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Vegetation effects on coastal foredune initiation: Wind tunnel experiments and field validation for three dune-building plants

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ABSTRACT

As the land-sea interface, foredunes buffer upland habitats with plants acting as ecosystem engineers shaping topography, and thereby affecting storm response and recovery. However, many ecogeomorphic feedbacks in coastal foredune formation and recovery remain uncertain in this dynamic environment. We carried out a series of wind tunnel experiments testing how the morphology, density, and configuration of three foredune pioneer dune building plant species influence the most basic stage of dune initiation — nebkha formation around individual plants. We established monocultures of native *Ammophila breviligulata* and *Panicum amarum* and invasive *Carex kobomugi* in 1 m × 1 m planter boxes of sand to simulate approximate natural and managed densities and planting configurations on the US Mid-Atlantic coast. We subjected each box to constant 8.25 m/s wind for 30 min in a moveable-bed unilateral-flow wind tunnel with an unvegetated upwind sand bed. We quantified resulting topography with sub-millimeter precision and related it to plant morphology, density, and configuration. Plant morphology, density, and configuration all influenced the resulting topography. Larger plants produced larger nebkha with greater relief, height, and sand volume. However, nebkha area, height, and planform shape varied among species, and taller plants did not necessarily produce taller nebkha. The erect grasses, *Ammophila* and *Panicum*, produced more elongated, high-relief nebkha compared to the low-lying *Carex*, which produced lower and more symmetrical equant nebkha. A staggered planting configuration produced greater net sediment accumulation than non-staggered. We validated these results against high-resolution field topographies of foredune nebkha and found strong agreement between the datasets. Our results provide species-specific parameters useful in designing foredune plantings and beach management and can be used to parameterize vegetation in models of foredune evolution associated with different plant species. By first understanding the underlying ecogeomorphic feedbacks involved in nebkha formation, we can more effectively scale up to forecast coastal foredune evolution and recovery.

1. Introduction

Ecosystem engineers directly or indirectly modify habitats by changing biotic and abiotic resources or physical habitat structure (Jones et al., 1994). Plants are capable engineers that can physically alter environments both when living and dead (Tanner, 2001; Badano and Cavieres, 2006; Bos et al., 2007; Hall Cushman et al., 2010). Vegetation is particularly important in the development of coastal foredunes, defined as the shore-parallel vegetated dune ridge in the backshore formed by aeolian sand deposition within vegetation (Hesp, 2002). The physical geomorphological processes surrounding foredune evolution have been studied extensively (Hesp and Walker, 2013; Feagin et al., 2015; Elko et al., 2016; Elko et al., 2019). Similarly, the spatial variability of foredune vegetation related to geomorphological processes was appreciated decades ago (Cowles, 1899; Ranwell, 1972; Carter, 1995). However, despite high investment in beach-dune management efforts (Wootton et al., 2016; Elko et al., 2019), the variability and mechanisms surrounding geomorphological processes and foredune vegetation have only recently gained heightened research attention (e.g. Stallins, 2005; Nield and Baas, 2008; Zarnetske et al., 2012; Durán Vinent and Moore, 2014; Zarnetske et al., 2015; Silva et al., 2016; Goldstein et al., 2017; Feagin et al., 2019; Hacker et al., 2019; Mullins

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et al., 2019). Our understanding of foredune ecogeomorphic feedbacks is limited (Stallins, 2006; Schlacher et al., 2008; Murray et al., 2008; Corenblit et al., 2011; Stallins and Corenblit, 2018). Efforts to model foredune initiation alongside storm response and recovery are thus constrained by an incomplete understanding of vegetation effects (Walker et al., 2017; Jackson and Nordstrom, 2019).

Foredunes are non-linear self-organizing complex adaptive habitats categorized by physical feedbacks between plants and topography (de Castro, 1995; Hesp, 2002; Nield and Baas, 2008; Hesp and Walker, 2013; Balke et al., 2014; Corenblit et al., 2015). Plants create, modify, and stabilize foredunes, while elevation and coastal processes (e.g. waves, overwash) influence vegetation structure and succession (Stallins, 2005; Durán Vinent and Moore, 2014; Zarnetske et al., 2015; Cheplick, 2016). These ecogeomorphic interactions modulate post-storm foredune recovery back to a pre-storm or new system state (Bendix and Hupp, 2000; Murray et al., 2008; Hesp et al., 2011; Wolner et al., 2013; Stallins and Corenblit, 2018). Aeolian sand transport is steered both by topography and vegetation over a range of physical, ecological, and geological timescales (Arens, 1996; Hesp et al., 2015). Across a landscape, beach physical characteristics vary (Durán Vinent and Moore, 2014; Houser and Mathew, 2011) and vegetation is heterogeneously distributed (Hesp, 1989), varying in morphology and density (Arens et al., 2001; Hesp et al., 2019). These characteristics create a spatiotemporally complex heterogenous system (Hilton et al., 2006; Charbonneau et al., 2017; Stallins and Corenblit, 2018).

Topographic heterogeneity is, in part, likely due to plant species-specific morphological traits impacting deposition (Hilton et al., 2006; Houser et al., 2008; Hacker et al., 2011, 2019). Above- and below-ground differences in plant species morphology and growth habit can yield noticeable species-level differences in the building and stabilizing of already established foredunes (Murray et al., 2008; Hacker et al., 2011; Zarnetske et al., 2012; Duran and Moore, 2013; Charbonneau et al., 2016; Charbonneau et al., 2017; Hacker et al., 2019). For example, some species are associated with more hummocky, erect, taller, or shorter established foredunes (Davies, 1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006; Hacker et al., 2011; Zarnetske et al., 2015; Hacker et al., 2019). Shoots create drag and surface cover, reducing wind and wave erosion (Tanaka et al., 2009; Silva et al., 2016; Feagin et al., 2019) and catch sediment, with species differing in capture efficiency, survival, morphology, establishment, density, and root versus shoot investment (Hesp, 1989; Arens et al., 2001; Zarnetske et al., 2012; Hesp et al., 2019). Changes in plant community structure can thus have cascading consequences on foredune morphology and stability (Wolner et al., 2013; Charbonneau et al., 2017; Bryant et al., 2019). Despite heightened coastal research since the 1960s (Jackson and Nordstrom, 2019), uncertainties remain as to the underlying causes of observed topographic heterogeneity associated with different plant species and densities (van Dijk et al., 1999; Arens et al., 2001; de M Luna et al., 2011; Duran and Moore, 2013; Durán Vinent and Moore, 2014; Zhang et al., 2015; Keijsers et al., 2016; Moore et al., 2016; Hesp et al., 2019).

Examining nebkha formation, one type of precursor to incipient (or embryo) foredune development (Hesp, 2002; Hesp and Walker, 2013), may yield insight into what factors of plant morphology and density are of greatest importance to backshore foredune initiation. Nebkha form from aeolian sand deposition around discrete individuals or groups of plants due to high localized drag and reduced wind velocity (Cooke et al., 1993; Hesp, 2002; Fig. 1). Nebkha vary in size from millimeters to

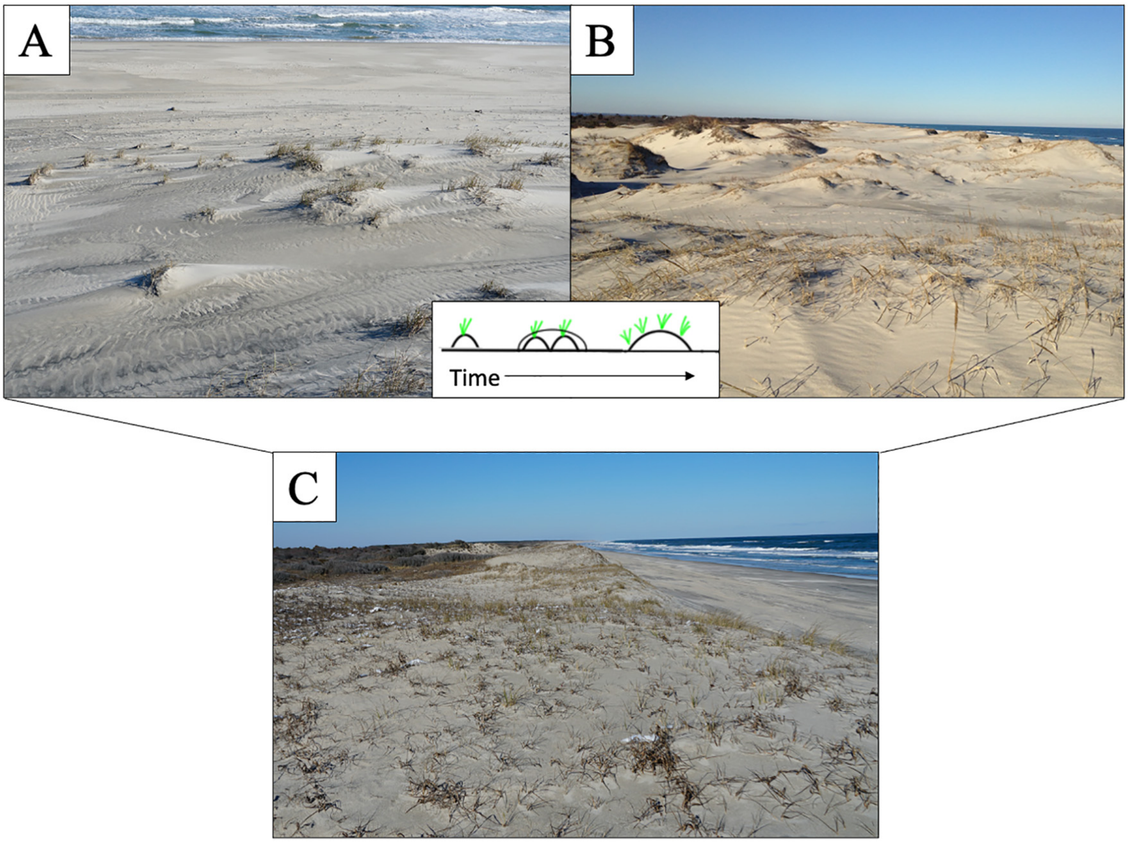

Fig. 1. Foredune initiation and development over time. Field photos depict (A) nebkha formed around individual plants on the backshore, (B) coalescence into larger nebkha containing multiple plant communities concentrated at their peaks and (C) a continuous foredune developed from the merging of larger nebkha. For scale, note the size of the plants in each image. These plants are all dormant *A. breviligulata* as the images were taken in winter.

meters, and can grow and merge over time as plants tiller and new nebkha emerge (Hesp, 1989; Cooke et al., 1993; Fig. 1). This deposition can ultimately form a continuous shore-parallel incipient foredune (Hesp, 1984, 1989, 2002, 2013; Fig. 1). Behind plants and the nebkha body, shielding and turbulent eddies create shadow dunes or tails (Hesp, 1981; Hesp and Smyth, 2017). These shadow dunes can vary in size by plant and nebkha shape (Raupach, 1992) and width, independent of plant height and sediment grain size (Hesp, 1981; Hesp and Smyth, 2017). Shadow dune and nebkha morphology are linked, although they are often examined separately (Hesp and Smyth, 2017). When nebkha are referred to in this publication, the nebkha and attached shadow dune complex are grouped as one entity (Charbonneau and Casper, 2018). Similar to studies of foredune ecogeomorphology, nebkha research has frequently focused on established field nebkha (Gillies et al., 2014; Hesp and Smyth, 2017). Nebkha can be thought of as the most basic unit or stage of foredune development whereby underlying physical-biological feedbacks that govern foredune evolution at a greater scale may be illuminated from examining their initiation.

To examine coupled ecogeomorphic relationships of nebkha formation as foredune precursors, we constructed a moveable-bed, unilateral-flow wind tunnel to test how three U.S. East Coast foredune pioneer plant species and their morphological traits, planting density, and planting configuration affect the initial size, shape, and volume of nebkha. We worked with dominant native and invasive foredune plants at natural and managed densities and configurations. After subjecting experimental stands to wind and sediment supply conditions typical of backshore environments, we related the size and shape of each resulting nebkha to the morphological traits of their individual plants (Fig. 1A), as well as to planting density and configuration. We tested the following hypotheses: (1) larger plants create larger nebkha; (2) a taller plant will build a taller, steeper nebkha; and (3) nebkha shape varies by plant species as a function of morphology and not as a function of plant size. Furthermore, we tested the same hypotheses against quantitative field observations to evaluate the ecological relevance of our findings for sandy beach-dune systems. By first understanding the underlying ecogeomorphic feedbacks of nebkha formation, we can more effectively scale up to forecast foredune evolution over time and develop more effective management strategies.

2. Materials and methods

2.1. Study species

We worked with three US East Coast dominant foredune building pioneers (Fig. 2A). Erect C_3 *Ammophila breviligulata* (0.66–1 m tall), is native to the US Mid-Atlantic and Great Lakes, and is a Pacific invasive grass (Hacker et al., 2011). C_4 bunchgrass *Panicum amarum* (1–2 m tall) is a US eastern seaboard and Gulf coast native known for high biomass production. *Carex kobomugi* (15–30 cm tall) is an Asia native sedge, and US invasive, with a low-lying semi-rosette growth form, small petiole angles, and blades touching or nearly touching the surface (Min, 2006). All species are rhizomatous, spreading laterally asexually in guerilla growth form, burial-tolerant, and with relatively long (15–50 cm) and narrow (<1.25 cm) leaf blades. Typical *A. breviligulata* and *C. kobomugi* field densities are ≈40 and ≈140 ramets m^{-2}, respectively (Charbonneau et al., 2016). *Panicum* field densities vary widely with plant age, initially having uniform density (≈100 ramets m^{-2}, 30 transects at Delaware State Seashore, September 2016), but typically thin to one dense clump per m^2 (Woodhouse, 1982). *Panicum amarum* and *A. breviligulata* are available commercially and planted in management efforts. *Carex kobomugi* was available and planted 1960–1990 in the Eastern US until its invasive qualities were documented (Wootton et al., 2005).

2.2. Wind tunnel and experimental plantings

We constructed a moveable-bed unilateral suction-flow wind tunnel, modified from the design of the Oregon State University O.H. Hinsdale Wave Research Lab wind tunnel (Zarnetske et al., 2012). In the wind tunnel, we controlled wind speed, wind duration, sediment supply, and grain size (Houser and Mathew, 2011), allowing us to focus on effects of varying plant species, density, and configuration. The wind tunnel chamber is 6.0 m long, 1.0 m wide, and 2.0 m high. Near the tunnel's longitudinal center, 3.6 m downwind, a 1.0 m × 1.0 m × 0.3 m wooden planter box containing established and fully rooted plants in sand, can be inserted and sealed flush with the chamber floor. The wind tunnel is located as a research and learning tool at the Ocean Country Vocation Technical School in NJ (Charbonneau and Casper, 2018). More details on the wind tunnel can be found at TheWindTunnel.weebly.com. The sand used was washover sand from Island Beach State Park, NJ medium quartz (mean grain size 0.300–0.350 mm). See Supplementary material S1 for grain size distributions.

In each planter box, we established a monoculture of rooted plants at one of three density treatments and two configurations relative to wind direction. In low, medium, and high density treatments, we spaced plants uniformly at 45.7 cm, 30.5 cm, and 15.25 cm apart, on center, respectively (Fig. 2B). Although high density plantings reflect some field-observed densities (Zarnetske et al., 2012; Charbonneau et al., 2016), this treatment produced nebkha around plant groups not individuals such that these data could not be evaluated in the same manner as the other densities. Therefore, the high density results are included in Supplementary material S2, but are otherwise excluded from further analysis or discussion herein. The low and medium densities reflect backshore Mid-Atlantic conditions and are the most common plant spacings used in beach and dune management projects (Savage and Woodhouse, 1968; Seneca et al., 1976; O'Connell, 2008; Wootton et al., 2016). Within density treatments, we tested two different plant configurations. Configuration 1 (2017), termed non-staggered, are planted in a regular hexagonal array oriented with distinct rows parallel to flow (Fig. 2B). Configuration 2 (2018), termed staggered, is a rotation of the non-staggered array 90°, producing a diagonal offset pattern (Fig. 2B). For each plant species, density, and configuration, we tested four replicate boxes and four “sand-only” control boxes lacking plants. See Supplementary material S3 for images of the treatments.

To measure the influence of plant traits on topography, we quantified individual plant morphological traits before subjecting them to the wind tunnel experiments. From bed-level, we measured plant: (1) stem base width as the distance between the two farthest stems perpendicular to wind flow, (2) height bent naturally and (3) height as tallest taut leaf. We counted: (4) total leaves and (5) total stems. Stem widths are not included for *C. kobomugi* as the stems tended to be buried, as they often are in the field, after leveling box beds pre-experiment. Post-experiment, we cut the shoots of all plants at the surface, without disturbing the bed and resultant topography, using shop shears. We measured biomass after drying for 72 h at 70 °C.

To minimize wind-tunnel edge effects on saltation (Bauer et al., 2004), we only analyzed nebkha away from the wall, outside of its boundary layer. All analyzed nebkha were ≥17 cm from the tunnel sides (Table 1) and nebkha morphology data are from the central 66 cm of the tunnel (i.e., 33 cm of the longitudinal centerline). Similar to many wind tunnel investigations, our experiments lacked full representation of turbulent motion due to the restricted length scale (Bauer et al., 2004). However, this physical limitation applied equally across all experimental treatments. Vertical profiles along the chamber length and width support the formation of established and consistent boundary layers. Our goal was to examine nebkha initiation in a flow setting conducive to aeolian sand transport and deposition. The controlled wind tunnel environment enabled us to draw robust conclusions regarding differences among treatments

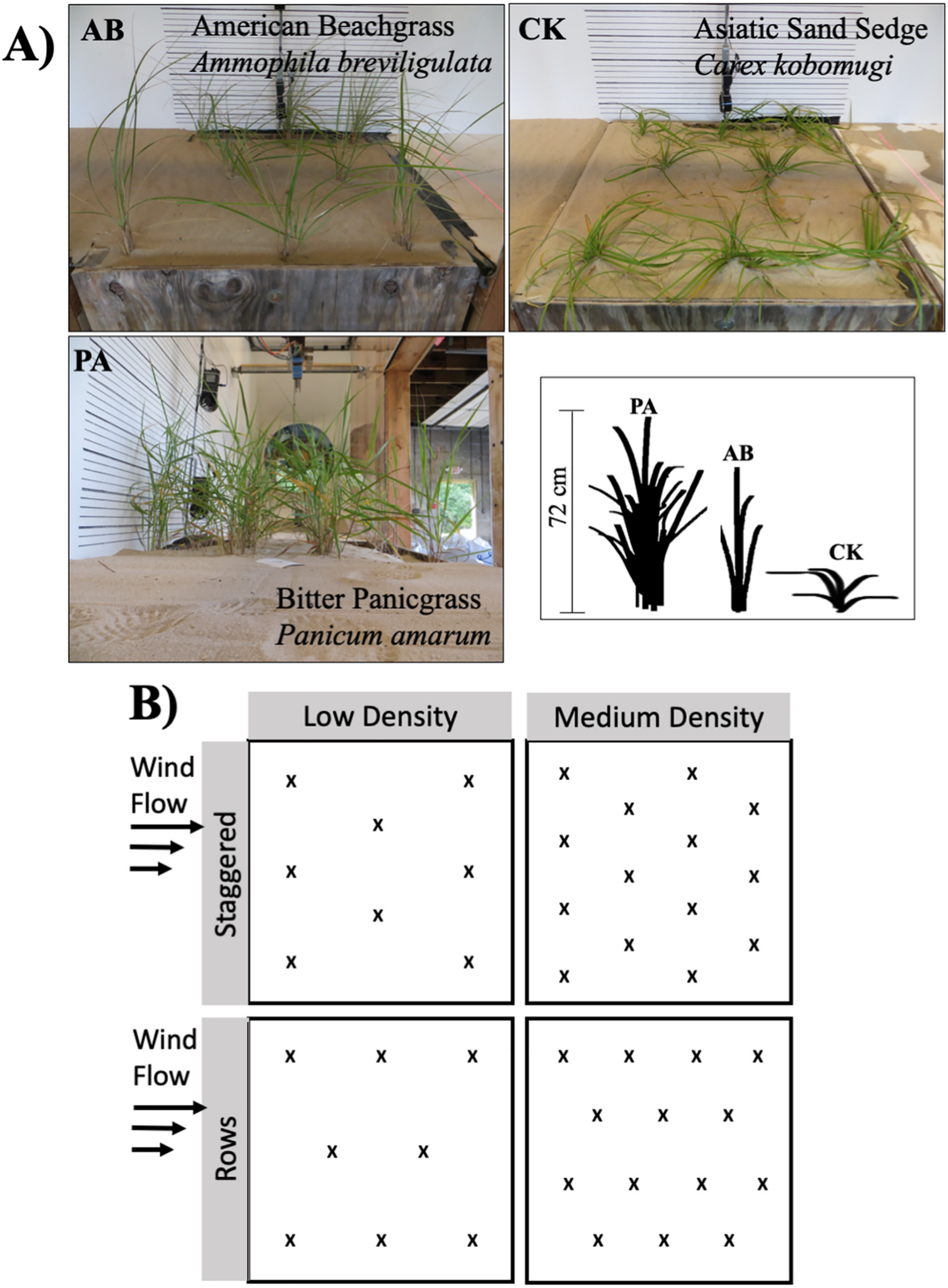

Fig. 2. Wind tunnel experimental setup. (A) We established two native Mid-Atlantic erect grasses (AB and PA) and one invasive low-lying sedge (CK) rooted in sand in 1 m × 1 m monoculture plant boxes. The top left schematic is to scale, showing relative differences in plant size and morphology across species. (B) The plants were planted at low or medium density and in a staggered or non-staggered configuration relative to the prevailing wind direction. There are, therefore, four density × configuration treatments with four replicates per species.

Table 1
Number of plants versus nebkha examined per density/configuration treatment. Sample sizes are exclusive of plant and nebkha within the wind tunnel wall boundary layer which are excluded from analyses. There were four replicates per species per density per configuration, staggered and non-staggered.

Box density	Plants/box	Non-staggered nebkha/box	Staggered nebkha/box
Low 45.7 cm	8	2	4
Medium 30.5 cm	14	7	6

in conditions representative of the range of fluid-sediment-vegetation interactions found in nature. Vertical and horizontal velocity profiles can be seen in Charbonneau and Casper (2018) with additional higher-resolution profiles measured throughout the wind tunnel chamber in Supplementary material S4.

2.3. Wind tunnel experiments and topographic quantification

We conducted experiments September 2017 (non-staggered) and 2018 (staggered) with green full grown plants. We leveled a continuous dry sand bed of 2.54 cm height along the chamber and in the box using a custom rake, taking care not to damage the plants. The flat upwind bed mimicked a dry sandy backshore of unlimited sediment supply for aeolian transport towards vegetation (Arens, 1996). We subjected each box to 30 min of 8.25 m/s velocity measured 60 cm above the center of the test area. We chose this speed and duration to allow maximum formation time within the bounds of our available sediment supply (≈25 tonnes across all boxes and runs). This speed is also consistent with the work of Zarnetske et al. (2012) and promoted accretion around the plants as opposed to scouring between the plants and shielding behind the plants (Järvelä, 2002).

Directly following the wind treatment, we quantified topography with an industrial class II laser 3D sensor, a SICK TriSpector1060. The sensor uses triangulation and integrated data processing to collect and mesh 2500 elevation (z) profiles, every 0.42 mm, along the Y axis into a digital elevation model (DEM). Each scan encompassed 66 cm of the box width (X), the full 1 m box length (Y), plus 0.125 m upwind and downwind. It is factory calibrated, producing true XYZ mm values in all DEMs. Because Class II lasers cannot penetrate live tissue, we necessarily clipped all aboveground plant material before these scans. We extracted topographic information from the scans with SOPAS Engineering Tool V2018.3 (Intelligence, 2019).

We also scanned each box prior to a wind tunnel run to assess initial elevation and account for any bed leveling error. We determined if erosive or accretionary forces built each nebkha by examining Δz, defined as nebkha peak height minus initial bed height. Elevation spikes in the initial scans (from laser canopy reflectance) made discerning the initial upwind elevations only possible in post-processing by leveling a horizontal fixed plane to the upwind sand surface in SOPAS per nebkha. In 2018, we improved this quantification by also installing a vertical wire stake at the front and back of each plant, marked at the sediment surface. We determined if Δz reflected accretion, erosion, or was equal post-experiment with marker visibility (Supplementary material S5) and used this method to assess the accuracy of our initial scan method.

We quantified volume, area, elevation, and shape per nebkha in SOPAS (Intelligence, 2019). We defined the bounds of each nebkha from elevation point clusters where each plant was located with the Blob Tool. This tool calculates basal area and volume (from object base) of each blob (i.e., nebkha). Nebkha elevation is base to peak, with peak location upwind, downwind, or within the plant. We measured nebkha slope from the peak and upwind extreme parallel to wind flow. At the peak, we measured the width (perpendicular to flow) and length (parallel to flow) of the nebkha base to quantify shape as planform eccentricity, the length/width ratio. Eccentricity values closer to 1 indicate a more equant nebkha while values >1 denote a longer wind-parallel axis, and <1 indicate that the wind perpendicular axis is longer than the wind parallel axis.

2.4. Field validation

We quantified naturally-formed backshore nebkha at Island Beach State Park (IBSP), New Jersey, USA (Fig. 3). IBSP is a ≈17 km microtidal barrier island sandy beach shoreline that has never been replenished. Total annual precipitation is 127 cm. Precipitation and wind speeds are lowest April–August, causing minimal sediment transport (Gares, 1992; NOAA Gauge 8531680). Conversely, the Atlantic Hurricane season is June 1 to November 30, with most storms occurring September to October (Gares, 1992). The most notable recent storm to impact IBSP was Hurricane Sandy (October 2012), although smaller storms even more recently have affected IBSP (Dohner et al., 2016). Much of the foredune toe and slope have been both naturally colonized and artificially planted where nebkha and incipient dunes develop.

Fall and Spring 2018, we field truthed backshore individual *A. breviligulata* and *C. kobomugi* nebkha and plants with the following criteria: (1) seaward of vegetation, no plants or obstructions upwind, (2) ≥50 cm from nearest neighbor, (3) located on flat backshore, (4) having a fully intact nebkha, and (5) being only composed of sand. We needed these criteria to establish fair comparisons between the field nebkha and our wind tunnel experiments. Specifically, we compared these data to the upwind wind tunnel plants and nebkha, which also meet these criteria. Where all conditions were met, we used pennies as ground control markers around the form. The pennies, with their fixed diameter and shape, provided scale and marked locations allowing for photogrammetric model accuracy checks. We measured the same plant morphological traits as at the wind tunnel and then without disturbing topography, harvested the aboveground biomass with garden shears. We used a 12.1-megapixel camera to collect 100 shadow-less photos per nebkha across all vantage points to generate one 3D model per nebkha.

We used Agisoft Metashape Professional Edition to create image-based 3D models of the field nebkha to then quantify nebkha volume, area, and planform shape. 3D model generation involved: (1) automatically aligning camera image locations; (2) manually improving camera alignment with markers; (3) generating a dense point cloud; (4) defining the scale; (5) creating a scale bar referenced DEM; (6) generating contours every 0.1-mm to determine where the nebkha and backshore surface intersected; and (7) using Agisoft tools to quantify nebkha morphological parameters (AgiSoft, 2018). See Supplementary material S6 for more details and a visual workflow of the 3D model creation. We produced 3D models of 18 nebkha, five each of *C. kobomugi* and *A. breviligulata*, which were paired spatially (<4 m apart), and four more *A. breviligulata* (all within 5 m of each other) from two locations (Fig. 4). We collected all 3D model images on the same day, such that we assume all plants per location were subject to equal formative abiotic conditions. We did not attempt to discern wind conditions beyond formative direction based on nebkha orientation. However, it is important to note that these nebkha would likely have developed over multiple transport events with varying sediment supply (Czarnes et al., 2000; Maun, 2009; Balke et al., 2014; Zarnetske et al., 2015) and multiple wetting and drying cycles occurring between and among events (Czarnes et al., 2000; Maun, 2009; Balke et al., 2014; Zarnetske et al., 2015).

2.5. Statistical analyses

To test our three hypotheses, we related plant and nebkha traits for both the field truth and wind tunnel data. We performed restricted

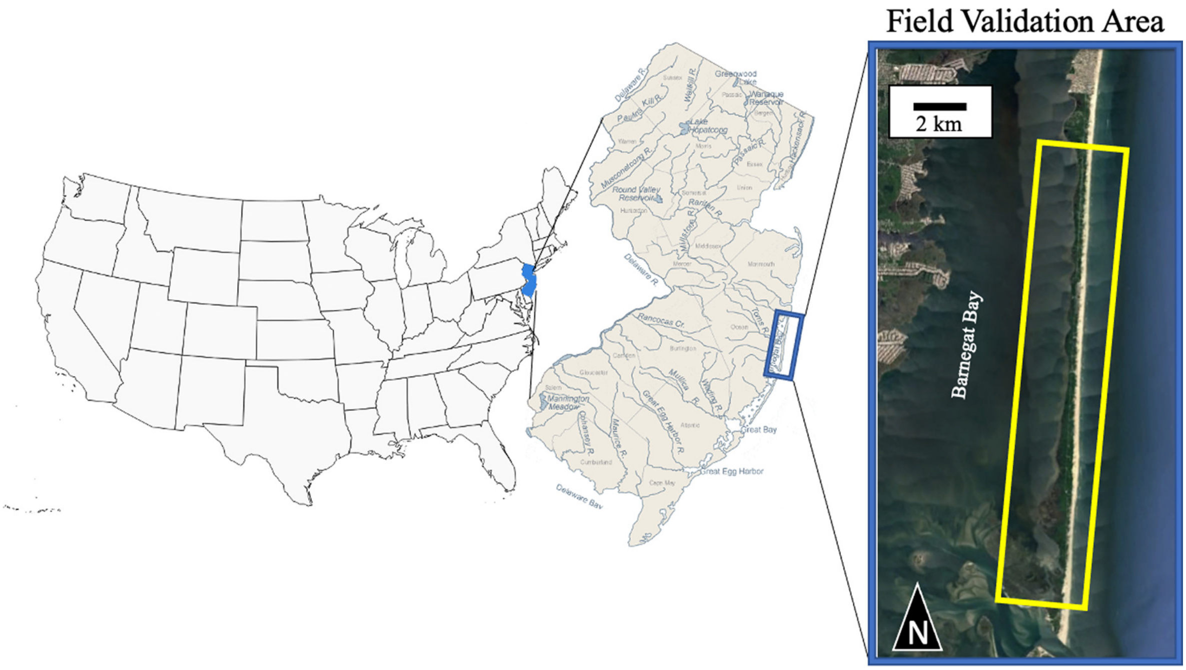

Fig. 3. Wind tunnel validation field site, Island Beach State Park, NJ, USA. Field validation was carried out in the backshore along the 17 km expanse of the park (39.7975° N, 74.0976° W). Map courtesy of Google Earth.

maximum likelihood linear mixed models (LMM), maintaining box (i.e., replicate) as a random effect. We performed ANCOVA of response variable and treatments with species as the covariate. In any ANCOVA and linear regressions, we controlled for a potential effect of box by examining mean results per box. All pairwise comparisons are Tukey HSD. We used JMP® Pro 14 for our analyses (JMP, 2019) and MATLAB® for Fig. 12 and our graphical abstract (MathWorks, Inc., 2018). Means are reported ± SE and all tests are two-tailed.

We first determined if accretionary forces built the wind tunnel nebkha. We separately examined if elevation change magnitude and direction (erosion or accretion) varied by species, density, plant row, and configuration with LMM. We also determined if the proportion of plants producing upwind erosion versus accretion varied by species using Fisher's Exact Test.

We performed correlation Principal Component Analyses (PCAs) on nebkha and plant variables to reduce variable dimensionality and collinearity (Graham, 2003). To determine how to structure the PCAs, we first examined if plant and nebkha traits varied across treatments. We performed separate LMM per plant trait examining the effect of density, species, configuration, and year by species interaction. Here, configuration differences reflect varying growth conditions in 2017 and 2018 (Fig. 5). We also performed nebkha trait LMMs as above. The LMMs revealed consistent nebkha variation across treatments, with varying magnitudes between species. Given this, we combined all treatments by constructing one PCA on the plant parameters, not including stem width, and one on nebkha parameters, not including shape (Table 2).

We largely tested our hypotheses based on the PC partial contributions of variables and loading magnitude and direction (Table 2). All variables loading on both plant and nebkha PC1 contributed in a similar positive way to the respective PC1 score, such that greater PC1 scores indicate a larger nebkha and plant with respect to all variables (Table 2). Nebkha PC2 represents nebkha relief, or height relative to area inversely related, whereby greater values represent taller nebkha with a smaller area (Table 2). We examined if nebkha PC1 and PC2 varied between species with LMM. To test Hypothesis (1), that nebkha size varies with plant size (plant PC1), we performed two ANCOVA analyses, with nebkha PC1 and volume (normalized via log transformation) as the independent variables; we further examined species differences with a Wilcoxon Rank Sum Test. For Hypothesis (2), that a taller plant builds a taller, steeper nebkha, we tested if nebkha PC2 variation was explained by plant size (plant PC1). Similarly, we also examined nebkha height and PC2 in the grasses in an LMM as a function of species, year, and their interaction knowing *P. amarum* was taller in 2017, but *A. breviligulata* was taller in 2018. To test Hypothesis (3), nebkha planform shape varies by plant species; we performed two LMM, one to test variation by density, configuration, and species and another by size (plant PC1) and species. We compared nebkha shape across species with Kruskal-Wallis, and Steel-Dwass pairwise comparisons.

We used Wilcoxon Signed-Rank tests to compare plant traits, and likewise, nebkha traits, between wind tunnel and field data. As previously mentioned, to ensure fair comparison between field and wind tunnel nebkha, we only compared field nebkha ($n = 13$) to wind tunnel nebkha that were in the first upwind row in both densities for *A. breviligulata* ($n = 21$). Specifically, for *C. kobomugi,* we only used upwind low density wind tunnel data to also maintain a more balanced sample size between field ($n = 5$) and wind tunnel replicates ($n = 7$). We separately compared nebkha height, area, volume, and planform shape between field and wind tunnel (1) *A. breviligulata* nebkha, (2) *C. kobomugi* nebkha, and (3) then explicitly compared *A. breviligulata* and *C. kobomugi* field nebkha pairs. As stated above, we used PCA and regression to test our three hypotheses, but only for *A. breviligulata* given the $n = 5$ field sample size for *C. kobomugi*.

3. Results

3.1. Plant morphological differences across treatments

The LMMs revealed that no plant traits differed between planting densities, but highlighted species differences in morphology and size 2017 and 2018. Generally, for most metrics, *C. kobomugi* was smallest and *P. amarum* was largest (Fig. 3). Both years, *A.* breviligulata had an equal number of leaves as *C.* kobomugi, and *P. amarum* had more

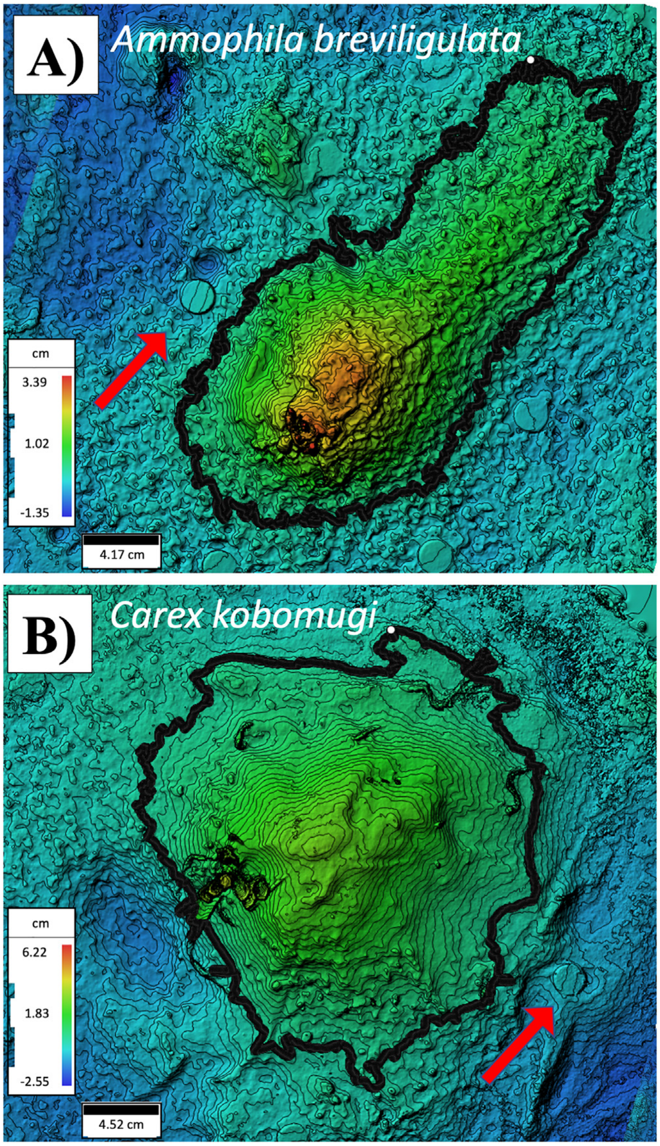

Fig. 4. An example of a nebkha 3D model created from a field (A) *A. breviligulata* and (B) *C. kobomugi*. Both in the field and wind tunnel, *A. breviligulata* produced more oblong nebkha than *C. kobomugi*, which produced more equant nebkha. The contours in both models are 0.1 mm, but both models are to different vertical and horizontal scales, despite equal formative conditions, because local microtopography shaped the scale of each 3D model. The thick black line indicates the edge of the nebkha base. The red arrows each point to a penny ground control marker and represent the presumed formative wind direction based on nebkha orientation.

stems than both ($F_{2,44} = 48.9$, $P < 0.0001$). Both years, *C. kobomugi* had the least number of stems and *P.* amarum had the most ($F_{2,32} = 80.02$, $P < 0.0001$) with all species having more stems in 2018 than 2017 ($F_{1,44} = 15.3$, $P < 0.001$). The two height metrics were equal across years, but there was a species × year interaction indicating that *C. kobomugi* was shortest both years, but in 2017 *A. breviligulata* was taller than *P. amarum* ($F_{2,45} = 44.61$, $P < 0.0001$) whereas in 2018 *P. amarum* was taller than *A. breviligulata* ($F_{2,42} = 205.51$, $P < 0.0001$). Stem widths in *P. amarum* and *A. breviligulata* were statistically equal across years with *P. amarum* stems wider than *A. breviligulata* stems ($F_{1,28} = 22.7$, $P < 0.0001$).

3.1.1. Wind tunnel nebkha formation

Nebkha only formed in treatments containing plants. In the control boxes without plants, transverse aeolian ripples of uniform size and shape formed. Elevation change per nebkha varied by species ($F_{2,45} = 5.83$, $P = 0.005$), and was greater for *P. amarum* (7.21 ± 1.04 mm) than for *A. breviligulata* (2.38 ± 1.0 mm). Change in elevation was also influenced by density ($F_{1,45} = 6.70$, $P = 0.01$) and configuration ($F_{1,45} = 9.59$, $P < 0.005$). Regardless of species, nebkha in the non-staggered medium density treatment had less elevation change than other treatments. Plants with upwind erosion had less elevation gain (5.11 ± 0.58 mm) than those accreting upwind (7.43 ± 0.90 mm; $F_{1,15} = 5.59$, $P = 0.02$). *Carex kobomugi* nebkha were formed by both upwind and downwind deposition whereas the two erect grasses predominantly had upwind scouring and downwind accretion (species comparison DF = 2, $\chi^2 = 23.76$, $P < 0.001$; Supplementary material S5). Regardless of configuration or density, the peaks of *A. breviligulata* (87%) and *P. amarum* (66%) nebkha were largely leeward versus split between upwind and downwind for *C. kobomugi* (51%; Supplementary material S5). Nebkha ranged in upwind and downwind slope 1–16° ($\bar{x} = 7.65 \pm 0.22°$), not reaching the assumed angle of repose ~30°.

3.2. Wind tunnel nebkha differences across treatments

Planting density did not statistically impact nebkha traits, but configuration did. Staggered treatments consistently produced larger nebkha in all size parameters, area ($F_{1,32} = 23.67$, $P < 0.0001$), height ($F_{1,37} = 8.02$, $P < 0.01$), and volume ($F_{1,38} = 18.61$, $P < 0.0001$). Nebkha planform shape did not vary between density or configuration treatments. The staggered configuration produced nebkha of approximately double the volume of the non-staggered configuration across all species (Table 3). For *C. kobomugi* and *A. breviligulata*, the staggered configuration produced nebkha with ~2× larger area than the non-staggered configuration. Planting row (i.e., front, back, middle) did not affect nebkha PC1 or PC2. Frontal area varied between species and densities, but was not quantified (Supplementary S3).

3.3. Wind tunnel nebkha differences across species

Ordination plots of nebkha PCAs highlight species differences in nebkha size and relief (Fig. 6). Examining nebkha PC1, both *A. breviligulata* and *C. kobomugi*, produced smaller nebkha than *P. amarum* ($F_{2,41} = 8.21$, $P = 0.001$). Examining nebkha height relative to surface area (nebkha PC2), *C. kobomugi* produced nebkha of lower relief and greater surface area, than both erect grasses which produced nebkha of statistically equivalent relief ($F_{2,38} = 7.38$, $P < 0.01$). LMM revealed that this result is driven by *C. kobomugi* and *P. amarum* producing nebkha of equivalent area ($F_{1,32} = 9.35$, $P < 0.001$), but *C. kobomugi* and *A. breviligulata* nebkha being equivalent in height ($F_{1,37} = 8.61$, $P < 0.001$; Fig. 7). Total biomass upwind of a plant did not impact nebkha PC1 (ANCOVA $P > 0.05$).

ANCOVA revealed that nebkha size (nebkha PC1) increased linearly with plant size (plant PC1), demonstrating that larger plants produced larger nebkha ($F_{1,44} = 5.47$, $P = 0.02$; Fig. 8). The slope and direction of this relationship did not significantly differ between species indicating a universal positive relationship between plant size and nebkha size between the species (Fig. 8). Similarly, larger plants, (i.e., greater plant PC1) built nebkha of greater log volume ($F_{3,44} = 9.48$, $P < 0.0001$). The slope of this relationship did not vary between the species although mean log nebkha volume did vary by species ($F_{2,44} = 5.89$, $P < 0.01$). *Carex kobomugi* and *A. breviligulata* produced nebkha of equivalent volume ($F_{1,38} = 13.75$, $P < 0.0001$), both smaller than *P. amarum* (Wilcoxon Rank Sum; $\chi^2 = 12.69$, DF = 2, $P < 0.01$; Fig. 9).

No clear pattern emerged supporting taller plants building taller nebkha. Nebkha PC2, representing nebkha area relative to height (Table 2), was unrelated to plant size (PC1), but varied by species. Recall that in 2017, *P. amarum* was taller than *A. breviligulata*, but in 2018 *P. amarum* was taller than *A. breviligulata* (Fig. 5). However, among

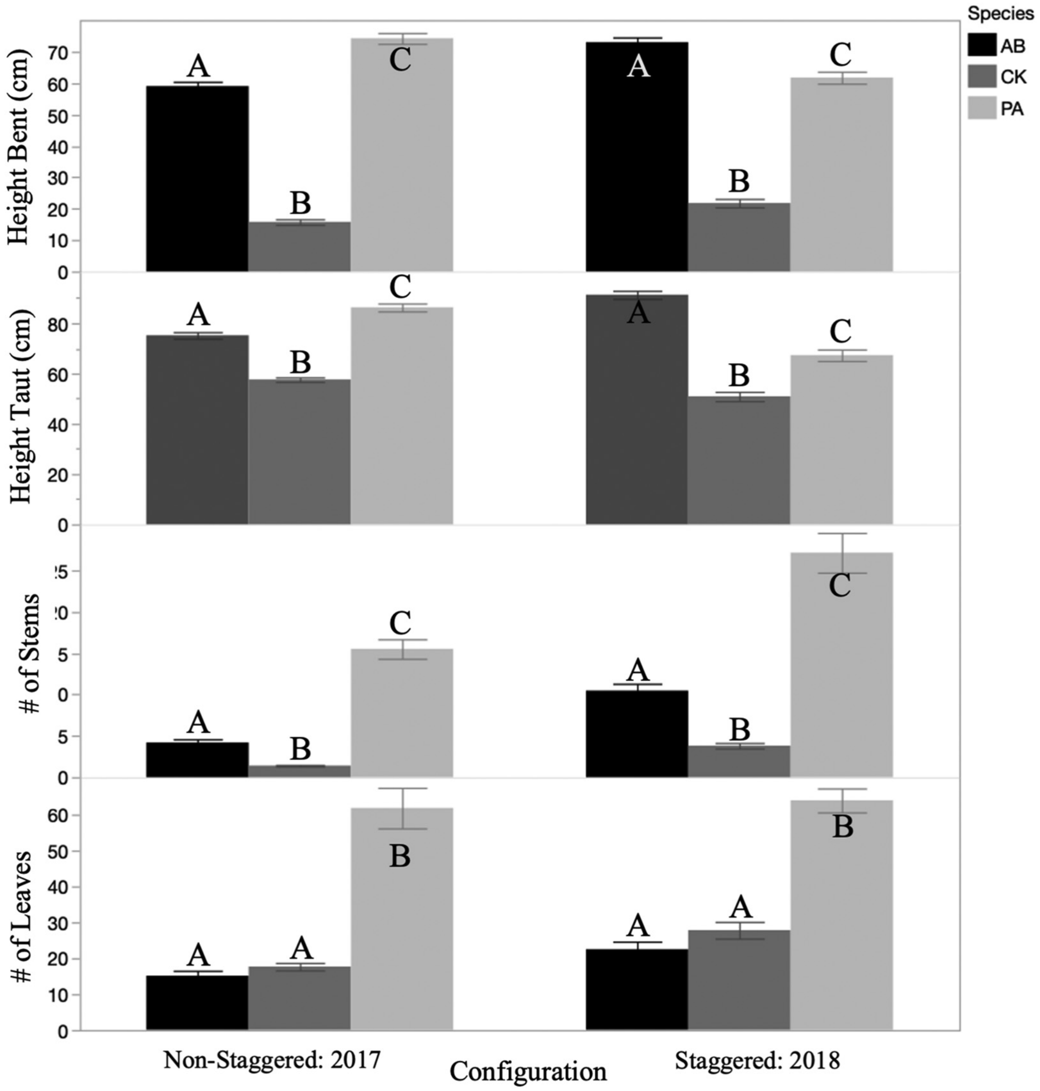

Fig. 5. Plant morphology traits across configurations reflecting differences by year. Plant traits did not vary between planting densities, but varied across species and configuration whereby configuration differences reflect different growth conditions in 2017 versus 2018. *Carex kobomugi* (CK) was consistently the smallest plant in all metrics. Note that in 2017 *P. amarum* (PA) was taller than *A. breviligulata* (AB), but in 2018 this relationship flipped. Error bars represent ± SE with different letters above species representing statistically different means from Tukey HSD pairwise comparisons.

these species there is no year by type interaction with nebkha height ($F_{1,25} = 1.56$, $P = 0.22$) or nebkha PC2 ($F_{1,25} = 0.01$, $P = 0.89$; Fig. 10). Nebkha PC2 did not vary between the two erect grasses ($P = 0.53$), and nebkha created by *P. amarum* were taller both years despite which plant species was taller ($F_{1,25} = 5.78$, $P = 0.02$; Fig. 10). Nebkha height is better explained by stem width than height as LMM revealed that a wider stem base produced taller nebkha in both erect grasses in the wind tunnel regardless of species (LMM: $F_{1,129} = 7.98$, $P < 0.01$). Maximum nebkha height achieved was 16 mm.

Nebkha planform shape did not vary by treatment, density ($P = 0.54$), configuration ($P = 0.42$) or plant size ($P = 0.85$), but varied by species ($F_{2,32} = 12.55$, $P < 0.0001$). *Carex kobomugi* created equant, fairly circular nebkha, reflective of its semi-rosette morphology. The two erect grasses, which did not differ in nebkha shape, produced oblong planar nebkha with flow-parallel elongation relative to wind direction (Figs. 11 and 4; Table 3). Mean representations of the nebkha produced by the three plant species are shown in Fig. 12. Examining LMM, no one morphological trait explained nebkha shape.

3.4. Field validation: field nebkha examinations

Field *A. breviligulata* nebkha were larger than those produced in the wind tunnel, but they were equal in planform shape and demonstrated the same observed relationships between plant and nebkha morphology. Field nebkha had greater area, height, and volume (Table 4) than the wind tunnel nebkha, despite wind tunnel *A. breviligulata* plants having more biomass (e.g., being larger). All *A. breviligulata* nebkha were oblong (with longer tails relative to their width along the prevailing wind direction), but the length to width ratio was greater in the field nebkha (Table 4). Plant and nebkha PC1 were positively linearly related in that larger plants created larger nebkha ($F_{1,11} = 6.31$, $R^2 = 0.36$, $P < 0.03$). Similarly, nebkha volume increased with greater plant size (PC1; $F_{1,11} = 5.11$, $R^2 = 0.32$, $P < 0.05$). Plant height was unrelated to nebkha height, but a wider stem base produced taller nebkha ($F_{1,1} = 5.44$, $P = 0.04$), while plant size (PC1) was unrelated to nebkha relief (i.e., height versus area).

Field *C. kobomugi* nebkha were larger than wind tunnel nebkha although planform shape was equal. Specifically, field nebkha had greater

Table 2

Loadings and relative contribution of the morphology variables for both the nebkha and plant PCA. We performed a PCA separately on plant and nebkha morphology traits. The eigenvalues are λ and the values in parentheses represent the percentage of variability explained by each variable in the PC and by its axis (λ). The PCA accounted for 96.9% and 90.8% of the variability in nebkha and plant morphology, respectively.

		Principal Component 1		Principal Component 2	
	Variable	Loading score	λ	Loading score	λ
Nebkha	Height	0.81 (27.4%)	2.37 (79.0%)	0.58 (63.8%)	0.54 17.9%
	Volume	0.97 (39.5%)		−0.09 (1.62%)	
	Area	0.89 (33.1%)		−0.43 (34.6%)	
Plants	# Leaves	0.74 (22.3%)	2.46 (61.5%)	0.58 (28.3%)	1.17 29.3%
	# Stems	0.80 (25.9%)		0.50 (21.4%)	
	Height (Taut)	0.72 (21.1%)		−0.65 (35.7%)	
	Height (Natural)	0.87 (30.7%)		−0.41 (14.7%)	

area ($Z = 2.76$, $P < 0.01$), volume ($Z = 2.27$, $P = 0.02$), and trended towards being taller ($Z = 1.85$, $P = 0.06$), despite wind tunnel *C. kobomugi* plants having greater biomass ($Z = 1.79$, $P = 0.05$). Although field nebkha were larger than wind tunnel nebkha, nebkha planform shape was equivalent ($\bar{x} = 1.18 \pm 0.25$, $P = 0.10$).

Consistent with wind tunnel findings, field nebkha did not vary between paired individuals of *A. breviligulata* and *C. kobomugi* in area, height, or volume, but varied in planform shape. Field *A. breviligulata* produced elongated ellipses with longer tails parallel to the wind compared to *C. kobomugi*, which produced more uniform, round nebkha ($\bar{x}_{AB} = 2.46 \pm 0.17$, $\bar{x}_{CK} = 1.44 \pm 0.16$, $Z = -2.51$, $P = 0.01$; Fig. 4). These results are consistent with findings in the wind tunnel, where nebkha formed by *A. breviligulata* and *C. kobomugi*, with no plants upwind of them, did not vary in nebkha area, height, angle or volume, but did vary in shape ($\bar{x}_{AB} = 1.93 \pm 0.35$, $\bar{x}_{CK} = 1.25 \pm 0.19$, $Z = -2.14$, $P = 0.03$).

4. Discussion

Our findings elucidate a strong feedback between plant ecosystem engineers and surface topography at the initial stages of foredune genesis in nebkha formation, both in a wind tunnel and field setting. We show that feedbacks are explained by plant traits. Specifically: (1) larger plants created larger nebkha regardless of species; (2) the anecdotal adage that a taller, steeper plant may build a taller steeper dune, is unsupported at initialization, as stem width in erect grasses better predicted nebkha height than plant height alone; and (3) morphological traits impacted nebkha shape, with the erect grasses *P. amarum* and *A. breviligulata* producing more elongated, planar nebkha than low-lying *C. kobomugi*. These relationships hold true regardless of planting density and configuration, although the staggered configuration produced larger nebkha than non-staggered despite equal formative conditions. For management, these results suggest planting more culms per planting hole and/or larger plants to increase nebkha formation and subsequent sediment volume retention. Using a staggered configuration to the prevailing wind may be most conducive for building larger nebkha more quickly over time while simultaneously initiating rapid formation of a foredune that would buffer upland areas during storm events.

4.1. Field validation

Simulations of natural phenomenon are not always field validated, but should be in a well-constructed experimental design (Dunham and Beaupre, 1998), and our field truthing corroborates our wind tunnel findings. The increased size (area, height, and volume) of field nebkha for *A. breviligulata* and *C. kobomugi* was the main difference from the wind tunnel results, despite the wind tunnel plants having been larger than the field plants. We attribute this difference to field nebkha having increased formation time (>30 min), and likely forming over multiple transport events under varied wetting and drying cycles (Czarnes et al., 2000; Maun, 2009; Balke et al., 2014; Zarnetske et al., 2015). Similarly, a recent wind tunnel study achieved nebkha elevations of 2–8 cm, but after allotting several hours of formation, compared to our 30 min run time (Hesp et al., 2019). Our results suggest that the underlying feedbacks that create variation in nebkha size and shape among species remain true in the field beyond initialization. Longer flow-parallel elongation in the field despite smaller plants likely stems from differences in wind velocity and stem width, both of which have been shown to impact shadow dune length (Hesp and Smyth, 2017). While field and wind tunnel plant stem widths were equivalent, the speeds of the formative field winds were unknown. Corroboration of the field and wind tunnel results show our findings are ecologically relevant and replicated in natural ecosystems.

4.2. The effect of plant morphology on nebkha size and shape

Larger plants formed larger nebkha both in the field and wind tunnel with nuances in variations. Until now, the theory that larger plants build larger aeolian forms, such as foredunes, was based entirely on observations of larger plants concomitantly occurring on larger dunes (Davies,

Table 3

Staggered planting configuration produced larger nebkha across all size metrics with variations in magnitude across species. Results are LMM holding box as a random effect and means are reported ± S.E.

	Species	Staggered	Non-staggered	Species effect	Configuration effect
Nebkha volume	*A. breviligulata*	19.15 ± 2.16 cm^3	10.77 ± 2.41 cm^3	$\underline{(CK = AB) \le PA}$ $F_{1,38} = 13.75$, $P < 0.0001$	$F_{1,38} = 18.61$, $P < 0.0001$
	P. amarum	41.15 ± 3.88 cm^3	22.79 ± 4.44 cm^3		
	C. kobomugi	22.83 ± 3.19 cm^3	13.32 ± 3.43 cm^3		
Nebkha height	*A. breviligulata*	7.26 ± 0.44 mm	6.50 ± 0.44 mm	$\underline{(CK = AB) \le PA}$ $F_{1,37} = 8.61$, $P < 0.001$	$F_{1,37} = 8.02$, $P < 0.01$
	P. amarum	9.45 ± 0.50 mm	7.01 ± 0.49 mm		
	C. kobomugi	6.45 ± 0.32 mm	5.88 ± 0.38 mm		
Nebkha area	*A. breviligulata*	55.28 ± 4.67 cm^2	42.31 ± 5.75 cm^2	$\underline{(PA = CK) \ge AB}$ $F_{1,32} = 9.35$, $P < 0.001$	$F_{1,32} = 23.67$, $P < 0.0001$
	P. amarum	108.97 ± 10.05 cm^2	65.23 ± 11.31 cm^2		
	C. kobomugi	95.02 ± 10.32 cm^2	52.31 ± 6.05 cm^2		

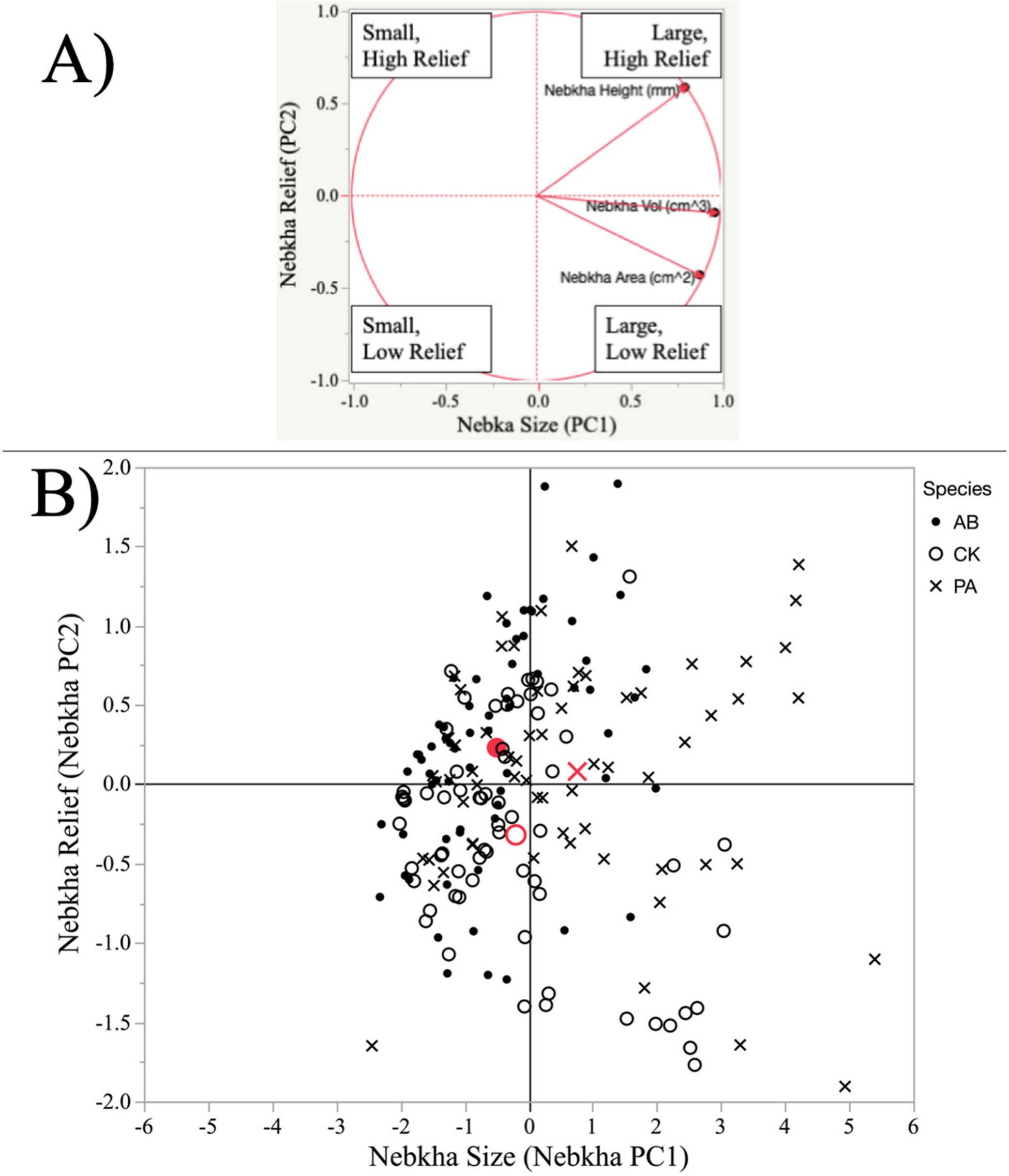

Fig. 6. Variation in nebkha size and shape across plant species explained by PCA. (A) Contribution of variables to the two principal components describing the variability in nebkha traits: volume, area, and height. PC1, loads fairly equally across all variables such that nebkha with large PC1 are of a larger size. PC2 loads heavily on nebkha height (negatively) and surface area (positively) as inverses, representing relative relief such that larger PC2 indicates greater relief than smaller PC2. (B) The ordination plot highlights species-specific differences in the size and relief of nebkha across species. Red points represent the mean for each species.

1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006; Hacker et al., 2011, 2019) with some exceptions (Charbonneau et al., 2017). Results presented here highlight the underlying feedbacks contributing to these associations and mirror findings surrounding artificial nebkha shapes where larger nebkha produced larger shadow dunes in their lee (Hesp and Smyth, 2017). This is similar to larger nebkha being established in the field around larger plant assemblages (Gillies et al., 2014). Compared to the aforementioned studies (Davies, 1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006; Hacker et al., 2011; Gillies et al., 2014; Hesp and Smyth, 2017; Hacker et al., 2019), we have reduced the scale to foredune initiation in nebkha genesis (Walker et al., 2017), and elucidated some of the drivers of the underlying feedbacks that enable larger plants to produce greater deposition.

At foredune initiation, the inherent morphological traits of the species influenced nebkha shape. Low-lying *C. kobomugi* produced more equant nebkha than erect grasses, but not necessarily shorter (Fig. 12), which does not support the notion that erect grasses are necessarily associated with or build taller and steeper foredunes (Davies, 1980; Wootton et al., 2005; Hacker et al., 2019). This shape relationship may carry though the life of the evolving foredune as suggested by comparing the lower, platform-like, established dunes of *Spinifex sericeus* versus *A. breviligulata* (Davies, 1980). Both are erect grasses, but their inflorescences are very different with that of *S. sericeus* being larger, shorter, and splaying horizontally ultimately driving differences in dune morphology (Davies, 1980). The results are consistent with nebkha length increasing with greater porosity, as observed with mesh objects (Gillies et al., 2017) and emergent and submerged vegetation (Yagci

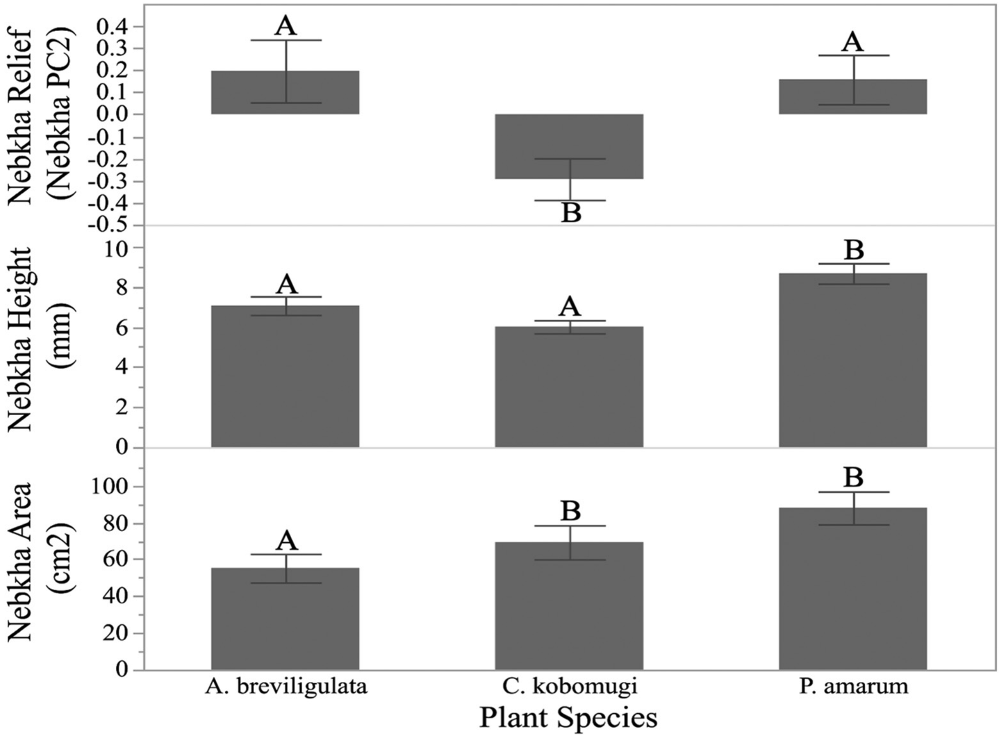

Fig. 7. Nebkha relief across plant species. *Carex kobomugi* created nebkha of lower relief than both erect grasses given its differences in nebkha height and area. Nebkha PC2 represents, as inverses, nebkha area (+) relative to height (−). *Carex kobomugi* nebkha had lower PC2 than both erect grasses, but examining the two variables loading on it, *C. kobomugi* produced equal nebkha height as the smaller erect grass *A. breviligulata* and equal area as the larger erect grass *P. amarum*. Error bars represent ± SE with different letters above species representing statistically different means from Tukey HSD pairwise comparisons. Means shown are mean value per box.

et al., 2016). Taller plants produce streamlined airflow and deposition around objects as shown by manipulating low-stem leaves on artificial erect plants (Hesp et al., 2019). In contrast, the low-lying stature of *C. kobomugi* has reduced porosity which should create increased turbulent kinetic energy and blade motion below the canopy, pushing topography into non-streamlined states (Raupach et al., 1996; Luhar and

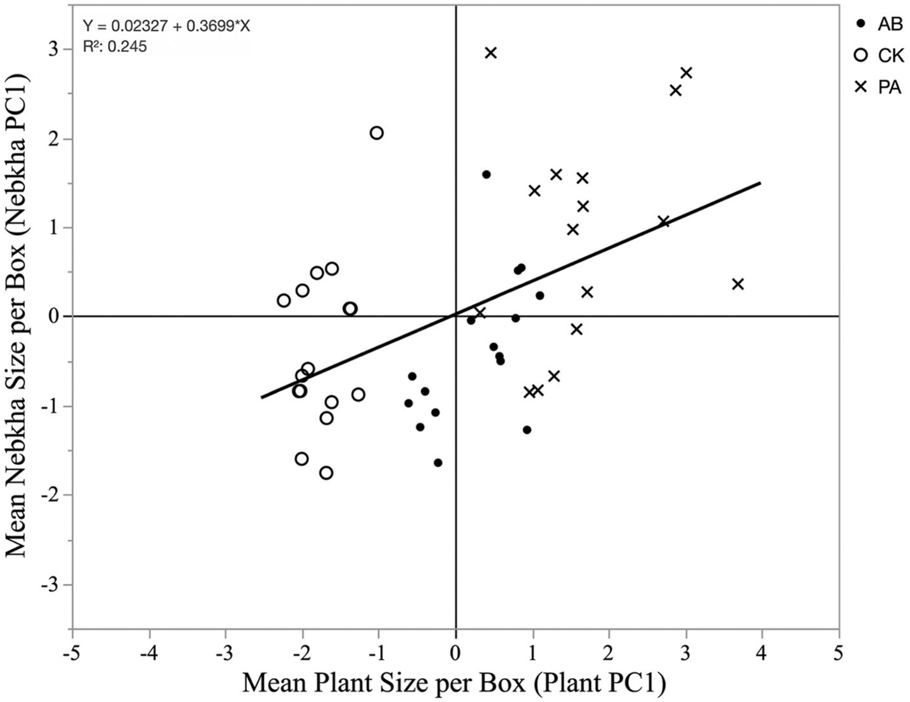

Fig. 8. Ordination plot of plant PC1 and nebkha PC1. Larger values for both axes indicate larger plants and nebkha, respectively, such that there is a positive linear relationship between plant size and nebkha size. Mean values per box are used to control for box as a potential confounding factor.

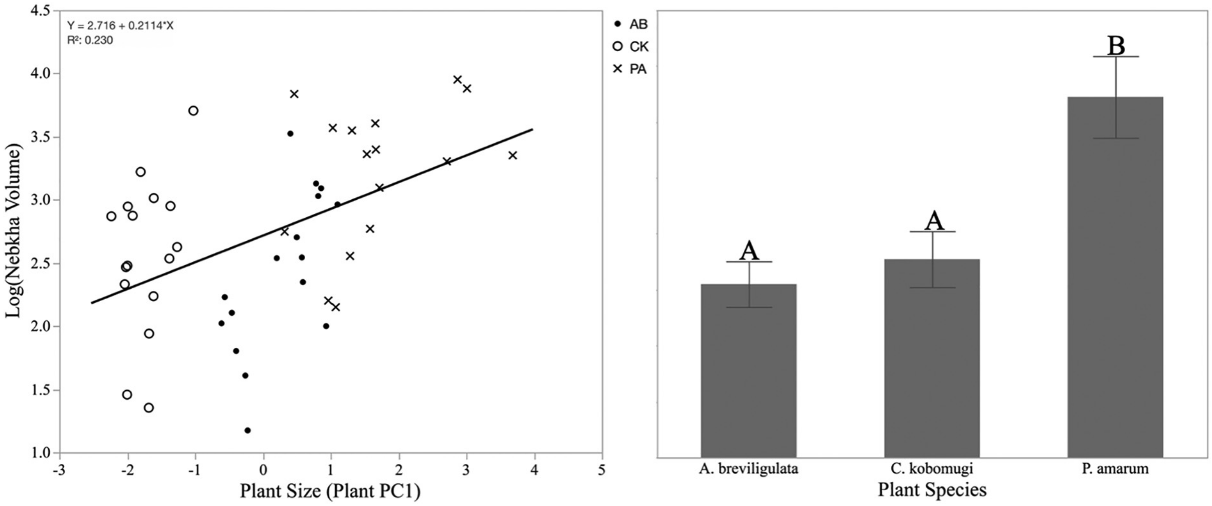

Fig. 9. Nebkha volume across plant species. Nebkha volume increased with increasing plant size with the largest plant species, *P. amarum* (PA) producing the largest nebkha. (A) All plants had increasing log (nebkha volume) with an equal slope across species with (B) *P. amarum* producing nebkha of greater volume than *A. breviligulata* (AB) and *C. kobomugi* (CK). (A) The data are normalized with log transformation and mean volume per box is used to control for box as a potential confounding factor.

Nepf, 2013; Boothroyd et al., 2016). Our wind tunnel results match studies of shrubs having increased deposition width and decreased deposition length with increasing horizontal complexity in low-lying leaves (Leenders et al., 2011).

Nebkha height was unrelated to plant height or size. Among the erect grasses, *P. amarum* built larger nebkha regardless of which grass was taller, while *C. kobomugi* and *A. breviligulata* nebkha were of equivalent height regardless of *A. breviligulata* being taller (Figs. 5 and 7). At the foredune level, crest height differences are attributed to vegetation height where lower profile plants have been noted (Davies, 1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006) or quantified on shorter established foredunes (Hacker et al., 2011, 2019). However,

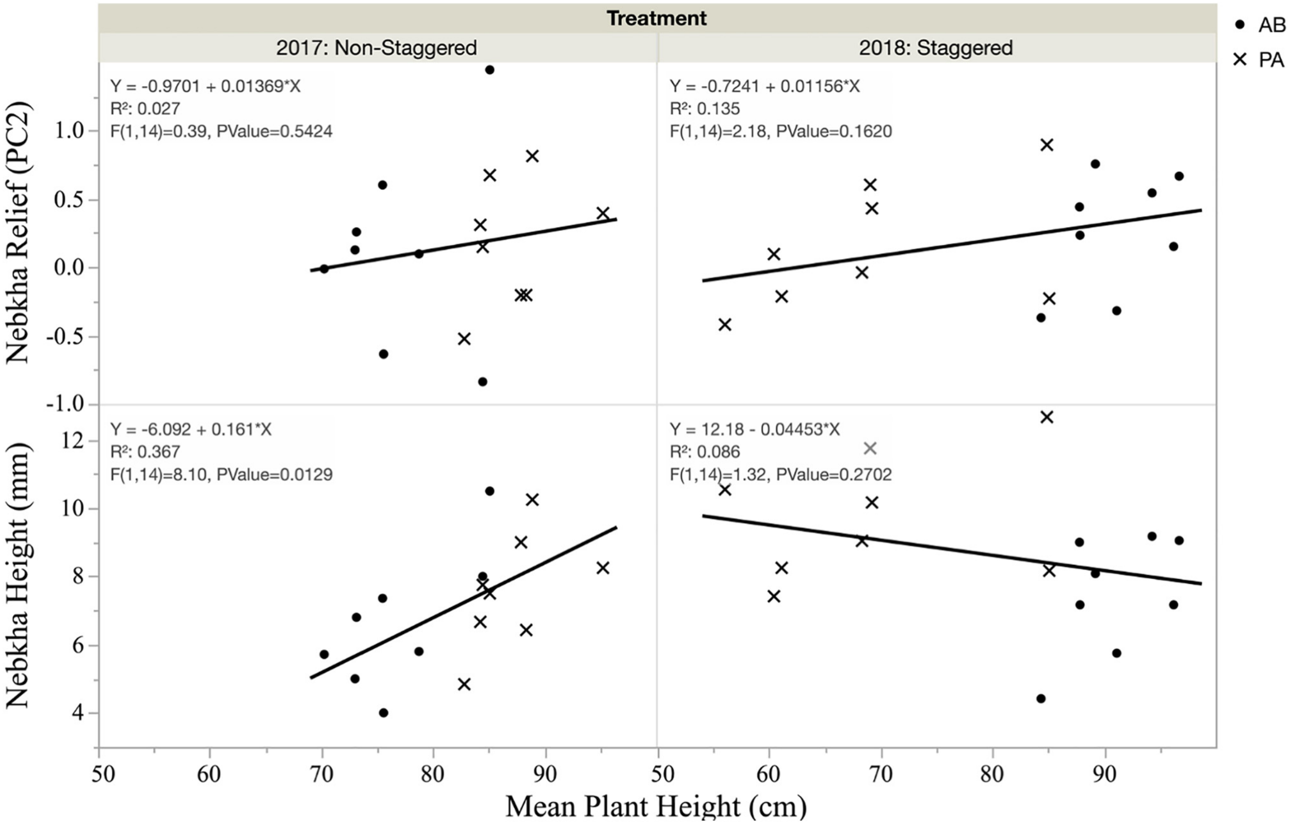

Fig. 10. Nebkha height relative to plant height. A taller plant does not necessarily build a taller nebkha as seen in the erect grasses *A. breviligulata* (AB) and *P. amarum* (PA). Nebkha height and relative relief (PC2: nebkha area (+) relative to height (−) as inverses) were both unrelated to plant height except for in 2017 when PA was taller than AB. However, we do not see the same relationship in 2018 when AB was taller than PA, suggesting that this relationship is due to other factors of plant morphology. The values represent the mean per box to control for box as a potential confounding factor.

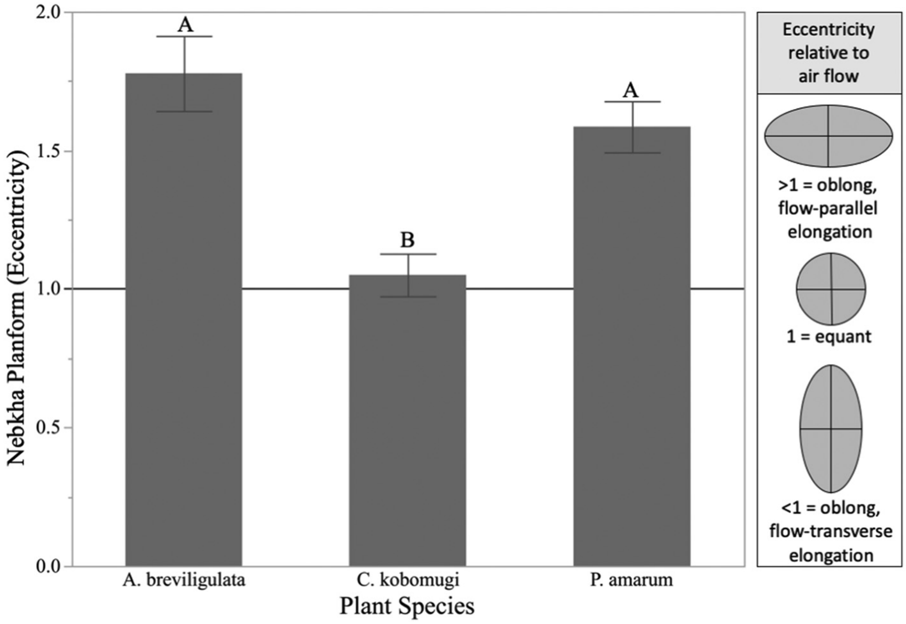

Fig. 11. Wind tunnel nebkha shape across plant species. Eccentricity is the ratio of the length and width of nebkha such that values >1 are longer than wider and values of 1 are equally long and wide along the prevailing wind direction. *Carex kobomugi* consistently produced more equant nebkha whereas the erect grasses, *P. amarum* and *A. breviligulata*, produced oblong or more planar nebkha. Different letters above species represent statistically different means from Tukey HSD pairwise comparisons.

greater plant height also tends to coincide with greater biomass and surface cover, both of which create increased trapping efficiency (de M Luna et al., 2011; Zarnetske et al., 2012) as exhibited here in *P. amarum*, but not *A. breviligulata*. This is interesting given that *A. breviligulata* and *P. amarum* have been found on dunes of similar size and shape in nature (Woodhouse et al., 1977; Hacker et al., 2019), but is also important to note that the species currently on a dune may not have necessarily built it (Charbonneau et al., 2017). Sediment size across locations may confound topographic variability created by plant morphology in nature as it can impact nebkha height, but this can be controlled for in a laboratory setting (Hesp, 1981; Hesp and Smyth, 2017). Greater stem width, which equates to greater frontal area and varies between species (Mullins et al., 2019), appears to be the paramount reason why *A. breviligulata* and *P. amarum* differed in nebkha height. This suggests that in foredune initiation, species identity may play a greater role than at higher densities due to both reduced neighbor interaction and frontal area (Pietri et al., 2009).

Sediment volume distribution, windward (sedge) versus leeward (erect grasses) of a plant, is attributable to plant morphology and height. This finding supports wider stem bases creating longer wake zones (Hesp, 1989), and overlapping wake zones leeward of erect plants having the potential to cause localized scour (Burri et al., 2011; Leenders et al., 2011). Instances of *C. kobomugi* windward scouring are also likely due leaf splay at the sediment surface increasing bed turbulence (Burri et al., 2011; Leenders et al., 2011; Luhar and Nepf, 2013). However, the leaf ends of *C. kobomugi* often became buried, no longer moving in the airstream, thus limiting blade motion that could trigger erosion and inciting deposition both upwind and downwind around the entirety of the relatively sheltered plant base (Pietri et al., 2009). Leaf flexibility, not measured here, relative to height and number of leaves, likely also impacts deposition as in air and water flow fields (Järvelä, 2002; Burri et al., 2011; Luhar and Nepf, 2013). The splayed and low-lying semi-rosette shape of *C. kobomugi* may also enable it to better retain accumulated grains (Charbonneau et al., 2016) than other plants (*A. breviligulata* = *C. kobomugi* nebkha volume). However, in the field, this phenomenon must be viewed in the context of how little sediment depth it takes to bury *C. kobomugi* or other shorter plants relative to taller erect grasses.

4.3. The effect of planting configuration and density on nebkha size

A staggered planting configuration produced nebkha with twice the volume of a non-staggered configuration. This is an important finding for coastal management and planting efforts. To our knowledge, managers have noted depositional differences from fencing configurations, but have not noted depositional differences from varying plant configuration; however, wind direction, which undoubtedly contributes to deposition variation, was not measured concomitantly (Savage and Woodhouse, 1968; Wootton et al., 2016). A staggered planting pattern relative to the prevailing wind direction eliminates or reduces wind alleys through rows, thereby increasing turbulent wake interactions between individuals and inducing greater deposition (Pietri et al., 2009). Regardless of configuration or density, deposition did not vary with plant row, indicating that sediment transported evenly throughout the stand and did not accumulate more in the first upwind or last downwind row as might have been expected from changes in frontal area (Hesp, 1983, 1989; Arens et al., 2001; Hesp et al., 2019).

Unexpectedly, density did not impact nebkha size. More objects theoretically equate to an increased roughness factor and greater wind dampening due to turbulence inducing deposition (Hesp, 1983, 1989; Zarnetske et al., 2012; Ortiz et al., 2013; Keijsers et al., 2014), and differing densities between species can sometimes exacerbate topographic species effects in developed foredunes, even in similarly erect grasses (Hacker et al., 2019). Lower densities often facilitate erosion (Keijsers et al., 2016) although they can, in some instances, enhance deposition (Burri et al., 2011). Our results are consistent with research on submerged and non-submerged vegetation, where flow reduction and deposition did not vary by density (Järvelä, 2002; Burri et al., 2011). Our two common management planting densities may not have been different enough to produce density-specific erosive or accretive effects. There may also be no correlation between vegetation density and accretion quantity, as has been suggested at the scale of an established foredune system

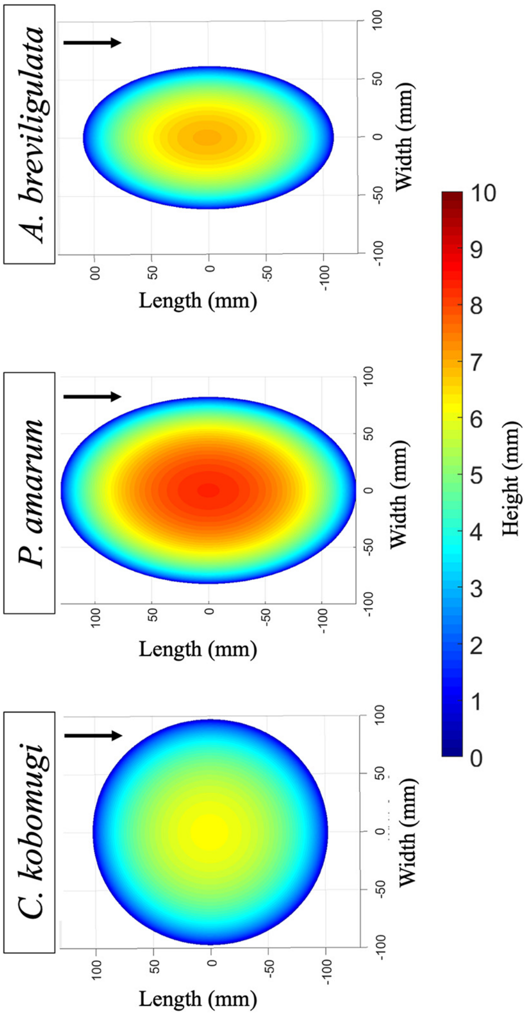

Fig. 12. To scale idealized representation of wind tunnel nebkha created by the three different foredune plant species. Nebkha differences were consistent across planting densities. The dimensions shown are based on the overall means for each plant species across density and configuration treatments. It is important to note that although these nebkha are small, our field validation data demonstrate these shape and size differences accrue and are maintained as the nebkha grow larger. The arrows depict the direction of wind flow.

and the timescale of years (Keijsers et al., 2015). However, our unanalyzed high density treatments forming melded nebkha among groups of plants suggest otherwise. Planting lower densities of larger plants may translate to equivalent accumulation as planting a greater number of smaller plants, but at reduced effort and monetary cost. Similarly, a 30.5 cm spacing, may represent a critical density, as has been suggested by Price (1961), below which roughness elements act independently instead of collectively.

4.4. Suggestions for future research

More is known about the effect of wind on rigid, submerged, and emergent vegetation than on flexible roughness elements or live plants (Järvelä, 2002; Burri et al., 2011). However, solid versus porous obstructions do not behave equivalently in flow conditions (Gillies et al., 2014). Plants undergo streamlining and compression, yielding more heterogeneous velocity fields than solid objects (Boothroyd et al., 2016; Yagci et al., 2016). In situ field experiments examining the ecosystem engineers that induce ecogeomorphic responses may thus yield different results than artificial proxies. The use of organic plant root proxies (Bryant et al., 2019) and live plants have recently been applied to simulate laboratory beach and dune wave-runup, although in studies using live plants it is critical that the plants be fully rooted and established as they would be naturally, otherwise the results may not hold bearing on reality (Silva et al., 2016; Feagin et al., 2019). Future endeavors using live plant material could incorporate irregularity in stand configuration as has been done with rigid pegs (Raupach et al., 2006) and artificial flexible plant proxies (Hesp et al., 2019). Additionally, the inclusion of heterogenous species assemblages and the correlation to turbulence generated at the canopy top versus stem-level would bolster the applicability of laboratory studies to natural settings (Nepf et al., 2007).

Ecogeomorphic sandy dune ecosystems across coastlines share many of the same anthropogenic challenges and functional similarities such that this research can contribute to a global framework for management and restoration of coastal interface habitats as suggested by Balke et al. (2014) and Corenblit et al. (2015). Scale constraints exist when studying beach-dune system evolution (Walker et al., 2017), and beach-dune research is often geologically focused (Jackson and Nordstrom, 2019). However, a more interdisciplinary approach, as applied here, appears needed to encapsulate the variability surrounding inherently complex ecogeomorphic systems (Stallins, 2006; Walker et al., 2017; Stallins and Corenblit, 2018). Ecogeomorphic systems are interdisciplinary by their very nature and as such, future research should seek to span disciplines, and laboratory experiments should be field-validated when broaching topics with management implications (Stallins, 2006; Schlacher et al., 2008; Murray et al., 2008; Corenblit et al., 2011; Stallins and Corenblit, 2018). Integrative ecogeomorphic studies have the potential to yield more realistic results of complex natural associations and thus more concrete suggestions for management by virtue of their improved systems perspective.

5. Conclusions

This research contributes to our fundamental understanding of the role of intraspecific variation in vegetation morphology, density, and configuration in impacting geomorphological processes in aeolian

Table 4
The *A. breviligulata* plants that formed the field nebkha were smaller than those in the wind tunnel, but they produced larger nebkha than in the wind tunnel. Nebkha shape was elongated in the wind tunnel and field, but field nebkha had greater elongation relative to their width parallel to the prevailing wind. N = 13 for each dataset.

	Field *A. breviligulata* Nebkha	Wind tunnel *A. breviligulata* Nebkha	Wilcoxon Rank Sum Test
Dry biomass	1.68 ± 0.37 g	6.26 ± 0.90 g	$Z = -3.98, P < 0.0001$
Nebkha area	331.90 ± 78.69 cm^2	56.26 ± 6.66 cm^2	$Z = 4.52, P < 0.0001$
Nebkha height	18.4 ± 1.58 mm	7.16 ± 0.62 mm	$Z = 4.56, P < 0.0001$
Nebkha volume	69.2 ± 23.5 cm^3	16.4 ± 2.5 cm^3	$Z = 2.92, P < 0.001$
Nebkha shape	3.01 ± 0.40	1.87 ± 0.34	$Z = 3.36, P < 0.001$

beach-dune systems. We demonstrated that larger plants build larger nebkha, lending experimental support to the commonly held belief that larger plants build larger foredunes. However, taller plants do not necessarily build taller and steeper nebkha. Rather, stem width, a proxy for frontal area, appears to better predict nebkha height. Differences in volumetric accumulation are directly dependent upon stand configuration relative to the prevailing wind direction. Planiform nebkha shape is unrelated to biomass and instead varies with species morphology with low-lying *C. kobomugi* producing more equant nebkha than both erect grasses. We focused on small-scale fundamental processes with applications to improve system scale predictions and modeling in future work. The field validation effort supported the laboratory-observed ecogeomorphic foredune initiation feedbacks and demonstrated that these relationships are maintained as the nebkha grows. The results have inherent management and modeling applications for species-specific vegetation parameterization to improve our understanding of spatiotemporal foredune evolution and recovery, storm response, and system state. For menegment, these results suggest that planting more culms per hole and larger plants staggered to the prevailing wind direction will result in more rapid accumulation, which can translate to reduced dune formation time. For modeling, we provide evidence of foredune plants acting as ecosystem engineers in beach and dune habitats such that vegetation should not be excluded when parameterizing future modeling efforts, where applicable. These results can be used for vegetation parameterization to yield more robust model results and provide a basis for testing hypotheses generated at the larger foredune scale. Understanding the efficacy of natural dune engineers will only be increasingly important as climate change and sea level rise impose heightened stress on critical ecogeomorphic habitats worldwide.

CRediT authorship contribution statement

Charbonneau secured funding to build the wind tunnel and conduct the research working, with Zarnetske designing its specifications based on previous blueprints. Wnek secured the wind tunnel location, and worked with students and Charbonneau collecting data. Charbonneau organized and oversaw the wind tunnel construction and carried out the research. Zarnetske, Wnek, Casper, and Barber each contributed to experimental design. Dohner and Charbonneau conducted field validation analyses. All authors contributed to the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geomorph.2021.107594.

References

AgiSoft, 2018. Agisoft Metashape User Manual - Professional Edition. Version 1 (5), 1–130.

Arens, S.M., 1996. Patterns of sand transport on vegetated foredunes. Geomorphology 17, 339–350.

Arens, S.M., Baas, A., Van Boxel, J.H., Kalkman, C., 2001. Influence of reed stem density on foredune development. Earth Surf. Process. Landf. 26, 1161–1176.

Badano, E.I., Cavieres, L.A., 2006. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. Diversity Distributions 12, 388–396.

Balke, T., Herman, P.M.J., Bouma, T.J., 2014. Critical transitions in disturbance-driven ecosystems: identifying Windows of Opportunity for recovery. J. Ecol. 102, 700–708.

Bauer, B.O., Houser, C.A., Nickling, W.G., 2004. Analysis of velocity profile measurements from wind-tunnel experiments with saltation. Geomorphology 59, 81–98.

Bendix, J., Hupp, C.R., 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrol. Process. 14, 2977–2990.

Boothroyd, R.J., Hardy, R.J., Warburton, J., Marjoribanks, T.I., 2016. The importance of accurately representing submerged vegetation morphology in the numerical prediction of complex river flow. Earth Surf. Process. Landf. 41, 567–576.

Bos, A.R., Bouma, T.J., de Kort, G.L.J., van Katwijk, M.M., 2007. Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. Estuar. Coast. Shelf Sci. 74, 344–348.

Bryant, D.B., Bryant, M.A., Sharp, J.A., Bell, G.L., Moore, C., 2019. The response of vegetated dunes to wave attack. Coast. Eng. 152, 103506.

Burri, K., Gromke, C., Lehning, M., Graf, F., 2011. Aeolian sediment transport over vegetation canopies: a wind tunnel study with live plants. Aeolian Res. 3, 1–9.

Carter, R.W.G., 1995. Coastal Environments: An Introduction to the Physical, Ecological and Cultural Systems of Coastlines. 5th ed. Academic Press, London.

Charbonneau, B.R., Casper, B.B., 2018. Wind tunnel tests inform Ammophila planting spacing for dune management. Shore & Beach 86, 37–46.

Charbonneau, B.R., Wnek, J.P., Langley, J.A., Lee, G., Balsamo, R.A., 2016. Above vs. belowground plant biomass along a barrier island: Implications for dune stabilization. J. Environ. Manag. 182, 126–133.

Charbonneau, B.R., Wootton, L.S., Wnek, J.P., Langley, J.A., Posner, M.A., 2017. A species effect on storm erosion: Invasive sedge stabilized dunes more than native grass during Hurricane Sandy. J. Appl. Ecol. 54, 1385–1394.

Cheplick, G.P., 2016. Changes in plant abundance on a coastal beach following two major storm surges 1. Journal of the Torrey Botanical Society 143, 180–191.

Corenblit, D., Baas, A., Bornette, G., Darrozes, J., Delmotte, S., Francis, R.A., Gurnell, A.M., Julien, F., Naiman, R.J., Steiger, J., 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. Earth Sci. Rev. 106, 307–331.

Cooke, R., Warren, A., Goudie, A., 1993. Desert Geomorphology. UCL Press, London.

Corenblit, D., Baas, A., Balke, T., Bouma, T., Fromard, F., Garófano-Gómez, V., González, E., Gurnell, A.M., Hortobágyi, B., Julien, F., Kim, D., Lambs, L., Stallins, J.A., Steiger, J., Tabacchi, E., Walcker, R., 2015. Engineer pioneer plants respond to and affect geomorphic constraints similarly along water-terrestrial interfaces world-wide. Glob. Ecol. Biogeogr. 24, 1363–1376.

Cowles, H.C., 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz. 27, 167–202.

Czarnes, S., Hallett, P.D., Bengough, A.G., Young, I.M., 2000. Root- and microbial-derived mucilages affect soil structure and water transport. Eur. J. Soil Sci. 51, 435–443.

Davies, J.L., 1980. Geographical Variation in Coastal Development. Longman, London.

de Castro, F., 1995. Computer simulation of the dynamics of a dune system. Ecol. Model. 78, 205–217.

de M Luna, M.C.M., Parteli, E.J.R., Durán, O., Herrmann, H.J., 2011. Model for the genesis of coastal dune fields with vegetation. Geomorphology 129, 215–224.

Dohner, S.M., Trembanis, A.C., Miller, D.C., 2016. A tale of three storms: morphologic response of Broadkill Beach, Delaware, following Superstorm Sandy, Hurricane Joaquin, and Winter Storm Jonas. Shore & Beach 84, 1–7.

Dunham, A.E., and S.J. Beaupre. 1998. Ecological experiments: scale, phenomenology, mechanism, and the illusion of generality. Á In: Resitarits, W. and Bernardo, J.(eds), Experimental ecology .... Pages 27–49.

Duran, O., Moore, L.J., 2013. Vegetation controls on the maximum size of coastal dunes. Proc. Natl. Acad. Sci. 110, 17217–17222.

Durán Vinent, O., Moore, L.J., 2014. Barrier island bistability induced by biophysical interactions. Nat. Clim. Chang. 5, 158–162.

Elko, N., Brodie, K., Stockdon, H., Nordstrom, K., 2016. Dune management challenges on developed coasts. Shore & Beach 84, 15–28.

Elko, N., Dietrich, C., Cialone, M., Stockdon, H., Bilskie, M.W., Boyd, B., Charbonneau, B.R., Cox, D., Dresback, K., Elgar, S., et al., 2019. Advancing the understanding of storm processes and impacts. Shore & Beach 87, 37–51.

Feagin, R.A., Figlus, J., Zinnert, J.C., Sigren, J., Martínez, M.L., Silva, R., Smith, W.K., Cox, D., Young, D.R., Carter, G., 2015. Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. Front. Ecol. Environ. 13, 203–210.

Feagin, R.A., Furman, M., Salgado, K., Martinez, M.L., Innocenti, R.A., Eubanks, K., Figlus, J., Huff, T.P., Sigren, J., Silva, R., 2019. The role of beach and sand dune vegetation in mediating wave run up erosion. Estuar. Coast. Shelf Sci. 219, 97–106.

Gares, P.A., 1992. Topographic changes associated with coastal dune blowouts at island beach state park, New Jersey. Earth Surf. Process. Landf. 17, 589–604.

Gillies, J.A., Nield, J.M., Nickling, W.G., 2014. Wind speed and sediment transport recovery in the lee of a vegetated and denuded nebkha within a nebkha dune field. Aeolian Res. 12, 135–141.

Gillies, J.A., Nickling, W.G., Nikolich, G., Etyemezian, V., 2017. A wind tunnel study of the aerodynamic and sand trapping properties of porous mesh 3-dimensional roughness elements. Aeolian Res. 25, 23–35.

Goldstein, E.B., Moore, L.J., Durán Vinent, O., 2017. Vegetation controls on maximum coastal foredune “hummockiness” and annealing time. Earth Surface Dynamics Discussions 1–15.

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815.

Hacker, S.D., Zarnetske, P., Seabloom, E., Ruggiero, P., Mull, J., Gerrity, S., Jones, C., 2011. Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact. Oikos 121, 138–148.

Hacker, S.D., Jay, K.R., Cohn, N., Goldstein, E.B., Hovenga, P.A., Itzkin, M., Moore, L.J., Mostow, R.S., Mullins, E.V., Ruggiero, P., 2019. Species-specific functional morphology of four US Atlantic Coast dune grasses: biogeographic implications for dune shape and coastal protection. Diversity 11 (82–16).

Hall Cushman, J., Waller, J.C., Hoak, D.R., 2010. Shrubs as ecosystem engineers in a coastal dune: influences on plant populations, communities and ecosystems. J. Veg. Sci. 21, 821–831.

Hesp, P.A., 1981. The formation of shadow dunes. J. Sediment. Petrol. 51, 101–112.

Hesp, P.A., 1983. Morphodynamics of incipient foredunes in New South Wales, Australia. Eolian Sediments and Processes. Elsevier, pp. 325–342.

Hesp, P.A., 1984. Foredune formation in SE Australia. In: Thom, B.G. (Ed.), Coastal Geomorphology in Australia. Academic Press, Sydney, pp. 60–97.

Hesp, P.A., 1989. A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes. International Association for Scientific Hydrology 54, 181–201.

Hesp, P.A., 2002. Foredunes and blowouts: initiation, geomorphology and dynamics. Geomorphology 48, 245–268.

Hesp, P.A., 2013. A 34 year record of foredune evolution, Dark Point, NSW, Australia. J. Coast. Res. 165, 1295–1300.

Hesp, P.A., Smyth, T.A.G., 2017. Nebkha flow dynamics and shadow dune formation. Geomorphology 282, 27–38.

Hesp, P.A., and I. J. Walker. 2013. Coastal dunes. In: Shroder, J. (Editor in Chief), Lancaster, N., Sherman, D.J., Baas, A.C.W. (Eds.), Treatise on Geomorphology. Academic Press, San Diego, CA, vol. 11, Aeolian Geomorphology, pp. 328–355.

Hesp, P.A., Martinez, M., da Silva, G.M., Rodríguez-Revelo, N., Gutierrez, E., Humanes, A., Laínez, D., Montaño, I., Palacios, V., Quesada, A., Storero, L., Trilla, G.G., Trochine, C., 2011. Transgressive dunefield landforms and vegetation associations, Doña Juana, Veracruz, Mexico. Earth Surf. Process. Landf. 36, 285–295.

Hesp, P.A., Smyth, T.A.G., Nielsen, P., Walker, I.J., Bauer, B.O., Davidson-Arnott, R., 2015. Flow deflection over a foredune. Geomorphology 230, 64–74.

Hesp, P.A., Dong, Y., Cheng, H., Booth, J.L., 2019. Wind flow and sedimentation in artificial vegetation: Field and wind tunnel experiments. Geomorphology 337, 165–182.

Hilton, M., Harvey, N., Hart, A., James, K., Arbuckle, C., 2006. The impact of exotic dune grass species on foredune development in Australia and New Zealand: a case study of *Ammophila arenaria* and *Thinopyrum junceiforme*. Aust. Geogr. 37, 313–334.

Houser, C., Mathew, S., 2011. Alongshore variation in foredune height in response to transport potential and sediment supply: South Padre Island, Texas. Geomorphology 125, 62–72.

Houser, C., Hapke, C., Hamilton, S., 2008. Controls on coastal dune morphology, shoreline erosion and barrier island response to extreme storms. Geomorphology 100, 223–240.

Intelligence, S. S. 2019. TriSpector1000 Operating Instructions:1–104.

Jackson, N.L., Nordstrom, K.F., 2019. Trends in research on beaches and dunes on sandy shores, 1969-2019. Geomorphology 1–13.

Järvelä, J., 2002. Flow resistance of flexible and stiff vegetation: a flume study with natural plants. J. Hydrol. 269, 44–54.

JMP®, 2019. Version Pro 14. SAS Institute Inc., Cary, NC.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Keijsers, J.G.S., Poortinga, A., Riksen, M.J.P.M., Maroulis, J., 2014. Spatio-temporal variability in accretion and erosion of coastal foredunes in the Netherlands: regional climate and local topography. PLoS One 9, e91115.

Keijsers, J.G.S., De Groot, A.V., Riksen, M.J.P.M., 2015. Vegetation and sedimentation on coastal foredunes. Geomorphology 228, 723–734.

Keijsers, J.G.S., De Groot, A.V., Riksen, M.J.P.M., 2016. Modeling the biogeomorphic evolution of coastal dunes in response to climate change. Journal of Geophysical Reseach Earth Surface 121, 1161–1181.

Leenders, J.K., Sterk, G., Van Boxel, J.H., 2011. Modelling wind-blown sediment transport around single vegetation elements. Earth Surf. Process. Landf. 36, 1218–1229.

Luhar, M., Nepf, H.M., 2013. From the blade scale to the reach scale: a characterization of aquatic vegetative drag. Adv. Water Resour. 51, 305–316.

MathWorks, Inc, 2018. MATLAB and Statistics and Machine Learning Toolbox Release 2018a. The MathWorks, Inc., Natick, Massachusetts, United States.

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press, Oxford, UK.

Min, B.M., 2006. Shoot growth and distribution pattern of *Carex kobomugi* in a natural stand. J. Plant Biol. 49, 224–230.

Moore, L.J., Durán Vinent, O., Ruggiero, P., 2016. Vegetation control allows autocyclic formation of multiple dunes on prograding coasts. Geology G37778, 1–4.

Mullins, E., Moore, L.J., Goldstein, E.B., Jass, T., Bruno, J., Durán Vinent, O., 2019. Investigating dune-building feedback at the plant level: insights from a multispecies field experiment. Earth Surf. Process. Landf. 60, 205–214.

Murray, A.B., Knaapen, M.A.F., Tal, M., Kirwan, M.L., 2008. Biomorphodynamics: physical-biological feedbacks that shape landscapes. Water Resour. Res. 44, W11301.

Nepf, H., Ghisalberti, M., White, B., Murphy, E., 2007. Retention time and dispersion associated with submerged aquatic canopies. Water Resources Research 43 (n/a–n/a).

Nield, J.M., Baas, A.C., 2008. Investigating parabolic and nebkha dune formation using a cellular automaton modelling approach. Earth Surf. Process. Landf. 33, 724–740.

O'Connell, J., 2008. Coastal dune protection and restoration, using “Cape” American beachgrass and fencing. Pages 1–17. Service, Woods Hole Sea Grant and Barnstable County Cooperative Extension.

Ortiz, A.C., Ashton, A., Nepf, H., 2013. Mean and turbulent velocity fields near rigid and flexible plants and the implications for deposition. J. Geophys. Res. Earth Surf. 118, 2585–2599.

Pietri, L., Petroff, A., Amielh, M., Anselmet, F., 2009. Turbulence characteristics within sparse and dense canopies. Environ. Fluid Mech. 9, 297–320.

Price, W.I.J., 1961. The effects of the characteristics of snow fences on the quantity and shape of the deposited snow. Agric. Ecosyst. Environ. 22-23, 89–98.

Ranwell, D.S., 1972. Ecology of Salt Marshes and Sand Dunes. Chapman and Hall, London.

Raupach, M.R., 1992. Drag and drag partition on rough surfaces. Bound.-Layer Meteorol. 60, 375–395.

Raupach, M.R., Finnigan, J.J., Brunei, Y., 1996. Coherent eddies and turbulence in vegetation canopies: the mixing-layer analogy. Bound.-Layer Meteorol. 78, 351–382.

Raupach, M.R., Hughes, D.E., Cleugh, H.A., 2006. Momentum absorption in rough-wall boundary layers with sparse roughness elements in random and clustered distributions. Bound.-Layer Meteorol. 120, 201–218.

Savage, R.P., Woodhouse, W.W., 1968. Creation and stabilization of coastal barrier dunes. Coast. Eng. Proc. 1 (11), 671–700.

Schlacher, T.A., Schoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, F., McLachlan, A., 2008. Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. Mar. Ecol. 29, 70–90.

Seneca, E.D., Woodhouse, W.W., Broome, S.W., 1976. Dune Stabilization With *Panicum amarum* Along the North Carolina Coast.

Silva, R., Martínez, M.L., Odériz, I., Mendoza, E., Feagin, R.A., 2016. Response of vegetated dune-beach systems to storm conditions. Coast. Eng. 109, 53–62.

Stallins, J.A., 2005. Stability domains in barrier island dune systems. Ecol. Complex. 2, 410–430.

Stallins, J.A., 2006. Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. Geomorphology 77, 207–216.

Stallins, J.A., Corenblit, D., 2018. Interdependence of geomorphic and ecologic resilience properties in a geographic context. Geomorphology 305, 76–93.

Tanaka, N., Nandasena, N.A.K., Jinadasa, K.B.S.N., Sasaki, Y., Tanimoto, K., Mowjood, M.I.M., 2009. Developing effective vegetation bioshield for tsunami protection. Civ. Eng. Environ. Syst. 26, 163–180.

Tanner, C.C., 2001. Plants as ecosystem engineers in subsurface-flow treatment wetlands. Water Science and Technology 44, 9–17.

Van Dijk, P.M., Arens, S.M., Van Boxel, J.H., 1999. Aeolian processes across transverse dunes. II: modelling the sediment transport and profile development. Earth Surf. Process. Landf. 24, 319–333.

Walker, I.J., Davidson-Arnott, R.G.D., Bauer, B.O., Hesp, P.A., Delgado-Fernandez, I., Ollerhead, J., Smyth, T.A.G., 2017. Scale-dependent perspectives on the geomorphology and evolution of beach-dune systems. Earth Sci. Rev. 171, 220–253.

Wolner, C.W.V., Moore, L.J., Young, D.R., Brantley, S.T., Bissett, S.N., McBride, R.A., 2013. Ecomorphodynamic feedbacks and barrier island response to disturbance: insights from the Virginia Barrier Islands, Mid-Atlantic Bight, USA. Geomorphology 199, 115–128.

Woodhouse Jr., W.W., 1982. Coastal sand dunes of the US. In: Lewis, R.R. (Ed.), Creation and Restoration of Coastal Plant Communities. CRC Press, Boca Raton, FL, pp. 1–43.

Woodhouse, W.W., Seneca Jr., E.D., Broome, S.W., 1977. Effect of Species on Dune Grass Growth 21:256–266.

Wootton, L.S., Halsey, S.D., Bevaart, K., McGough, A., Ondreicka, J., Patel, P., 2005. When invasive species have benefits as well as costs: managing *Carex kobomugi* (Asiatic sand sedge) in New Jersey's coastal dunes. Biol. Invasions 7, 1017–1027.

Wootton, L., Miller, J., Miller, C., Peek, M., Williams, A., Rowe, P., 2016. NJ Sea Grant Consortium Dune Manual. Pages 1–77.

Yagci, O., Celik, M.F., Kitsikoudis, V., Kirca, V.S.O., Hodoglu, C., Valyrakis, M., Duran, Z., Kaya, S., 2016. Scour patterns around isolated vegetation elements. Adv. Water Resour. 97, 251–265.

Zarnetske, P.L., Hacker, S.D., Seabloom, E.W., Ruggiero, P., Killian, J.R., Maddux, T.B., Cox, D., 2012. Biophysical feedback mediates effects of invasive grasses on coastal dune shape. Ecology 93, 1439–1450.

Zarnetske, P.L., Ruggiero, P., Seabloom, E.W., Hacker, S.D., 2015. Coastal foredune evolution: the relative influence of vegetation and sand supply in the US Pacific Northwest. J. R. Soc. Interface 12, 20150017.

Zhang, W., Schneider, R., Kolb, J., Teichmann, T., Dudzinska-Nowak, J., Harff, J., Hanebuth, T.J.J., 2015. Land–sea interaction and morphogenesis of coastal foredunes—a modeling case study from the southern Baltic Sea coast. Coast. Eng. 99, 148–166.