



Lateral vegetation growth rates exert control on coastal foredune “hummockiness” and coalescing time

Evan B. Goldstein¹, Laura J. Moore¹, and Orencio Durán Vincent²

¹Department of Geological Sciences, University of North Carolina at Chapel Hill, 104 South Rd, Mitchell Hall, Chapel Hill, NC 27599, USA

²Department of Physical Sciences, Virginia Institute of Marine Science, College of William and Mary, P.O. Box 1346, Gloucester Point, Virginia 23062, USA

Correspondence to: Evan B. Goldstein (evan.goldstein@unc.edu)

Received: 9 January 2017 – Discussion started: 19 January 2017

Revised: 12 June 2017 – Accepted: 19 June 2017 – Published: 8 August 2017

Abstract. Coastal foredunes form along sandy, low-sloped coastlines and range in shape from continuous dune ridges to hummocky features, which are characterized by alongshore-variable dune crest elevations. Initially scattered dune-building plants and species that grow slowly in the lateral direction have been implicated as a cause of foredune “hummockiness”. Our goal in this work is to explore how the initial configuration of vegetation and vegetation growth characteristics control the development of hummocky coastal dunes including the maximum hummockiness of a given dune field. We find that given sufficient time and absent external forcing, hummocky foredunes coalesce to form continuous dune ridges. Model results yield a predictive rule for the timescale of coalescing and the height of the coalesced dune that depends on initial plant dispersal and two parameters that control the lateral and vertical growth of vegetation, respectively. Our findings agree with previous observational and conceptual work – whether or not hummockiness will be maintained depends on the timescale of coalescing relative to the recurrence interval of high-water events that reset dune building in low areas between hummocks. Additionally, our model reproduces the observed tendency for foredunes to be hummocky along the southeast coast of the US where lateral vegetation growth rates are slower and thus coalescing times are likely longer.

1 Introduction

Vegetated coastal foredunes display various morphologies in the alongshore direction, ranging on a spectrum from continuous to hummocky (i.e., varying in dune crest elevation). Examples of hummocky foredunes from Fort Fisher State Recreation Area, NC, US, are shown in Fig. 1. As described below, three explanations have been used (separately and in conjunction) to explain the existence of hummocky vegetated foredunes at a given site – initial configuration (i.e., spatial distribution) of plants, the rate of plant lateral expansion, and forcing or boundary conditions that control the pace and style of the biophysical feedback that gives rise to coastal dune growth.

New coastal dunes can be initiated when there is sufficient cross-shore width seaward of the existing foredune for plants to colonize (e.g., Hesp, 2002) or when elevated water levels destroy existing dunes. The presence of plants causes the deposition of sand (e.g., Hesp, 1989; Arens 1996; Kuriyama et al., 2005), leading to the formation of small dunes (Hesp, 1981; Pye, 1983). These incipient dunes have a typology that depends on the mechanism (plant, seed, rhizome, flotsam, etc.) and alongshore continuity of plant establishment (Hesp, 1989, 2002; Hesp and Walker, 2013), and variability in the location where plants initially grow can cause the formation of hummocky dunes. For example, Godfrey (1977) noted that in some settings vegetation initializes from drift lines (wrack), so discontinuous drift lines would cause an initially discontinuous or patchy development of dune plants (and therefore discontinuous dunes). Therefore, continuous



Figure 1. Ground-based photo of 1–2 m hummocky foredunes covered with *Uniola paniculata* at Fort Fisher State Recreation Area, NC, USA. (Note the person in the center left wearing black with a 2 m fixed height survey pole for scale). The hummocky foredunes are seaward of an older continuous dune ridge.

or discontinuous plant initialization (in the alongshore direction) can control the initial alongshore continuity of the foredune (continuous or hummocky).

Given a discontinuous initial plant configuration, the spaces between plant sites infill through the establishment of new plants and/or the lateral expansion of existing plants via rhizomes (e.g., Keijsers et al., 2015). In this way, plant dynamics can also control the existence of hummocky dunes. Some plants grow laterally faster than others – Godfrey and coworkers (Godfrey, 1977; Godfrey and Godfrey, 1973; Godfrey et al., 1979) found that dunes of the northeastern US had more continuous ridges than the hummocky isolated dunes of the southeastern US, which they attributed to differences in plant lateral growth rates for the dominant species in each region.

Geologic and geomorphic templates have also been used to explain variability in dune height. Low areas without dunes can remain low because of shell or coarse-grained lags, a high water table that causes plant stress, and/or climatic conditions such as cold temperatures prohibiting plant growth (e.g., Mountney and Russell, 2006, 2009; Wolner et al., 2013; Ruz and Hesp, 2014; Ruz et al., 2017a). Godfrey (1977) hypothesized that barrier island orientation relative to the prevailing winds exerts a control on foredune morphology, with taller dunes occurring when winds blow directly onshore, perpendicular to the shoreline. Sediment supply has also been implicated in causing alongshore dune height variability – specifically that a geomorphic and geologic framework influences the morphology of bars, beaches and sediment supply, therefore controlling the height of coastal dunes (Houser et al., 2008; Houser and Mathew, 2011).

These proposed mechanisms may explain the formation of hummocky dunes, though foredunes, once formed, are dynamic features, evolving and growing through time. Both mature hummocky dunes as well as continuous dune ridges may evolve from initially hummocky dunes. Ritchie and Penland (1988, 1990) developed a conceptual model of coastal foredune development following flattening of foredune topography by a storm, stating that a mature, continuous foredune can develop from a washover terrace given sufficient time. The transition from washover terrace (a low surface) to a continuous dune requires individual incipient dunes to grow and merge, eventually developing into a single continuous ridge. (Ritchie and Penland, 1988, 1990; Pye, 1983; Carter and Wilson, 1990; Davidson-Arnott and Fisher, 1992; Mathew et al., 2010; Montreuil et al., 2013). Such a conceptual model, consistent with widely observed field conditions, does not address why some initially hummocky foredunes coalesce to a linear foredune ridge, while others remain hummocky, having variable dune height in the alongshore direction, though Godfrey (1977) discussed the potential for recurring storm events to prevent the coalescing of hummocky dunes, even in locations where vegetation grows rapidly in the lateral direction.

In this contribution we develop and explore a model of coastal foredune growth and hummocky dune evolution – that is consistent with this previous work – to better understand the mechanisms behind the development of hummocky foredunes in the alongshore direction. Previous work by Moore et al. (2016) has investigated the cross-shore dynamics. Our work here is a quantitative investigation of several of the hypotheses of Godfrey (1977), notably that vegetation exerts a fundamental control on alongshore dune morphology. Our findings suggest that, given no preexisting template and suf-

ficient time prior to the occurrence of a storm event, along-shore hummocky dunes eventually coalesce to form a continuous coastal foredune ridge. Model results are well explained by a predictive rule for both the coalescing timescale and the height of the coalesced dune that depend on the initial spatial distribution of dune vegetation (which controls the location of incipient dunes) and the lateral and vertical growth rate of vegetation.

2 Eco-morphodynamic model

We use a recently developed model of coastal dunes that includes the lateral propagation of vegetation (Moore et al., 2016). This model is based on the coastal dune model of Durán and Moore (2013), itself based on previous models used to study a variety of dunes (e.g., Parteli et al., 2009; Durán and Herrmann, 2006; Durán et al., 2010). We briefly summarize the model and the vegetation formulation below.

Given an initial topography $h(x, y)$ and a vegetation field, the model computes the bed shear stress perturbation due to the presence of a non-flat topography (Weng et al., 1991), modified by a separation bubble (when there is flow separation; Kroy et al., 2002) and the subsequent shear stress reduction due to vegetation (Raupach et al., 1993). From the bed shear stress field, the local nonuniform sand flux and sand flux divergence is then computed at every position (Kroy et al., 2002; Durán et al., 2010) – this determines the temporal change in topography. Sand avalanching occurs down the steepest descent gradient when topography exceeds the angle of repose. After the topography has been updated, the change in the vegetation field is calculated (itself dependent on the local accretion/erosion rate).

We use a simplified version of the vegetation formulation presented in Moore et al. (2016), which is itself a modification of earlier models (Durán and Moore, 2013; Durán and Moore, 2015; Durán and Herrmann, 2006). We now present the simplified vegetation model and then discuss the physical interpretation for the two key sensitivity parameters.

The vegetation is parameterized by the cover fraction ρ_{veg} . The growth and propagation of vegetation is modeled by an advection equation of the form

$$\frac{d\rho_{\text{veg}}}{dt} = C |\nabla \rho_{\text{veg}}| + G_0 \rho_{\text{veg}} (1 - \rho_{\text{veg}}), \quad (1)$$

where the first term is the lateral propagation of vegetation at rate C due to rhizome growth and the second term is the local growth of biomass to maximum cover $\rho_{\text{veg}} = 1$. The intrinsic growth rate (G_0) is assumed to increase with the deposition rate $\max\left(\frac{dh}{dt}, 0\right)$ and to vanish near the shoreline ($x < L_{\text{veg}}$, where x is the distance to the shoreline). This is represented by a Heaviside function (Θ) that is unity when distance to the shoreline is sufficient for plant growth ($((x - L_{\text{veg}}) > 0)$) and 0 otherwise:

$$G_0 = H_v^{-1} \max\left(\frac{dh}{dt}, 0\right) \Theta(x - L_{\text{veg}}). \quad (2)$$

The lateral vegetation propagation rate C is also assumed to increase with the deposition rate and to vanish for steep slopes ($\tan\theta_c < |\nabla h|$; where θ_c is 15° and is based on field observations from Moore et al. (2016). This is represented by a Heaviside function (Θ) that is unity when the slope of the land surface is not beyond a threshold ($(\tan\theta_c - |\nabla h|) > 0$) and 0 otherwise:

$$C = \beta \max\left(\frac{dh}{dt}, 0\right) \Theta(\tan\theta_c - |\nabla h|). \quad (3)$$

This formulation of vegetation growth has two parameters that reflect the sensitivity of plants to changes in surface topography. First, the intrinsic growth rate (G_0) of vegetation in the logistic model is sensitive to plant burial, to simulate the behavior of dune-building plants that are stimulated by burial (e.g., Maun and Perumal, 1999; Maun, 2004; Gilbert and Ripley, 2010). This sensitivity term H_v , with dimensions of $[L]$, encodes the efficiency of vertical plant growth after burial. Larger H_v results in smaller values of G_0 and therefore slower plant growth, implying that burial is more effective at reducing plant basal area. Second, the lateral propagation of vegetation is sensitive to burial rate and the spatial gradient of cover density. Here, the dimensionless coefficient β can be interpreted as the efficiency of rhizome propagation after burial. A larger β results in faster plant propagation from place to place. Note that vertical growth rate relies exclusively on H_v , but lateral expansion relies on the spatial gradient of vegetation cover and therefore depends indirectly on H_v . If H_v is large, the vertical growth rate is slower and this will cascade to slowness in lateral growth rate (and vice versa).

The model is integrated into a two-dimensional grid (64 m alongshore and 100 m cross-shore with 1 m grid size) with periodic alongshore boundary conditions. The shoreline is set to a fixed location and vegetation is “seeded” in one band at an identical cross-shore location (40 m from the shoreline). There is a gap in this seeding located near the center of the model domain. The seeded “line” represents the development of vegetation around a drift line of wrack and is set at the seaward vegetation limit of plant growth (e.g., Durán and Moore, 2013; Kuriyama et al., 2005). As a consequence, vegetation does not propagate seaward in model experiments. We track the evolution of the unplanted gap as a single representative example of an initially unvegetated gap in an along-shore foredune. In the absence of observational data that reveal the degree to which dune-building vegetation establishes via seed versus lateral propagation, beyond the initial seeding we allow plants to establish in unvegetated cells only by lateral propagation, which can be thought of as encompassing establishment via both mechanisms.

Forcing conditions (i.e., undisturbed shear velocity $U^* = 0.35 \text{ m s}^{-1}$) are kept constant for all model experiments,

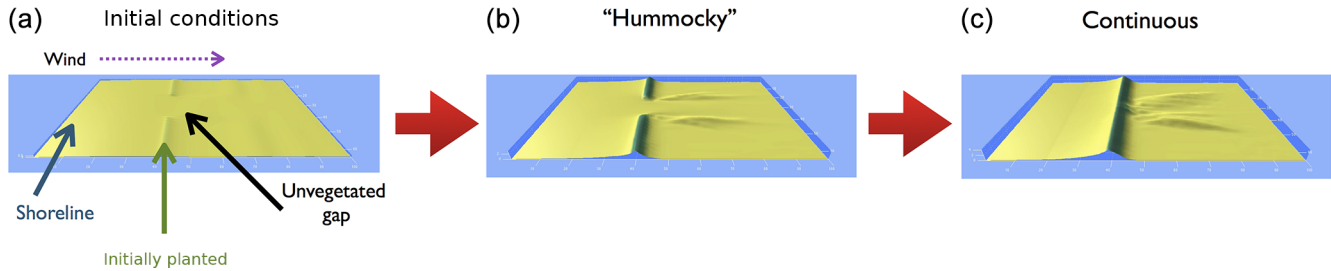


Figure 2. Numerical model definition sketch. (a) Initial conditions. (b) Formation of foredune and the infilling of the initially unvegetated gap. (c) The final continuous foredune ridge at the maximum theoretical dune height.

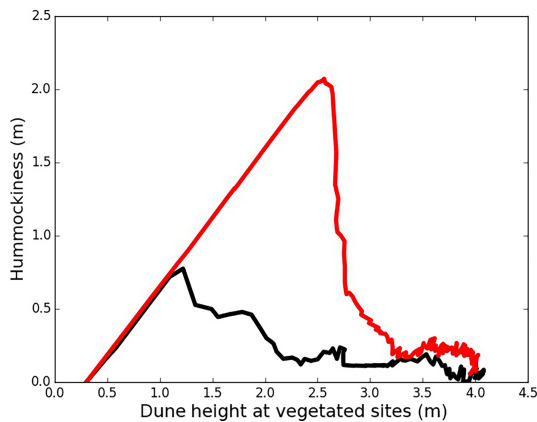


Figure 3. Phase plot of two numerical model experiments – the experiment in black has a larger growth parameter (β) and therefore faster lateral growth and lower hummockiness than the red experiment. All model iterations begin at (0.3, 0), reflecting the initial height of the planar sloping surface (0.3 m) at the location of the dune vegetation plantings. As the model iterates, the hummocky dunes develop, as vegetated sites grow in height more than unvegetated sites (which must wait for vegetation to grow before increasing in height). After vegetation propagates to these sites, a continuous foredune ridge develops and hummockiness reduces to zero. The maximum hummockiness and the trajectory through phase space is set by gap size (w), the vertical vegetation growth parameter (H_{veg}) and the lateral vegetation growth parameter (β).

but we vary the characteristics of the model vegetation to mimic variability in vertical and lateral plant growth rates. Experiments are shown for a range of vegetation lateral growth parameter values spanning over 1 order of magnitude ($10 \geq \beta \geq 0.1$), vertical growth parameter values spanning 1 order of magnitude ($0.4 \text{ m} \geq H_v \geq 0.04 \text{ m}$) and unvegetated gap sizes (10–20 m).

3 Results

From the initial condition, the model domain evolves to fill in the unvegetated gap (Fig. 2). Initially, the vegetation grows from the planted location in the vertical and lateral direction. Initially planted locations evolve into developed foredunes.

Within the unvegetated gap, only minor vertical elevation changes occur prior to the establishment of vegetation (via lateral propagation from the vegetated line). After the establishment of vegetation, the initially unvegetated sites become vegetated and grow vertically into a mature foredune. In the final model state, there is no evidence in the former dune gap to suggest that the site was once unvegetated. All model results yield a consistent maximum dune height of between 3.6 and 3.9 m.

We now focus on the lag in height between the unplanted gap and the surrounding planted dune – we refer to this difference as “hummockiness”, the difference in elevation between the dune under the initially planted area compared to the central location at the initially unvegetated gap. Hummockiness first increases with time as the initially unplanted site lags behind the planted locations in both vegetation cover and vertical elevation. Figure 3 is a partial phase plane for model results displaying hummockiness plotted against the height at the planted dune site. This partial phase space allows for the inspection of the trajectory of model results as they evolve from hummocky dunes to coalesced dunes. Initial trajectories all start at the (0.3, 0) mark (the beach is initially at an elevation of 0.3 m, with 0 hummockiness), and evolve in a clockwise fashion as the initially planted sites grow vertically at a faster rate than the unvegetated gap. After the propagation of vegetation into the initially unvegetated gap, the dune in the gap grows vertically at a rate faster than the vegetated sites (which has slowed in vertical growth as it nears the maximum theoretical dune height). This leads all trajectories toward a hummockiness of 0. Note that no timescale is shown in this phase space.

Two trajectories are shown in Fig. 3 to illustrate that the maximum hummockiness (the peak) is a function of H_v and β . As the lateral vegetation growth parameter (β) decreases from 10 to 0.1, the lateral growth rate slows down, which increases the variability in alongshore dune crest heights – hummockiness tends to increase (Fig. 4a). On the other hand, an increase in the vertical parameter H_v (plants are more sensitive to burial) slows the growth rate of vegetation, thereby increasing the maximum hummockiness (Fig. 4a). The unvegetated gap width also plays a role in controlling hum-

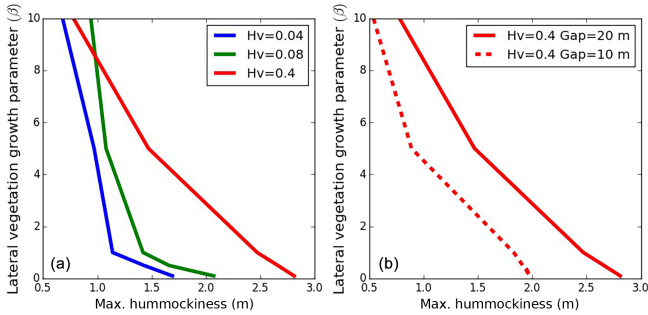


Figure 4. (a) Maximum hummockiness (m) as a function of H_v (vertical vegetation growth parameter) and β (lateral vegetation growth parameter). (b) Maximum hummockiness (m) as a function of β and unvegetated dune gap size.

mockiness as smaller initially unvegetated gap widths result in faster dune coalescing (Fig. 4b).

The general behavior of hummockiness and coalescing lends itself to heuristic analysis. Since the development of coastal dunes relies on the feedback between vegetation growth and aeolian sediment transport, maximum hummockiness occurs at the moment just before the center of a given gap transitions from unvegetated to vegetated (at which point the surrounding vegetated dunes have grown for some time). Therefore, maximum hummockiness is related to gap size and lateral propagation of plants – which from Eqs. (2) and (3) depends on β and H_v (via the spatial gradient in vegetation cover). For example, small gap size, high β (fast lateral growth of vegetation) and low H_v (fast vertical growth of vegetation) lead to low maximum hummockiness and vice versa. Results from all model simulations conform to this general behavior (Fig. 4a and b).

Gap size, lateral growth rate of vegetation and vertical plant sensitivity also impact model timescales for the along-shore coalescing of hummocky dunes. Maximum hummockiness occurs later (Fig. 5a) and dunes take longer to coalesce (Fig. 5b) with the decreasing lateral growth rate of vegetation, increasing plant sensitivity to burial and increasing gap size.

The lateral propagation rate (P) of the dune is defined as the time needed to propagate the crest a given lateral (along-shore) distance – the lateral spreading rate of the dune crest. This rate encompasses the spreading rate of the plant and the biophysical feedbacks that lead to dune growth. The lateral dune propagation rate is defined as $P = (0.5 \times W)/T_a$, where $(0.5 \times W)$ is the half width of the gap (W) and T_c is the time to coalescing. The half width of the gap is used since all model experiments include unvegetated gaps that fill in from both sides. Within the limits of the model experiments, results are well described by an equation of the form

$$P = K_1\beta + \frac{K_2}{H_v}, \quad (4)$$

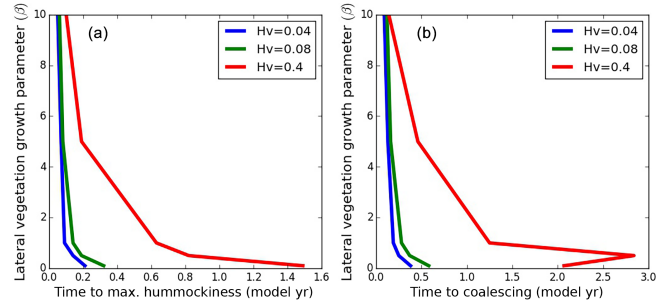


Figure 5. The impact of changes in the vertical vegetation growth parameter (H_v) and lateral vegetation growth parameter (β) on (a) the time of maximum hummockiness and (b) the time when coalescing occurs.

where K_1 and K_2 are dimensional parameters (6.5 m yr^{-1} and $1.9 \text{ m}^2 \text{ yr}^{-1}$). A high β (fast lateral growth of vegetation) and low H_v (fast vertical growth of vegetation) lead to fast lateral propagation of the dune crest. Figure 6 shows the modeled vs. predicted propagation times derived from Eq. (4).

Rewriting Eq. (4), the coalescing time can be written as

$$T_c = \frac{W}{K_1\beta + \frac{K_2}{H_v}} \text{ or } T_c = \frac{WH_v}{K_1\beta H_v + K_2}. \quad (5)$$

Following Durán and Moore (2013), we assume in the model a constant wind shear velocity ($U^* = 0.35 \text{ m s}^{-1}$) that represents typical wind conditions during dune growth. Because in reality conditions sufficient for transport do not occur all the time, Durán and Moore (2013) suggest that model time can be converted to real time by multiplying model time by a factor (r_t) that varies from 0 to 1 and represents the fraction of time there is no transport. Therefore, reduction in the flux of sand from beach to dune, because of low wind speeds, large grain sizes or narrow beaches, can be encapsulated through variation in r_t and has an effect similar to decreasing β and increasing H_v .

The height of the dune crest at the moment of coalescing (H_c) can be described by

$$H_c = H_{\max} \left(1 - e^{-\left(\frac{T_c}{T_f}\right)} \right) + Z, \quad (6)$$

where H_{\max} is maximum dune size, T_f is the formation time of the planted sites and Z is the initial beach elevation at the site of dune nucleation (here 0.3). Both H_{\max} and T_f are functions of the seaward vegetation growth limit as well as other relevant parameters, defined in Durán and Moore (2013). Figure 7 is the modeled vs. predicted dune height at coalescing calculated from Eq. (6).

4 Discussion and Implications

Godfrey (1977) and Godfrey et al. (1979) observed that foredunes change from irregular, hummocky dunes in the

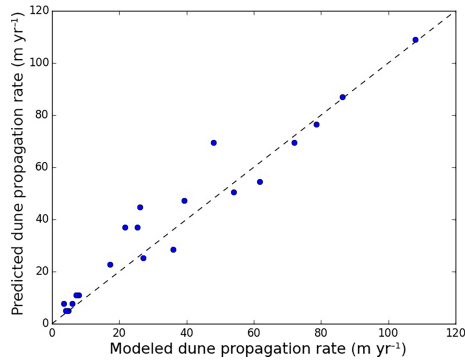


Figure 6. Modeled lateral dune propagation rate vs. predicted propagation rate from Eq. (4). Black line is 1 : 1.

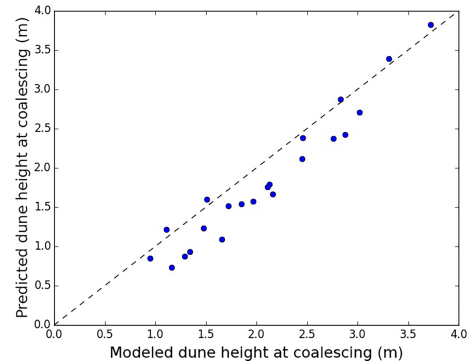


Figure 7. Modeled dune elevation at coalescing vs. predicted dune elevation at coalescing from Eq. (6). Black line is 1 : 1.

southeastern US to contiguous long-crested dunes in the northeastern US. This change in observed dune morphology is attributed to changes in foredune species dominance (Godfrey and Godfrey, 1973; van der Valk, 1975; Woodhouse et al., 1977; Godfrey, 1977; Godfrey et al., 1979). From Virginia northward, foredunes are dominated by *Amphiphila breviligulata* (American beachgrass), while south of Virginia, *Uniola paniculata* (sea oats) dominates foredunes (Wagner, 1964; Godfrey, 1977; Duncan and Duncan, 1987; Lonard et al., 2011). On the east coast, *A. breviligulata* and *U. paniculata* exhibit similar rates of vertical growth (including the adapted response of increasing growth rates when buried by moderate amounts of sand; Disraeli, 1984; Maun, 2004; Ehrenfeld, 1990; Lonard et al., 2011; Wagner, 1964). However, *A. breviligulata* and *U. paniculata* exhibit differences in rates of lateral growth: 1–3 and 0.6–1 m yr⁻¹ respectively (Woodhouse et al., 1977; Ehrenfeld, 1990; Lonard et al., 2011). The slower lateral growth rate of *U. paniculata* provides a potential explanation for the observation of hummocky dunes along the southeastern US coast. This species-specific control on dune morphology likely arises from differences in growth form, similar to observations that explain species-specific dune morphology along the US west coast (Hacker et al., 2012; Zarnetske et al., 2012). We can understand these differences in the context of model findings – though *A. breviligulata* and *U. paniculata* may have similar vertical growth characteristics (H_v is identical), their lateral growth rates (encoded here as β) are different, resulting in differences in dune hummockiness (Fig. 4a) and coalescing time (Fig. 5b). The dominant dune-building plant of the southeastern US has a slower lateral growth rate and therefore a longer coalescing time, likely leading to the increased prevalence of hummocky foredunes in this region. Evidence that even *U. paniculata* can form continuous dune ridges is present on Sapelo Island, Georgia, US. The lack of a major hurricane strike in this region (Bossak et al., 2014) is manifest in the continuous ridge topography even though the foredune is dominated by *U. paniculata* (Monge and Stallins, 2016; Stallins, 2005; Stallins and Parker, 2003).

However, the numerical finding that hummocky dunes always coalesce if given sufficient time suggests that differences in species-specific lateral growth rates alone are not sufficient to explain hummockiness that persists through time. A more complete explanation likely comes from combining our finding that coalescing time lengthens with decreasing lateral growth rate of the dominant dune-building grass, with the suggestion by several studies that low areas (and therefore hummocks) are maintained by overwash during high-water events (Godfrey, 1977; Hosier and Cleary, 1977; Ritchie and Penland, 1988). We can understand this using Eq. (7) – if the recurrence time for high-water events (R) is shorter than the coalescing time T_c , existing hummockiness will likely be maintained because low areas are more likely to be overwashed than adjacent higher dunes on either side. When this occurs, the dune-building process in the low areas is reset, increasing hummockiness until vegetation again becomes established in the overwashed zone. Conversely, if $R \gg T_c$, hummockiness will tend to decrease through time because there will be sufficient time between storms for coalescing to occur. Along the southeast US coast, it appears that $R < T_c$ given the previous observations that hummocky dunes are prevalent there and given the slow lateral growth rate of *U. paniculata*. Thus, although hummockiness appears to be an intrinsic feature of foredunes along the southeast coast of the US, model results suggest that hummockiness is actually a transient characteristic of foredunes that only becomes persistent when coalescing time is slow relative to the frequency of storms capable of resetting the dune-building process in the low areas between hummocks.

In the case of $R > T_c$, environmental conditions may be conducive to bistable dynamics in the alongshore direction – similar to the cross-shore models of Durán Vinent and Moore (2015) and Goldstein and Moore (2016) – with alternating stretches of dunes near the maximum height and lower intervening areas. In addition to storms, other factors such as a high water table, low sediment supply, grain size variability, development of shell lag and climatic conditions may also result in the suppression of the coalescing of coastal

foredunes (Mountney and Russell, 2006, 2009; Wolner et al., 2013; Hoonhout and de Vries, 2016; Ruz and Hesp, 2014; Ruz et al., 2017a). Feedbacks between the wind, dune vegetation and sediment transport that are specific to hummocky dunes may also alter the rates of coalescing (Barrineau and Ellis, 2013; Gillies et al., 2014), such as the development of high wind velocity regions located adjacent to hummocky dune forms (Hesp and Smyth, 2017). Work here does not address observations of older foredune ridges that lose their continuous morphology as a result of plant succession, erosion via rain and flow in rivulets, or trampling (Levin et al., 2009, 2017). Additionally the potential for lag between fast cross-shore beach recovery time vs. slower cross-shore vegetation recovery time (e.g., Castelle et al., 2017; Keijsers et al., 2016; Ruz et al., 2017b) could introduce novel dynamics that are not explored in this work.

There exists a potential for climate change to alter the range of the two dominant species of dune-building grasses along the US east coast. Plantings of *A. breviligulata* south of VA tend to die as a result of blight, pests, drought intolerance and intolerance of high temperature (Seneca, 1972; Singer et al., 1973; van der Valk, 1975; Woodhouse et al., 1977; Odum et al., 1987; Seliskar and Huettel, 1993). A warming climate might lead to further northward expansion of *U. paniculata*, which is currently restricted in northward extent by temperature (Seneca, 1972; Godfrey, 1977) – a northern expansion of the range has already been observed (Zinnert et al., 2011; Stalter and Lamont, 1990, 2000) and is being sought in selective breeding trials (USDA, 2013). Additionally, glasshouse experiments have reported that *A. breviligulata* is negatively impacted by competition with *U. paniculata* (Harris et al. 2017; Brown et al., 2017). Because changes in β between these two dune-building species affect variability in along-shore dune height, a change in the dominant dune-building species from *A. breviligulata* to *U. paniculata* has the potential to decrease the protection provided by dunes during high-water events. Changes in storminess may also impact the hummockiness of coastal foredunes, with an increase in storm intensity or frequency leading to a greater tendency for dunes to be hummocky and therefore to provide less protection to habitats behind them. Here, we have focused on the development of hummocky dunes from an initially flat condition, but Lazarus and Armstrong (2015) discuss the potential for storm events to create regularly spaced overwash throats (via self-organization) that could also set up hummocky dune topography. Although beyond the scope of this effort, observational work aimed at assessing the relationships among storm frequency/magnitude, species composition of dune-building vegetation and dune development (e.g., van Puijenbroek et al., 2017a, b) will be useful in addressing the future implications of model results presented here as climate change is anticipated to alter each of these factors.

Data availability. Model code used in this paper is available on the website of EBG and also by request.

Appendix A: Variables

Symbol	Variable name
h	Elevation
t	Time
ρ_{veg}	Vegetation cover fraction
C	Lateral vegetation propagation rate
G_0	Intrinsic growth rate
L_{veg}	Seaward limit of vegetation growth
θ_c	Critical topographic angle where vegetation stops expanding laterally
H_v	Vertical vegetation growth sensitivity term
β	Lateral vegetation growth sensitivity term
W	Half width of unvegetated gap (i.e., half width of plant spacing)
P	Lateral propagation rate of dune
T_c	Time to coalescing
K_1	Dimensional parameter
K_2	Dimensional parameter
H_{max}	Maximum dune size
T_f	Dune formation time at planted sites (time to H_{max})
Z	Initial beach elevation at site of dunes
R	Recurrence time for high-water events

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

Acknowledgements. Evan B. Goldstein thanks Theo Jass and Elsemarie deVries for valuable discussions regarding this work. We thank two anonymous reviewers for comments on the paper. Funding was provided by NSF-GLD (EAR-1324973) and the Virginia Coast Reserve Long-Term Ecological Research Program (NSF DEB-123773).

Edited by: Andreas Baas

Reviewed by: two anonymous referees

References

- Arens, S. M.: Patterns of sand transport on vegetated foredunes, *Geomorphology*, 17, 339–350, [https://doi.org/10.1016/0169-555X\(96\)00016-5](https://doi.org/10.1016/0169-555X(96)00016-5), 1996.
- Barrineau, C. P. and Ellis, J. T.: Sediment transport and wind flow around hummocks, *Aeolian Res.*, 8, 19–27, <https://doi.org/10.1016/j.aeolia.2012.10.002>, 2013.
- Bossak, B. H., Keihany, S. S., Welford, M. R., and Gibney, E. J.: Coastal Georgia Is Not Immune to Hurricane History, 1851–2012, *Southeast. Geogr.*, 54.3, 323–333, 2014.
- Brown, J. K., Zinnert, J. C., and Young, D. R.: Emergent interactions influence functional traits and success of dune building ecosystem engineers, *J. Plant Ecol.*, <https://doi.org/10.1093/jpe/rtx033>, in press, 2017.
- Carter, R. W. G. and Wilson, P.: The geomorphological, ecological and pedological development of coastal foredunes at Magilligan Point, Northern Ireland, *Coastal dunes: form and process*, John Wiley and Sons, London, 129–157, 1990.
- Castelle, B., Bujan, S., Ferreira, S., and Dodet, G.: Fore-dune morphological changes and beach recovery from the extreme 2013/2014 winter at a high-energy sandy coast, *Mar. Geol.*, 385, 41–55, 2017.
- Davidson-Arnott, R. G. and Fisher, J. D.: Spatial and temporal controls on overwash occurrence on a Great Lakes barrier spit, *Can. J. Earth Sci.*, 29, 102–117, <https://doi.org/10.1139/e92-011>, 1992.
- Disraeli, D. J.: The effect of sand deposits on the growth and morphology of *Ammophila breviligulata*, *J. Ecol.*, 72, 145–154, <https://doi.org/10.2307/2260010>, 1984.
- Duncan, W. H. and Duncan, M. B.: *The Smithsonian guide to sea-side plants of the Gulf and Atlantic Coasts from Louisiana to Massachusetts*, Smithsonian Institution Press, Washington, DC, 400 pp., 1987.
- Durán, O. and Herrmann, H. J.: Vegetation against dune mobility, *Phys. Rev. Lett.*, 97, 188001, <https://doi.org/10.1103/PhysRevLett.97.188001>, 2006.
- Durán, O. and Moore, L. J.: Vegetation controls on the maximum size of coastal dunes, *P. Natl. Acad. Sci.*, 110, 17217–17222, <https://doi.org/10.1073/pnas.1307580110>, 2013.
- Durán Vinent, O. and Moore, L. J.: Barrier island bistability induced by biophysical interactions, *Nature Climate Change*, 5, 158–162, <https://doi.org/10.1038/nclimate2474>, 2015.
- Durán, O., Parteli, E. J., and Herrmann, H. J.: A continuous model for sand dunes: Review, new developments and application to barchan dunes and barchan dune fields, *Earth Surf. Proc. Land.*, 35, 1591–1600, <https://doi.org/10.1002/esp.2070>, 2010.
- Ehrenfeld, J. G.: Dynamics and processes of barrier-island vegetation, *Rev. Aquat. Sci.*, 2, 437–480, 1990.
- Gilbert, M. E. and Ripley, B. S.: Resolving the differences in plant burial responses, *Austral Ecol.*, 35, 53–59, <https://doi.org/10.1111/j.1442-9993.2009.02011.x>, 2010.
- Gillies, J. A., Nield, J. M., and Nickling, W. G.: Wind speed and sediment transport recovery in the lee of a vegetated and denuded nebkha within a nebkha dune field, *Aeolian Research*, 12, 135–141, <https://doi.org/10.1016/j.aeolia.2013.12.005>, 2014.
- Godfrey, P. J.: Climate, plant response and development of dunes on barrier beaches along the US east coast, *Int. J. Biometeorol.*, 21, 203–215, 1977.
- Godfrey, P. J. and Godfrey, M. M.: Comparison of ecological and geomorphic interactions between altered and unaltered barrier island systems in North Carolina, in: *Coastal Geomorphology*, edited by: Coates, D. R., State University, New York, NY, 239–257, 1973.
- Godfrey, P. J., Leatherman S. P., and Zaremba, R.: A geobotanical approach to classification of barrier beach systems, in: *Barrier islands: From the Gulf of St. Lawrence to the Gulf of Mexico*, edited by: Leatherman, S. P., Academic Press, New York, NY, 99–126, 1979.
- Goldstein, E. B. and Moore, L. J.: Stability and bistability in a one-dimensional model of coastal fore-dune height, *J. Geophys. Res.-Earth*, 121, 964–977, <https://doi.org/10.1002/2015JF003783>, 2016.
- Hacker, S. D., Zarnetske, P., Seabloom, E., Ruggiero, P., Mull, J., Gerrity, S., and Jones, C.: Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact, *Oikos*, 121, 138–148, <https://doi.org/10.1111/j.1600-0706.2011.18887.x>, 2012.
- Harris, A. L., Zinnert, J. C., and Young, D. R.: Differential response of barrier island dune grasses to species interactions and burial, *Plant Ecol.*, 218, 609–619, <https://doi.org/10.1007/s11258-017-0715-0>, 2017.
- Hesp, P. A.: The formation of shadow dunes, *J. Sediment. Res.*, 51, 0101–0112, <https://doi.org/10.1306/212F7C1B-2B24-11D7-8648000102C1865D>, 1981.
- Hesp, P. A.: A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes, in: *Coastal Sand Dunes*, edited by: Gimingham, C. H., Ritchie, W., Willetts, B. B., and Willis, A. J., Proceedings of Royal Society, Edinburgh, 96B, 181–201, 1989.
- Hesp, P. A.: Fore-dunes and blowouts: initiation, geomorphology and dynamics, *Geomorphology*, 48, 245–268, [https://doi.org/10.1016/S0169-555X\(02\)00184-8](https://doi.org/10.1016/S0169-555X(02)00184-8), 2002.
- Hesp, P. A. and Smyth, T. A.: Nebkha flow dynamics and shadow dune formation, *Geomorphology*, 282, 27–38, <https://doi.org/10.1016/j.geomorph.2016.12.026>, 2017.
- Hesp, P. A. and Walker, I. J.: *Fundamentals of Aeolian Sediment Transport: Coastal dunes*. Ch. 11.17, Vol. 11: *Aeolian Geomorphology, Treatise on Geomorphology*, edited by: Shroder, J. F., Elsevier Academic Press, San Diego, Calif., 328–355, 2013.
- Hoonhout, B. M. and de Vries, S.: A process-based model for aeolian sediment transport and spatiotemporal varying sed-

- iment availability, *J. Geophys. Res.-Earth*, 121, 1555–1575, <https://doi.org/10.1002/2015JF003692>, 2016.
- Hosier, P. E. and Cleary, W. J.: Cyclic geomorphic patterns of washover on a barrier island in southeastern NC, *Environ. Geol.*, 2, 23–31, <https://doi.org/10.1007/BF02430662>, 1977.
- Houser, C. and Mathew, S.: Alongshore variation in foredune height in response to transport potential and sediment supply: South Padre Island, Texas, *Geomorphology*, 125, 62–72, <https://doi.org/10.1016/j.geomorph.2010.07.028>, 2011.
- Houser, C., Hapke, C., and Hamilton, S.: Controls on coastal dune morphology, shoreline erosion and barrier island response to extreme storms, *Geomorphology*, 100, 223–240, <https://doi.org/10.1016/j.geomorph.2007.12.007>, 2008.
- Keijsers, J. G. S., De Groot, A. V., and Riksen, M. J. P. M.: Vegetation and sedimentation on coastal foredunes, *Geomorphology*, 228, 723–734, <https://doi.org/10.1016/j.geomorph.2014.10.027>, 2015.
- Keijsers, J. G. S., De Groot, A. V., and Riksen, M. J. P. M.: Modeling the biogeomorphic evolution of coastal dunes in response to climate change, *J. Geophys. Res.-Earth*, 121, 1161–1181, <https://doi.org/10.1002/2015JF003815>, 2016.
- Lazarus, E. D. and Armstrong, S.: Self-organized pattern formation in coastal barrier washover deposits, *Geology*, 43, 363–366, <https://doi.org/10.1130/G36329.1>, 2015.
- Kroy, K., Sauermann, G., and Herrmann, H. J.: Minimal model for sand dunes, *Phys. Rev. Lett.*, 88, 054301, <https://doi.org/10.1103/PhysRevLett.88.054301>, 2002.
- Kuriyama, Y., Mochizuki, N., and Nakashima, T.: Influence of vegetation on aeolian sand transport rate from a backshore to a foredune at Hasaki, Japan, *Sedimentology*, 52, 1123–1132, <https://doi.org/10.1111/j.1365-3091.2005.00734.x>, 2005.
- Levin, N., Tsoar, H., Herrmann, H. J., Maia, L. P., and Claudino-Sales, V.: Modelling the formation of residual dune ridges behind barchan dunes in North-east Brazil, *Sedimentology*, 56, 1623–1641, <https://doi.org/10.1111/j.1365-3091.2009.01048.x>, 2009.
- Levin, N., Jablon, P. E., Phinn, S., and Collins, K.: Coastal dune activity and foredune formation on Moreton Island, Australia, 1944–2015, *Aeolian Research*, 25, 107–121, [doi:10.1016/j.aeolia.2017.03.005](https://doi.org/10.1016/j.aeolia.2017.03.005), 2017.
- Lonard, R. L., Judd, F. W., and Stalter, R.: Biological flora of coastal dunes and wetlands: *Uniola paniculata* L., *J. Coastal Res.*, 27, 984–993, <https://doi.org/10.2112/JCOASTRES-D-10-00167.1>, 2011.
- Mathew, S., Davidson-Arnott, R. G., and Ollerhead, J.: Evolution of a beach-dune system following a catastrophic storm overwash event: Greenwich Dunes, Prince Edward Island, 1936–2005, *Canadian J. Earth Sci.*, 47, 273–290, <https://doi.org/10.1139/E09-078>, 2010.
- Maun, M. A.: Burial of plants as a selection force in sand dunes, in: *Coastal Dunes: Ecology and Conservation*, edited by: Martínez, M. L. and Psuty, N. P., Springer-Verlag, Heidelberg, Germany, 119–136, 2004.
- Maun, M. A. and Perumal, J.: Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand, *Ecol. Lett.*, 2, 14–18, <https://doi.org/10.1046/j.1461-0248.1999.21048.x>, 1999.
- Monge, J. A. and Stallins, J. A.: Properties of dune topographic state space for six barrier islands of the US southeastern Atlantic coast, *Phys. Geogr.*, 37, 452–475, <https://doi.org/10.1080/02723646.2016.1230041>, 2016.
- Montreuil, A. L., Bullard, J. E., Chandler, J. H., and Millett, J.: Decadal and seasonal development of embryo dunes on an accreting macrotidal beach: North Lincolnshire, UK, *Earth Surf. Proc. Land.*, 38, 1851–1868, <https://doi.org/10.1002/esp.3432>, 2013.
- Moore, L. J., Vinent, O. D., and Ruggiero, P.: Vegetation control allows autocyclic formation of multiple dunes on prograding coasts, *Geology*, 44, 559–562, <https://doi.org/10.1130/G37778.1>, 2016.
- Mountney, N. P. and Russell, A. J.: Coastal aeolian dune development, Solheimasandur, southern Iceland, *Sediment. Geol.*, 192, 167–181, <https://doi.org/10.1016/j.sedgeo.2006.04.004>, 2006.
- Mountney, N. P. and Russell, A. J.: Aeolian dune-field development in a water table-controlled system: Skeiðarársandur, Southern Iceland, *Sedimentology*, 56, 2107–2131, <https://doi.org/10.1111/j.1365-3091.2009.01072.x>, 2009.
- Odum, W. E., Smith, T. J., and Dolan, R.: Suppression of natural disturbance: long-term ecological change of the outer banks of North Carolina, in: *Landscape Heterogeneity and Disturbance*, edited by: Turner, M. G., Springer-Verlag, New York, NY, 123–134, 1987.
- Parteli, E. J., Durán, O., Tsoar, H., Schwämmle, V., and Herrmann, H. J.: Dune formation under bimodal winds, *P. Natl. Acad. Sci. USA*, 106, 22085–22089, <https://doi.org/10.1073/pnas.0808646106>, 2009.
- Pye, K.: Coastal dunes, *Prog. Phys. Geog.*, 7, 531–557, <https://doi.org/10.1177/030913338300700403>, 1983.
- Raupach, M. R., Gillette, D. A., and Leys, J. F.: The effect of roughness elements on wind erosion threshold, *J. Geophys. Res.*, 98, 3023, <https://doi.org/10.1029/92JD01922>, 1993.
- Ritchie, W. and Penland, S.: Rapid dune changes associated with overwash processes on the deltaic coast of South Louisiana, *Mar. Geol.*, 81, 97–122, [https://doi.org/10.1016/0025-3227\(88\)90020-5](https://doi.org/10.1016/0025-3227(88)90020-5), 1988.
- Ritchie, W. and Penland, S.: Aeolian sand bodies of the south Louisiana coast, *Coastal dunes form and process*, John Wiley and Sons, London, 105–127, 1990.
- Ruz, M.-H. and Hesp, P. A.: *Geomorphology of high latitude coastal dunes*, edited by: *Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences*, edited by: Martini, I. P. and Wanless, H. R., The Geological Society London, Spec. Publications 388, <https://doi.org/10.1144/SP388.17>, 2014.
- Ruz, M. H., Héquette, A., and Marin, D.: Development of large nebkhas along an accreting macrotidal coastline, Northern France, *Aeolian Research*, 24, 1–14, <https://doi.org/10.1016/j.aeolia.2016.11.002>, 2017a.
- Ruz, M. H., Héquette, A., Marin, D., Sipka, V., Crapoulet, A., and Cartier, A.: Development of an incipient foredune field along a prograding macrotidal shoreline, northern France, *Géomorphologie: relief, processus, environnement*, 23, 37–50, <https://doi.org/10.4000/geomorphologie.11638>, 2017b.
- Seliskar, D. M. and Huettel, R. N.: Nematode Involvement in the Dieout of *Ammophila breviligulata* (Poaceae) on the Mid-Atlantic Coastal Dunes of the United States, *J. Coastal Res.*, 9, 97–103, 1993.
- Seneca, E. D.: Seedling Response to Salinity in Four Dune Grasses from the Outer Banks of North Carolina, *Ecology*, 53, 465–471, <https://doi.org/10.2307/1934234>, 1972.

- Singer, R., Lucas, L. T., and Warren, T. B.: The Marasmius-Blight Fungus, *Mycologia*, 65, 468–473, <https://doi.org/10.2307/3758118>, 1973.
- Stallins, J. A.: Stability domains in barrier island dune systems, *Ecol. Complex.*, 2, 410–430, <https://doi.org/10.1016/j.ecocom.2005.04.011>, 2005.
- Stallins, J. A. and Parker, A. J.: The influence of complex systems interactions on barrier island dune vegetation pattern and process, *Ann. Assoc. Am. Geogr.*, 93, 13–29, <https://doi.org/10.1111/1467-8306.93102>, 2003.
- Stalter, R. and Lamont, S. E.: The Vascular Flora of Assateague Island, Virginia, *B. Torrey Bot. Club*, 117, 48–56, <https://doi.org/10.2307/2997128>, 1990.
- Stalter, R. and Lamont, S. E.: Vascular Flora of Fisherman Island, Virginia, *J. Torrey Bot. Soc.*, 127, 324–332, <https://doi.org/10.2307/3088651>, 2000.
- USDA: Progress Report of Activities 2013, Cape May Plant Materials Center, available at: http://www.nrcs.usda.gov/Internet/FSE_PLANTMATERIALS/publications/njpmcra12114.pdf (last access: January 2017), 2013.
- van der Valk, A. G.: The Floristic Composition and Structure of Fore-dune Plant Communities of Cape Hatteras National Seashore, *Chesapeake Science*, 16, 115–126, 1975.
- van Puijenbroek, M. E. B., Limpens, J., De Groot, A. V., Riksen, M. J. P. M., Gleichman, M., Slim, P. A., van Dobben, H. F., and Berendse, F.: Embryo dune development drivers: beach morphology, growing season precipitation, and storms, *Earth Surf. Proc. Land.*, <https://doi.org/10.1002/esp.4144>, in press, 2017a.
- van Puijenbroek, M. E. B., Nolet, C., de Groot, A. V., Suomalainen, J. M., Riksen, M. J. P. M., Berendse, F., and Limpens, J.: Exploring the contributions of vegetation and dune size to early dune building using unmanned aerial vehicle (UAV)-imaging, *Biogeosciences Discuss.*, <https://doi.org/10.5194/bg-2017-170>, in review, 2017b.
- Wagner, R. H.: Ecology of *Uniola paniculata* in the dune-strand habitat of North Carolina, *Ecol. Monogr.*, 34, 79–96, <https://doi.org/10.2307/1948464>, 1964.
- Weng, W. S., Hunt, J. C. R., Carruthers, D. J., Warren, A., Wiggs, G. F. S., Livingstone, I., and Castro, I.: Air flow and sand transport over sand-dunes, *Aeolian Grain Transport, Acta Mech Supp.*, edited by: Barndorff-Nielsen, O. and Willetts, B., Springer, Vienna, Vol. 2, 1–22, 1991.
- Wolner, C. W. V., Moore, L. J., Young, D. R., Brantley, S. T., Bissett, S. N., and McBride, R. A.: Ecomorphodynamic feedbacks and barrier island response to disturbance: Insights from the Virginia Barrier Islands, Mid-Atlantic Bight, USA, *Geomorphology*, 199, 115–128, <https://doi.org/10.1016/j.geomorph.2013.03.035>, 2013.
- Woodhouse, W. W., Seneca, E. D., and Broome, S. W.: Effect of Species on Dune Grass Growth International, *Journal of Biometeorology*, 21, 256–266, 1977.
- Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B., and Cox, D.: Biophysical feedback mediates effects of invasive grasses on coastal dune shape, *Ecology*, 93, 1439–1450, <https://doi.org/10.1890/11-1112.1>, 2012.
- Zinnert, J. C., Shiflett, S. A., Vick, J. K., and Young, D. R.: Woody vegetative cover dynamics in response to recent climate change on an Atlantic Coast barrier island using Landsat TM imagery, *Geocarto International*, 26, 595–612, <https://doi.org/10.1080/10106049.2011.621031>, 2011.