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The onset of coastal foredune formation at variable levels of ecological complexity

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Gaps in our understanding of the interplay between biotic and abiotic forces shaping coastal dunes inhibit our ability to fully understand their evolution and predict topographic changes. The theoretical evolution of a dune system begins with nebkha formation. This formation begins around individual dune-building plants, which grow over time around groups of plants. Individual nebkha mounds can meld into one another, growing in size and complexity based on the dune-building vegetation population. To better understand ecogeomorphological feedbacks driving these relationships, we tested how plant density impacts nebkha formation by *Ammophila breviligulata* in both a laboratory and a field setting. Laboratory tests consisted of using a wind tunnel to control abiotic forces, focusing on the effects of varying plant density in nebkha formation. We tested three low densities commonly supporting backshore nebkha: an individual (one plant) and small groups (five and nine plants). In the field, we used both remote sensing and field techniques to quantify the relationship between stem density and the nebkha shape and size of backshore *A. breviligulata* nebkha. In the wind tunnel, stem density was not as strong a predictor of nebkha size or shape as number of leaves and aboveground biomass, both of which increased with growing stem and plant densities. Stem density was a strong predictor of nebkha size and shape, with increasing variability at increasing densities in both the laboratory and field. *In situ* measurements of stem density are performed inconsistently among field experiments due to the effort required. Therefore, strong allometric scaling among *A. breviligulata* morphology metrics can help overcome limitations around what can be collected in the field or in a modeled environment containing limited plant metrics. *In situ*, vegetation stabilization frequently allowed the nebkha to grow steeper than would be expected based on grain size and the angle of repose. These differences in field and laboratory nebkha highlight the importance of grounding laboratory work in field collections for the interpretation of their results in nature. Understanding the underlying ecogeomorphic feedbacks involved in nebkha formation is critical to scaling up modeling efforts to forecast coastal foredune evolution, recovery, and storm response in the face of climate change.

KEYWORDS

aeolian transport, *Ammophila breviligulata* (American beachgrass), backshore, ecogeomorphology, nebkha, remote sensing, topographic evolution, wind tunnel

1 Introduction

Sandy beaches and coastal dunes are natural and nature-based features at the interface of land and sea, making them highly vulnerable to the impacts of sea-level rise and climate change. In natural, managed, or built settings, the habitats buffer upland areas and provide invaluable ecosystem services, including flood and erosion reduction (Maun, 2009; Jackson and Nordstrom, 2012). The foredune—defined as the shore-parallel vegetated dune ridge in the backshore formed by aeolian sand deposition within vegetation—serves as the first line of defense, protecting upland areas during storms (Hesp, 2002). Around the world, many natural dunes have been eroded and or replaced by artificially built dunes, which are more restricted in potential size and shape and therefore respond differently to storm events (Nordstrom et al., 2000). The upland areas buffered by these dunes and dune-like features often include both coastal habitats and infrastructure; for the latter, population growth and economic expansion continue despite the inherent and increasing risk of coastal hazards associated with climate change (IPCC, 2022). Modeling these systems under different stressors can help predict their responses to future events, enabling adaptive management strategies (Zinnert et al., 2017).

Within a system, dunes exhibit high spatiotemporal topographic variability and correspondingly variable storm responses, largely driven by the prestorm state relative to storm surge (Houser et al., 2008; Houser and Mathew, 2011). Prestorm state is influenced by both physical and biological processes; while physical processes in this system have been extensively studied for decades, biological processes have received substantially less research attention (Jackson and Nordstrom, 2020). Dunes are recognized as ecogeomorphic habitats shaped by a complex interplay between biotic and abiotic forces, though this appreciation is relatively recent (Corenblit et al., 2015; Zinnert et al., 2017; Stallins et al., 2020). Biotic and abiotic forces are linked: wind transports sand, while plants modify wind flow and trap sand, thereby building topographic features. These features, in turn, influence wind flow and sedimentation patterns. Dune-building plants respond positively to burial, increasing in vigor and thereby enhancing entrapment, sediment retention, and topographic change, creating a positive feedback loop for the vegetation and dune development (Hesp, 1989; Stallins and Parker, 2003; Maun, 2009; Walker et al., 2017). There is positive feedback between vegetation, topography, and sand transport, but these relationships are nonlinear, can increase in complexity over time, and remain generally poorly understood (Charbonneau et al., 2021; Costas et al., 2024). This biotic–abiotic interplay ultimately impacts both topographic variability and storm response.

Dune and beach modeling efforts reflect the current state of our understanding of these systems and are therefore limited in their inclusion of biological and ecogeomorphic relationships (Piercy et al., 2023). During storms, foredune change is highly dependent on beach characteristics, dune height, dune width, and vegetation supporting the dunes, the latter of which we do not fully understand mechanistically (Houser et al., 2008; Houser and Mathew, 2011; Charbonneau et al., 2017). Both bottom-up and top-down controls can shape dune topographic variability (Stallins et al., 2020). Dune-building species maintain inter- and intraspecific variability in morphology and density, and research on the impacts of these factors on dune topography and stability has grown in the last decade (e.g., Zarnetske et al., 2012; Hacker et al., 2019; Charbonneau et al., 2021; Walker and Zinnert, 2022). Vegetation morphology and density are impacted by both biological and physical factors, with potentially compounding effects on dune morphology (Maun, 2009; Zarnetske et al., 2012; Hacker et al., 2019; Charbonneau et al., 2021; Hesp et al., 2021b); studies on these relationships have been predominantly descriptive (McGuirk et al., 2022). Moreover, existing models of beach-dune systems, including plant morphology metrics, are limited or vary in the parameters included (Piercy et al., 2023). A universally included metric or the use of allometric scaling could both help overcome the issue, but it requires more research for implementation. As our appreciation of ecogeomorphic relationships has increased, so has the number of studies looking to quantitatively understand them (McGuirk et al., 2022), in turn improving the potential for and practice of including this information in modeling and management efforts (Piercy et al., 2023).

Considering that foredunes are complex, nonlinear, self-organizing habitats, studying their inception—when fewer subsequent formative events have occurred—may reduce complexity and allow clearer insight into ecogeomorphic relationships. Nebkha formation is a precursor to incipient (or embryo) foredune development (Hesp, 2002; Figure 1). Nebkha are aeolian-formed accumulations of sand around vegetation that represent the onset of dune formation (Cooke et al., 1993; Hesp, 2002; Figure 1). Over time, they vary in size from millimeters to meters, vertically or horizontally, and discrete nebkha can merge over time as space becomes limited due to plant tillering (i.e., new stems emerging from the same plant), nebkha growth, and the emergence of new nebkha, all of which are impacted by sedimentation and rainfall (Hesp, 1989; Cooke et al., 1993; Hesp et al., 2021a; Figure 1). Over time, merging nebkha can form a continuous, shore-parallel incipient foredune or phalanx defense against storm surge (Hesp, 2002; Hesp et al., 2021a). Nebkha and their plants also shield areas downwind, resulting in shadow dunes or tails in their lee (Hesp and Smyth, 2017). Shadow dune morphology and nebkha morphology are linked, and in this publication, the nebkha and attached shadow dune complex are grouped and referred to as one entity, the nebkha (Hesp and Smyth, 2017; Charbonneau et al., 2021). Most Nebkha research was focused on established nebkha rather than their inception (e.g., Gillies et al., 2014; Hesp and Smyth, 2017), but research interest in nebkha has increased recently (Goudie, 2022).

Backshore nebkha formed by plant individuals and groups can be thought of as the most basic unit or stage of foredune development; we believe that underlying feedbacks governing foredune evolution at a greater scale may be illuminated from examining their initiation. With this in mind, we aimed to examine nebkha genesis around plant individuals and groups in a wind tunnel setting, controlling physical factors and varying plant density. The laboratory work is complemented by fieldwork examining the size and shape of established backshore nebkha relative to the plant population or community supporting them. This work is a continuation of the work of Charbonneau et al. (2021), which focused on nebkha formation around individual plants in uniform stands of different species, morphologies, and planting configurations that are common in dune grass planting efforts. We expect that increasing biological complexity at greater plant density will result in greater variability in nebkha size and shape in both field and laboratory settings. Data of this nature, at

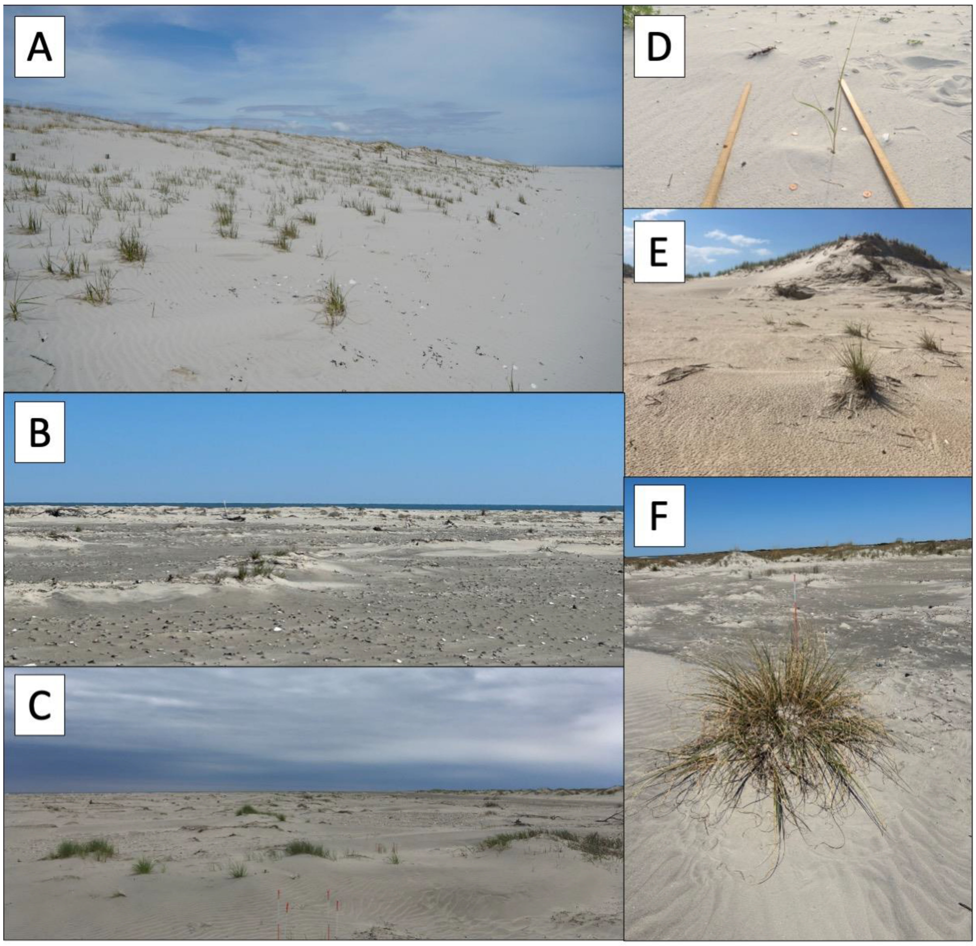

FIGURE 1
Dunes form in sandy beach backshores, and their inception begins with sediment accumulation around plant individuals or single-species populations as nebkha **(A–F)**. Backshore nebkha can vary in size and shape supported by monocultures of dune-builder grasses **(A–F)**. Individual nebkha **(D–F)** can be supported by an individual plant with only one stem (**D**; pennies for scale) or with multiple stems **(E)** and nebkha are also supported by groups of individuals **(F)**.

the onset and early stages of nebkha formation, can help us better understand the early stages of dune development, such as by identifying which vegetation morphological features (i.e., number of stems and leaves, plant height, shape, etc.) most impact resulting nebkha shape and size, which at a larger dune scale are factors that impact storm response. Quantifying the relationship between vegetation morphology features and resulting nebkha dimensions enables use within coastal protection project planning in the design, modeling, and decision phases. These relationships are particularly valuable for natural and nature-based solution projects, where hard and soft structures are combined for additional protection and ecosystem benefits.

2 Methods

This research combines both laboratory and fieldwork to better understand the initial stages of dune formation. Laboratory experiments were conducted using a wind tunnel, while complementary fieldwork was intended to validate/test the laboratory findings in natural conditions (Dunham and Beaupre, 1988). In the wind tunnel, we controlled wind speed, wind duration, sediment supply, and grain size, focusing on the effects of varying plant density on nebkha formation. In the field, we quantified preexisting backshore nebkha and related their morphology to the plants supporting them, accounting for the greater variability in physical and biological conditions present in nature compared to the laboratory.

2.1 Study species

American beachgrass (*Ammophila breviligulata*, Fern.) is a prevalent native species found along the sandy beaches of the US mid-Atlantic and Great Lakes and a widespread introduced invasive species along the US Pacific Coast (Hacker et al., 2011; Zarnetske et al., 2012). This xeric, erect C_3 perennial grass (0.66–1 m tall) has relatively long (15–50 cm) and narrow (< 1.25 cm) leaf blades and prominent rhizomes that can expand 2–3 m per year, producing a guerilla growth form (Maun, 1984). The species is burial-tolerant, increasing vigor and altering resource allocation in response to burial (Maun, 2009; Brown and Zinnert, 2018). High density and rapid lateral spread in dune-building species can lead to increased sand accretion and the construction of taller and wider dunes compared to species with lower lateral spread and density (Hacker et al., 2019). *Ammophila breviligulata* thrives in the backshore, where dunes are initiated, and in the foredunes, where it builds, maintains, and restores habitat as an ecosystem engineer (Hacker et al., 2011; Zarnetske et al., 2012; Charbonneau et al., 2021). It is, however, outcompeted by later successional species in secondary and gray dune habitats (Maun, 2009). Reproduction occurs predominantly through asexual tillering (Maun, 1984; Slaymaker et al., 2015) or the growth of new ramets along lateral rhizomes. Both tillering and new ramet production typically occur at the beginning of the growing season rather than during it, and individual plants usually produce multiple stems (Zarnetske et al., 2012; Charbonneau, 2019). In the US mid-Atlantic, plants begin to break dormancy in mid-February, are fully emerged by mid-May, and the growing season continues until September or October, when the plants senesce and enter dormancy (Charbonneau, 2019).

2.2 Laboratory experiment

2.2.1 Wind tunnel and experimental design

The laboratory experiment was conducted at the Ocean County Vocational Technical School Wind Tunnel in Waretown, NJ, USA (Charbonneau et al., 2021). The laboratory is 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). The wind tunnel chamber is 6.0 m long, 1.0 m wide, and 2.0 m high. Downwind, 3.6 m into the chamber, is an opening where 1.0 m × 1.0 m × 0.3 m wooden planter boxes can be inserted. It is in these boxes that we established rooted planting configurations in sand. A box is sealed into the chamber flush with the floor, and both are leveled with a continuous dry sand bed (2.54 cm bed height, medium quartz sand, mean grain size of 0.300–0.350 mm), mimicking a dry sandy backshore for aeolian transport toward vegetation (Arens, 1996; Charbonneau et al., 2021). Additional wind tunnel details can be found at TheWindTunnel.weebly.com and in Charbonneau et al. (2021).

We planted a total of 30 boxes (1 m × 1 m × 0.3 m) in monocultures across two experimental treatments and one control treatment on 13 and 14 April 2019. The experimental treatments corresponded to medium- (five plants) and high-density (nine plants) populations, with all individuals in a group supporting a single nebkha, compared to a single-plant low-density control. The experimental densities and staggered diamond configurations were designed to reflect natural plant arrangements observed along the backbeach at Island Beach State Park, NJ, USA, on 12 April 2019 (Figure 2). Sample sizes included 10 boxes per treatment (20 experimental and 10 control boxes). Bare sand boxes were not included because previous trials under the same conditions produced uniform transverse aeolian ripples (Charbonneau et al., 2021). Leading/upwind edge individuals were positioned 7.6 cm from the box edge, and plants within each group configuration were spaced 4 cm apart at the center to minimize edge effects. All plants were positioned at least 40 cm or more from the wind tunnel sidewalls, well outside the boundary layer, which begins ≈ 7.5 cm from the wall (Supplementary Material S1). Similarly, all plants sat < 40 cm tall and were pulled taut vertically, well outside the ceiling boundary layer (Supplementary Material S1). The sand used was medium quartz with a mean grain size of 0.300–0.350 mm, sourced from Island Beach State Park, NJ, USA. Detailed grain size distributions can be found in Charbonneau et al. (2021; Supplementary Material S1).

Runs consisted of exposing each box to 30 min of wind at 8.25 m/s, measured 60 cm above the box center. This speed and duration allowed maximum sediment transport within the bounds of our sediment supply (≈ 25 tons across all runs). These conditions were

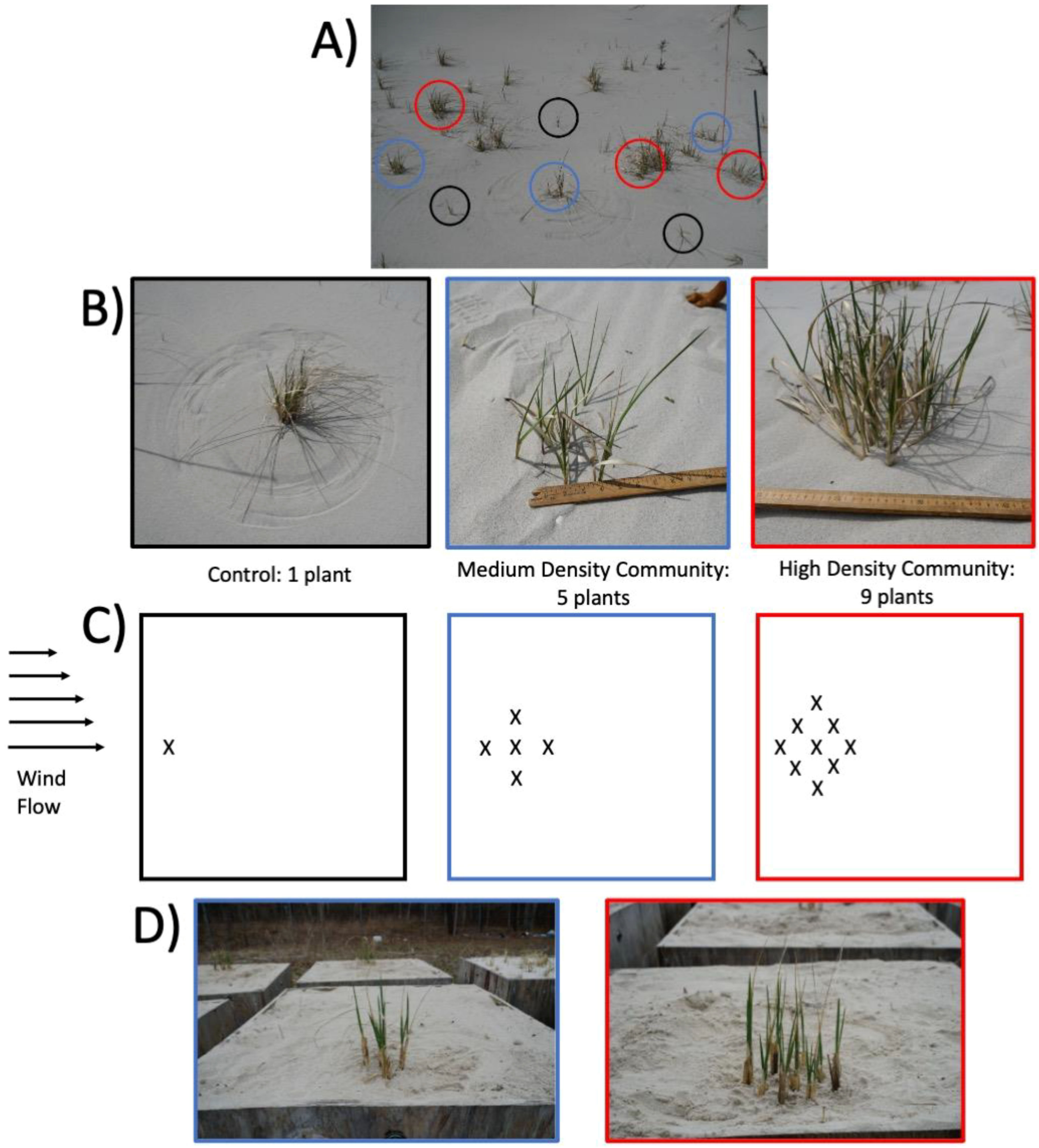

FIGURE 2
Commonly observed backshore *A. breviligulata* population group configurations and their laboratory replication in wind-tunnel boxes. Plants are typically singular or in groups sprinkled along the back beach **(A, B)**. Individual group sizes frequently encountered were five or nine plants in a diamond-like configuration **(A, B)**, which we replicated as our medium- and high-density laboratory treatments **(C, D)**. Each 1-m^2 box was individually sealed into a wind tunnel and provided the same abiotic scenario (i.e., sand availability and wind speed and direction) to build nebkha.

the same as in Charbonneau et al. (2021) and consistent with other laboratory experiments, most notably those of Järvelä (2002) and Zarnetske et al. (2012), designed to promote accretion rather than scouring and shielding. Prior to each box run, we measured plant morphometrics for each individual. From bed level, we measured: (1) stem width as the distance between the two farthest stems perpendicular to wind flow, (2) height bent naturally, and (3) height as the tallest taut leaf. We counted (4) total leaves and (5) total stems. After the experiment, shoots from all plants were cut at the surface—without disturbing the bed and resultant topography—using shop shears to measure biomass after drying for 72 h at 70°C.

2.2.2 Data processing and analyses

Following Charbonneau et al. (2021), immediately after wind tunnel runs, we quantified box topography with an industrial class II laser 3D sensor, the SICK TriSpector1060. This sensor collects and meshes elevation (z) profiles every 0.42 mm along the y-axis to generate a digital elevation model (DEM) with true xyz millimeter values. Scans encompass all plants within the 66-cm box width (x) and 1-m box length (y), plus 0.125 m upwind and downwind of each box. As class II lasers cannot penetrate live tissue, all aboveground biomass was removed postrun and prescan. Each box was also scanned prior to its run, with the plants in place, to account for any bed-leveling errors during postprocessing (Charbonneau et al., 2021). We assessed whether erosive or accretionary forces visibly built nebkha using marked vertical wire stakes at the front and back of leading and trailing edge plants, and confirmed these observations in postprocessing by calculating Δz, defined as peak elevation minus initial bed elevation (i.e., nebkha height).

We extracted localized topographic information from the scans with SOPAS Engineering Tool V2025.1 (SICK AG, 2019). The quantified topographic parameters included nebkha volume, area, height, and shape per box. Nebkha boundaries were defined from clusters of elevation points identified with the Blob Tool, which typically spans the plant bounds and extends downwind, represents the nebkha, and the tool calculates its basal area and volume (from the object base). Once defined, we measured the elevation from base to peak, recorded the peak location, and measured the longest x- and y-axes.

Postprocessing revealed that nebkha formed around the plants in all wind tunnel runs. However, for three medium-density and two high-density boxes, the nebkha edges relative to the sand bed were not discernible enough with the methods used in SOPAS, resulting in a sample size of 10 low/control, seven medium, and eight high-density nebkha, where each box had between three to 56 stems within it, among the one to nine plants.

2.3 Field validation

2.3.1 Fieldwork

Fieldwork was conducted on the southern portion of Hog Island, VA, USA (37°22′13.8252″ N, 75°43′4.6236″ W), a barrier island in the Virginia Coast Reserve Long-Term Ecological Research site (Figure 3). The sand in this area is fine, with a mean grain size of ~ 0.16 mm (Fenster et al., 2016). Over the past several years, southern Hog Island has been accreting, creating a wide beach where new dune hummocks were established by several species, including *A. breviligulata*, *Panicum amarum*, *Spartina patens*, and *Uniola paniculata* (Sabo et al., 2024). In September 2024, we randomly selected a range of nebkha formed by monocultures of *A. breviligulata* along 780 m of shoreline (n = 61). The number of stems on each nebkha was counted, ranging from one to 30 stems. Each selected nebkha was at least 5 m from the edge of nearby vegetation patches. We recorded the location and elevation at the base of each nebkha using a Trimble R10–2 TSC7 RTK GPS receiver, with vertical and horizontal precisions of 15 and 10 mm, respectively (Trimble Inc., Westminster, CO, USA).

2.3.2 Data processing and analyses

To quantify the effect of stem number on nebkha formation, we extracted several nebkha morphometrics from digital elevation imagery collected in October 2024. Imagery was acquired at 100 m altitude using a DJI Phantom 4 Pro RTK unoccupied aerial system (UAS) (SZ DJI Technology Co. Ltd., Shenzhen, China), which features a 20-MP 1-in. CMOS sensor. The resulting imagery had a resolution of 3 cm pixel^{-1}, a horizontal precision of 0.4 cm, and a vertical precision of 1.2 cm. Vertical accuracy, based on ground control points surveyed with a Trimble R10 RTK system, was 0.062 cm. Raw UAS imagery was processed into point clouds from UAS flight paths with 70% horizontal and 80% vertical overlap using Inverse Distance Weighting in Agisoft Metashape Pro version 1.7 (Agisoft, St. Petersburg, Russia). From this, DEMs were derived using structure-from-motion (SfM) and tiling processes, and were georeferenced during processing with the same Trimble R10 RTK ground control points.

We analyzed the resulting DEMS using Esri ArcGIS Pro. Using the dynamic range adjustment feature, we overlaid DEMs with known Ammophila nebkha documented by RTK GPS in the field (Figure 4). At an observable scale of 1:20, nebkha areas were manually extracted based on slope changes relative to the surrounding topography, creating polygon features. Raster

FIGURE 3
(A) The field site component of the research was conducted on the southern portion of Hog Island, Virginia, USA (37°22′13.8252″ N, 75°43′4.6236″ W). This site is a barrier island that is one of many long-term ecological research (LTER) sites maintained in the USA for the purpose of studying scientific processes in a relatively unaltered or natural state free of direct management or anthropogenic intervention. **(B)** Purple dots mark the locations of *A. breviligulata* nebkha mounds surveyed and used in the analysis.

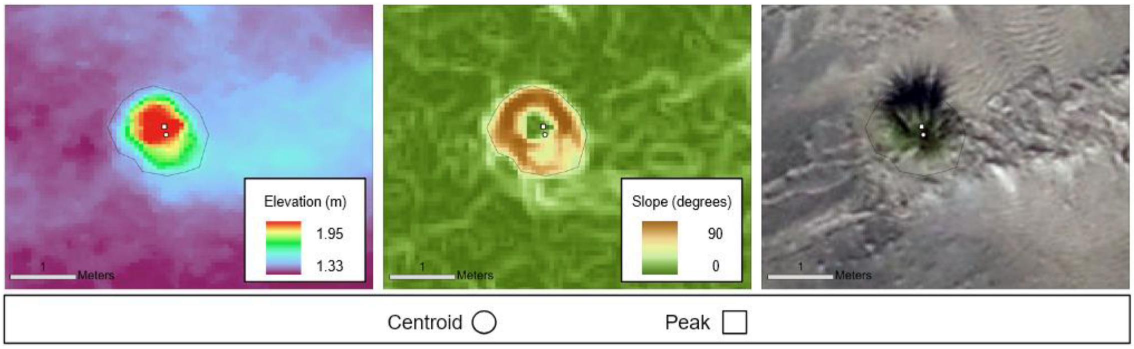

FIGURE 4
Digital elevation model (left) observed using dynamic range adjustment, surface parameter layer depicting slope (center), and orthomosaic (right) image at 1:20 range. Centroid is defined as the geometric center, and peak elevation is from the base of the nebkha, supported by *A. breviligulata*, to the elevation maxima, which represents nebkha peak height. Only the digital elevation model was used for discerning nebkha.

elevation data were used to confirm slope-based changes, with elevation differences of at least > 2 cm indicating the nebkha edge (accounting for horizontal error in the imagery). Orthomosaic imagery was also evaluated to confirm nebkha vegetation. Nebkha showing no discernible change in slope or elevation from the surrounding topography were excluded from further analysis. Following these methods, several field nebkha were not distinguishable from the imagery (n = 22), and we were able to identify 39 total nebkha of varying sizes, supported by three to 30 A. *breviligulata* stems. After extracting nebkha areas, we quantified geometric centroid, maximum elevation, volume, and long-shore and cross-shore dimensions from the peak elevation and geometric centroid. The centroid is defined as the geometric center, and peak elevation is calculated as the difference between the elevation maxima of the base of the nebkha, where this metric represents the nebkha height. We created a slope raster from the DEM, allowing documentation of the south/southwestern slope for each identified nebkha, reflecting the dominant wind direction on Hog Island during September and October 2024, as recorded by a meteorological station on Hog Island, VA, USA.

2.4 Statistical analyses

Means are reported ± standard error (SE), and unless otherwise noted, all tests are two-tailed. Statistical analyses were performed using JMP Pro 18.0 (JMP, 2019). Nebkha height measurements were taken from the base of the nebkha to its elevation maximum (i.e., peak). Normality of all data was assessed in JMP using a Goodness-of-Fit test and by examining residual plots for homoscedasticity. When normality was not met, plant morphology data and field data were log-transformed; additional details are provided below.

To analyze the plant morphology data from the wind tunnel tests on the individual plant level, we employed nonparametric methods due to a heavy right skew in most metrics. Transformation was not viable: while a log transformation normalized the distribution of the number of leaves, other metrics remained skewed, necessitating nonparametric analyses. Metrics including plant height, stem width, biomass, and the number of stems and leaves were compared between treatments using Kruskal–Wallis tests, with pairwise comparisons conducted via the Wilcoxon method as the nonparametric equivalent to analysis of variance (ANOVA). Relationships between variables were assessed using Spearman's Rho (ρ) as a nonparametric correlation measure. Aggregated metrics per box—total stems, total leaves, and total biomass—were normally distributed; these were analyzed across density treatments using ANOVA with Tukey Honestly Significant Difference (HSD) pairwise comparisons, and linear regression was applied to examine relationships among morphological variables.

We analyzed the Nebkha wind tunnel data, which were not transformed, using both qualitative and quantitative tests. Linear regression was used to test how plant parameters, at the box level, relate to nebkha size and shape metrics. Nebkha size metrics included nebkha volume (cm^3), surface area (cm^2), length (mm), width (mm), and height (mm). Nebkha shape metrics included relief (height relative to area) and planform eccentricity (length/width ratio). Metrics were compared between treatments using ANOVA with Tukey HSD pairwise comparisons. Analysis of covariance (ANCOVA) was used to test whether differences in nebkha size across treatments could be attributed to the total number of stems and total number of leaves. Multiple regression models were used to determine which plant variables (i.e., total number of leaves, total number of stems, total dry weight, average plant height (bent sitting natural), density treatment) most parsimoniously explained nebkha size metrics (i.e., volume, surface area, height). All possible models were analyzed, and the Akaike information criterion corrected for small sample size (AICc) was used to determine the top models.

The following field variables were log-transformed to meet normality assumptions: stem number, nebkha area, volume, alongshore distance, cross-shore distance, peak nebkha elevation, nebkha height, and the alongshore and cross-shore differences of the peak and centroid. Pearson's correlation was used to assess relationships between base nebkha elevation and stem number, as well as between alongshore/cross-shore peak–centroid differences and peak elevation. Linear regressions were used to evaluate the effect of stem number on dune nebkha metrics (i.e., area, volume, alongshore, cross-shore, nebkha height, slope, and position of the peak relative to the centroid alongshore and cross-shore).

3 Results

3.1 Plant morphology of wind tunnel *A. breviligulata* plants

Individual plants in the low-density control treatment were larger compared to those in the two population-level treatments. Plants in the medium- and high-density treatments had fewer leaves (χ^2 = 20.1, degrees of freedom (df) = 2, $p < 0.0001$), fewer stems (χ^2 = 18.3, df = 2, $p < 0.0001$), and also lower biomass ($\bar{x}$ = 2.92 g ± 0.20 g; χ^2 = 16.1, df = 2, $p = 0.0003$) than low-density treatment individual plants ($\bar{x}$ = 11.42 g ± 0.90 g). Low-density plants were also twice as wide ($\bar{x}$ = 2.2 cm ± 0.33 cm; χ^2 = 13.5, df = 2, $p = 0.001$) as plants in the medium- and high-density treatments ($\bar{x}$ = 1.1 cm ± 0.05 cm). Plant height did not vary between treatments when naturally bent ($\bar{x}$ = 23.5 cm ± 0.37 cm); however, medium-density plants were shorter when pulled taut ($\bar{x}$ = 27.2 cm ± 0.77 cm; χ^2 = 8.6, df = 2, $p = 0.01$) compared to low- and high-density plants, which were taller ($\bar{x}$ = 29.3 cm ± 0.49 cm).

Almost all plant metrics were significantly positively related to each other (see Supplementary Material S2 for measures of association using Spearman's ρ and the distribution of plant morphology metrics). Among these, the number of leaves and number of stems exhibited the strongest relationship (ρ = 0.90, $p \leq 0.0001$), indicating that plants with more stems tend to have more leaves and vice versa. The next two strongest correlations were between biomass and the number of leaves (ρ = 0.63, $p \leq 0.0001$), followed by biomass and the number of stems (ρ = 0.61, $p \leq 0.0001$).

The total number of leaves and stems per box varied, and as would be expected with the experimental design, the high-density treatment had more total stems ($F_{2,\ 22}$ = 68.4, $p < 0.0001$) and total leaves ($F_{2,\ 22}$ = 53.0, $p < 0.0001$) than both other treatments, and the medium-density treatment had more leaves and stems than the low-density boxes (see Table 1 for mean stems, leaves, and biomass per box). The total number of stems in a box was strongly positively related to the total number of leaves in a box (R^2 = 0.93, $F_{1,\ 23}$ = 319.6, $p < 0.0001$). Despite individual plants varying in height within the density treatments, the average height of plants, sitting bent or taut, did not vary across treatments ($p > 0.05$).

Low-, medium-, and high-density treatments contained one, five, and nine plants, respectively. Many topographic variables were associated with density treatment, driven by increased plant biomass and greater variability in plant morphological traits at higher densities. Means are reported ± SE, and pairwise comparisons across densities were performed using Wilcoxon tests; all comparisons were statistically significant.

3.2 Wind tunnel nebkha size

With the exception of nebkha height and width, all size metrics were significantly positively correlated. A full correlation matrix of these metrics is provided in Supplementary Material S3.

Nebkha surface area varied across the different density treatments, predominantly driven by differences in the total number of leaves in each replicate (Figure 5). Surface area was greater in the high-density treatment than in the other two lower-density treatments ($F_{2,\ 22}$ = 11.6, $p = 0.002$). The top five models among all possible models for predicting the nebkha surface area are represented in Table 1. ANCOVA examining the effects of total leaves, density, and their interaction indicated that the relationship between nebkha surface area and total leaves did not differ by density (R^2 = 0.60, $F_{5,\ 19}$ = 5.70, $p = 0.002$).

Density refers to the density treatment as low, medium, or high, and plant height is the average plant height in a replicate, measured as *A. breviligulata* plants sat bent naturally.

Nebkha volume varied across the different density treatments, with this variation driven primarily by differences in total biomass (Figure 5). Nebkha volume was greater in the high-density treatments compared to the low- and medium-density treatments ($F_{2,\ 22}$ = 9.8, $p = 0.0009$). The top five models for predicting nebkha volume are summarized in Table 2. ANCOVA examining the effects of total leaves, density, and their interaction indicated that the differences in nebkha volume among density treatments were largely driven by variations in leaf number (R^2 = 0.57, $F_{5,\ 19}$ = 5.09, $p = 0.004$; Table 1). Similarly, ANCOVA assessing biomass, density, and their interaction revealed that differences in nebkha volume by density were primarily due to variations in biomass across treatments R^2 = 0.69, $F_{5,\ 19}$ = 8.38, $p = 0.0003$; Table 1).

Nebkha height showed a trend of varying across treatments, driven by the high-density treatment producing nebkha of greater

TABLE 1 Plant morphology metrics per wind tunnel plant density treatment.

	Low density (L)	Medium density (M)	High density (H)	Comparisons across densities
Stems per wind tunnel box (#)	12.9 ± 1.8	27.9 ± 2.2	45.1 ± 2.1	L < M < H
Leaves per wind tunnel box (#)	46.2 ± 6.3	86.3 ± 7.6	144.1 ± 7.1	L < M < H
Biomass per wind tunnel box (g)	11.4 ± 2.8	15.0 ± 3.3	27.2 ± 3.1	(L = M) < H

Low-, medium-, and high-density treatments contained one, five, and nine plants, respectively. Many topographic variables were associated with density treatment, driven by increased plant biomass and greater variability in plant morphological traits at higher densities. Means are reported ± SE, and pairwise comparisons across densities were performed using Wilcoxon tests; all comparisons were statistically significant at a nn alpha level (α) of 0.05, P < 0.05.

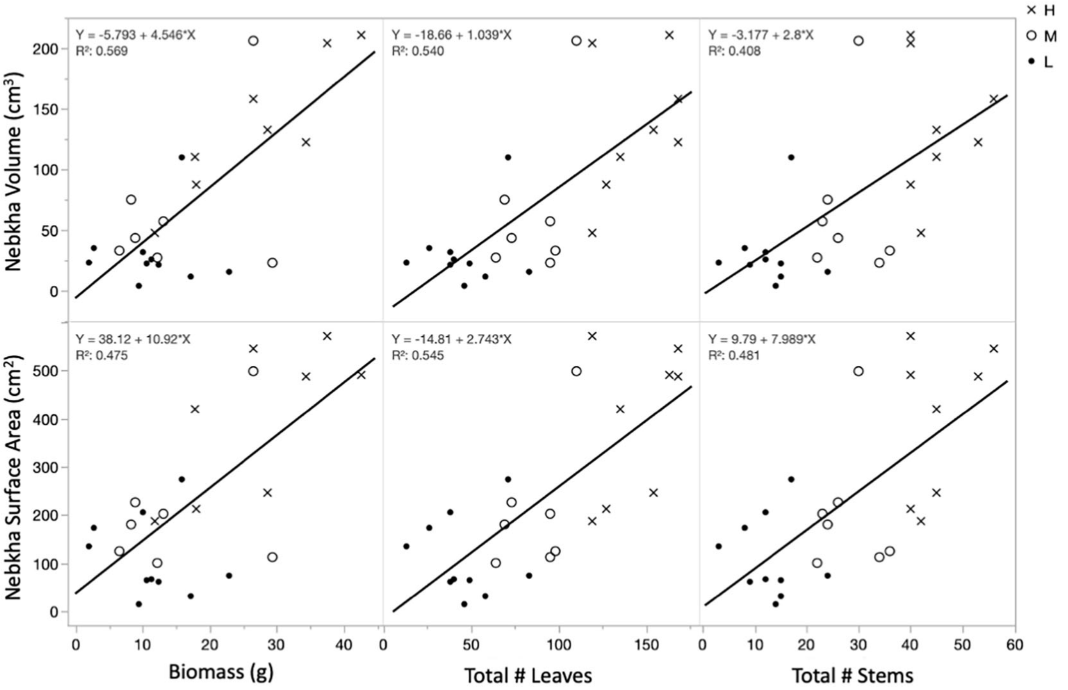

FIGURE 5
Nebkha volume and surface area, for wind tunnel nebkha, are both most strongly positively related to the total number of leaves and biomass of *A. breviligulata*, as the most prevalent variables in the top five models for both of these variables. The total number of stems is shown, given that it is a common model variable used to predict topographic changes, but these results show that much more variability can be captured using the number of leaves or biomass, both of which are tightly related to the number of stems. It is also important to note that plant morphology varies within plant populations, but density differences in topography are driven by these differences, not the treatment itself, as revealed with ANCOVA. Points represent the three different density treatments: low (L: one plant), medium (M: five plants), and high (H: nine plants). All *p*-values are < 0.0001.

TABLE 2 **The top five models for predicting *A. breviligulata*-built nebkha size metrics—specifically, nebkha surface area, volume, and height—for wind tunnel nebkha.**

Model dependent variable	Model independent variables	Adjusted R^2	AIC	RMSE	F-value	P-value
Nebkha surface area	Total leaves	0.525	314.8	118.6	27.58	< 0.0001
	Total leaves and biomass	0.541	315.7	116.6	15.14	< 0.0001
	Biomass and density	0.535	316.0	117.3	14.86	< 0.0001
	Total stems and biomass	0.529	316.3	118.1	14.51	< 0.0001
	Total leaves and density	0.516	317.0	119.6	13.84	< 0.0001
Nebkha volume	Total leaves and biomass	0.590	264.5	41.88	28.34	< 0.0001
	Biomass and density	0.584	264.9	42.19	17.91	< 0.0001
	Biomass	0.550	265.1	43.93	30.34	< 0.0001
	Total leaves and total stems	0.580	265.2	42.43	17.59	< 0.0001
	Biomass and plant height	0.576	265.4	42.61	17.35	< 0.0001
Nebkha height	Biomass and plant height	0.287	129.8	2.83	5.84	0.009
	Total leaves	0.189	131.3	3.02	6.60	0.01
	Biomass	0.174	131.8	3.05	6.05	0.02
	Density	0.161	132.2	3.07	5.62	0.03
	Total leaves and plant height	0.201	132.7	3.00	4.03	0.03

Density refers to the density treatment as low, medium, or high, and plant height is the average plant height in a replicate, measured as *A. breviligulata* plants sat bent naturally.

height than the low-density treatment ($F_{2, 22}$ = 3.2, p = 0.06). The top five models of all possible models for predicting nebkha height are presented in Table 2. Generally, height was not strongly predicted by plant morphological variables (Adj R^2 range: 0.174–0.287) compared to how well both surface area and volume could be predicted by them. Nebkha height appears driven by volume and surface area (R^2 = 0.65, $F_{2, 22}$ = 20.68, p < 0.0001; Supplementary Material S3); an effects test shows that both independent variables significantly impact nebkha height, but a stronger relationship exists with volume (F = 25.61, p < 0.0001) than with area (F = 10.43, p = 0.004), where volume alone accounts for 48.8% of the variability in nebkha height (Figure 6).

3.3 Wind tunnel nebkha shape

Nebkha shape across all three treatments was ellipsoidal in the prevailing wind direction, as eccentricity—the ratio of nebkha length to width—did not vary by treatment ($\bar{x}$ = 1.41 ± 0.11). Similarly, relief did not vary among treatments. Supporting this, an ANCOVA examining the effect of surface area on height with density as a covariate revealed that the relationship between height and area did not differ by density (p > 0.05). Nebkha width ($F_{2, 22}$ = 7.02, p = 0.004) and length ($F_{2, 22}$ = 7.86, p = 0.002) both varied by treatment, with high-density treatments producing nebkha that were longer and wider than those in the low-density treatment. Nebkha length was not related to plant height (p = 0.51) but was positively related to the number of stems (R^2 = 0.39, $F_{1, 22}$ = 13.93, p = 0.001). Eccentricity showed a trend of increasing (length growing more than width) with increasing number (R^2 = 0.15, $F_{1, 22}$ = 4.02, p = 0.06). Supporting these findings, the distance of the centroid from the upwind nebkha edge increased with stem number (R^2 = 0.35, $F_{1, 22}$ = 11.86, Pp < 0.01), whereas the peak location did not vary with the number of stems.

The nebkha peak was always located within or just behind the plants, and its position varied by density. Typically, the peak did not coincide with the nebkha centroid; only three instances had the centroid at the peak, and in most cases, the centroid was behind the plants. In the low- and medium-density treatments, nebkha peaks were behind the plants (15 of 17 replicates)—more than expected by chance—whereas in the high-density treatment, six of eight peaks were within the plants (Fisher's exact; χ^2 = 10.1, df = 2, N = 25, p < 0.001). Further examination revealed that nebkha with peaks within the plants had more stems ($\bar{x}$ = 43.1 ± 2.60) than those with centroids behind the plants ($\bar{x}$ = 21.6 ± 3.11; $t_{20.2}$ = 5.33, p < 0.0001). The maximum upwind angle recorded for wind tunnel nebkha was 18° ($\bar{x}$ = 6.4° ± 0.78°).

3.4 Field nebkha size

Multiple size metrics of field nebkha were significantly positively correlated; a full correlation matrix is provided in Supplementary Material S4. The number of stems in nebkha formed by *A. breviligulata* ranged from three to 30 and occurred within an elevation range of 1.11–1.54 m above sea level. No significant correlation was observed between total stem number and base elevation (p > 0.05). Field nebkha surface area ranged from 0.20 to 4.47 m^2 and was weakly but positively related to stem number (R^2 = 0.17, $F_{1, 37}$ = 7.70, p = 0.009; Figure 7). Nebkha height (measured peak to base) ranged from 0.04 to 0.68 m and showed a strong positive relationship with stem number (R^2 = 0.71, $F_{1, 37}$ = 91.15, p < 0.0001; Figure 7). Nebkha volume ranged from 0.013 to

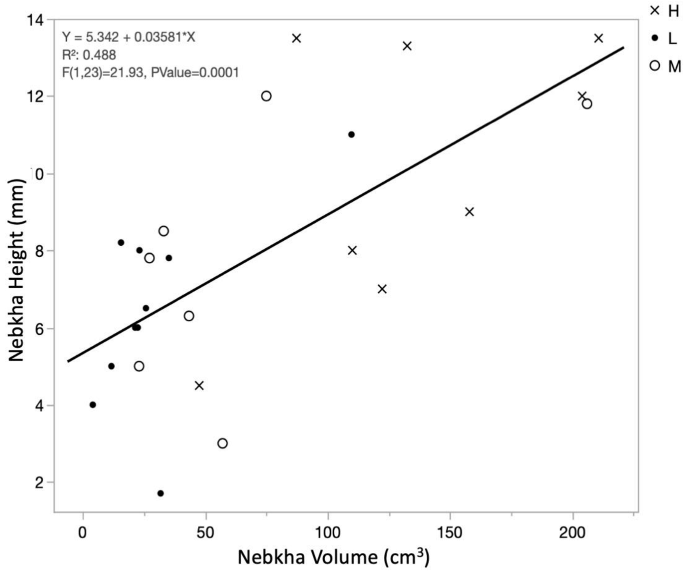

FIGURE 6
For wind tunnel nebkha, nebkha height was not strongly predicted by *A. breviligulata* plant morphology metrics (e.g., biomass, number of stems, etc.) but was strongly positively related to nebkha volume, which can be predicted by this variable. Points represent the three different density treatments: low (L: one plant), medium (M: five plants), and high (H: nine plants).

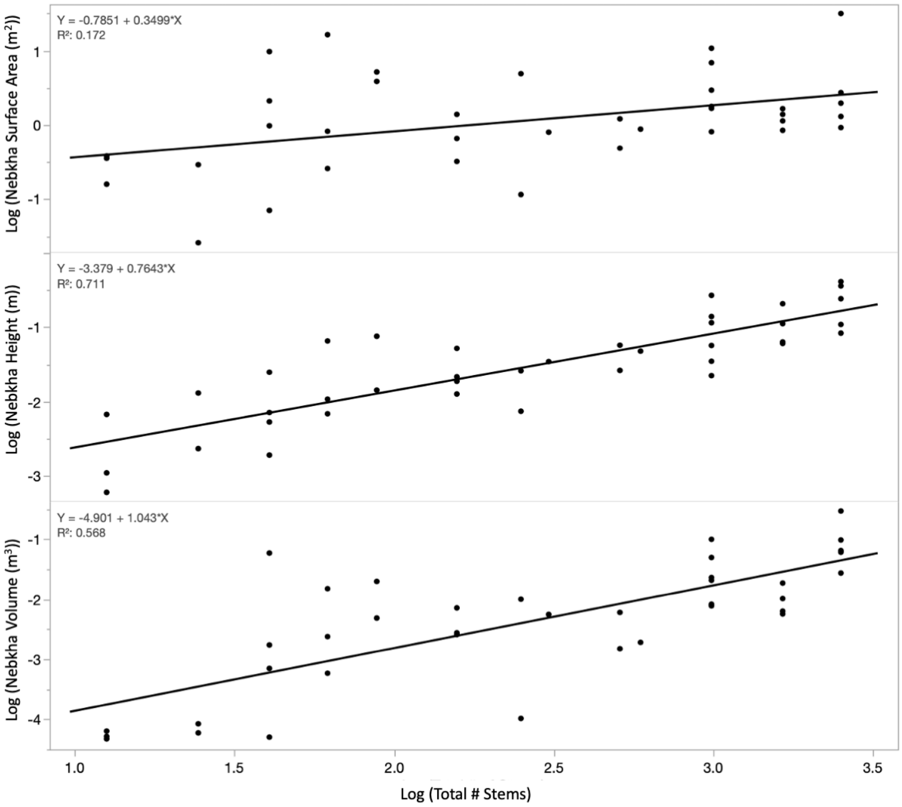

FIGURE 7
For field nebkha, nebkha height, surface area, and volume are all positively related to the total number of *A. breviligulata* stems supporting them. All *p*-values are < 0.0001, with the exception of the total number of stems and surface area, which maintained a *p*-value of 0.009.

0.59 m^3 and was also positively related to stem number (R^2 = 0.57, $F_{1,3\ 7}$ = 48.74, $p < 0.0001$; Figure 7).

3.5 Field nebkha shape

The Nebkha shape appears somewhat related to the number of stems. Nebkha were slightly longer alongshore (0.52–2.68 m), with a slightly stronger relationship with total stems (R^2 = 0.23, $F_{1,\ 37}$ = 11.17, p = 0.002) relative to cross-shore length (0.47–2.09 m, R^2 = 0.17, $F_{1,\ 37}$ = 7.84, p = 0.008). The number of stems did not affect nebkha eccentricity, the ratio of nebkha length to width ($p > 0.05$), where the mean eccentricity of field nebkha was 0.99 ± 0.05, indicating a fairly circular nebkha shape. This result suggests both nebkha length and width increase concomitantly in the field; supporting this, both alongshore width (R^2 = 0.17, $F_{1,\ 37}$ = 7.84, p = 0.01) and length (R^2 = 0.23, $F_{1,\ 37}$ = 11.17, p = 0.001) had a positive relationship with the number of stems. Nebkha slopes ($\bar{x}$ = 28.3 ± 1.9) had a wide angle range from 6.9° to 51.3°, and slope was positively related to the number of stems (R^2 = 0.54, $F_{1,\ 37}$ = 43.16, $p < 0.0001$, Figure 8). Of 39 nebkha, 13 had slopes at or above a theoretical angle of repose for medium-sized grains (Bagnold, 1960; Sloss et al., 2012; Figure 8), and taller nebkha maintained elevated angles of repose (R^2 = 0.69, $F_{1,\ 37}$ = 80.67, $p < 0.0001$).

The mean position of the nebkha peak relative to the centroid was within 9 cm alongshore and 6 cm cross-shore, although substantial variation was observed across all dune nebkha. Despite this variability, both the peak and centroid were consistently located within the plant stems, and the number of stems had no significant effect on the placement of the nebkha peak relative to the centroid alongshore or cross-shore ($p > 0.05$ for both).

4 Discussion

4.1 Allometric relationships among *A. breviligulata* plant traits

Allometry, the scaling of form, is apparent in *A. breviligulata*. Here, all plant morphological parameters were highly correlated (Supplementary Material S2); thus, larger plants were larger across all measured parameters, a pattern observed in several dune species. Early work on *Ammophila arenaria* and *Elymus mollis* demonstrates allometric relationships between biomass and leaf area mediated by nitrogen availability (Pavlik, 1983). In the field, allometric relationships among population- and community-level root metrics of *Spartina patens* and *A. breviligulata* have been

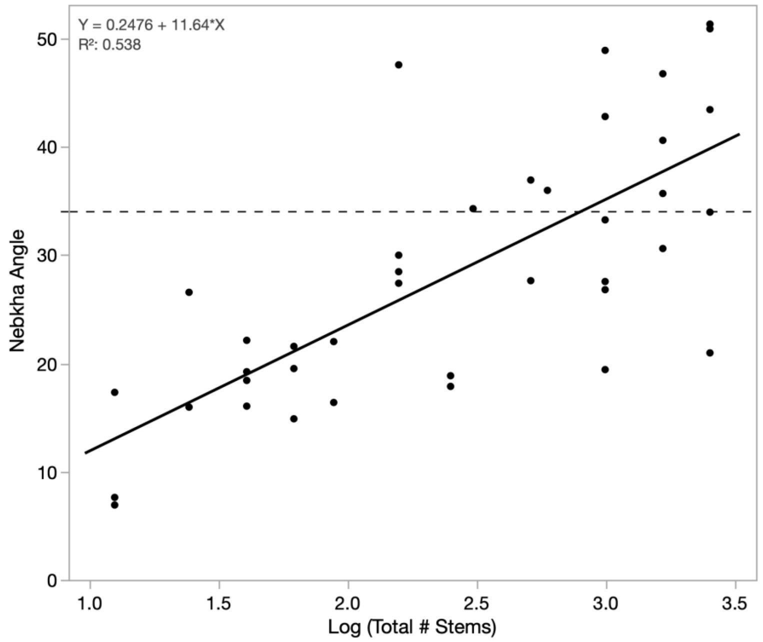

FIGURE 8
For field nebkha, the upwind slope (nebkha angle) is positively related to the total number of *A. breviligulata* stems. The angle measured represents the stoss upwind nebkha slope relative to the predominant southwest wind direction on Hog Island, VA, USA. The dotted line represents a theoretical angle of repose (34°) for medium-sized grains, and stem densities ranged from 3 to 30.

described (Snook and Day, 1995). Correlations among plant traits have been observed for *A. breviligulata*, *Panicum amarum*, *S. patens*, *Uniola paniculata*, and the invasive species *Carex kobomugi* (Jass, 2015; Charbonneau et al., 2021), although not explicitly considered in the framework of allometric scaling or theory. Comparisons of morphological variables between dune-builder species exist (e.g., Hacker et al., 2019; Charbonneau et al., 2021; Walker and Zinnert, 2022), with these differences typically linked to preexisting topography (McGuirk et al., 2022). In contrast, in this study, we observed nebkha topographic formation to identify morphological metrics with the greatest physical influence.

Employing allometric equations in existing dune models can be an efficient way to expand or incorporate modeled ecogeomorphic relationships. Allometric equations have been used in tree models for decades, including mangroves and shrubs, but there are known issues with universality and site- or species-specific variability (Komiyama and Poungparn, 2005; 2008; Brantley and Young, 2007; Reeves et al., 2022). Woody plants cannot necessarily be harvested or measured quickly or inexpensively to tailor models to specific sites, making this issue difficult to overcome (Komiyama et al., 2008). While dune grasses may vary across species (Pavlik, 1983; Gao et al., 2024), site data, including biomass, can be collected relatively quickly and inexpensively, making site-specific issues less prohibitive. Our observed strong coupling of morphological parameters suggests that stem density could be measured across a site and then used to extrapolate other parameters, such as biomass and number of leaves —the two strongest predictors (over 50% variability) of nebkha size metrics, including volume and surface area. Despite this, dune model options remain limited, as most models incorporating plants beyond a roughness component rely on percent cover to drive ecogeomorphic relationships (Piercy et al., 2023). Only two of nine known exceptions exist—de Luna et al. (2011) and Charbonneau et al. (2022)—highlighting the need to expand the range of vegetation parameters in existing models or to better understand the relationships between percent cover and morphology.

4.2 Stem density effects on nebkha morphology

Wind tunnel differences in nebkha surface area and volume across density treatments were an artifact of a strong positive relationship with leaves, aboveground biomass, and stem density. Interestingly, the relationships were stronger for the former two parameters (leaf density and aboveground biomass) than for stem density (Figure 5) and were more prominent in top models predicting nebkha size (Table 2). Stem density is commonly used to estimate abundance, and relationships have been observed between stem density and sand capture relative to dune size and shape (e.g., Zarnetske et al., 2012; Hacker et al., 2019; Charbonneau et al., 2021). Grasses maintain numerous leaves per stem, but leaves are more easily buried than stems as they are more flexible, often less upright, with some species having leaf parts close to or at the sand surface (Hacker et al., 2019; Walker and Zinnert, 2022). Burial reduces leaf number in *A. breviligulata* (Harris et al., 2017) and leaf-to-stem ratios in related species, *A. arenaria*, triggering subsequent tillering (Sykes and Wilson, 1990). While leaves and biomass could not be measured in the field, stem density showed a strong positive relationship with nebkha size metrics (Figure 7) and, interestingly, was not influenced by establishment location (relative to elevation), despite lower-elevation areas being more prone to overwash (Reeves et al., 2022). It is also worth noting that we observed increasing variability in nebkha size parameters with rising stem density in both the field and wind tunnel, with the lowest standard error at reduced stem numbers (< 15) and lower density treatments (Figures 5, 7). Based on the recent work of Costas et al. (2024), at higher plant densities—or as nebkha grow and merge—these relationships may become nonlinear. Stems are easier to measure in the field, and the strong correlation between the number of leaves and stems in *A. breviligulata* demonstrated here supports the continued use and collection of stem density as a field metric.

Observed field nebkha slopes document plant stabilization. Of 39 nebkha, 15 had slopes above a theoretical angle of repose, 30°, for medium-fine grains, where Sloss et al. (2012) note that slopes can be increased to up to 50° by dense vegetation (Bagnold, 1960). Field nebkha slope was positively related to stem density, but our results also suggest slope is not related to density alone – field nebkha at the maximum observed stem density (30 stems) maintained 50° slopes, whereas others with the same density were at or below 30°, and nebkha with 10–20 stems maintained slopes at or near 50° (Figure 8). While we did not collect and analyze sediment samples, these results suggest that grain aggregation resulting in greater slopes is possible without soil stabilization (Bagnold, 1960). While roots provide structural stability and, as noted in Cooke et al. (1993), can influence nebkha slope, much of this stability likely arises directly from arbuscular mycorrhizal fungi (AMF; Daynes et al., 2013). AMF hyphae and their secreted compounds bind grains and physically entangle them with roots (see Figure 4 of Feagin et al., 2015), and dune-builder species such as *A. breviligulata* engage in mutualistic relationships with AMF (e.g., Maun, 2009; Walker and Zinnert, 2022). In *A. breviligulata*, AMF increases stem density from the same plant by 31% (Gemma and Koske, 1997). Observed patterns in slope, stem density, and nebkha height suggest that, at the foredune level, vegetation densities may contribute to greater accrued topographic height than would be expected from physical processes alone.

Differences in the relationships observed with nebkha height may be a function of differences in available time and space for the resultant topography to evolve. In the field, nebkha height had the strongest relationship with stem density among all nebkha parameters (Figure 7) but was also related to nebkha volume and surface area (Supplementary Material S4). In the wind tunnel, nebkha height was more related to nebkha volume and surface area than to plant morphology or density metrics (Figure 7). Both available space and sediment supply were controlled in the laboratory, and plant-influenced topography was measured shortly after a wind event, allowing for a direct test of planting density on resulting nebkha topography. Conversely, field nebkha formed and evolved over multiple sand transport events, as suggested by the absence of tails indicating the predominant wind direction during deposition, and they maintained distances of more than a meter between individual nebkha (Cooke et al., 1993; Sloss et al., 2012). Over the course of field nebkha evolution, there was greater potential for ecogeomorphic interactions (i.e., plant burial and growth in response to sand transport), which was not present in the wind tunnel experiment. Field wind directions were also more variable than in the controlled wind tunnel. Although winds from the south/southwest were most prominent in the month preceding our imagery collection, the most frequent wind directions over longer timeframes originate from the south/southwest and the north/northwest (Priestas et al., 2015), likely contributing to overall nebkha shape.

The shape of the field nebkha, compared to those created in the wind tunnel, documents topographic stabilization by plants. Wind tunnel nebkha formed by erect grasses were ellipsoid, both here and in Charbonneau et al. (2021), forming around and behind plants in a full nebkha-shadow dune complex (Hesp and Smyth, 2017). Laboratory simulations of sand flow around objects (Hesp and Smyth, 2017) and backshore transport to artificial plants (Hesp et al., 2019) also produced tails. In contrast, field nebkha were circular around plant groups, distinctly lacking tails. In light of the aforementioned studies, this suggests tails are ephemeral in nature unless stabilized, with the area among plants theoretically stabilized both above and below ground. Nebkha width increased in both the field and wind tunnel with greater stem densities or larger areas of plant influence. Nebkha eccentricity and length were only related to stem density at high wind tunnel stem densities, where broader zones of influence produced greater elongation in downwind sheltered areas—a pattern that appears biologically irrelevant and underscores the importance of integrating laboratory and field observations (Dunham and Beaupre, 1988). These differences can suggest that the shapes of foredunes and nebkha complexes formed by the same species may not be directly related. In this context, topographic changes around plants in the main nebkha body are relevant for dune modeling, whereas the tails are ephemeral and contribute negligibly to overall topographic change.

Nebkha peak locations varied, with potential ecogeomorphic implications for where dune plants expand to offer new obstructions for topography building. In the wind tunnel, peaks were within the plants in the high-density treatments and downwind of the plants in the low- and medium-density treatments. All field nebkha peaks were in the plants, but as previously discussed, this may be because the tails or any downwind deposition were eroded. These results support flow deceleration with increasing density, resulting in increased deposition around plants—a finding observed in dunes as well as other canopied systems (e.g., Hesp, 1989; Gillies et al., 2014; Hesp et al., 2019; Finnigan, 2000). From a biological perspective, increasing stem densities may enhance deposition within the canopy, which is more likely to trigger the burial-vigor response characteristic of dune-building plants (Sykes and Wilson, 1990; Maun, 2009; Brown and Zinnert, 2018). This supports the notion that nebkha tails are ephemeral and largely separate from the main body from a dune evolution perspective. Paradoxically, while sand deposition within the plants promotes tillering (Disraeli, 1984; Maun, 2009) in the main nebkha body, downwind shielding and the resulting deposition may also facilitate stand expansion and subsequent nebkha growth in the lee of the main body (Maun, 2009; Gao et al., 2023). Recent findings by Gao et al. (2023) indicate that leeward tillering may occur or that leeward shielding reduces stress, allowing seedlings to establish. Together, our laboratory and field results suggest that burial responses and stem/leaf density influence nebkha size, although the processes driving nebkha shape evolution remain incompletely understood.

5 Conclusions

This work adds to the relatively limited number of quantitative studies examining plant morphology and dune topography at inception (McGuirk et al., 2022). We sought to better understand the underlying mechanisms of nebkha formation, whereas most studies of plant morphology examine the completed dune form and aim to infer the mechanistic history after the fact. Overall, the results highlight how plants stabilize the topography they support and provide insight into the plant morphological and density variables that most strongly predict topographic variability in nebkha size and shape metrics. Simulations of natural phenomena in laboratory settings are not always validated with field measurements to ensure the simulation aligns with reality, but they should be incorporated in a well-constructed experimental design (Dunham and Beaupre, 1988). This approach is supported by our work, where separate interpretations of laboratory and field data would have led to different conclusions than when analyzed together. In the wind tunnel, both the number of leaves and biomass were stronger predictors of nebkha volume and surface area than the number of stems, a commonly used metric in modeling efforts. In the field, however, these metrics are harder to measure than stem density, which was also a strong predictor of nebkha morphology and shape. This likely reflects the ecogeomorphic interactions between plant growth and sand burial. Our results regarding relationships between plant morphology metrics, allometry, and growing topographic variability at increasing plant densities are relevant for modeling efforts. Similarly, the demonstrated stabilizing role observed in *A. breviligulata* here, and presumably mirrored in other dune-builder species, highlights how the ecogeomorphic feedback between nebkha and plant can result in variability in topographies that might not be predictable when examining physical properties alone. These results showcase dune vegetation as ecosystem engineers with critical roles in the dune-building process and continued geomorphic evolution of dune systems, which need to be quantitatively represented in dune system modeling, management, and natural and nature-based project design.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

BC: Writing – original draft, Formal analysis, Methodology, Project administration, Data curation, Visualization, Resources, Investigation, Validation, Conceptualization, Writing – review & editing, Funding acquisition, Supervision. JZ: Validation, Supervision, Project administration, Data curation, Writing – review & editing, Methodology, Investigation, Writing – original draft, Funding acquisition, Resources, Visualization, Formal analysis. JW: Funding acquisition, Conceptualization, Writing – review & editing, Supervision, Methodology, Project administration, Resources, Investigation. AW: Project administration, Resources, Conceptualization, Supervision, Writing – review & editing, Investigation, Methodology. EM: Formal analysis, Investigation, Writing – review & editing, Methodology. KM: Formal analysis, Methodology, Investigation, Writing – review & editing. AS: Writing – original draft, Writing – review & editing, Investigation, Formal analysis, Methodology, Visualization, Validation. SD: Investigation, Validation, Methodology, Formal analysis, Writing – review & editing.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1691144/full#supplementary-material

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