2021

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

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Geomorphology

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--Manuscript Draft--

Manuscript Number:	GEOMOR-10306R2
Article Type:	Research Paper
Keywords:	Biogeomorphic and Ecogeomorphic Systems; Ecogeomorphology; Ecosystem Engineers; Nebkha
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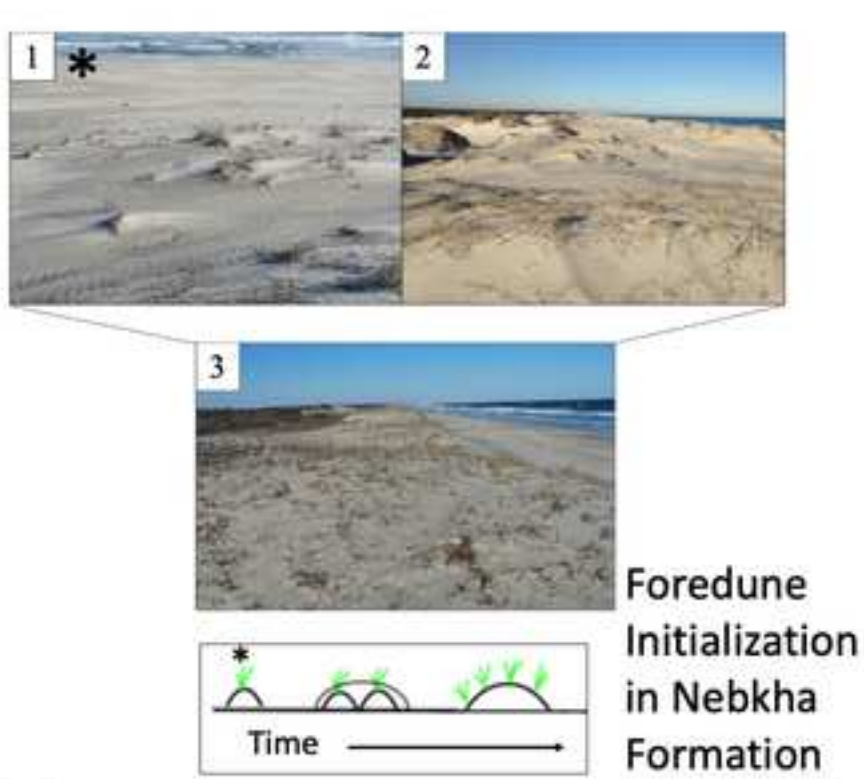
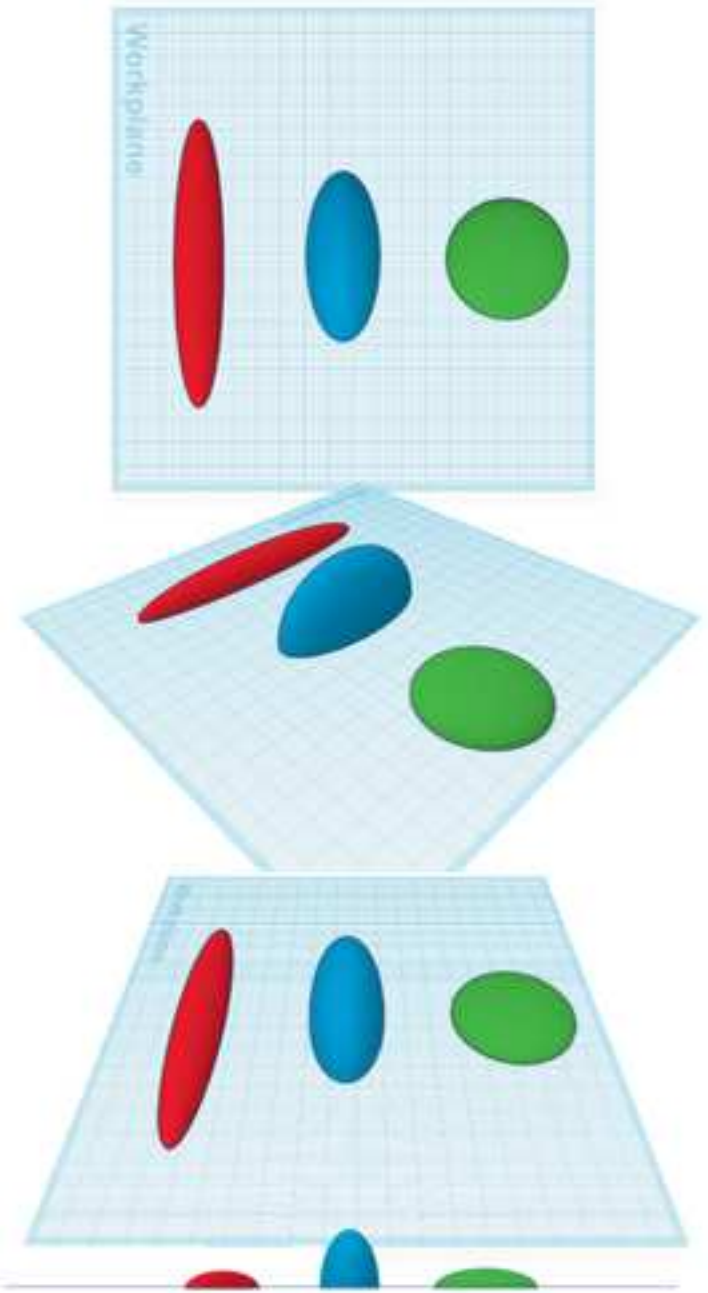
Abstract:	As the land-sea interface, foredunes buffer upland habitats with plants acting as ecosystem engineers shaping topography, and thereby, affecting storm response and recovery. However, many ecogeomorphic feedbacks in coastal foredune formation and recovery remain uncertain in this dynamic environment. We carried out a series of wind tunnel experiments testing how the morphology, density, and configuration of three foredune pioneer dune builder 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 1m x 1m 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-minutes 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 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.

graphical abstract





Running head: PLANT FOREDUNE INITIATION

Title: 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 builder 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 1m x 1m 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-minutes 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 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.

KEYWORDS: Biogeomorphic and Ecogeomorphic Systems, Ecogeomorphology, Ecosystem Engineers, Nebkha

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, physically altering environments both when living and dead (Tanner, 2001; Badano and Cavieres, 2006: Bos et al., 2007; Hall 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; Neild 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 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; Neild 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, the 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., 1992; Hesp, 2002; Fig. 1). Nebkha vary in size from millimeters to 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 and as such, 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 and not as a function of plant size, with lower-lying plants creating more circular nebkha. Furthermore, we tested the same hypotheses against quantitative field observations to evaluate the ecological relevance of our findings for sandy beaches. Our findings demonstrate that dune plant growth form, and configuration, influence nebkha size and shape. 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.

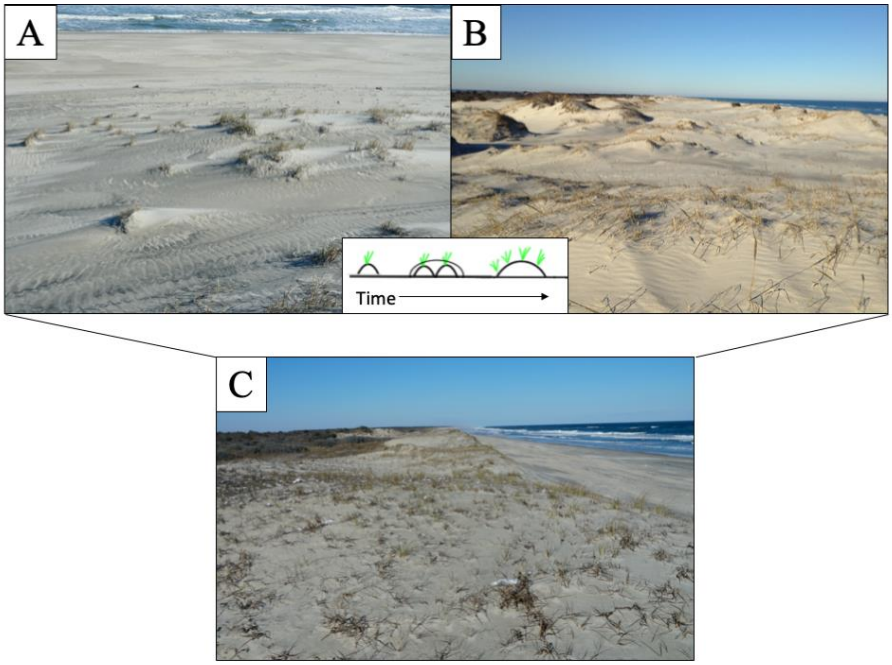


Fig. 1: Foredune initiation and development over time. Field photos depict (A) small nebkha formed around individual plants on the backshore, (B) coalescence into larger nebkha containing multiple plant communities concentrated at their peaks and (C) a continuous foredune developed

from the merging of larger nebkha. For scale, note the size of the plants in each image which are all dormant *A. breviligulata* as the images were taken in winter.

MATERIALS and METHODS

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, semi-rosette growth form, small petiole angles, and blades touching or nearly touching the surface (Min, 2006). All 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).

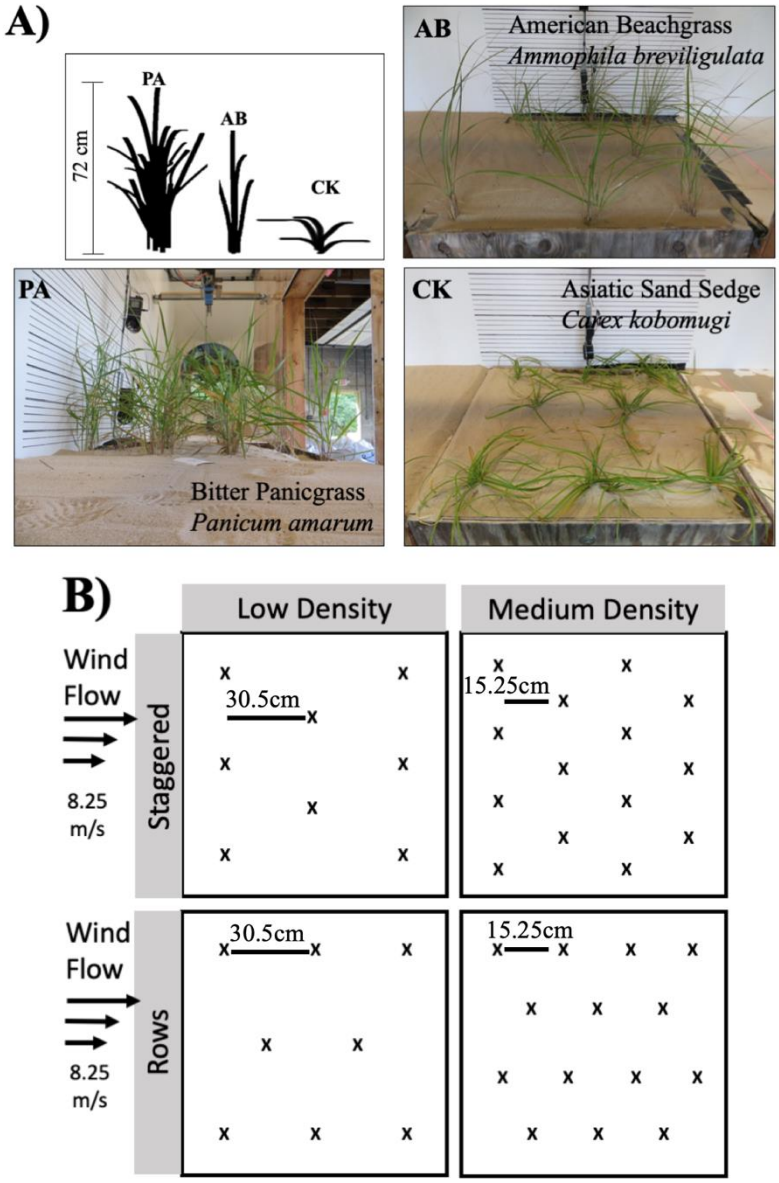


Fig. 2: Wind tunnel experimental setup. (A) We established two native Mid-Atlantic erect grasses (AB and PA) and one invasive low-lying sedge (CK) rooted in sand in 1m x 1m monoculture plant boxes. The top left schematic is to scale, showing relative differences in plant size and morphology across species. (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 x configuration treatments with four replicates in each per species.

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 velocity, 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 longitudinal center, 3.6 m downwind, a 1.0 m x 1.0 m x 0.3 m wooden planter box containing established and fully roots 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. Therefore, these data could not be evaluated in the same manner as the other densities. 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 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 90º, 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 treatmentsz≈˙.

To measure the influence of plant traits on topography, we quantified individual plant morphology traits per plant before subjecting them to wind tunnel experiments. From bed-level, we measured plant: (1) stem width between the two farthest stems perpendicular to the wind, (2) height, bent naturally and (3) height, 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 levelling box beds pre-experiment. Post-experiment, we cut the shoots of all plants at the surface using shears and measured biomass after drying for 72 hr at 70°C.

To minimize wind-tunnel edge effects on saltation (Bauer et al., 2004), we only analyzed nebkha buffered from the wall. 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 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 throughout the wind tunnel chamber available in Supplementary Material S4.

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. 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

Wind Tunnel Experiments and Topographic Quantification

We conducted experiments September 2017 (non-staggered) and 2018 (staggered) with green full grown plants. We levelled 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 plants and shielding behind plants (Järvelä, 2002).

Directly following the wind treatment, we quantified the 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, 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.

Field Validation

We quantified naturally-formed backshore nebkha at Island Beach State Park (IBSP), New Jersey, USA (Fig. 3). IBSP is a ≈17km micro-tidal 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 recent notable storm to impact IBSP was Hurricane Sandy (October 2012), although other smaller storms have affected IBSP more recently (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.

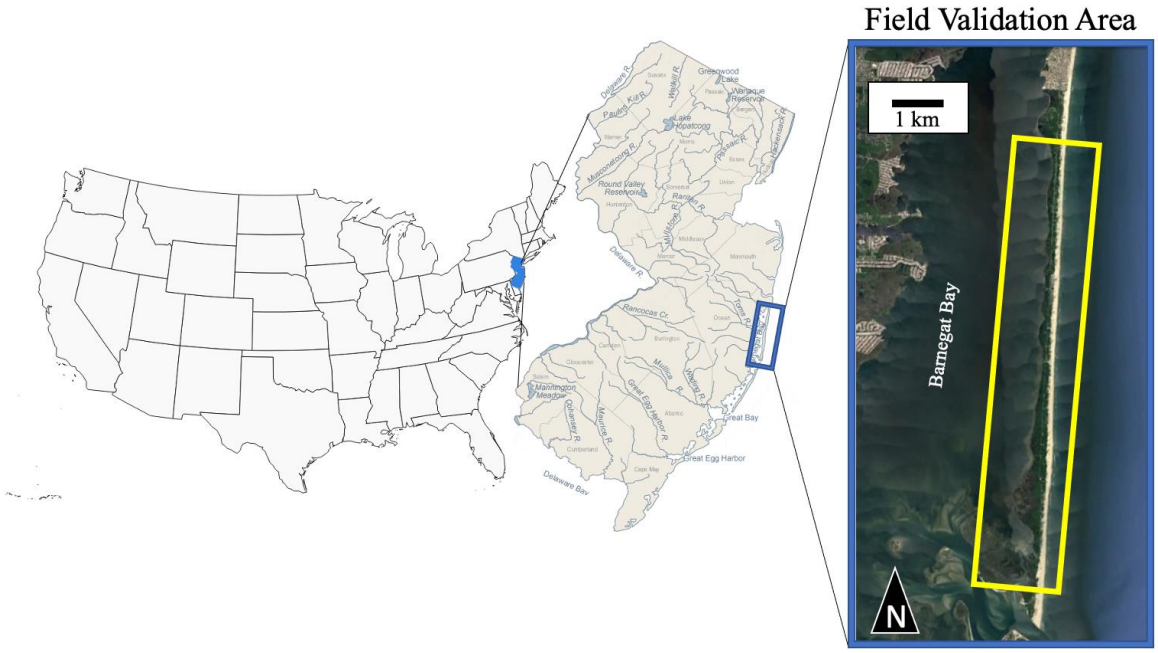


Fig. 3: Wind tunnel validation field site, Island Beach State Park, NJ, USA. Field validation was carried out in the backshore along the 17 km expanse of the park (39.7975° N, 74.0976° W). Map courtesy of Google Earth.

Fall and Spring 2018, we field truthed backshore individual *A. breviligulata* and *C. kobomugi* 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 nebkha and backshore surface intersection; and (7) using Agisoft tools to quantify nebkha morphological parameters (AgiSoft, 2018). See Supplementary Material S6 for more details and visual workflow of the 3D models. We produced 3D models of 18 nebkha, five each of *C. kobomugi* and *A. breviligulata*, 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).

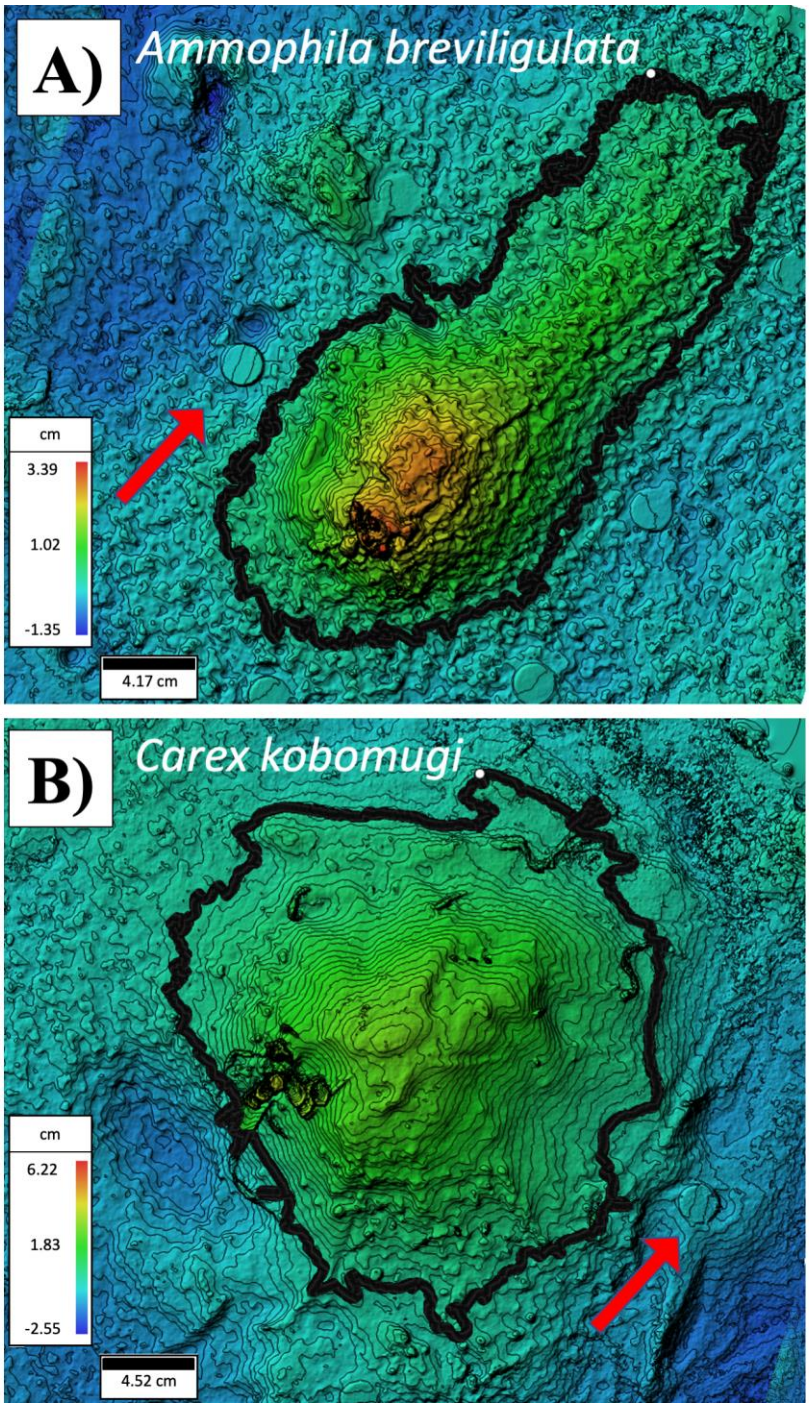


Fig. 4: An example of a nebkha 3D models created from field (A) *A. breviligulata* and (B) *C. kobomugi*. Both in the field nebkha and wind tunnel, *A. breviligulata* produced more oblong nebkha than *C. kobomugi*, which produced more equant nebkha. The contours in both models are 0.1 mm, but both models 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.

Statistical Analyses

We related plant and nebkha traits, for the field truth and wind tunnel data, to test our three hypotheses. We performed restricted 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 control 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 figure 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 plant the parameters, not including stem width, and one on nebkha parameters, not including shape (Table 2).

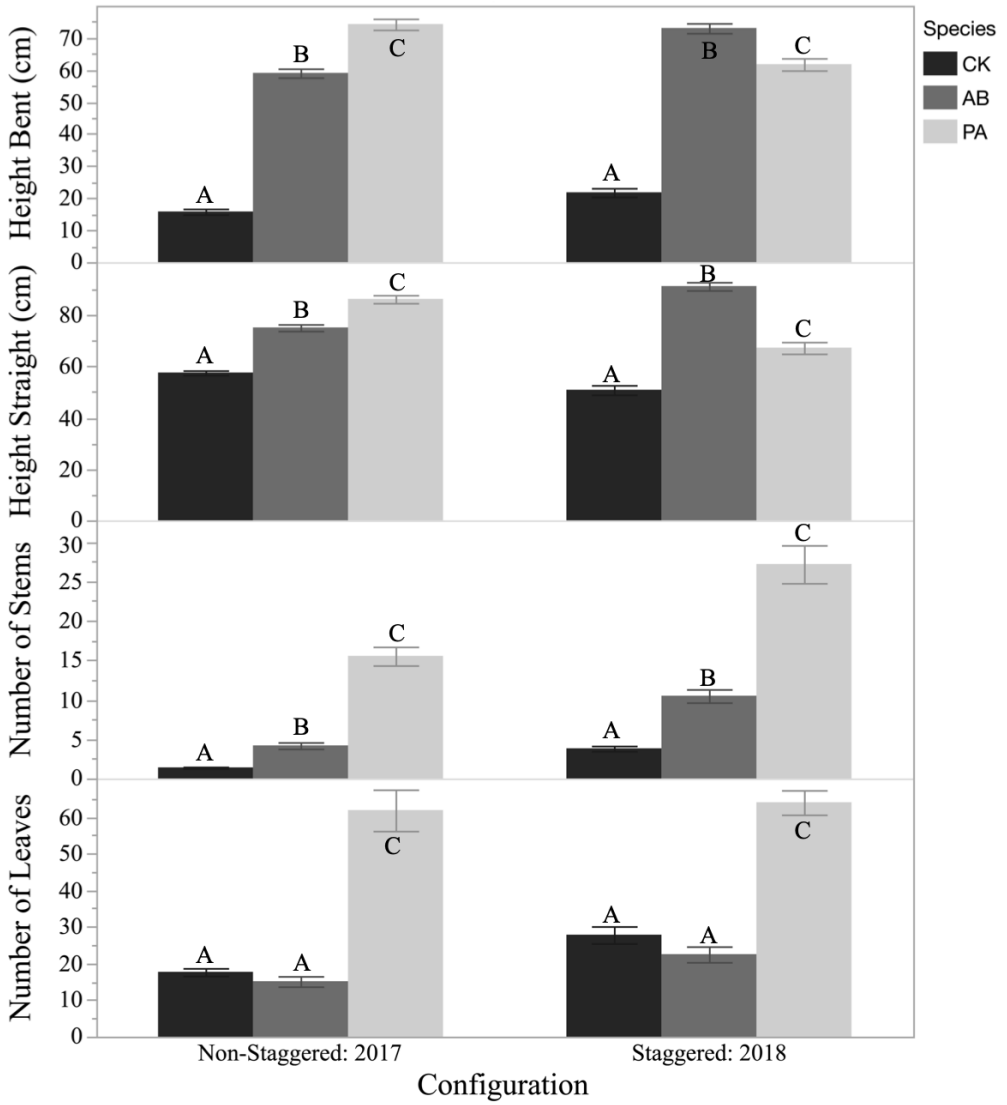


Fig. 5: Plant morphology traits across configurations reflecting differences in year. Plant traits did not vary between planting densities, but varied across species and configuration. *Carex kobomugi* (CK) was consistently the smallest plant in all metrics. Note that in 2017 *P. amarum* (PA) was taller 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.

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, equating to greater PC1 scores indicates a larger nebkha and plant with respect to all variables (Table 2). Nebkha PC2 represents nebkha relief, or height relative to area inversely related, 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 by 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 nebkha, we tested if nebkha PC2 variation was explained by plant size (plant PC1). Similarly, we examined nebkha height and PC2 in the grasses in an LMM as a function of species, year, and their interaction knowing *P. amarum* was tallest 2017, but *A. breviligulata* was tallest 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.

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 in 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%)	

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.*

RESULTS

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 *Carex* was smallest and *Panicum* was largest (Fig. 3). Both years, *Ammophila* had an equal number of leaves as *Carex*, and *Panicum* had more stems than both ($F_{2,44} = 48.9$, $P < 0.0001$). Both years, *Carex* had the least number of stems and *Panicum* 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 X year interaction indicating that *Carex* was shortest both years, but in 2017 *Ammophila* was taller than *Panicum (*$F_{2,45} = 44.61$, $P < 0.0001$) whereas in 2018 *Panicum* was taller than *Ammophila (*$F_{2,42}$

392 = 205.51, $P < 0.0001$). Stem widths in *Panicum* and *Ammophila* were statistically equal across
393 years with *Panicum* stems wider than *Ammophila* stems ($F_{1,28} = 22.7$, $P < 0.0001$).
394
395 *Wind Tunnel Nebkha Formation*
396 Nebkha only formed in treatments containing plants. In the control boxes without plants,
397 transverse aeolian ripples of uniform size and shape formed. Elevation change per nebkha varied
398 by species ($F_{2,45} = 5.83$, $P = 0.005$), and was greater for *P. amarum* (7.21 ± 1.04 mm) than for *A.*
399 *breviligulata* (2.38 ± 1.0 mm). Change in elevation was also influenced by density ($F_{1,45} = 6.70$,
400 $P = 0.01$) and configuration ($F_{1,45} = 9.59$, $P < 0.005$). Regardless of species, nebkha in the non-
401 staggered medium density treatment had less elevation change than other treatments. Plants with
402 upwind erosion had less elevation gain (5.11 ± 0.58 mm) than those accreting upwind (7.43 ±
403 0.90 mm; $F_{1,15} = 5.59$, $P = 0.02$). *Carex kobomugi* nebkha were formed by both upwind and
404 downwind deposition whereas the two erect grasses predominantly had upwind scouring and
405 downwind accretion (species comparison DF = 2, $\chi^2 = 23.76$, $P < 0.001$; Supplementary Material
406 S5). Regardless of configuration or density, the peaks of *A. breviligulata* (87 %) and *P. amarum*
407 (66 %) nebkha were largely leeward versus split between upwind and downwind for *C.*
408 *kobomugi* (51 %; Supplementary Material S5). Nebkha ranged in upwind and downwind slope 1-
409 16° ($\bar{x} = 7.65 \pm 0.22°$), not reaching the assumed angle of repose ~30°.
410
411 *Wind Tunnel Nebkha Differences Across Treatments*
412 Planting density did not statistically impact nebkha traits, but configuration did.
413 Staggered treatments consistently produced larger nebkha in all size parameters, area ($F_{1,32} =$
414 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 ~2x larger area than the non-staggered configuration. Planting row (i.e., front, back, middle) did not affect nebkha PC1 or PC2. Basal/frontal area varied between species and densities, but was not quantified (Supplementary S3).

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.

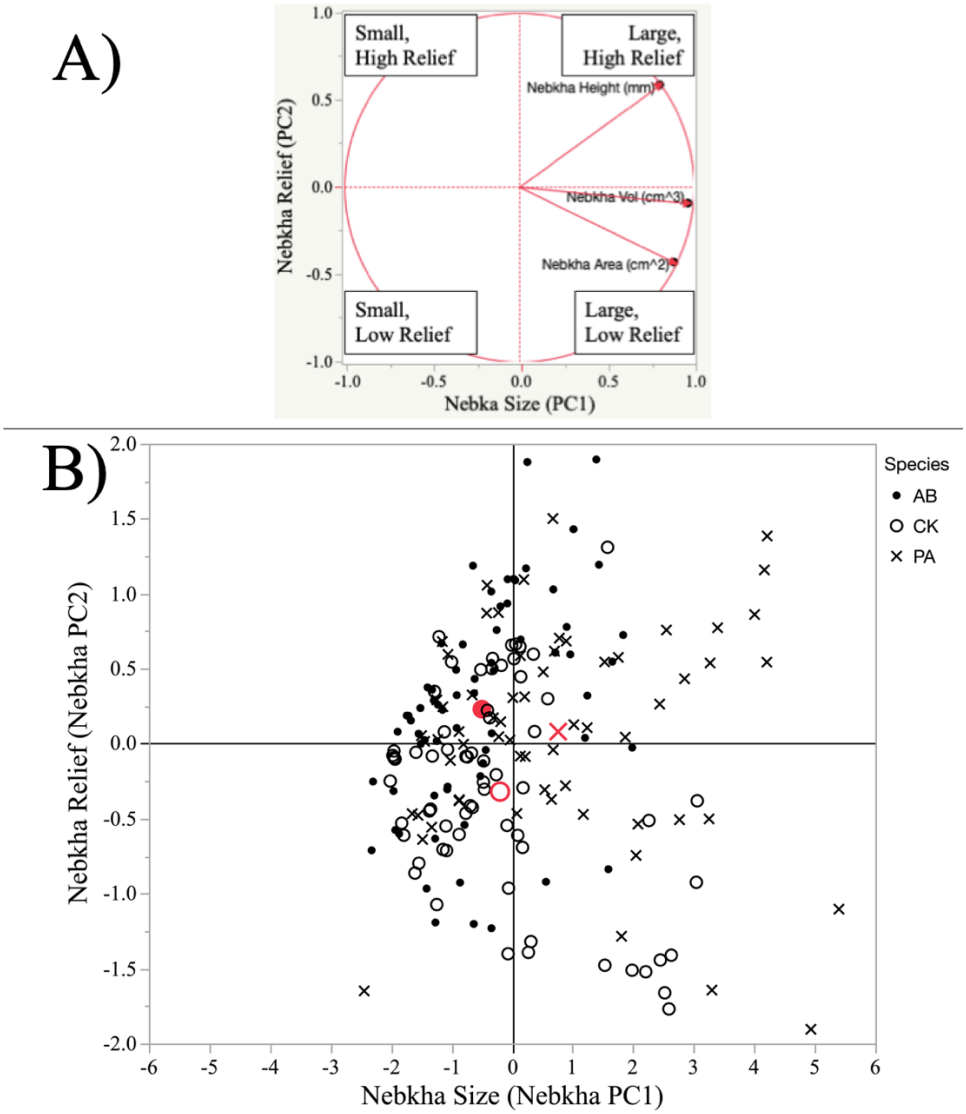
	Species	Staggered	Non-Staggered	Species Effect	Configuration Effect
Nebkha Volume	*A. breviligulata*	19.15 ± 2.16 cm^3	10.77 ± 2.41 cm^3	(CK = AB) < PA $F_{1,38}$ = 13.75, P < 0.0001	$F_{1,38}$ = 18.61, P < 0.0001
	P. amarum	41.15 ± 3.88 cm^3	22.79 ± 4.44 cm^3		
	C. kobomugi	22.83 ± 3.19 cm^3	13.32 ± 3.43 cm^3		
Nebkha Height	*A. breviligulata*	7.26 ± 0.44 mm	6.50 ± 0.44 mm	(CK = AB) < 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	(PA = CK) > 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		

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 *Ammophila 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.*

433 *breviligulata* nebkha being equivalent in height ($F_{1,37} = 8.61$, $P < 0.001$; Fig. 7). Amount of

434 biomass upwind of a plant did not impact nebkha PC1 (ANCOVA $P > 0.05$).



435
436 **Fig. 6:** Variation in nebkha size and shape across plant species explained by PCA. (A)
437 Contribution of variables to the two principal components describing the variability in nebkha
438 traits: volume, area, and height. PC1, loads fairly equally across all variables such that nebkha
439 with large PC1 are of a larger size. PC2 loads heavily on nebkha height (negatively) and surface
440 area (positively) as inverses, representing relative relief such that larger PC2 indicates greater
441 relief than smaller PC2. (B) The ordination plot highlights species-specific differences in the size
442 and relief of nebkha across species. Red points represent the mean for each species.
443

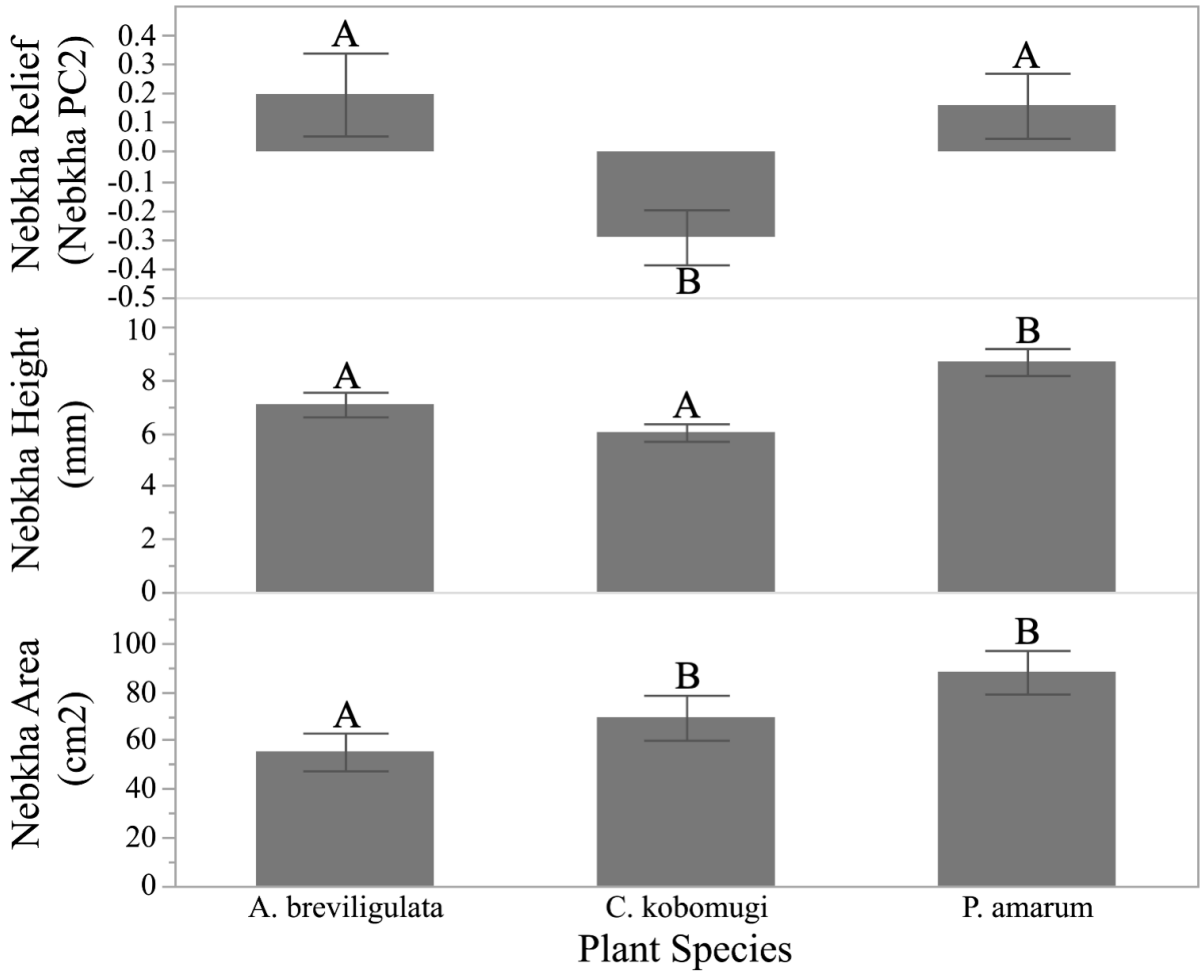
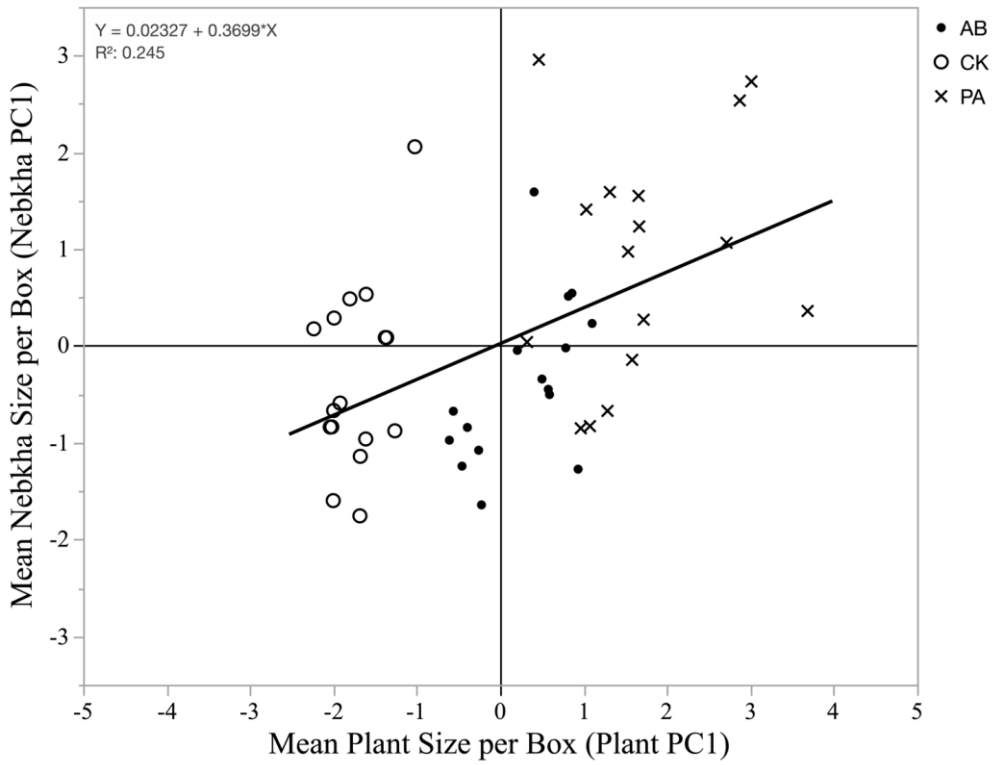


Fig. 7: Nebkha relief across plant species. Relief varied as a function of nebkha height and area across species with *C. kobomugi* creating nebkha representative of both erect grasses. Nebkha PC2 represents, as inverses, nebkha area (+) relative to height (-). *Carex kobomugi* nebkha had lower PC2 than 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 to 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.

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

459 volume ($F_{3,44}$ = 9.48, P < 0.0001). The slope of this relationship did not vary between the species
460 although mean log nebkha volume did vary by species ($F_{2,44}$ = 5.89, *P* < 0.01). *Carex kobomugi*
461 and *A. breviligulata* produced nebkha of equivalent volume ($F_{1,38}$ = 13.75, *P* < 0.0001), both
462 smaller than *P. amarum* (Wilcoxon Rank Sum; χ^2 = 12.69, DF = 2, *P* < 0.01; Fig. 9).



463
464 **Fig. 8:** Ordination plot of plant PC1 and nebkha PC1. Larger values for both axes indicate larger
465 plants and nebkha, respectively, such that there is a positive linear relationship between plant
466 size and nebkha size.
467

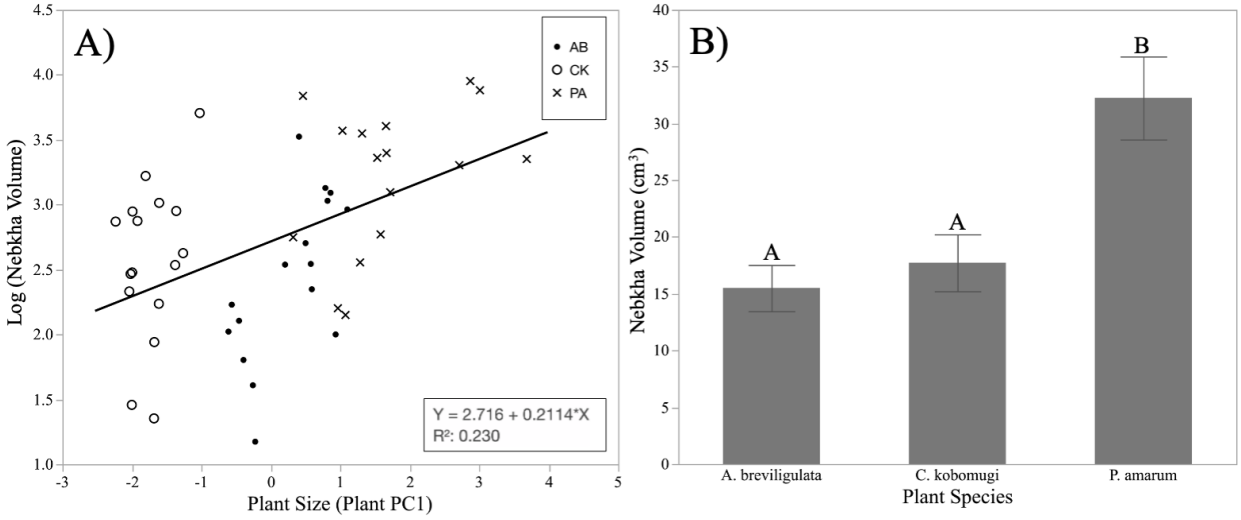


Fig. 9: Nebkha volume and plant species and identity. Nebkha volume increased with increasing plant size with the largest plant species, *P. amarum* (PA) producing the largest nebkha. (A) All plants had increasing log (nebkha volume) with the same slope across species with (B) the largest plant, *P. amarum* (PA) 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.

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* < *A. breviligulata* (Fig. 5). However, among 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, height relative to surface area, did not vary between the two erect grasses (P = 0.53), and nebkha created by *P, amarum* were taller both years despite which species was taller ($F_{1,25}$ =5.78, P = 0.02; Fig. 10). Nebkha height is better explained by plant width than height as LMMs revealed that a wider stem base produced taller nebkha both in the field for *A. breviligulata* ($F_{1,1}$ = 5.44, P = 0.04) and 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.

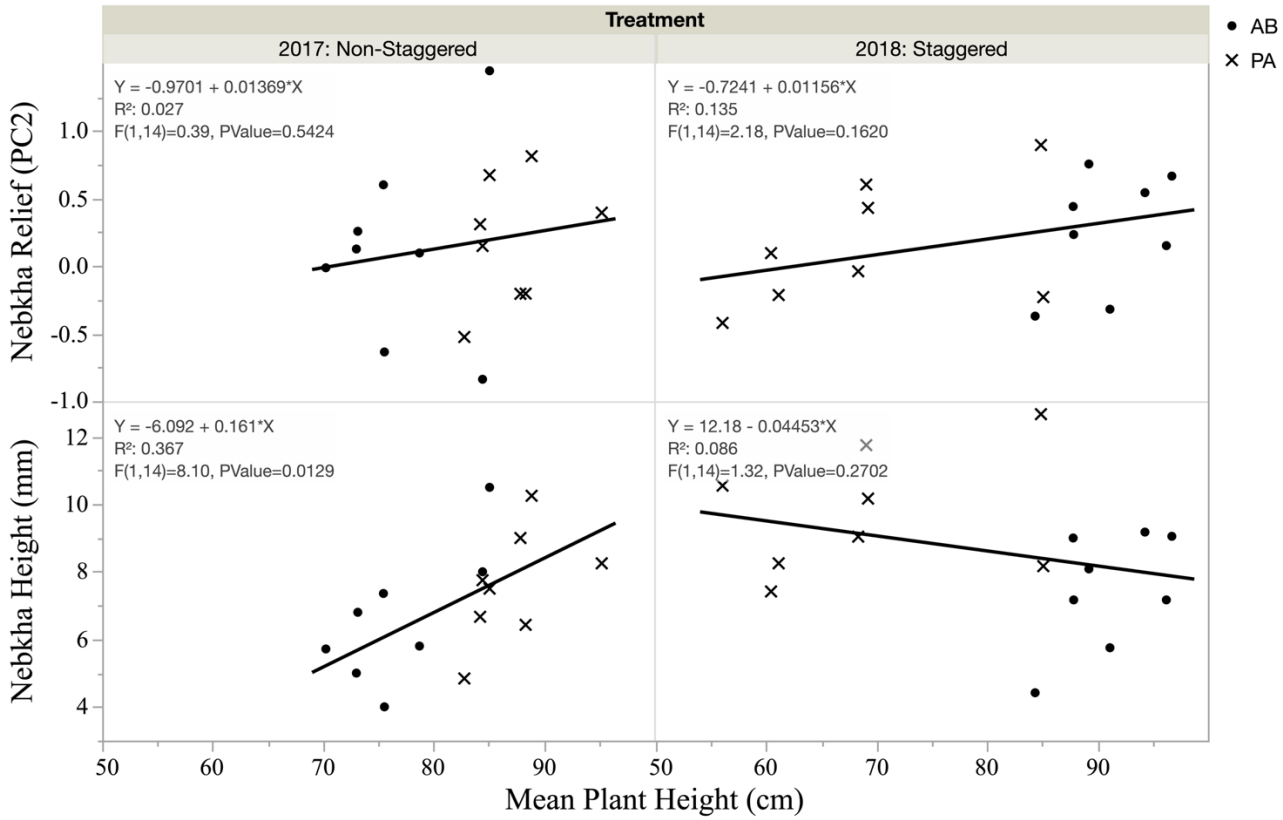


Fig. 10: Nebkha height relative to plant height. A taller plant does not necessarily build a taller nebkha as seen in the erect grasses *P. amarum* (PA) and *A. breviligulata* (AB). Nebkha height and relative relief (PC2: nebkha area (+) relative to height (-) as inverses) were both unrelated to plant 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 replicate to control for box as a potential confounding factor.

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. The two erect grasses, which did not differ in nebkha shape, produced oblong planar nebkha, with flow-parallel elongation relative to wind direction (Fig. 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.

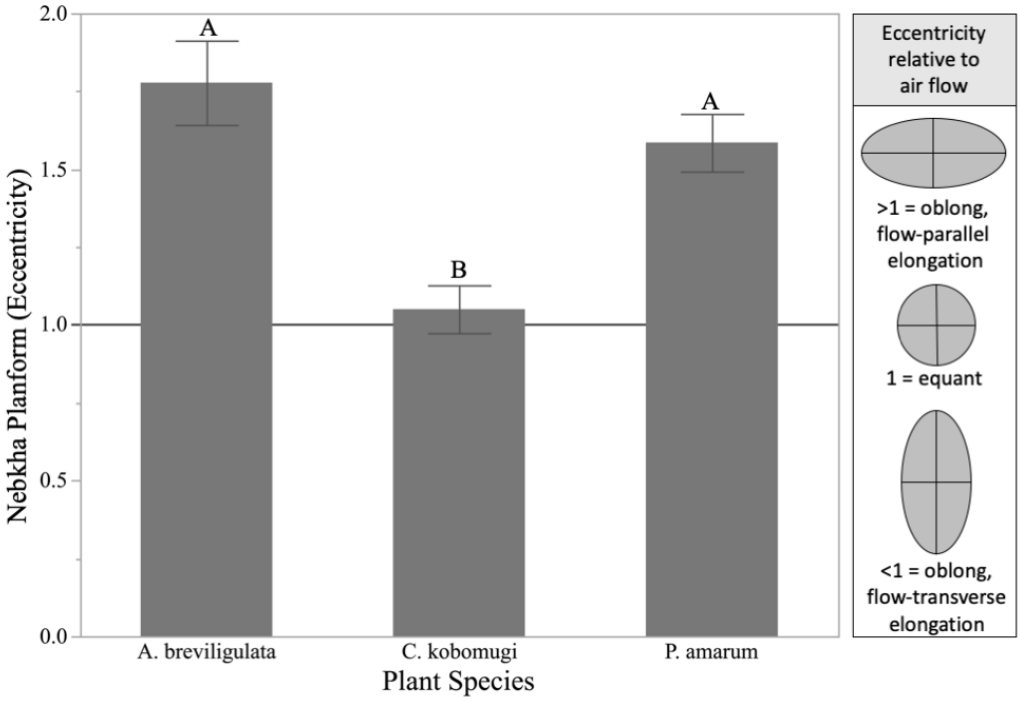


Fig. 11: Wind tunnel nebkha shape across plant species. Eccentricity is the ratio of the length and width of nebkha such that values > 1 are longer than wider and values of 1 are equally long and wide along the prevailing wind direction. *Carex kobomugi* consistently produced more equant nebkha whereas 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.

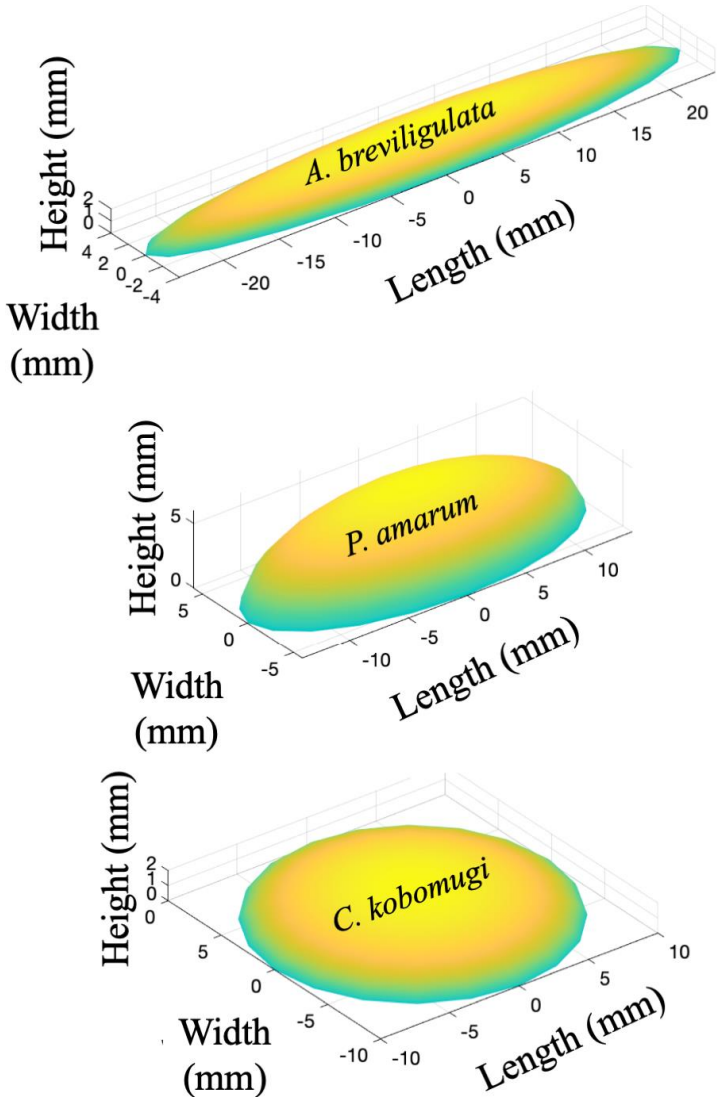


Fig. 12: To scale idealized representation of wind tunnel nebkha created by the three different foredune plant species. Nebkha differences were consistent across planting densities. The dimensions shown are based on the overall means for each plant species across density and configuration treatments.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

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 held the same observed relationships between plant and nebkha morphology as in the lab setting. Field nebkha displayed greater area, height, and volume (Table 4), despite wind tunnel *A. breviligulata* having more biomass. All *A. breviligulata* nebkha were oblong (longer tails relative to width) but the length to width ratio was greater in the field

524 nebkha (Table 4). Plant and nebkha PC1 were positively linearly related in that larger plants
525 created larger nebkha ($F_{1,11} = 6.31$, $R^2 = 0.36$, $P < 0.03$). Similarly, nebkha volume increased
526 with greater plant size (PC1; $F_{1,11} = 5.11$, $R^2 = 0.32$, $P < 0.05$). Plant height was unrelated to
527 nebkha height while plant size (PC1) was unrelated to nebkha relief (i.e., height versus area).

528 **Table 4.** The *A. breviligulata* plants that formed the field nebkha were smaller than those in the
529 wind tunnel, but they produced larger nebkha than in the wind tunnel. Nebkha shape was
530 elongated in the wind tunnel and field, but field nebkha had greater elongation relative to their
531 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, $P < 0.001$

532

533 Field *C. kobomugi* nebkha were larger than wind tunnel nebkha although planform shape
534 was equal. Specifically, field nebkha had greater area (Z = 2.76, $P < 0.01$), volume (Z = 2.27, P
535 = 0.02), and trended towards being taller (Z = 1.85, $P = 0.06$), despite *C. kobomugi* plants in the
536 wind tunnel having greater biomass (Z = 1.79, $P = 0.05$). Although field nebkha were larger than
537 those in the wind tunnel, nebkha planform shape was equivalent ($\bar{x} = 1.18 \pm 0.25$, $P = 0.10$).

538 Consistent with wind tunnel findings, field nebkha did not vary between paired
539 individuals of *A. breviligulata* and *C. kobomugi* in area, height, or volume, but varied in
540 planform shape. Field *A. breviligulata* produced elongated ellipses with longer tails parallel to
541 the wind compared to *C. kobomugi*, which produced more uniform, round nebkha ($\bar{x}_{AB} = 2.46 \pm$
542 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
543 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 ± 0.35, $\bar{x}_{CK}$ = 1.25 ± 0.19, Z = -2.14, *P* = 0.03).

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.

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 minutes), 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 minute run time (Hesp et al., 2019). Our results suggest that the underlying feedbacks or principals 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 likely stems from differences in wind velocity and stem width, 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.

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, 1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006; Hacker et al., 2011, 2019) with some exceptions (Charbonneau et a., 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

590 Smyth, 2017; Hacker et al., 2019), we have reduced the scale to foredune initiation in nebkha
591 genesis (Walker et al., 2017), and elucidated some of the drivers of the underlying feedbacks that
592 enable larger plants to produce greater deposition.

593 At foredune initiation, the inherent morphological traits of the species influenced nebkha
594 shape. Low-lying *C. kobomugi* produced more equant nebkha than erect grasses, supporting the
595 notion that erect grasses, such as *A. breviligulata* are associated with taller and steeper foredunes
596 (Davies, 1980; Wootton et al., 2005; Hacker et al., 2019). This relationship may carry though the
597 life of the evolving foredune as suggested by comparing the lower platform-like established
598 dunes of *Spinifex sericeus* versus *A. breviligulata* (Davies, 1980). Both are erect grasses, but
599 their inflorescences are very different with that of *S. sericeus* being larger, shorter, and splaying
600 horizontally ultimately driving differences in dune morphology (Davies, 1980). The results are
601 consistent with nebkha length increasing with greater porosity, as observed with mesh objects
602 (Gillies et al., 2017) as well as emergent and submerged vegetation (Yagci et al., 2016). Taller
603 plants produce streamlined airflow and deposition around objects as shown by manipulating low-
604 stem leaves on artificial erect plants (Hesp et al., 2019). In contrast, the low-lying stature of *C.*
605 *kobomugi* has reduced porosity which should create increased turbulent kinetic energy and blade
606 motion below the canopy, pushing topography into non-streamlined states (Raupach et al., 1996;
607 Luhar and Nepf, 2013; Boothroyd et al., 2016). Our wind tunnel results match studies of shrubs
608 having increased deposition width and decrease deposition length with increasing horizontal
609 complexity in low-lying leaves (Leenders et al., 2011).

610 Nebkha height was unrelated to plant height or size. Among the erect grasses, *Panicum*
611 built larger nebkha regardless of which grass was taller, while *Carex* and *Ammophila* nebkha
612 were of equivalent height regardless of *Ammophila* being taller (Fig. 5 and 7). At the foredune

613 level, crest height differences are attributed to vegetation height where lower profile plants have
614 been noted (Davies, 1980; Hesp, 1989; Wootton et al., 2005; Hilton et al., 2006) or quantified on
615 shorter established foredunes (Hacker et al., 2011 and 2019). However, greater plant height also
616 tends to coincide with greater biomass and surface cover, both of which create increased trapping
617 efficiency (de M Luna et al., 2011; Zarnetske et al., 2012) as exhibited here in *P. amarum*, but
618 not *A. breviligulata*. This is interesting given that *P. amarum* and *A. breviligulata* have been
619 found on dunes of similar size and shape in nature (Woodhouse et al., 1977; Hacker et al., 2019),
620 but is also important to note that the species currently on a dune may not have necessarily built it
621 (Charbonneau et al., 2017). Sediment size across locations may confound topographic variability
622 created by plant morphology in nature as it can impact nebkha height, but this can be controlled
623 for in a laboratory setting (Hesp, 1981; Hesp and Smyth, 2017). Greater stem width, which
624 equates to greater basal/frontal area and has varies between species (Mullins et al., 2019),
625 appears to be the paramount reason why *P. amarum* and *A. breviligulata* differed in nebkha
626 height. This suggests that in foredune initiation, species identity may play a greater role than at
627 higher densities due to reduced neighbor interaction and basal/frontal area (Pietri et al., 2009).
628 Sediment volume distribution, windward (sedge) versus leeward (erect grasses) of a plant
629 is attributable to plant morphology and height. This finding supports wider stem bases creating
630 longer wake zones (Hesp, 1989), and overlapping wake zones leeward of erect plants having the
631 potential to cause localized scour (Burri et al., 2011; Leenders et al., 2011). Instances of *C.*
632 *kobomugi* windward scouring are also likely due leaf splay at the sediment surface increasing
633 bed turbulence (Burri et al., 2011; Leenders et al., 2011; Luhar and Nepf, 2013). However, the
634 leaf ends of *C. kobomugi* often became buried, no longer moving in the airstream, thus limiting
635 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* relative to the taller erect grasses.

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 noted no 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 basal/frontal area (Hesp, 1983 and 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 and 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 and the timescale of years (Keijsers et al., 2015). However, our unanalyzed high density treatments forming melded nebkha among groups of plants suggests 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.

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 has recently been applied to simulate laboratory storm 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 hold little bearing on reality (Silva et al., 2016; Feagin et al., 2019). Future endeavors on 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 similarly 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 field-validated laboratory experiments 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.

CONCLUSIONS

This research contributes to our fundamental understanding of the role of intraspecific variation in vegetation morphology, density, and configuration to impact geomorphological processes in aeolian beach-dune systems. We demonstrated that larger plants built 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 basal/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 varied 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 suggested 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. 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 plants acting as ecosystem engineers in foredune habitats such that they should not be excluded as factors in modeling efforts. These reustls 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.

AUTHOR CONTRIBUTIONS

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.

ACKNOWLEDGEMENTS

This research was conducted with Government support under contract FA9550-11-C-0028 and awarded by the Department of Defense, Air Force Office of Scientific Research, National Defense Science and Engineering Graduate (NDSEG) Fellowship, 32 CFR 168a. The wind tunnel was funded and supported by the US Coastal Research Program (USCRP) with USACE ERDC and USGS (Contract #W912HZ18P0090) organized by the American Shore and Beach Preservation Society and USACE ERDC BAA CHL-15 (Contract #W912HZ-16-P-0088). The following entities within New Jersey donated resources without which the wind tunnel would not exist: NJDEP, Island Beach State Park, NJ FWS, NJ Ocean County School (OCVTS) Board, and Marine Academy of Technology and Environmental Studies (MATES). We Ed Crawford and Anthony Reo, as well as the following local and national sponsors that donated invaluable resources and expertise: Air Systems Engineering, Coastal Transplants, HandyMan Pros, Motion Industries, Moxley Electronics, One Ton Bag LLC, Pineland's Nursery, EMCO Industrial Plastics, and SICK Sensor Intelligence. Peter Petraitis and Arthur Dunham are thanked for statistical expertise.

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