lines 218 - 220:

  The 5 cm threshold is the minimum that can be accurately derived from the images and corresponds with visual estimates of nebkha dune foot; Pixels above 5 cm indicated sand deposition, and a slope of 15º has been earlier identified by Baas et al (2002), as the slope for a shadow dune.

o Authors said that there are 11 blocks landward from the foredune in line 236 . However only 10 blocks could be seen in Figure 2.

- There are 11 blocks landward from the foredune, however in our figure 2 one block was cut off by the edge of the figure. We changed figure 2 to show all the blocks.

o In Figure 4, the markers for seaward and landward cannot be differentiated. They should not be the same.

- We changed the markers for the seaward and landward situated dunes, so that they can be differentiated.

o I truly enjoyed the discussion part. I checked the references and found them all correct and found them all correct (i.e. references cited in the text are in the list and vice versa). The manuscript is well written. I could not find grammatical errors or awkward sentences that would distract me as a reader. On the contrary, the text is easy to follow. I believe the manuscript should proceed to publication after the revision outlined above. UAV systems are becoming more and more accessible to a wider community and hence I believe contributions such as the one outlined in this paper will be welcome by a number of other coastal researchers.

- Thank you for your comments, we are glad you liked our discussion.

Reviewer 2

This is an interesting topic , sadly very poorly written.

- Line 55- there are multiple papers outlining how incipient or embryo dunes develop in multiple countries so this is patently wrong – remove or rephrase.
  - We agree that there are many paper that describe the formation of incipient foredunes or embryo dunes. However there are not so many papers that quantify the factors that determine the speed of early dune development. We adapted the sentence at line 56 to reflect this.
- Lines 57 to 63- actually Hesp stated that incipient foredunes are initiated in several ways and by nebkha and shadow dune formation is only ONE way. If the authors are going to review how incipient foredunes are formed they need to state all the other ways too – e.g. by aeolian deposition in continuous alongshore canopies of vegetation as well as discrete nebkha. And it's: incipient foredunes" NOT incipient dunes" - the latter describes any type of dune...
  - In our study site dune formation is initiated by the establishment of vegetation and the formation of a nebkha and shadow dune. Since the formation of an incipient foredune by sand deposition within the continuous alongshore vegetation did not occur in our study site, we would rather not add this process to our introduction. We clarified throughout our MS that we are studying nebkha dunes.
- Lines 79-80 these refs are very recent – the more comprehensive reviews of e.g. effect of veg density and distribution are in hesp papers – 1983, 1988 for example so cite these and Arens papers.
  - We only cited the more recent papers to limit word counts. We added some additional older references including Hesp from 1983 and 1988 as well as the papers by Arens, to give a more comprehensive overview.
- Lines 91-92. You need to explain better WHY u think greater dune size should mean greater accretion/deposition. Is it because u think if a dune is big then it obviously has a greater sediment supply than a small dune? BUT what about age? How has this been taken into account? A dune might be small because its young/in early development stage, a big one because it's been sitting there for 200 years or gets regular scarping, scarp fill, crest growth due to that... Also is it because a larger vegetation patch would produce a larger nebkha and therefore would be able to collect more sand? There are multiple answers here and you must discuss there and later in the discussion/conclusions the impacts of these on your results.
  - We changed our hypotheses at line 103 – 109 to clarify our expectations:

    We expected that nebka dune growth would be a function of vegetation density, initial dune size, and shelter, with the function being modulated by season and degree of shelter. We hypothesised that:

    1. *Nebkha dunes with high vegetation density grow fastest irrespective of season or shelter*
    2. *In summer, growth of nebkha dunes is linearly related to initial dune size with small dunes growing at the same rate than big dunes. Exposed dunes grow faster than sheltered dunes because of higher sand supply.*
    3. *In winter dune growth is no longer linearly related to initial dunes size, as small dunes are more susceptible to storm erosion than big dunes. Exposed dunes grow slower than sheltered dunes because of higher storm erosion.*
  - The dunes in our study are quite young, most of the nebkha dunes (ca. 95%) have developed within 5 years. Age is important as it will affect the size of the nebkha dunes, however age is difficult to measure. Furthermore, in coastal systems the dune size can also decrease by sea water inundation during large storms, this erosion will weaken the correlation between age and nebkha dune size. At the study site section we mention the age of our nebkha dunes.
  - The area of the vegetation patch can indeed have a large effect on the sand deposition and thereby nebkha dune growth. We therefore did some additional analysis to test the effect of vegetation area on nebkha dune growth. In our study site the vegetation area was correlated to the dune size. We checked whether the vegetation area is a better predictor for nebkha dune growth than dune size, however this was not the case. Especially for the dunes seaward of the foredune, vegetation area only explained 36% of the variation, whereas dune size explains 90% of the variation. We included these results and discuss this in the discussion, the results are at line 368 – 372 and the discussions at line 529 - 533.
- Lines 92-93: WHY? Because of snow cover, more wave energy and erosion, wet sand WHAT? Please explain.

- We think that exposed dunes grow faster in summer, because there is no storm erosion and therefore more net sand deposition, the sheltered dunes will grow slower because they have less sand supply. In winter storms result in sand erosion, potentially leading to negative growth for the exposed dunes. The sheltered dunes are protected from the storm and will still have a positive growth and therefore have an increased growth in winter. To clarify our expectation we changed the hypotheses, see above new version.

o Lines 101-102: WHAT 3 types of dunes? You haven't said before this that there are 3 types. In line 100 u say dunes are formed by 1, 2 or a mixture*...* is that what u mean by saying 3 TYPES of dunes? In which case they are NOT types.(im convinced even by this stage you do not understand how dunes are classified*...*) they are ALL incipient foredunes formed in diff species or mixtures of species. REWRITE. Elucidate please!

  - We will change the sentence to reflect that these are all nebkha dunes, with different species composition. We checked the manuscript to clarify that we are always talking about nebkha dunes and that the different dunes consist of different plant species.

o It is NOT obvious until one gets into the methods section that you are mostly, or entirely talking about incipient foredunes and mostly nebkha and shadow dunes. You need to state this clearly at the start of the paper and also in the abstract.

  - We indeed study nebkha dunes only. We changed the text accordingly.

o Lines 275-276: dune height - WHY? Because these are older since they are more landward? Explain 289-290: obviously because they formed earlier and are older and have had a greater time to collect sand. How about stating these kinds of associations when u state your results?

  - The sheltered dunes are not much older than the exposed dunes, five years at most. Nevertheless, we agree that the height differences between sheltered and exposed dunes cannot be contributed to their position only, but can be a function of their slightly older age too. We added this explanation to the MS at line 319 - 321.

o Also u are omitting the important papers on flow and sedimentation in patches or veg- etation – classic study of diff patch density by Qian et al; Liu papers, Bouma paper on flow in veg patches underwater etc. – these all provide excellent explanations of how density controls nebkha development and need to be reviewed and cited.

  Bouma, T.J., van Duren, L.A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T., Herman, P.M.J., 2007. Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. Continental Shelf Research 27, 1020–1045.

  Dong.,Z., Wanyin, L., Guangqiang, Q., Ping, L., 2008.Wind tunnel simulations of the three-dimensional airflow patterns around shrubs. Journal of Geophysical Research 113: F202016, doi: 10.1029/2007JF000880

  - We thank you for calling attention to these nice papers; we incorporated them into our MS, making our discussion stronger.

• Lines 337-340: it's strange and weird that you state dune vol is related to dune volume! Of course it is as it's the same thing. *...* Rewrite to explain better what you are correlating here.

  - We meant that the absolute change in dune volume was related to the initial dune volume, we rewrote this sentence to make it more clear.

o Line 358: YOU MEAN: "The aim of this study was to explore the contributions of vegetation and dune size to NEBKHA dune development" - add this word otherwise its totally confusing and non-obvious what u are talking about; i.e. ANY dune development??!

  - We changed this to nebkha dune development.

o Line 359 – now your aim is ONLY about degree of shelter? What about the other aims stated at the start of the paper??

  - The main aim of our study is to explore the contributions of vegetation and dune size to nebkha dune development. Our secondary aim is to understand how the contribution of vegetation and dune size is modified by the degree of shelter. We changed the sentence at line 446 – 448 to better reflect this.

o Lines 368-369: because you have failed to adequately review the literature you are stating untruths here. One of the great papers to fully show how seasons control foredune growth is the one by Davidson-Arnott (ref in Hesp 2002 paper maybe). Check his book which has the model in it I think. At any case remove the statement that this is the first to relate foredune growth to seasonal change.

  - You are entirely correct that we are not the first paper to show how seasons control vegetated dune growth. Davidson-Arnott and Law (1990) show that the amount of sand deposition at a foredune depends on the season, where in winter more sand is deposited than in summer. Montreuil et al. (2013) showed that embryo dunes show a seasonal cycle of summer growth and winter erosion. As far as we know, we are the first paper to show that the effect of vegetation and dune size on nebkha dune development differs between a winter and summer. We changed the sentence at line 457 – 460 to clarify this.

- Lines 390-393: the referencing of the transverse dune lit here doesn't compute. Shadow dunes and/or nebkha do not at all have the same flow dynamics as transverse dunes. You need to rethink this entire idea and writing. Shadow dunes for example are controlled by paired horizontal flow vortices and max slope angle (hesp 1981). Nebkha vol and height is largely controlled by veg density and nebkha age and rate of plant growth....

  - You are correct that it is not correct to compare nebkha dunes with transverse dunes. We therefore removed the sentence.

  - The sentence is replaced by the following sentence at line 467 - 471:

    The linear relationship between initial dune volume and dune volume change found for the nebkha dunes in our study indicates that different dune sizes have similar effect on the wind flow pattern per unit of area, which indicates scale invariance (Hallet, 1990). Scale invariance has been used for modelling nebkha and foredune development (Baas, 2002; Durán Vinent and Moore, 2013), but has not yet been validated for nebkha dunes to our knowledge.

- Lines 415-416- and less storm surge, wet high tide beach, etc on the sheltered side??

  - In these lines we refer to our result that dune growth of sheltered nebkha dunes was higher in winter than growth of sheltered dunes in summer. It seems reasonable to assume that this result is related to a higher sand deposition in winter, than to differences in storm surge or wet high tide beach. We will change the sentence to clarify our result, to the following:

    Interestingly, the sheltered dunes had a slightly higher dune growth in winter compared to summer. This increase in dune growth for sheltered dunes can perhaps be explained by more frequent and/or intensive aeolian transport events during winter resulting into higher sand supply to the sheltered dunes (Davidson-Arnott and Law, 1990).

- Line 418 and subsequent lines: You are NOT describing "veg characteristics" here. BE specific – u are at least first describing the effect of veg species differences or combinations of species, NOT density, distribution, height etc. So be specific – rewrite.

  OK I see that you discuss these other factors next BUT would be better to still rewrite the first part to make it clear you are first just talking about species differences. Lines 448-449: there are several studies showing that ammophila does trap more sand generally compared to other species due to its high density clump-like nature so cite some of these.

  - You are correct that we first discuss the difference in dune growth formed by different plant species. To make the title better reflect the section we renamed the title to vegetation. Furthermore, we were more specific in the subsequent lines on our results.

  - We added a reference that reported that *A. arenaria* can trap more sand compared to other dune building species.

- lines 514-515: I don't see anywhere a decent explanation of why this is the case. You need to better explain this conclusion.

  - Thank you for calling attention to this . Indeed, we only looked at the difference in dune growth for dunes with different species composition. We will change the sentence at line 641 to the following:

    Species composition does not affect dune growth over summer, but does affect dune growth during winter, particularly at exposed sites.

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

Short running head: Dune size and vegetation

Marinka E.B. van Puijenbroek[1], Corjan Nolet[2], Alma V. de Groot[3], Juha M. Suomalainen[4,5], Michel J.P.M. Riksen[2], Frank Berendse[1] and Juul Limpens[1]

[1]Plant Ecology and Nature Conservation Group (PEN), Wageningen University & Research Wageningen, P.O. Box 47, 6700 AA, The Netherlands

[2]Soil Physics and Land Management Group, Wageningen University & Research, Wageningen, P.O. Box 47, 6700 AA, The Netherlands

[3]Wageningen Marine Research, Wageningen University & Research, Den Helder, Ankerpark 27, 1781 AG, The Netherlands

[4]Laboratory of Geo-Information and Remote Sensing, Wageningen University & Research, Wageningen, P.O. Box 47, 6700 AA, The Netherlands

[5]Finnish Geospatial Research Institute, National Land Survey of Finland, Kirkkonummi, Finland

Correspondence to: Marinka E.B. van Puijenbroek (marinka.vanpuijenbroek@wur.nl)

Abstract

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

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

We found that a positive change in dune volume (dune growth) was linearly related to initial dune volume over summer but not over winter. Big dunes accumulated more sand than small dunes due to their larger surface area. Exposed dunes increased more in volume (0.81% per dune per week) than sheltered dunes (0.2% per dune per week) over summer, while the opposite occurred over winter. Vegetation characteristics did not significantly affect dune growth in summer, but did significantly affect dune growth in winter. Over winter, dunes dominated by *Ammophila arenaria*, a grass species with high vegetation density throughout the year, increased more in volume than dunes dominated by

Elytrigia juncea, a grass species with lower vegetation density (0.43 vs. 0.42 (m^3/m^3)/week). The effect of species was irrespective of dune size or distance to the sea.

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

Key words: ~~Biogeomorphology,~~ ~~embryo~~ Nebkha dunes, *Ammophila arenaria*, *Elytrigia juncea*, beach-dune interaction, landform morphology, the Netherlands

1. Introduction

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

Field Code Changed

Dune development is the result of an interaction between vegetation and aeolian processes and starts above the high-water line by the establishment of dune-building plant species (Maun, 2009). Once vegetation establishes on the bare beach, it forms a roughness element that facilitates local sand deposition and reduces erosion, forming a small dune within discrete clumps of vegetation (Dong et al., 2008; Hesp, 2002)~~(Hesp, 2002)~~. At the lee side of these small clumps of vegetation a shadow dune develops by sand deposition, this shadow dune has a ridge parallel to the wind direction (Clemmensen, 1986; Gunatilaka and Mwango, 1989; Hesp, 1981)~~(Hesp, 1981)~~. Vegetation and shadow dune together are known as ~~embryo~~ nebkha dunes, embryo dunes or incipient foredunes ~~dunes~~ (Hesp, 2002; Hesp and Smyth, 2017). The~~ir~~ further development of these nebkha dunes strongly depends on the balance between summer accumulation of sand and vegetation growth and winter erosion of sand and loss of

Field Code Changed

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom)

Field Code Changed

Formatted: Font: (Default) Verdana, 8.5 pt

Field Code Changed

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Verdana, 8.5 pt, Dutch (Netherlands) vegetation (Montreuil et al., 2013). Summer growth and winter erosion depend on weather conditions, such as wind speed, precipitation and storm intensity (Montreuil et al., 2013; van Puijenbroek et al., 2017). As a result, net dune growth can differ from year to year. Over time the smaller vegetated dunes can develop into an established foredune that forms the first line of coastal defense against flooding.

Most research on coastal dune growth and erosion have focussed on processes and factors that influence the supply of sand to the dunes and the effect of storm intensity on dune erosion (Anthony, 2013; Haerens et al., 2012; Houser et al., 2008; Keijsers et al., 2014; Saye et al., 2005; de Vries et al., 2012). However, how coastal nebkha dune growth and erosion rates are influenced by the individual dune characteristics, such as dune size, vegetation and degree of sheltering are less well studied. Dune size affects the wind flow pattern, thus affecting sand deposition (Walker and Nickling, 2002) for example increasing height or length of the shadow dune (Hesp, 1981; Hesp and Smyth, 2017). Dune size also influences storm erosion: Claudino-Sales (2008) found that foredunes with a higher volume were less sensitive to erosion. Whether the latter also applies to ~~embryo~~ nebkha dunes, is unknown. Differences in vegetation density between plant species are known to modify sand deposition (Arens, 1996; Hesp, 1983; Keijsers et al., 2014; Zarnetske et al., 2012), storm erosion (Charbonneau et al., 2017; Seabloom et al., 2013), and dune morphology (Du et al., 2010; Hacker et al., 2012; Hesp, 1988)~~, and growth (Charbonneau et al., 2017; Hacker et al., 2012; Seabloom et al., 2013; Zarnetske et al., 2012)~~. Sheltering by other nebkha dunes can decrease the sand supply but can also reduce erosion by waves (Arens, 1996; Lima et al., 2015; Luo et al., 2014; Montreuil et al., 2013)~~(Arens, 1996; Montreuil et al., 2013)~~. Although dune size, vegetation and sheltering are known to be important for individual nebkha dune development, the relative contributions of these factors are unknown.

Field Code Changed

Field Code Changed

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Dutch (Netherlands)

Field Code Changed

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom)

Formatted: Font: (Default) Times New Roman, 12 pt

Field Code Changed

Formatted: Font: (Default) Verdana, 8.5 pt, English (United Kingdom)

Formatted: English (United Kingdom)

Field Code Changed

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Dutch (Netherlands)

Formatted: Dutch (Netherlands)

In this study, we explored the contribution of vegetation and dune size to dune development. Using an unmanned aerial vehicle (UAV) with camera we monitored a natural nebkha dune field for one year. From the aerial images we constructed ~~a~~ digital terrain models (DTM) and ~~an~~ orthomosaics. From the DTM's and orthomosaics we extracted detailed data on dune size (dune area, volume and maximum height), vegetation characteristics and the degree of sheltering. We related changes in dune volume (dune growth) to initial dune size, ~~and~~ vegetation ~~to changes in dune volume~~and sheltering over a summer (April - August) and winter period (November - April). We expected that nebkha dune growth ~~to~~ would be a function of ~~dune size and vegetation density~~vegetation density, initial dune size, and shelter, with the function being modulated by season and degree of shelter. We hypothesised that: ~~, dune growth being the largest for big dunes with high vegetation density. We also expected that the effect of sheltering on dune growth would depend on season: exposed dunes growing faster in summer, but slower in winter.~~

1. Nebkha dunes with high vegetation density grow faster irrespective of season or shelter.
2. In summer, growth of nebkha dunes is linearly related to initial dune size, with small dunes growing at the same rate as big dunes. Exposed dunes grow faster than sheltered dunes because of higher sand supply.
3. In winter dune growth is no longer linearly related to initial dune size, as small dunes are more susceptible to storm erosion than big dunes. Exposed dunes grow slower than sheltered dunes because of higher storm erosion.

Formatted: List Paragraph, Numbered + Level: 1 + Numbering Style: 1, 2, 3, … + Start at: 1 + Alignment: Left + Aligned at: 18.8 mm + Indent at: 25.2 mm

Formatted: Font: (Default) Times New Roman, 12 pt

Formatted: Font: (Default) Times New Roman, 12 pt, Bold

Formatted: Normal, No bullets or numbering

2. Methods

2.1 Study ~~area~~site

We monitored 8 hectares (200 m x 400 m) of a natural dune field with a large range of dune sizes at 'the Hors', the southern tip of the barrier island at Texel, the Netherlands, coordinates: 52°59'43.70"N, 4°43'47.53"E (Fig. 1). The Hors is a wide dissipative beach with a high degree of hydrodynamic reworking of the sand, which results in a high transport potential and opportunity for dunes to develop. ~~In the last 20 years many vegetated dunes have developed on the beach.~~ In the last 5 years, between 2010 and 2015, many nebkha dunes have developed on the beach~~At this area permanent dunes are formed~~ by plant species *Ammophila arenaria*, *Elytrigia juncea* or a mixture of both species. These three ~~types of vegetated dunes~~dunes with different species composition occur~~red~~ at similar distances from the sea, making this area ideal for ~~testing~~ exploring the effects of dune size and species composition on dune growth. *A. arenaria* and *E. juncea* differ in their vegetation characteristics: *A. arenaria* grows in dense patches, whereas *E. juncea* has a more sparse growth form. This difference in growth form probably also results into a different dune morphology: *A. arenaria* forms higher 'hummocky' shaped dunes, whereas *E. juncea* builds broader and lower dunes (Bakker, 1976; Hacker et al., 2012). The monitoring area is bisected by a low (maximum height of 7 m NAP, i.e. above the mean sea level near Amsterdam), continuous foredune ridge that runs parallel to the shore. The nebkha dunes that occur at the seaward side of this foredune are more exposed to the sea, while the nebkha dunes occurring at the landward side of the foredune are more sheltered from the sea, enabling us to explore whether the effects of dune size and vegetation are modified by the degree of shelter especially since the age difference between the seaward and landward nebkha dunes is at most 5 years. The foredune in our monitoring area has a maximum height of 7m NAP (NAP refers to Amsterdam Ordnance Date, which refers to mean sea level near Amsterdam).

2.2 Weather conditions

Formatted: Indent: First line: 0 mm

Summer conditions during our study period were similar to previous years, while winter conditions were calmer than usual (Supplementary S1). The precipitation during the growing season was 276 mm, and the average temperature in June and July was 16 °C. The most common wind direction was South to South-West. The most common wind speed in summer was 4 - 5 m s^{-1}, and the maximum wind speed was 13 m s^{-1}. In winter the wind speed was higher compared to summer, the most common wind speed was 5 – 6 m s^{-1} and the maximum wind speed was 19 m s^{-1}. We registered one storm during the study period. This storm, however, could be classified as relatively weak. The highest water level was 211 cm NAP; compared to 248 cm NAP and 254 cm NAP from previous years. The storm, which was the first of the season, occurred after the beginning of our mapping campaign.

2.2 3 Data collection

Three UAV flights in November (2015), April (2015) and August (2016) were carried out with a rotary octocopter UAV system (Aerialtronics Altura Pro AT8 v1) and camera equipment of WageningenUR *Unmanned Aerial Remote Sensing Facility* (Fig. 1). The octocopter was equipped with a Canon EOS 700D single-lens reflex camera with a 28mm f/2.8 Voigtländer Color Scopar SL-II N objective. The camera sensor was modified to give a false colour output. The red channel of the camera had been converted to be sensitive in the near-infrared, with centre point around 720nm. The blue channel of the camera had been extended to also cover the UV region of the spectrum. The green channel was left with almost original response. The false colour modification enabled the calculation of a modified Normalised Difference Vegetation Index (NDVI), a commonly used measure for vitality and/or cover of the vegetation (Carlson and Ripley, 1997). Aerial images were acquired by auto-piloted flights at an altitude of 80 m at 4 – 5 m s^{-1} velocity. The camera was set to take one image per second. The auto-piloted flights enabled us to have the same flight paths for each of the three mapping campaigns. The flight paths ensured that images had a minimum of 85% forward and 65% side-way overlap. Four flights of 10 minutes were needed to cover the study area, yielding up to 900 RAW false colour images per mapping campaign. Five ground control points were permanently placed in the flight area and measured with a RTK-DGPS Trimble R6 Model 3 (TSC3) to calibrate our images with coordinates. During our mapping campaign, a Spectralon reference panel was measured with our camera immediately before take-off and after landing.

2.3 4 Radiometric calibration

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

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

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

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

2.~~4~~ 5 Photogrammetric reconstruction

The large overlap between the consecutive images was necessary for photogrammetric software to successfully process the aerial images into a 3D point cloud (Fig. 2). The 3D point cloud was generated using Agisoft Photoscan Professional (v. 1.2.6), using the Structure-from-Motion (SfM) and Multi-View Stereo (MVS) algorithms (Fonstad et al., 2013; Westoby et al., 2012). The correlated 3D points are georeferenced to match the ground control points, and contain pixel intensity values of the input imagery. From this 3D point cloud we interpolated a 5 cm pixel size digital surface model (DSM) and a

1 cm pixel size orthomosaic image. The vertical error distribution of a DSM produced by UAV photogrammetry is expected to be equivalent to airborne LIDAR data and terrestrial laser scanning (Hugenholtz et al., 2013; Mancini et al., 2013). The DSM included also vegetation, which resulted in a vertical error in dune height in areas where vegetation is present. We removed the vegetation from the point cloud by identifying and removing the vegetation points. Vegetation points were removed by distinguishing vegetation from sand using k-means clustering of the 3-D point cloud with NDVI using the Hartigan and Wong (1979) algorithm in R (R Core Team, 2016). The holes in the point cloud that arose by removing the vegetation were filled by using LAStools (the tool Blast2dem) (Isenburg, 2016), which resulted in a Digital Terrain Model (DTM) without vegetation.

We checked the accuracy of the Photogrammetric reconstruction by measuring the vertical error, the repeatability of the method and the degree in which NDVI predicted the biomass of the vegetation. The vertical error of the DTM was assessed during a combined mapping and flight campaign in August 2015 by measuring the elevation for 1100 points distributed over the flight area with an RTK-DGPS Trimble R6 Model 3 (TSC3) and comparing the measured point measurements with the DTM. The repeatability of the UAV photogrammetry was tested by repeating the same flight path five times in November 2015 and comparing the similarity between the five DSMs. The NDVI measurements were tested by clipping the vegetation flush with the sand surface for six *A. arenaria* and seven *E. juncea* dunes and relating the biomass of the vegetation to the NDVI values.

2.5 6 Defining dunes

To be able to relate dune growth to characteristics of an individual nebkha dune including its shadow dune, we first had to define individual dunes from the DTM. We followed a step-wise procedure for each of our mapping campaigns (November, April, and August) using ArcGIS 10.3 (ESRI, 2016) that resulted into different polygons in which each individual dune~~s~~ expanded or decreased in volume over the study period. Dune ~~size~~ volume and growth were later calculated using the same polygons for each measurement campaign through time (see next section). To define the polygons we used the step-wise procedure described below: 1) we constructed a baseline raster by calculating the average elevation in a circle of 5m radius around each pixel in the DTM. A higher or lower radius resulted in either a too low or too high baseline. 2) We then qualified pixels of the DTM as dunes, if they were 5 cm or higher above a baseline raster, or had a slope of 15° or higher. The 5 cm threshold is the minimum that can be accurately derived from the images and corresponds with visual estimates of nebkha dune foot; a slope of 15º has been earlier identified by Baas et al (2002), as the slope for a shadow dune. From these selected ‘dune’ pixels we created dune polygons. 3) Dune polygons of consecutive campaigns were overlaid to construct the largest dune-covered area during the study period. 4) Each polygon was visually checked for minimum size and presence of vegetation: dunes consisting of only one clump of vegetation (0.4 m^2 or smaller) and dunes with no vegetation were discarded to derive conservative estimates of nebkha dune volume and growth.

Field Code Changed

2.~~6~~ 7 Variables

For each nebkha dune and for each mapping campaign we extracted dune volume (m^3), max height (m) and horizontal area (m^2) from the dune polygons (see previous section) in the DTM. We calculated changes in dune volume, i.e. ~~the~~ absolute ~~change in dune volume~~dune growth (m^3/week) by subtracting the current dune volume (V_t) from the volume of the previous mapping campaign (V_{t-1}), ~~and we corrected~~ correcting for the number of weeks between the mapping campaigns. To explore relationships irrespective of dune~~s~~ size, we also calculated the relative dune growth (m^3/m^3/week). ~~change in dune volume per week as (V_t/V_{t-1})/week. Where V_t is the dune volume and V_{t-1} the dune volume of the previous mapping campaign.~~

We manually identified the species composition on each nebkha dune from the orthomosaic. Species identification was verified in the field for a random subset of 100 dunes (23%) in May 2016. To this end we created 2 transects from the southwest border to the northeast border of the area, along which ~~. For these transects~~ we determined the species on each nebkha dune ~~in the field in May 2016~~. We compared the presence of species in the field with the orthomosaic, and adjusted the species composition if necessary. In our dataset, dunes have either *A. arenaria*, *E. juncea* vegetation, or a mixture of both species. A dune was defined as covered by a mixture of both species, when it had distinct vegetation patches of both species present. For each nebkha dune and mapping campaign we also extracted the vegetation density and the maximum plant height. To assess vegetation density we first distinguished vegetated pixels from non-vegetated pixels based on the orthomosaic using k-means classification of the NDVI using the MacQueen (1967) algorithm. Hereafter, the vegetation area (m^2) and vegetation density (NDVI/cm^2 dune) ~~was~~ were calculated by summing the NDVI values of all vegetated pixels within the dune polygon (vegetation area) and then dividing this summed NDVI by the

Field Code Changed

total number of cm^2 pixels within the dune polygon (vegetation density). The maximum plant height was calculated by subtracting the DTM (with vegetation) from the DSM (without vegetation).

Sheltering can affect the sand supply and storm erosion. We used two methods to define the ~~extent~~ degree of sheltering. Firstly, we distinguished whether a nebkha dune was seaward or landward from the foredune. Secondly we determined how much ~~a~~ the dune was clustered with other dunes. We extracted the degree of clustering for each dune by calculating the mean height from the DTM in a 25 m radius around the dune. All data extraction from the DSM, DTM and orthomosaic were done in R (R Core Team, 2016).

2.~~7~~ 8 Statistical analysis

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

Field Code Changed

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

Thirdly, we analysed how the relative changes in dune volume over winter and summer depended on dune size and vegetation characteristics in separated linear mixed models (Pinheiro et al., 2016). To correct for spatial autocorrelation and species distribution we ran this analyses on a subset of 236 (54%) dunes. To this end we first explored the degree of spatial autocorrelation in our dataset by creating a variogram. To account for the spatial autocorrelation of 25 m in our dataset we imposed a 50 m x 50 m grid over our study area; all dunes that were located within a grid cell (referred to as block) were assumed to show spatial autocorrelation to some extent. This spatial autocorrelation was corrected for in our statistical model by including block as a random intercept. We had 10 blocks seaward from the foredune and 11 blocks landward from the foredune (Fig. ~~2~~3), in which all species combinations occurred (*A. arenaria* dunes, *E. juncea* dunes and *A. arenaria* + *E. juncea* dunes). By only including dunes that were located within a block in the analysis, our selection was biased towards smaller dunes, since larger dunes often fell within multiple blocks. We do expect that the effect of vegetation is more apparent for these smaller dune compared to larger dunes. To better distinguish between effects of species compositions and vegetation structure we used two different models. The effect of species composition was tested in a model with dune volume, maximum dune height, clustering and species, whereas the effect of vegetation structure was tested in a model with dune volume, maximum dune height, dune clustering, vegetation density and maximum plant height as explanatory variables. Within each model we used the initial conditions for the explanatory variables, with initial conditions being the values at the start of each measurement campaign. We included all two-way interactions. We selected the best model by using Akaike information criterion (AIC). As we were mainly interested in the importance of the explanatory variables relative to each other, we calculated the standardised estimates for all the models by scaling the explanatory data.

The normality and homogeneity of the variance of the data was visually checked. All statistical analyses were conducted in R (R Core Team, 2016). In the results we use statistic notation to show the results of the ANOVA and linear regression models. We mention the F- value (ANOVA) or t-value (linear regression), which indicates the difference of the explanatory variable to the variation in the data. The p-value indicates the probability that the null-hypothesis is correct, we used a p-value of 0.05 as a cut off to reject the null-hypothesis. The number in subscript indicates the degrees of freedom.

3. Results

3.1 Nebkha Dune dune characteristics

Within the 8 hectare nebkha dune field we distinguished 434 432 polygons that were covered with nebkha dunes for at least one moment during our mapping campaigns (Supplementary material S2). Half of these Most of the dunes were were covered by *E. juncea* dunes vegetation (50.023%), followed by *A. arenaria* dunes vegetation (28.112%) and mixed a mixture of both plant species dunes (2221.668%) in August 2016. Species composition of the dunes changed along a gradient from sea to land. Close to the sea dunes were vegetated by *E. juncea*, while, further from the sea, dunes were also vegetated by *A. arenaria* alone, or in a mix with *E. juncea* (Fig. 23). Landward of the foredune dunes were also vegetated by *E. juncea*, *A. arenaria* alone, or a mix of both species. The foredune bisecting our study area was mainly vegetated with *A. arenaria*.

In August 2016 dune area, volume and maximum height differed significantly between nebkha dunes differing in species composition (volume: F$_{2,}$~~$_{428}$~~$_{426}$=3.~~05~~02, p=0.~~048~~049; max. height: F$_{2,}$~~$_{428}$~~$_{426}$=~~59~~58.~~6~~8, p < 0.001), but did not differ between dunes contrasting in shelter. Dunes with a mix of *E. juncea* and *A. arenaria* had overall the highest volume and maximum height, whereas ~~*E. juncea*~~ dunes with *E. juncea* had the lowest volume and height. ~~*A. arenaria* d~~Dunes with *A. arenaria* had the largest range in dune volume (Fig. ~~3A~~4A, B, C). For ~~*E. juncea*~~ dunes with *E. juncea* seaward from the foredune the distance between nebkha dunes was higher, and thus clustering lower, than for ~~compared~~ to ~~*A. arenaria*~~ dunes with *A. arenaria* and dunes with both species (F$_{2,}$~~$_{428}$~~$_{426}$=~~52~~51.5, p<0.001).~~, the distance between dunes landward from the foredune was overall smaller than dunes seaward from the foredune (Fig. 3D, $F_{1,428}$=70.2, p<0.001).~~ The dune volume did not significantly differ between dunes seaward and landward from the foredune (volume: F$_{1,}$~~$_{428}$~~$_{426}$=0.~~76~~75, p=0.39~~),~~). In contrast, ~~but~~ the dune height above NAP as well as the degree of clustering (Fig. 4D) were~~was~~ significantly higher for dunes landward from the foredune (dune height: F$_{1,}$~~$_{428}$~~$_{426}$=15.9, p<0.001, clustering: $F_{1,426}$=70.2, p<0.001); we cannot exclude that part of these effects were related to the slightly older age (max. 5 years) of the nebkha dunes landward of the foredune.~~.~~

For the statistical model with relative change in dune volume as response variable, we had to correct for species distribution and spatial autocorrelation. We created a grid, with blocks of 50 m x 50 m, and we selected dunes that fell within a block. In total, we selected 236 dunes, which consisted of 41.95% of dunes with *E. juncea* ~~dunes~~, 36.02% of dunes with *A. arenaria* ~~dunes~~, and 22.03% of dunes with both species. ~~These~~ This subset of dunes had an overall lower dunes size compared to all the nebkha dunes in the dune field, but had overall similar dune morphology and vegetation characteristics (Supplementary data ~~S2~~S3).

Figure 3 approximately here

Vegetation characteristics depended on the plant species dominating the dunes and on the degree of shelter. ~~*E. juncea*~~ Nebkha dunes with *E. juncea* had significantly the lowest vegetation density, ~~*A. arenaria*~~ nebkha dunes with *A. arenaria* the highest and nebkha dunes which consisted of both species had an intermediate vegetation density (Fig. ~~3E~~4E, $F_{2,}$~~$_{428}$~~$_{426}$=~~49~~48.~~30~~91, p<0.001). Similar to vegetation density, ~~*E. juncea*~~ nebkha dunes with *E. juncea* also had the lowest maximum plant height, whereas ~~*A. arenaria* and~~ nebkha dunes with *A. arenaria* and consisting of both species had the highest maximum plant height (Fig. ~~3F~~4F, $F_{2,}$~~$_{428}$~~$_{426}$=42.~~70~~38, p<0.001). Nebkha ~~Dunes~~ dunes landward from the foredune had significantly higher vegetation densities compared to seaward dunes ($F_{1,}$~~$_{428}$~~$_{426}$=45.~~7~~49, p<0.001), which is probably caused the calmer conditions landward from the foredune, which benefits plant growth or the slightly older age of these nebkha dunes. There was no significant difference in maximum plant height between nebkha dunes seaward and landward from the foredune ($F_{1,}$~~$_{428}$~~$_{426}$=0.41, p=0.52). Nebkha dunes with *E. juncea* had the smallest vegetation area (0.35±0.047m^2), nebkha dunes with mixed vegetation the largest vegetation area (10.90±3.05 m^2) and nebkha dunes with *A. arenaria* have an intermediate vegetation area (7.25±4.18 m^2). The vegetation area on a nebkha dune is larger landward from the foredune (9.61±3.96 m^2), compared to seaward of the foredune (2.04±0.41 m^2). The vegetation area was correlated to dune volume (linear regression: t_{430} = 25.29, p < 0.001), however this relationship was stronger for nebkha dunes landward from the foredune, compared to nebkha dunes seaward from the foredune (R^2 = 0.99 vs. R^2 = 0.69).

3.2 Change in nebkha dune number and volume

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

3.2.1 Summer

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

Over summer, most nebkha dunes increased in dune volume, including the foredune which increased over summer with 0.28% per week, reaching a volume of 64,444 m^3 in August. Only 4.~~15~~16% of the nebkha dunes showed a small decrease in the volume with a mean of -0.041±0.014 m^3/week. Changes in dune volume were positively related to the initial dune volume (Fig. ~~4A~~5A, t-

~~value$_{430}$~~value$_{428}$= 57.~~20~~11, $p<0.001$) and were higher for nebkha dunes seaward of the foredune compared to nebkha dunes landward of the foredune, resulting in a significant effect of shelter (t-~~value$_{430}$~~value$_{428}$=~~-41.70~~2.72, p~~<0.001~~=0.0069). The absolute changes in dune volume were also positively related to vegetation area, however this relationship depended on the sheltering (vegetation area*sheltering by foredune: t-value$_{428}$ = 25.29, $p > 0.001$). Nebkha dune vegetation area explained more variation in the change in dune volume for dunes landward of the foredune, compared to dunes seaward of the foredune (R^2= 0.98 vs. R^2 = 0.36).

Figure 4 approximately here

~~Over summer~~Compared to the absolute change in dune volume, the relative change in dune volume (m^3/m^3/week) was mainly influenced by sheltering, ~~were the relative change in dune volume was higher~~with dunes seaward of the foredune ~~compared~~ growing faster than dunes to landward of the foredune (Fig. ~~5A~~6A). We found no significant difference in relative change in dune volume between dunes with different species composition (Fig. ~~5A~~6A, Table 1). In our statistical model plant height had a statistically significant effect on the relative dune growth. However, when tested in a single linear mixed model with block as random intercept, plant height had a R^2 of 0.0038, thus hardly explaining any variation in relative dune growth (Table 2). Several dune size variables were significant, but the individual variation explained by initial dune volume~~,~~ and dune height was very low, their R^2 ranging between 0.05 – 0.0033. The significant interactions between variables were mostly caused by the slight correlations between the explanatory variables. The clustering of nebkha dunes (i.e. the average height within 25 m of each dune) did not significantly affect the relative dune growth. We tested whether the effect of clustering was masked by the use of blocks as random intercept, since the amount of clustering was different between the blocks. We re-analysed the data without the blocks as random factor and again found ~~again~~ no effect of clustering on the relative growth rate of dunes.

Table 1 & 2 approximately here

3.2.2 Winter

Over winter (November – April) 7.85% of the 344 nebkha dunes disappeared, of which 40.74% were ~~*E. juncea*~~ dunes with *E. juncea*, 55.56% were ~~*A. arenaria*~~ dunes with *A. arenaria* and 3.70% were dunes with both species. These nebkha dunes disappeared both seaward (40.74%) and landward (59.26%) from the foredune and were overall quite small with an average volume of 2.23 ± 0.19 m^3.

Despite the decreasing number of nebkha dunes over winter, dunes ~~Over winter dunes still~~ increased in volume, the large foredune even increased with 0.22% per week. However on average the change~~s~~ in absolute dune volume was less positive than over summer, 21.~~20~~30% of the dunes decreased -0.061±0.015 (SE) m^3/week in volume, particularly seaward of the foredune. 25.00% of these decreased dunes were covered with *A. arenaria* , 50.00% with *E. juncea* and 25.00% with both species. The absolute change in dune volume between November and April was positively related to the initial dune volume in November (Fig. ~~4B~~5B, t-~~value$_{430}$~~value$_{428}$=2.12, p=0.~~033~~034), but was only significant for dunes landward of the foredune. Dunes seaward of the foredune showed no relationship between absolute change in dune volume and the dune volume in November (shelter: t-~~value$_{430}$~~value$_{428}$=~~16.37~~ 3.00, p~~<0.001~~=0.0029). Similar to initial dune volume, the vegetated area only explained variation in dune volume for the dunes landward from the foredune (vegetated area * sheltering by foredune: t-value$_{428}$ = 16.17, p<0.001).

The relative change in dune volume was influenced by species composition and degree of shelter (Table 1). Nebkha ~~Dunes~~ dunes with *E. juncea* increased relatively less in volume than dunes with *A. arenaria* ~~dunes~~ (Fig. ~~5B~~6B); this effect was only significant for dunes seaward of the foredune. We found no significant relationship between relative change in dune volume and vegetation density or maximum plant height (Table 2). There was a significant interaction between vegetation density and sheltering by the foredune, which could be related to the higher vegetation density at the dunes landward of the foredune. Initial ~~D~~dune volume, and sheltering~~the position relative to the foredune~~, had ~~a~~ significant negative effects on the relative change in dune volume, whereas clustering had a positive significant effect, but the relationships ~~was~~ were very weak (R^2 between 0.002 – 0.05).

3.3 Net nebkha dune growth

Taken over the whole observation period November – August, ~~Net~~the absolute nebkha dune growth (m^3/week) ~~per week over the whole observation period November – August~~ was higher at the seaward side of the foredune than at the sheltered landward side (slope seaward dunes: 0.37%, slope landward dunes: 0.25%, dune volume*position from foredune: t-~~value$_{430}$~~ value$_{428}$ = -11.7, p<0.001). Similarly, the relative dune growth (m^3/m^3)/week of the ~~S~~seaward dunes was also ~~also had a~~ slightly higher ~~relative change in dune volume over November to August compared to~~ than the landward dunes (seaward dunes: 0.27 ± 0.00009 ~~(m^3/m^3)/week~~ (means±SE), landward dunes: 0.026±0.0001 ~~(m^3/m^3)/week~~, F-value$_{1,230}$ = 18.51, p<0.001).

3.4 Accuracy of photogrammetric reconstruction

We checked the accuracy of the Photogrammetric reconstruction by measuring the vertical error, the repeatability of the method and the degree in which NDVI predicted the biomass of the vegetation. The average vertical error was 7.3 ± 0.2 cm, with 80% of the measured points having a vertical error between -10 and 10 cm (Fig. S4.1). The vertical error increased with increasing distance from a ground control point, at 150 m from a ground control point there was a vertical error of 20 cm (Fig. S4.2). A vertical error of 10 cm could result in a deviation 3 – 6% in the dune volume, whereas the vertical error of 20 cm would result in a deviation of 5 – 12% in the dune volume (Table S4.1). The deviation depends however on the average elevation of a dune, a nebkha dune with a higher average elevation will have lower deviation of the vertical error than a nebkha dune with a low average elevation.

The source of error due to different conditions during consecutive mapping campaigns was limited (Table S4.2). The difference between the DSMs of different flights with the same flight paths at the same day was on average 3.9±3.9e^{-6} cm, with 80% of the raster cells of the DSM had a difference between -0.07 and 0.07 cm (Fig. S4.3).

Formatted: Indent: First line: 12.5 mm

The degree in which NDVI represented vegetation biomass differed between species. The summed NDVI of a nebka dune with *A. arenaria* showed a trend with the biomass of *A. arenaria* (t_4 = 2.43, p = 0.07, R^2 = 0.6), for nebkha dune consisting of *E. juncea* the summed NDVI was not significantly related to the biomass of the vegetation (t_5 = 1.43, p = 0.21, R^2 = 0.29).

Formatted: Font: Not Bold

4. Discussion

The aim of this study was to explore the contributions of vegetation and dune size (i.e. initial dune volume) to nebkha dune development expressed as change in dune volume. ~~and~~ In addition, we were interested in how ~~how~~ the~~se~~ effects of vegetation and dune size on nebkha dune development ~~are~~ were modified by the degree of shelter. ~~We expected dune growth to be a function of dune size and vegetation density, dune growth being the largest for big dunes with high vegetation density. We also expected that the effect of sheltering on dune growth would depend on season: exposed dunes growing faster in summer, but slower in winter.~~ Our results show that the contribution of vegetation and dune size depended on season and degree of shelter. In summer dune volume change (m^3/week) was explained by initial dune ~~size~~ volume and to a lesser extent by dune height, while species composition, vegetation height or density had no effect. In winter dune volume change was explained by vegetation and ~~dune size~~initial dune volume, depending on the degree of shelter. Exposed nebkha dunes with sparsely growing *E. juncea* grew less in volume than exposed nebkha dunes with densely growing *A. arenaria*. In contrast~~, growth~~, growth of sheltered nebkha dunes was a function of initial dune volume. These findings are the first to show that the ~~relative contribution~~effect of vegetation and dune size ~~for~~ on the nebkha dune development depends on season. ~~over a winter and summer season, and these~~ These results can be used ~~for~~ to improve modelling of coastal dune development.

4.1 Dune size

4.1.1 Summer growth

We found a positive linear relationship between the initial dune volume and the absolute change in dune volume over summer. It is known that nebkha dunes affect sedimentation by changing the wind flow patterns (Dong et al., 2004; Li et al., 2008). Previous studies have found that with increased dune volume the area where the wind speed is reduced increases, which result in higher sedimentation rates

(Hesp, 1981; Hesp and Smyth, 2017). The linear relationship between initial dune volume and dune ~~growth~~ volume change found for the nebkha dunes in our study indicates that different dune sizes have similar effect on the wind flow pattern per unit of area, which indicates scale invariance (Hallet, 1990). Scale invariance has been used for modelling nebkha and foredune development (Baas, 2002; Durán Vinent and Moore, 2013), but not yet been validated for nebkha dunes to our knowledge. ~~This result has also been found in a modelling study by Walmsey and Howard (1985), who found that different sized desert barchan dunes experienced similar disruptions of wind flow patterns, suggesting similar relative rates of deposition and erosion.~~

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

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom)

Formatted: English (United Kingdom)

Formatted: Font color: Red

Formatted: Font color: Red

Formatted: Font color: Red

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

4.1.2 Winter

In winter initial dune size was only a good predictor for growth of the nebkha dunes occurring landward of the foredune. For these sheltered dunes, increases in volume (m^3/week) ~~growth~~ again followed a linear relationship with initial dune volume. The absence of a relationship between initial dune ~~size~~ volume and dune growth for the exposed dunes occurring seaward form the foredune, suggests that dune erosion is less dependent on initial dune size than dune growth. Dune erosion has mainly been attributed to wave run-up during storms (Haerens et al., 2012; Vellinga, 1982). Therefore, it seems reasonable to assume that the degree of erosion depends on whether the dune can be reached by high energy waves. Large dunes that are reached by high water levels can erode substantially, whereas small dunes can have no erosion if they are protected by other dunes from the high water.

Interestingly, the sheltered nebkha dunes had a slightly higher dune growth in winter compared to summer. This increase in dune growth for sheltered nebkha dunes can perhaps be explained by more frequent and/or intensive aeolian transport events during winter resulting into higher sand supply to the sheltered dunes (Davidson-Arnott and Law, 1990).

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom)

4.2 Vegetation ~~characteristics~~

Vegetation characteristics were a poor predictor of dune volume change over the summer period, but were a significant predictor for dune volume change over winter. Over summer dune growth did not differ between nebkha dunes covered by different dune building plant species when corrected for dune size. Similarly we did not find a clear effect of vegetation density and plant height on dune growth. This results contrast with other studies that report a significant difference in the ability of species to trap sand mediated by differences in shoot density and cover (Keijsers et al., 2015; Zarnetske et al., 2012). Perhaps the discrepancy with our study can be explained by the differences in spatial scale used between studies. We studied dune volume change at the scale of a nebkha dune including its shadow dune, whereas the other studies focussed on the scale of the vegetation patch (Bouma et al., 2007; Dong et al., 2008; Hesp, 1981, 1983; Keijsers et al., 2015; Zarnetske et al., 2012), where species specifics effects are probably more pronounced than at the scale of the whole dune. Our results support findings of ~~Also~~ Al-Awadhi and Al-Dousari (2013) ~~found~~ who reported that the effects of vegetation on dune growth are scale dependent for coastal nebkha dunes. They found that the linear relationship between shrub vegetation characteristics and dune morphology levels off for bigger dunes. In our statistical models we selected the smaller nebkha dunes, which was a consequence of only selecting dunes that

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom) were located within one block. However even for these smaller nebkha dunes vegetation had no significant effect on relative dune growth. The vegetated area of the nebkha dunes did have a positive relationship with the change in dune volume, however this relationship could be caused by co-variation between the vegetated area and dune size, big dunes generally having a higher vegetated area. Since initial dune volume was generally a better predictor for change in dune volume than the vegetated area, our results suggest initial dune volume to be the better predictor for modelling.

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

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

Formatted: Font: (Default) Times New Roman, 12 pt, English (United Kingdom)

4.3 Application of UAV monitoring for nebkha dune development

Formatted: Font: (Default) Times New Roman, 12 pt, Bold

Measurements on the accuracy of the photogrammetric reconstruction shows that the vertical error is between 0 cm – 20 cm, where most of the DTM pixels have a vertical error between 0 cm – 10 cm, resulting into a deviation of dune volume between 3 – 12%. We do not expect this variation to affect our results however, since the measurement error is random in nature and not systematic making explanatory variables less significant rather than more significant. The vertical error increased with increasing distance from the ground control markers, for future studies a maximum distance of 70 m from each raster pixel to a ground control marker would be better than the 150 m we used. In our statistical models for relative dune volume change (m^3/m^3/week) we accounted for the increasing vertical error with increasing distance from the ground control marker by including blocks as a random factor, since the nebkha dunes within a block have similar distances to a ground control marker.

The vegetation density, expressed as NDVI/cm^2 dune, was not significantly correlated with the biomass. The poor relationship is likely a result of the low sample size (six or seven samples), in combination with the high contribution of non-green parts, such as stems and dead litter, that give no or weak NDVI signal. Since stems and dead litter do affect the wind flow pattern and attenuate waves, the poor relationship between NDVI and biomass could explain why we did not find an effect of vegetation density on dune growth and erosion. We did not measure the accuracy of the plant height, and can therefore not say how well the maximum plant height represents the real plant height, however it is probably an under-representation, since outliers are removed during photogrammetric processing.

Formatted: Font: Not Bold

4.~~3~~ 4 Implication for dune development

4.~~3~~4.1 Net dune growth

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

During winter, storms determine the erosion of nebkha dunes seaward of the foredune. Multiple low intensity storms can lead to more erosion than one high intensity storm (Dissanayake et al., 2015;

Field Code Changed

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

Sand supply and storm intensity are also affected by local conditions as beach morphology. A minimum beach width is needed to reach maximum aeolian transport, the fetch length (Delgado-Fernandez, 2010; Dong et al., 2004; Shao and Raupach, 1992). Our study site had a wide beach (0.9 km wide), and we assume that the maximum aeolian transport was reached. The net growth of our foredune was approximately 30 m^3 per m foredune parallel to the sea for a period of 10 months. This growth rate does also occur at other places along the Dutch coast, but is not very common (Keijsers et al., 2014). Storm intensity is also influenced by beach morphology. The presence of intertidal bars and a wide beach can reduce the storm intensity by wave attenuation (Anthony, 2013; Ruggiero et al., 2004). Therefore we can assume that the net dune growth we found in our study will depend on the beach morphology. On smaller beaches we expect the net dune growth to be lower compared to wider beaches, due to the lower sand supply by reduced fetch length and higher storm erosion of dune (van Puijenbroek et al., 2017)

4.4.2 Vegetation

For coastal dune development vegetation is essential, however the species-composition of the vegetation seems less important than we assumed: species did not seem to affect dune growth over the summer, but did affect dune growth over winter.

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

Field Code Changed

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

4.4.4 Application

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

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

5. Conclusions

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

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

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

Data availability Data will be made available through the 4TU.Center for Research Data (http://researchdata.4tu.nl/home/)

Field Code Changed

Author contributions MvP, CN and JS performed UAV flights and image calibration. MvP, CN and JL analysed the data. MvP, CN, JS, AdG, MR, FB and JL provided guidance on the scope and design of the project, and contributed to the writing of the manuscript.

Supporting information

Additional supporting information can be found in the online version of this article:
~~Appendix~~ Supplement S1 Weather conditions in our study site for 2013 - 2016
Supplement S2 DTM, DSM and orthomosaic of each mapping campaign
~~Appendix~~ Supplement ~~S2~~ S3 Nebkha dune morphology of selected dunes
Supplement S4 Accuracy photogrammetric reconstruction

Formatted: Font: Not Bold

References

Al-Awadhi, J. M. and Al-Dousari, A. M.: Morphological characteristics and development of coastal nabkhas, north-east Kuwait, Int. J. Earth Sci., 102(3), 949–958, doi:10.1007/s00531-012-0833-9, 2013.

Anthony, E. J.: Storms, shoreface morphodynamics, sand supply, and the accretion and erosion of coastal dune barriers in the southern North Sea, Geomorphology, 199, 8–21, doi:10.1016/j.geomorph.2012.06.007, 2013.

Arens, S. M.: Patterns of sand transport on vegetated foredunes, Geomorphology, 17(4), 339–350, doi:10.1016/0169-555X(96)00016-5, 1996.

Baas, A. C. W.: Chaos, fractals and self-organization in coastal geomorphology: simulating dune landscapes in vegetated environments, Geomorphology, 48(1–3), 309–328, doi:10.1016/S0169-555X(02)00187-3, 2002.

Bakker, J. P.: Phytogeographical aspects of the vegetation of the outer dunes in the Atlantic province of Europe, J. Biogeogr., 3(2), 85–104, 1976.

Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T. and Herman, P. M. J.: Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments, Cont. Shelf Res., 27(8), 1020–1045, doi:10.1016/j.csr.2005.12.019, 2007.

Carlson, T. N. and Ripley, D. A.: On the relation between NDVI, fractional vegetation cover, and leaf area index, Remote Sens. Environ., 62(3), 241–252, doi:10.1016/S0034-4257(97)00104-1, 1997.

Carter, R. W. G.: Near-future sea level impacts on coastal dune landscapes, Landsc. Ecol., 6(1–2), 29–39, doi:10.1007/BF00157742, 1991.

Charbonneau, B. R., Wootton, L. S., Wnek, J. P., Langley, J. A. and Posner, M. A.: A species effect on storm erosion: Invasive sedge stabilized dunes more than native grass during Hurricane Sandy, J. Appl. Ecol., n/a-n/a, doi:10.1111/1365-2664.12846, 2017.

Claudino-Sales, V., Wang, P. and Horwitz, M. H.: Factors controlling the survival of coastal dunes during multiple hurricane impacts in 2004 and 2005: Santa Rosa barrier island, Florida, Geomorphology, 95(3–4), 295–315, doi:10.1016/j.geomorph.2007.06.004, 2008.

Clemmensen, L. B.: Storm-generated eolian sand shadows and their sedimentary structures, Vejers Strand, Denmark, J. Sediment. Res., 56(4), 520–527, doi:10.1306/212F8977-2B24-11D7-8648000102C1865D, 1986.

Davidson-Arnott, R. G. D. and Law, M. N.: Seasonal patterns and controls on sediment supply to coastal foredunes, Long Point Lake Erie., in Coastal Dunes: Forms and Process, pp. 177–200, Wiley, London, UK., 1990.

Delgado-Fernandez, I.: A review of the application of the fetch effect to modelling sand supply to coastal foredunes, Aeolian Res., 2(2–3), 61–70, doi:10.1016/j.aeolia.2010.04.001, 2010.

Dissanayake, P., Brown, J., Wisse, P. and Karunarathna, H.: Comparison of storm cluster vs isolated event impacts on beach/dune morphodynamics, Estuar. Coast. Shelf Sci., 164, 301–312, doi:10.1016/j.ecss.2015.07.040, 2015.

Dong, Z., Wang, H., Liu, X. and Wang, X.: The blown sand flux over a sandy surface: a wind tunnel investigation on the fetch effect, Geomorphology, 57(1–2), 117–127, doi:10.1016/S0169-555X(03)00087-4, 2004.

Dong, Z., Luo, W., Qian, G. and Lu, P.: Wind tunnel simulation of the three-dimensional airflow patterns around shrubs, J. Geophys. Res. Earth Surf., 113(F2), F02016, doi:10.1029/2007JF000880, 2008.

Du, J., Yan, P. and Dong, Y.: The progress and prospects of nebkhas in arid areas, J. Geogr. Sci., 20(5), 712–728, doi:10.1007/s11442-010-0806-5, 2010.

Durán Vinent, O. and Moore, L. J.: Vegetation controls on the maximum size of coastal dunes, Proc. Natl. Acad. Sci., 110(43), 17217–17222, doi:10.1073/pnas.1307580110, 2013.

ESRI: ArcGIS Desktop: Release 10.3, CA: Environmental Systems Research, Redlands, US., 2016.

Everard, M., Jones, L. and Watts, B.: Have we neglected the societal importance of sand dunes? An ecosystem services perspective, Aquat. Conserv. Mar. Freshw. Ecosyst., 20(4), 476–487, doi:10.1002/aqc.1114, 2010.

Feagin, R. A., Sherman, D. J. and Grant, W. E.: Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats, Front. Ecol. Environ., 3(7), 359–364, doi:10.1890/1540-9295(2005)003[0359:CEGSRA]2.0.CO;2, 2005.

Ferreira, Ó.: The role of storm groups in the erosion of sandy coasts, Earth Surf. Process. Landf., 31(8), 1058–1060, doi:10.1002/esp.1378, 2006.

Fonstad, M. a., Dietrich, J. T., Courville, B. C., Jensen, J. L. and Carbonneau, P. E.: Topographic structure from motion: a new development in photogrammetric measurement, Earth Surf. Process. Landf., 38(4), 421–430, doi:10.1002/esp.3366, 2013.

Fox, J. and Weisberg, S.: An {R} Companion to Applied Regression, Sage, Thousand Oaks, US., 2011.

Gunatilaka, A. and Mwango, S. B.: Flow separation and the internal structure of shadow dunes, Sediment. Geol., 61(1), 125–134, doi:10.1016/0037-0738(89)90045-6, 1989.

Hacker, S. D., Zarnetske, P., Seabloom, E., Ruggiero, P., Mull, J., Gerrity, S. and Jones, C.: Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact, Oikos, 121(1), 138–148, doi:10.1111/j.1600-0706.2011.18887.x, 2012.

Haerens, P., Bolle, A., Trouw, K. and Houthuys, R.: Definition of storm thresholds for significant morphological change of the sandy beaches along the Belgian coastline, Geomorphology, 143–144, 104–117, doi:10.1016/j.geomorph.2011.09.015, 2012.

Hallet, B.: Spatial self-organization in geomorphology: from periodic bedforms and patterned ground to scale-invariant topography, Earth-Sci. Rev., 29(1), 57–75, doi:10.1016/0012-8252(0)90028-T, 1990.

Hartigan, J. A. and Wong, M. A.: Algorithm AS 136: A K-Means Clustering Algorithm, J. R. Stat. Soc. Ser. C Appl. Stat., 28(1), 100–108, doi:10.2307/2346830, 1979.

Hesp, P.: Morphology, dynamics and internal stratification of some established foredunes in southeast australia, Sediment. Geol., 55, 17–41, 1988.

Hesp, P.: Foredunes and blowouts: initiation, geomorphology and dynamics, Geomorphology, 48(1–3), 245–268, doi:10.1016/S0169-555X(02)00184-8, 2002.

Hesp, P. A.: The formation of shadow dunes, J. Sediment. Res., 51(1), 101–112, doi:10.1306/212F7C1B-2B24-11D7-8648000102C1865D, 1981.

Hesp, P. A.: Morphodynamics of incipient foredunes in NSW, Australia., in Eolian Sediments and Processes, edited by M. E. Brookfield and T. S. Ahlbrandt, pp. 325–342, Elsevier, Amsterdam., 1983.

Hesp, P. A. and Smyth, T. A. G.: Nebkha flow dynamics and shadow dune formation, Geomorphology, 282, 27–38, doi:10.1016/j.geomorph.2016.12.026, 2017.

Hothorn, T., Bretz, F. and Westfall, P.: Simultaneous Inference in General Parametric Models, Biom. J., 50(3), 346–363, 2008.

Houser, C., Hapke, C. and Hamilton, S.: Controls on coastal dune morphology, shoreline erosion and barrier island response to extreme storms, Geomorphology, 100(3–4), 223–240, doi:10.1016/j.geomorph.2007.12.007, 2008.

Isenburg, M.: LAStools - efficient LiDAR processing software (version 160730, academic). [online] Available from: http://rapidlasso.com/LAStools, 2016.

Keijsers, J. G. S., Poortinga, A., Riksen, M. J. P. M. and Maroulis, J.: Spatio-Temporal Variability in Accretion and Erosion of Coastal Foredunes in the Netherlands: Regional Climate and Local Topography, PLoS ONE, 9(3), e91115, doi:10.1371/journal.pone.0091115, 2014.

Keijsers, J. G. S., De Groot, A. V. and Riksen, M. J. P. M.: Vegetation and sedimentation on coastal foredunes, Geomorphology, 228, 723–734, doi:10.1016/j.geomorph.2014.10.027, 2015.

Keijsers, J. G. S., De Groot, A. V. and Riksen, M. J. P. M.: Modeling the biogeomorphic evolution of coastal dunes in response to climate change, J. Geophys. Res. Earth Surf., 121(6), 2015JF003815, doi:10.1002/2015JF003815, 2016.

Koch, E. W., Barbier, E. B., Silliman, B. R., Reed, D. J., Perillo, G. M., Hacker, S. D., Granek, E. F., Primavera, J. H., Muthiga, N., Polasky, S., Halpern, B. S., Kennedy, C. J., Kappel, C. V. and Wolanski, E.: Non-linearity in ecosystem services: temporal and spatial variability in coastal protection, Front. Ecol. Environ., 7(1), 29–37, doi:10.1890/080126, 2009.

Li, Z., Wu, S., Dale, J., Ge, L., He, M., Wang, X., Jin, J., Ma, R., Liu, J. and Li, W.: Wind tunnel experiments of air flow patterns over nabkhas modeled after those from the Hotan River basin, Xinjiang, China (I): non-vegetated, Front. Earth Sci. China, 2(3), 333–339, doi:10.1007/s11707-008-0019-8, 2008.

Lima, P. H. S. de, Janzen, J. G. and Nepf, H. M.: Flow patterns around two neighboring patches of emergent vegetation and possible implications for deposition and vegetation growth, Environ. Fluid Mech., 15(4), 881–898, doi:10.1007/s10652-015-9395-2, 2015.

Luo, W., Dong, Z., Qian, G. and Lu, J.: Near-wake flow patterns in the lee of adjacent obstacles and their implications for the formation of sand drifts: A wind tunnel simulation of the effects of gap spacing, Geomorphology, 213(Supplement C), 190–200, doi:10.1016/j.geomorph.2014.01.008, 2014.

MacQueen, J.: Some methods for classification and analysis of multivariate observations, in Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability, edited by L. M. Le Cam and J. Neyman, pp. 281–297, University of California Press, Berkeley, US. [online] Available from: http://projecteuclid.org/euclid.bsmsp/1200512992 (Accessed 2 February 2017), 1967.

Martínez, M. L. and Psuty, N. P.: Coastal Dunes: Ecology and Conservation, Springer-Verslag, Berlin, Heidelberg, Germany., 2008.

Maun, M. A.: The Biology of Coastal Sand Dunes, Oxford University Press, New York, US., 2009.

Montreuil, A.-L., Bullard, J. E., Chandler, J. H. and Millett, J.: Decadal and seasonal development of embryo dunes on an accreting macrotidal beach: North Lincolnshire, UK, Earth Surf. Process. Landf., 38(15), 1851–1868, doi:10.1002/esp.3432, 2013.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team: nlme: Linear and Nonlinear Mixed Effects models. [online] Available from: http://CRAN.R-project.org/package=nlme, 2016.

van Puijenbroek, M. E. B., Limpens, J., De Groot, A. V., Riksen, M. J. P. M., Gleichman, M., Slim, P. A., van Dobben, H. F. and Berendse, F.: Embryo dune development drivers: beach morphology, Growing season precipitation, and storms, Earth Surf. Process. Landf., 1–12, doi:10.1002/esp.4144, 2017.

R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. [online] Available from: http://www.r-project.org, 2016.

Ruggiero, P., Holman, R. A. and Beach, R. A.: Wave run-up on a high-energy dissipative beach, J. Geophys. Res. Oceans, 109(C6), C06025, doi:10.1029/2003JC002160, 2004.

Saye, S. E., van der Wal, D., Pye, K. and Blott, S. J.: Beach–dune morphological relationships and erosion/accretion: An investigation at five sites in England and Wales using LIDAR data, Geomorphology, 72(1–4), 128–155, doi:10.1016/j.geomorph.2005.05.007, 2005.

Seabloom, E. W., Ruggiero, P., Hacker, S. D., Mull, J. and Zarnetske, P.: Invasive grasses, climate change, and exposure to storm-wave overtopping in coastal dune ecosystems., Glob. Change Biol., 19(3), 824–32, doi:10.1111/gcb.12078, 2013.

Shao, Y. and Raupach, M. R.: The overshoot and equilibration of saltation, J. Geophys. Res., 97(D18), 20559–20564, 1992.

Silva, R., Martínez, M. L., Odériz, I., Mendoza, E. and Feagin, R. A.: Response of vegetated dune–beach systems to storm conditions, Coast. Eng., 109, 53–62, doi:10.1016/j.coastaleng.2015.12.007, 2016.

Suomalainen, J., Anders, N., Iqbal, S., Roerink, G., Franke, J., Wenting, P., Hünniger, D., Bartholomeus, H., Becker, R. and Kooistra, L.: A Lightweight Hyperspectral Mapping System and Photogrammetric Processing Chain for Unmanned Aerial Vehicles, Remote Sens., 6(11), 11013–11030, doi:10.3390/rs61111013, 2014.

Vellinga, P.: Beach and dune erosion during storm surges, Coast. Eng., 6(4), 361–387, doi:10.1016/0378-3839(82)90007-2, 1982.

de Vries, S., Southgate, H. N., Kanning, W. and Ranasinghe, R.: Dune behavior and aeolian transport on decadal timescales, Coast. Eng., 67, 41–53, doi:10.1016/j.coastaleng.2012.04.002, 2012.

Walker, I. J. and Nickling, W. G.: Dynamics of secondary airflow and sediment transport over and in the lee of transverse dunes, Prog. Phys. Geogr., 26(1), 47–75, doi:10.1191/0309133302pp325ra, 2002.

Westhoff, V., Bakker, P. A., van Leeuwen, C. G. and van der Voo, E. E.: Wilde planten, flora en vegetatie in onze natuurgebieden, Natuurmonumenten, 's-Graveland, The Netherlands., 1970.

Westoby, M. J., Brasington, J., Glasser, N. F., Hambrey, M. J. and Reynolds, J. M.: "Structure-from-Motion" photogrammetry: A low-cost, effective tool for geoscience applications, Geomorphology, 179, 300–314, doi:10.1016/j.geomorph.2012.08.021, 2012.

Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B. and Cox, D.: Biophysical feedback mediates effects of invasive grasses on coastal dune shape., Ecology, 93(6), 1439–50, 2012.

Table 1. Statistical models for the relative change in dune volume between April – August (summer) and November – April (winter) for nebkha dunes. In this model we tested the effect of species, -dune size, and degree of sheltering. The data was analysed with a general linear mixed model with blocks as random intercept. The standardized estimates and level of significance are shown for the models. Model selection was performed with AIC (Akaike information criterion) as selection criteria. Marginal R^2 is the variation explained by the fixed factors, whereas the conditional R^2 is the variation explained by the fixed and random factors.

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

Akaike Inf. Crit.	-632.60	-685.45	-673.10	-709.11
Bayesian Inf. Crit.	-555.08	-641.04	-595.57	-661.35

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

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

Model with vegetation characteristics	*Dependent variable:*			
	Relative change in dune volume			
	Summer		*Winter*	
	Full model	Model selection	Full model	Model selection
Main effects				
Intercept	1.24***	1.24***	0.90***	0.81***
Vegetation density	-0.003		-0.05	-0.03
Max. plant height	0.15	0.14**	0.04	
Dune volume	8.65***	6.62***	-2.72	-3.67**
Clustering	-0.21	-0.23	0.29	0.40**
Max. dune height	-0.44*	-0.41**	0.07	0.17
Sheltering by foredune	0.26*	0.29*	-0.28*	-0.25**
Veg. density * max. plant height	-0.01		0.001	
Veg. density * dune volume	0.83		0.92	
Veg. density * clustering	-0.03		0.078	0.06
Veg. density * max. dune height	0.04		-0.03	
Veg. density * Shel. by foredune	-0.005		-0.03	-0.04**
Max. plant height * dune volume	-0.58		-0.19	
Max. plant height * Clustering	0.02		-0.06	
Max. plant height * max. dune height	-0.11	-0.10**	0.04	
Max. plant height * Shel. by foredune	0.004		-0.01	
Dune volume * clustering	-6.37**	-6.30***	4.51**	4.65***
Dune volume * max. dune height	-1.54		-1.11	
Dune volume * Shel. by foredune	1.63	1.95*	-2.23*	-1.82**
Clustering * max. dune height	0.40*	0.41**	-0.32	-0.42**

Clustering * Shel. by foredune	-0.15	-0.17*	0.05	
Max. dune height * Shel. by foredune	-0.16	-0.16*	0.28**	0.31***
Marginal R^2	0.33	0.31	0.24	0.21
Conditional R^2	0.37	0.35	0.42	0.40
Observations	236	236	236	236
Akaike Inf. Crit.	-622.85	-674.05	-656.46	-704.97
Bayesian Inf. Crit.	-542.07	-626.28	-575.68	-657.20

Note:
$^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

Figure captions

Fig. 1 A) Overview of the Hors on Texel, the Netherlands. The white lines show the flight path for the four different flights. The points show the position of the ground control markers. The white polygon is the monitoring area, which is 200 m x 400 m. B) Photograph of the study site with the UAV used to monitor the nebkha dunes.

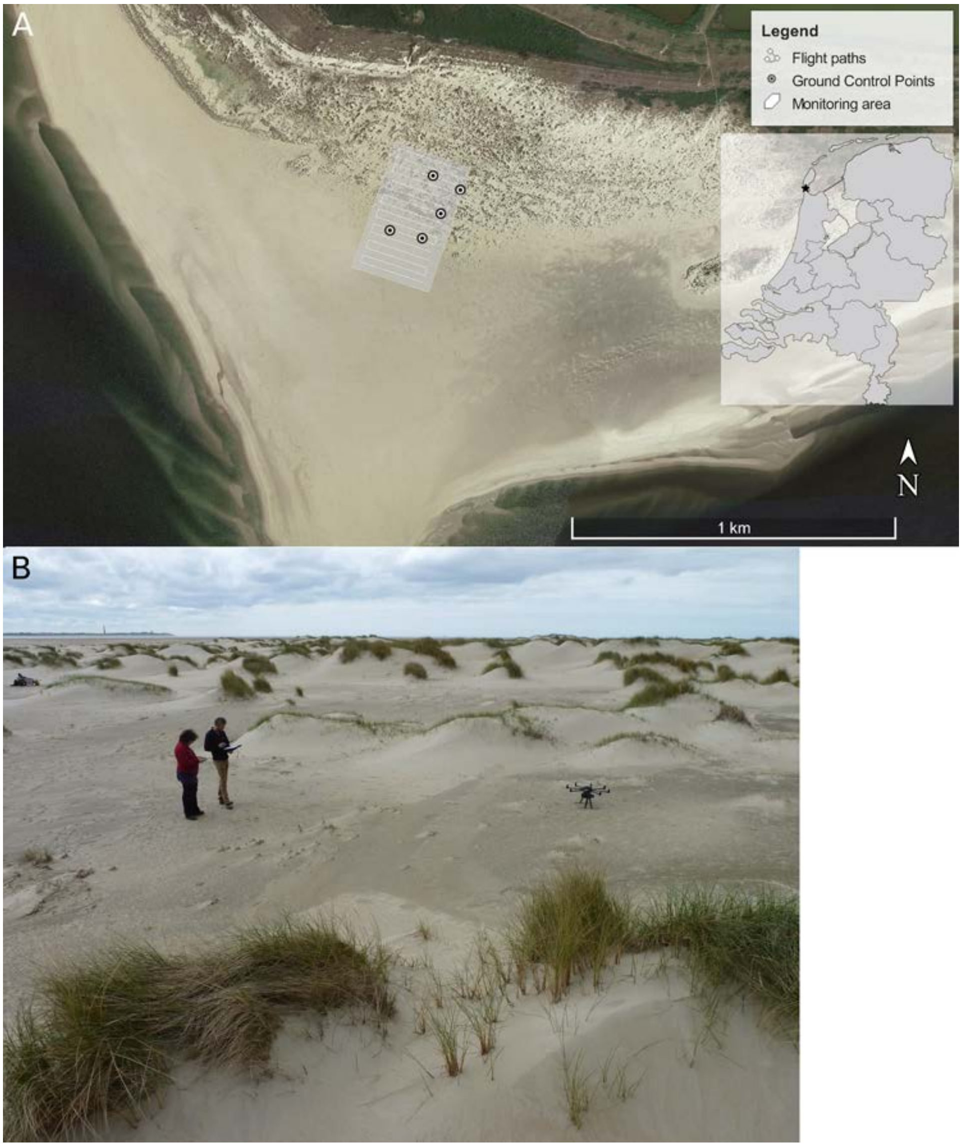
Fig. 2 Workflow of the methodology. The 3D point cloud from the photogrammetry was used to construct a DSM, DTM and NDVI orthomosaic. The DTM and NDVI orthomosaic where used to define the nebkha dunes. The explanatory variables for the statistical models were derived from the DSM, DTM and NDVI orthomosaic. For a more detailed explanation see methods.

Fig. 3 Overview of the monitoring area. A) The elevation is shown with the Digital Terrain Model (m NAP), the green pixel indicates grass cover and the polygons indicate the nebkha dunes. B) The colour indicates the species present on the nebkha dune and the squares the blocks. The foredune in the middle of the monitoring area is excluded from the statistical analysis. Some dunes ~~that~~ were cut-off by the edge of the DTM, we discarded these dunes.

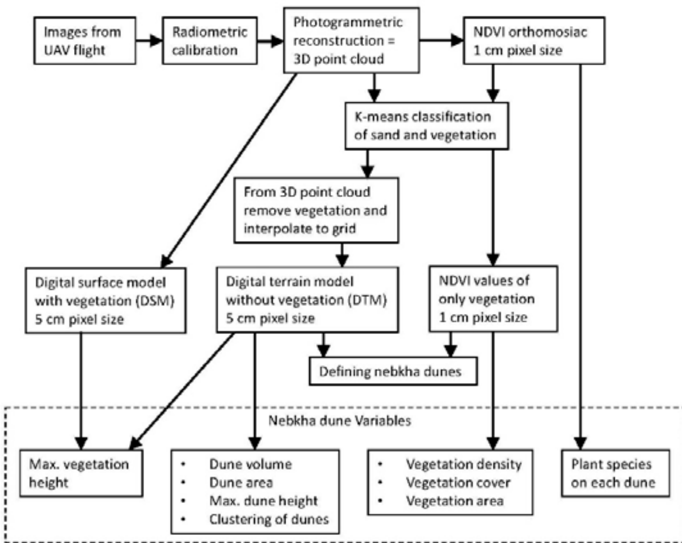
Fig. 4 Different dune characteristics for nebkha dunes in August with *A. arenaria*, *E. juncea* and a mix of both species separated for dunes seaward and landward of the foredune: A) Dune area, B) Maximum dune height, C) Dune volume, D) Clustering: mean height around a 25m radius around the dune, E) Vegetation density, F) Plant height. The letters denote the significant difference between the bars. Seaward of the foredune there were 41 ~~*A. arenaria*~~ dunes with *A. arenaria*, ~~198~~ 193 ~~*E. juncea*~~ dunes with *E. juncea*, and 53 dunes with both species, landward of the foredune there were 81 ~~*A. arenaria*~~ dunes with *A. arenaria*, 23 ~~*E. juncea*~~ dunes with *E. juncea*, and 41 dunes with both species. NAP refers to Amsterdam Ordnance Date, which refers to mean sea level near Amsterdam

Fig. 5 The relationship between initial dune volume (m^3) and the absolute change in dune volume (m^3/week) for: A) summer (April – August); B) winter (November – April). The data is shown for nebkha dunes seaward and landward of the foredune. The black line shows the regression prediction, the grey dashed line the 95% confidence interval. The formulas are the result of a linear regression model.

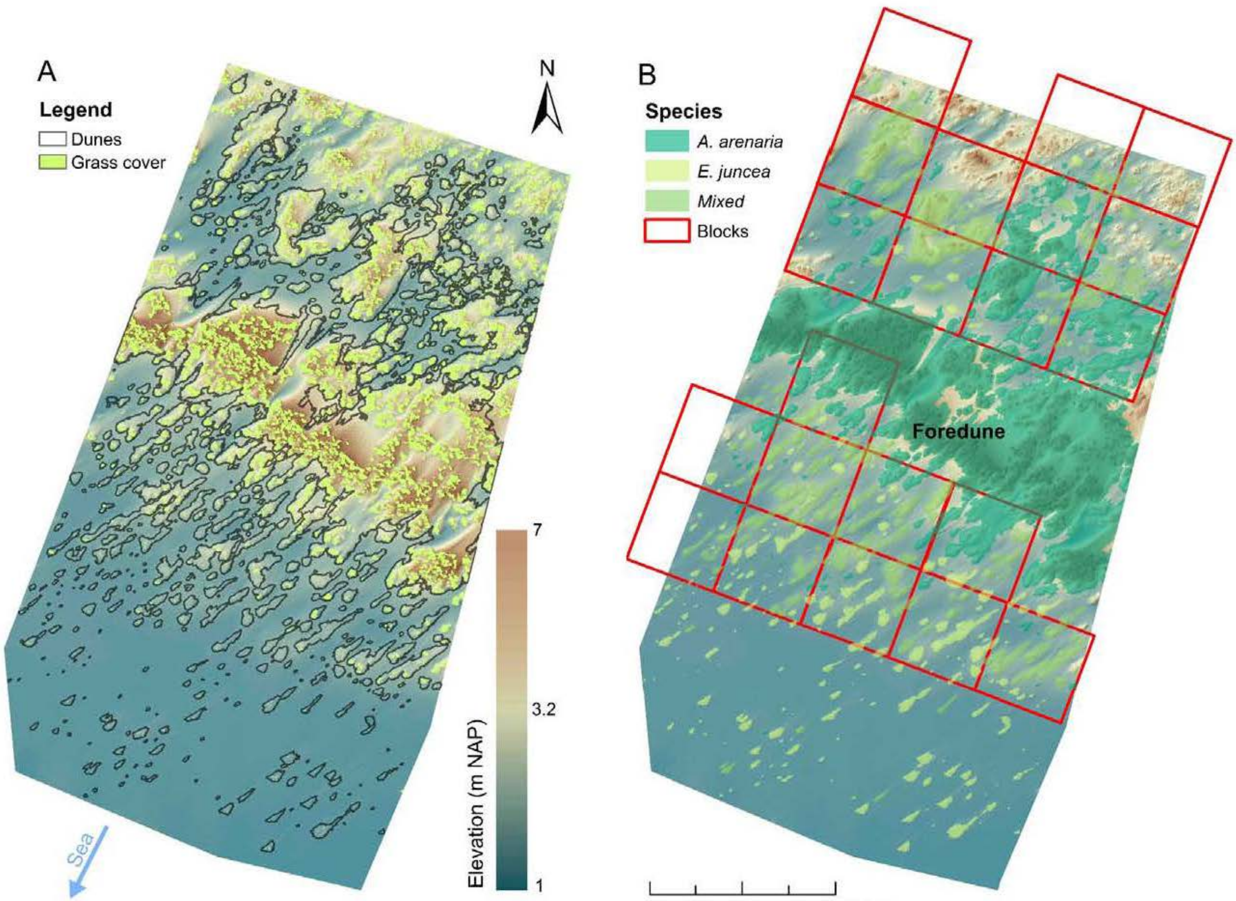
Fig. 6 Relative change in dune volume (m^3/m^3)/week for nebkha dunes with *A. arenaria*, *E. juncea* and a mix of both species and separated for dunes seaward and landward of the foredune for: A) summer, April – August; B) winter, November – April. The letters denote the significant difference between the bars. Seaward of the foredune there were 28 ~~*A. arenaria*~~ dunes with *A. arenaria*, 77 ~~*E. juncea*~~ dunes with *E. juncea*, and 28 dunes with both species, landward from the foredune there were 57 ~~*A. arenaria*~~ dunes with *A. arenaria*, 22 ~~*E. juncea*~~ dunes with *E. juncea*, and 25 dunes with both species.


A
Legend
Flight paths
Ground Control Points
Monitoring area
N
1 km
B

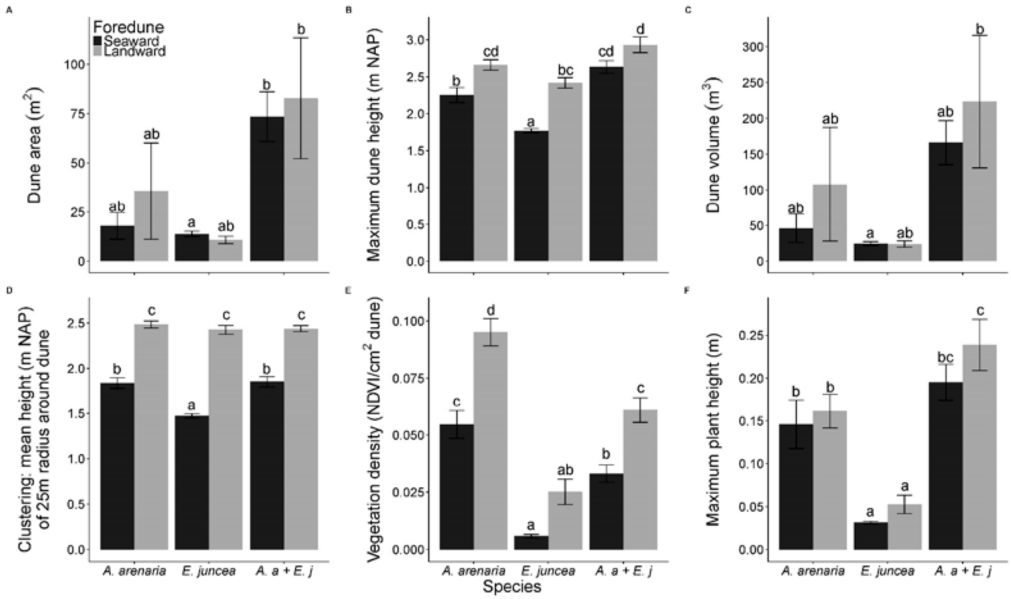
864

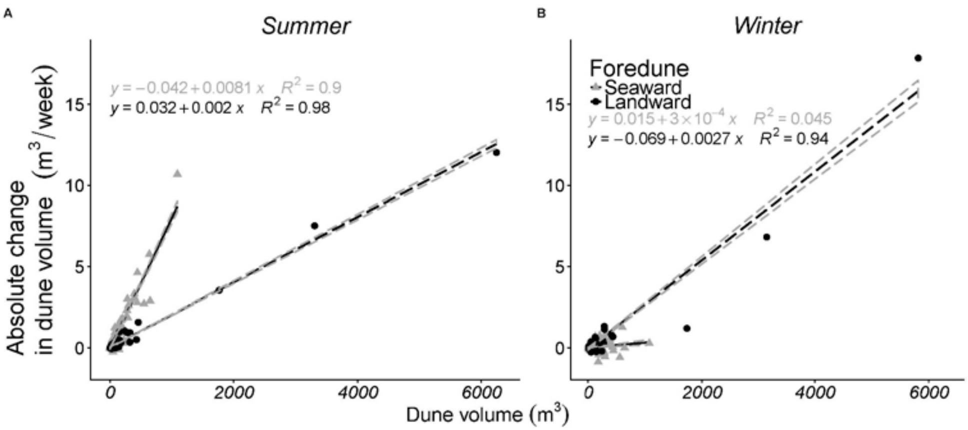


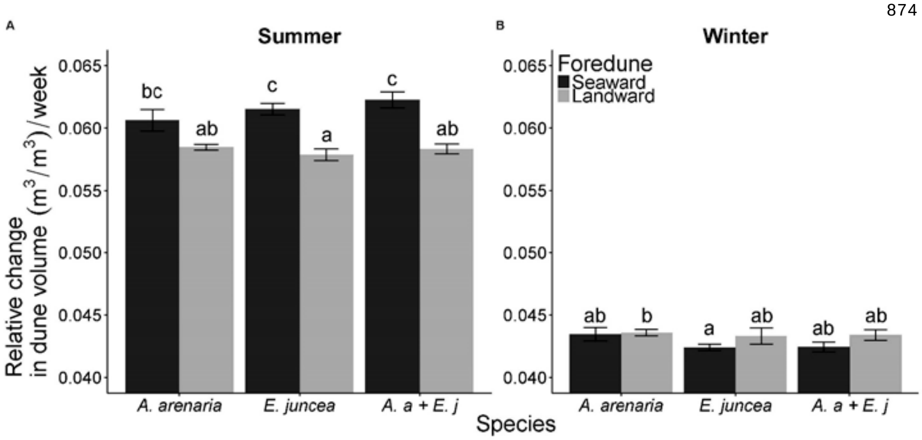
Images from UAV flight
Radiometric calibration
Photogrammetric reconstruction = 3D point cloud
NDVI orthomosiac 1 cm pixel size
K-means classification of sand and vegetation
From 3D point cloud remove vegetation and interpolate to grid
Digital surface model with vegetation (DSM) 5 cm pixel size
Digital terrain model without vegetation (DTM) 5 cm pixel size
NDVI values of only vegetation 1 cm pixel size
Defining nebkha dunes
Nebkha dune Variables
Max. vegetation height
Dune volume
Dune area
Max. dune height
Clustering of dunes
Vegetation density
Vegetation cover
Vegetation area
Plant species on each dune



A
Legend
Dunes
Grass cover
N
Elevation (m NAP)
7
3.2
1
Sea
B
Species
A. arenaria
E. juncea
Mixed
Blocks
Foredune
0 25 50 100 Meters


A
B
C
D
E
F
Foredune
Seaward
Landward
Dune area (m2)
Maximum dune height (m NAP)
Dune volume (m3)
Clustering: mean height (m NAP) of 25m radius around dune
Vegetation density (NDVI/cm2 dune)
Maximum plant height (m)
A. arenaria
E. juncea
A. a + E. j
Species


A
Summer
B
Winter
Absolute change in dune volume (m3/week)
y = −0.042 + 0.0081 x R2 = 0.9
y = 0.032 + 0.002 x R2 = 0.98
Foredune
Seaward
Landward
y = 0.015 + 3 × 10−4 x R2 = 0.045
y = −0.069 + 0.0027 x R2 = 0.94
Dune volume (m3)
0
5
10
15
0
2000
4000
6000


A
Summer
B
Winter
Foredune
Seaward
Landward
Relative change
in dune volume (m3/m3)/week
0.065
0.060
0.055
0.050
0.045
0.040
bc
ab
c
a
c
ab
ab
b
a
ab
ab
ab
A. arenaria
E. juncea
A. a + E. j
Species