Biophysical feedback mediates effects of invasive grasses on coastal dune shape

PHOEBE L. ZARNETSKE,[1,6] SALLY D. HACKER,[1] ERIC W. SEABLOOM,[2] PETER RUGGIERO,[3] JASON R. KILLIAN,[4] TIMOTHY B. MADDUX,[4] AND DANIEL COX[5]

[1]*Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, Oregon 97331 USA*
[2]*Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, Minnesota 55108 USA*
[3]*College of Earth, Oceanic, and Atmospheric Sciences, Oregon State University, 104 CEOAS Administration Building, Corvallis, Oregon 97331 USA*
[4]*O. H. Hinsdale Wave Research Laboratory, Oregon State University, 220 Owen Hall, Corvallis, Oregon 97331 USA*
[5]*Civil and Construction Engineering, Oregon State University, 220 Owen Hall, Corvallis, Oregon 97331 USA*

Abstract. Vegetation at the aquatic–terrestrial interface can alter landscape features through its growth and interactions with sediment and fluids. Even similar species may impart different effects due to variation in their interactions and feedbacks with the environment. Consequently, replacement of one engineering species by another can cause significant change in the physical environment. Here we investigate the species-specific ecological mechanisms influencing the geomorphology of U.S. Pacific Northwest coastal dunes. Over the last century, this system changed from open, shifting sand dunes with sparse vegetation (including native beach grass, *Elymus mollis*), to densely vegetated continuous foredune ridges resulting from the introduction and subsequent invasions of two nonnative grass species (*Ammophila arenaria* and *Ammophila breviligulata*), each of which is associated with different dune shapes and sediment supply rates along the coast. Here we propose a biophysical feedback responsible for differences in dune shape, and we investigate two, non-mutually exclusive ecological mechanisms for these differences: (1) species differ in their ability to capture sand and (2) species differ in their growth habit in response to sand deposition. To investigate sand capture, we used a moveable bed wind tunnel experiment and found that increasing tiller density increased sand capture efficiency and that, under different experimental densities, the native grass had higher sand capture efficiency compared to the *Ammophila* congeners. However, the greater densities of nonnative grasses under field conditions suggest that they have greater potential to capture more sand overall. We used a mesocosm experiment to look at plant growth responses to sand deposition and found that, in response to increasing sand supply rates, *A. arenaria* produced higher-density vertical tillers (characteristic of higher sand capture efficiency), while *A. breviligulata* and *E. mollis* responded with lower-density lateral tiller growth (characteristic of lower sand capture efficiency). Combined, these experiments provide evidence for a species-specific effect on coastal dune shape. Understanding how dominant ecosystem engineers, especially nonnative ones, differ in their interactions with abiotic factors is necessary to better parameterize coastal vulnerability models and inform management practices related to both coastal protection ecosystem services and ecosystem restoration.

Key words: Ammophila arenaria; Ammophila breviligulata; *ecomorphology; ecosystem engineer; ecosystem service;* Elymus mollis; *foredune; geomorphology; invasive species; sediment deposition; sediment transport; wind tunnel.*

INTRODUCTION

Aquatic–terrestrial interface environments are dynamic systems mediated by strong feedbacks among sediment (e.g., silt, mud, sand), a fluid medium (air or water), and vegetation. These biological and physical interactions and associated feedbacks modify system dynamics, leading to striking landscape features such as marsh platforms and channels, river topologies, and coastal dunes (e.g., Fisher et al. 2007, Murray et al. 2008; Gutierrez et al., *in press*). To understand how these features evolve, it is important to investigate the interplay between ecomorphology, an organism's form and function, and geomorphology, a physical landform and its function. Understanding this interplay is necessary to anticipate the ecological and physical changes that can occur with species invasions, land use alterations, and climate change (e.g., Hacker and Dethier 2006, Murray et al. 2008, Koch et al. 2009; Gutierrez et al., *in press*).

Species that engineer their habitat are particularly influential within interface environments because they physically modify a variety of abiotic materials through their own structure and growth habit (Jones et al. 1994, 2010). In turn, these species affect ecosystem services through their ability to modify the structure and function of these environments (Barbier et al. 2011). For example, vegetation in river systems can alter river geomorphology, specifically channel braiding patterns and bank structure, which in turn mediates effects of flow, increases bank stability, and reduces erosion: all key to future vegetation growth (Murray and Paola 2003, Tal and Paola 2010). Vegetation in estuarine and subtidal environments (e.g., seagrasses, cordgrasses, mangroves, algae) captures and stabilizes sediment, creating intertidal habitat complexity for diverse aquatic species (Duarte 2000, Langlois et al. 2003, Kirwan and Murray 2007, Aburto-Oropeza et al. 2008), and also attenuates waves through its structure, reducing coastal vulnerability (Danielsen et al. 2005, Barbier et al. 2008). Some of the best examples come from aeolian environments where vegetation (e.g., grasses, sedges, shrubs, forbs) captures wind-blown sediment, creating dunes (Hesp 1989, 1991, Arens et al. 2001; see Plate 1), and increasing coastal protection by reducing wave overtopping (Sallenger 2000). Dune-building grasses also affect biodiversity by speeding up ecological succession (Cowles 1899) and creating habitat complexity with xeric, exposed environments on dune crests adjacent to marshy, protected inter-dune swales (e.g., Snyder and Boss 2002).

Changes in the physical environment can also influence ecological changes in community composition, succession trajectories, and vegetation growth form (e.g., Corenblit et al. 2008, Murray et al. 2008, Bouma et al. 2010, Hacker et al. 2012). Variations in the frequency or intensity of physical forces such as wind velocity, sediment supply, and wave conditions, can lead to further modification of the physical and biological environment. Many of the landscape features we observe today are the result of numerous feedbacks between shifting species compositions and environmental conditions. Therefore, understanding the relative roles of biological vs. physical forces in the context of interface environments is necessary to make robust predictions about the future of these environments and the ecosystem services they provide under intense human influence and climate change.

Here we investigate a dune interface environment on the Pacific Northwest coast of North America that is highly invaded by nonnative grasses. In this system, sand, wind, ocean currents, waves, and vegetation interact to form landscape features that provide important functions and services along the coast. The vegetation in this system is primarily composed of three similar sand-binding beach grass species (two nonnative invaders, *Ammophila arenaria* and *Ammophila breviligulata*, and one native, *Elymus mollis*). The purposeful introduction and subsequent spread of *Ammophila* led to the development of vegetated and stabilized foredune ridges, replacing the open shifting dunes characterized by low-density native vegetation (Cooper 1958). Today, these foredune ridges protect coastal communities and infrastructure from wave overtopping and inundation (Sallenger 2000), but also have implications for native dune species and habitat conservation (Seabloom and Wiedemann 1994, Wiedemann and Pickart 1996, Zarnetske et al. 2010, Hacker et al. 2012).

The introductions of the two *Ammophila* species are linked to variability in dune geomorphology. Dunes dominated by *A. arenaria* tend to be taller and narrower than dunes dominated by *A. breviligulata* (Seabloom and Wiedemann 1994, Hacker et al. 2012). Species-specific morphological differences (e.g., extent of lateral spreading growth habit) suggest that the three species may vary with respect to their ability to capture sand and in their growth response to subsequent sand deposition (Hacker et al. 2012). However, the species-specific mechanisms involved in sand capture and foredune development have not yet been measured in this system.

These observations are potentially confounded by covarying gradients in sediment supply along the Oregon and Washington coast (Ruggiero et al. 2005, Kaminsky et al. 2010, Ruggiero et al. 2011, Hacker et al. 2012). Due to significant human interventions (e.g., jetties at the mouth of the Columbia River) and natural variability in forcing conditions, sediment supply in the region varies across a wide range of temporal and spatial scales. Along the northwest Oregon and southwest Washington coast, sediment supply to beaches and dunes is variable but mostly positive (Kaminsky et al. 2010). Here, the foredunes are typically low and wide, and *A. breviligulata* is the dominant foredune grass. In contrast, along the central and southern Oregon coast, sediment supply is lower and more stable, the foredunes are taller and narrower, and *A. arenaria* is the dominant foredune grass. Differences in sediment supply play a strong role in controlling coastal dune geomorphology (Hesp 1989, Psuty 1992). However, Hacker et al. (2012) found that, with similar sediment supply conditions (as measured by shoreline change rates [SCR] $\pm$ 2 m/yr, where SCR is taken as a proxy for sediment supply), dunes dominated by *A. arenaria* were taller than those dominated by *A. breviligulata*. The differences in dune shape documented in Hacker et al. (2012) imply that the two species differ in their ability to control dune shape.

Here we experimentally decouple the effects of species identity from sand supply to determine the ecological mechanisms responsible for the dune shape variability documented in Hacker et al. (2012). We propose the following biophysical feedback to explain differences in physical features (geomorphology) associated with different vegetation in aquatic–terrestrial interface environments (Fig. 1a), and specifically differences in dune

A

Geomorphology

B   Dune geomorphology

FIG. 1. (A) Conceptual diagram showing the important biophysical feedback between vegetation and sediment in aquatic–terrestrial interface systems. Vegetation characteristics (growth habit, density) and sediment supply form the basis for the sediment capture process, which is continually modified through feedbacks between vegetation growth and sediment capture. (B) Expected feedbacks and resulting dune geomorphology for this coastal dune study system based on data from Hacker et al. (2012) for native beach grass (*Elymus mollis*) and two nonnative grass species, (*Ammophila arenaria* and *Ammophila breviligulata*).
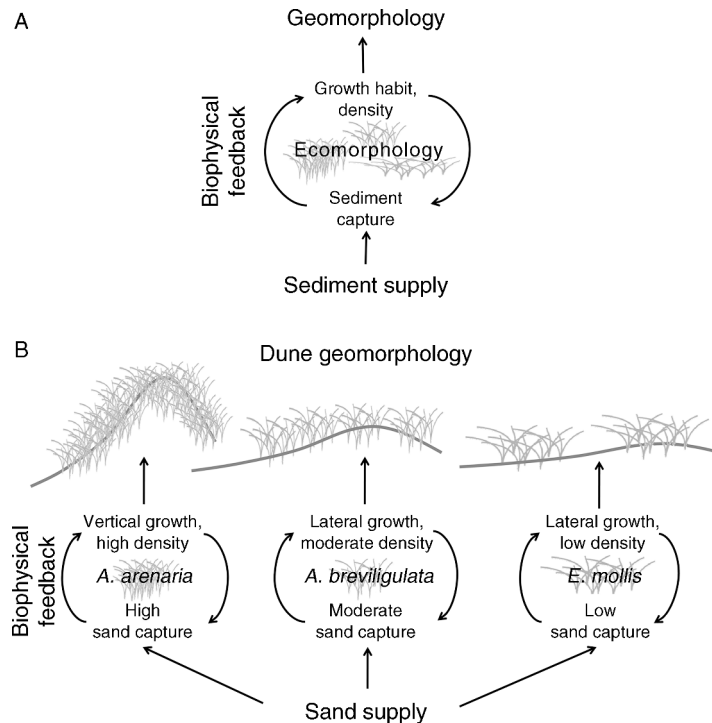
shape associated with the three species of grasses (Fig. 1b). First, differences in the form (growth habit and density) of species lead to initial differences in function (sediment capture ability) (Fig. 1a, ecomorphology). Second, species vary in their growth response to sediment deposition (Fig. 1a, growth habit, density). Third, deposition-induced changes in plant growth alter sediment capture (Fig. 1a, sediment capture). For this coastal dune system, we suggest that the feedback reinforces species-specific sediment capture ability, eventually resulting in differences in dune shape with *A. arenaria* building taller, narrower dunes, *A. breviligulata* building lower, wider dunes, and *E. mollis* building the shortest, widest dunes (Fig. 1b, Hacker et al. 2012).

Within the context of the feedback hypothesized above, we propose two non-mutually exclusive mechanisms: (1) species differ in their ability to capture sand and (2) species differ in their growth habit in response to sand deposition. We controlled sand supply in two experiments to investigate the ecological mechanisms important to dune shape. First, we used a moveable-bed wind tunnel to investigate the influence of species and tiller density on sand capture ability. Second, we used a mesocosm experiment to investigate the effects of sand supply on the growth response of species.

METHODS

We used three species of beach grasses in the study: *A. arenaria* (originally from Europe), *A. breviligulata* (originally from the east coast of North America and

the Great Lakes), and *Elymus mollis* (native to the Pacific coast of North America). Superficially, these species appear similar, but each differs in a variety of plant morphological and growth habitat features (Appendix A; also see Hacker et al. 2012). Specifically, *A. arenaria* has numerous tillers with stiff blades and grows in a tussock form while *A. breviligulata* has moderate numbers of tillers with more flaccid blades, and grows in a less clumped distribution. Finally, *E. mollis* produces few tillers with limp blades, and grows in a more even distribution.

Assessing sand capture efficiency

We constructed a moveable bed wind tunnel at the O. H. Hinsdale Wave Research Laboratory (HWRL), Corvallis, Oregon, USA, to perform sand capture efficiency experiments (see Appendix B: Fig. B1 for details on tunnel design and instrumentation). We collected 3000 adult tillers with intact rhizomes of each of the three grass species from the foredune face in Fort Stevens State Park, Clatsop Plains, Oregon (46°09′46″ N, 123°58′15″ W) in May 2008. We planted tillers in 1 m^2 × 0.3 m tall boxes filled with Oregon beach sand (median grain size: 0.24 mm) at HWRL. Species were planted at three density blocks (125, 250, and 500 tillers/ m^2; Appendix B: Fig. B2), reflecting a range of field densities on coastal foredune faces in the Pacific Northwest (Appendix A). In total, we used 28 boxes (three replicates per species by density combination, one sand-only box).

We controlled the abiotic components of the experiment (supply of dry beach sand, wind velocity), so that we could isolate biotic factors influencing the sand capture outcome. Prior to an experimental run, each box was leveled to its surface with dry beach sand and placed into the wind tunnel test section. Windward (upstream) of the test section, a loaded bed of dry sand simulated a ground-level backshore beach environment, and unidirectional air flow transported sand toward the test section (downstream). To assess sand capture during low vs. high wind conditions, we subjected each box to each of the following conditions, in random order: (1) 6 m/s wind for 4800 s and (2) 9.5 m/s wind for 1200 s. We used test runs to determine these speed and duration combinations such that total sediment supply from the upstream sand bed (in $kg \cdot m^{-1} \cdot s^{-1}$) remained approximately constant across each experimental run. We calculated the sand provided to each test box (s_{in}) as the difference between the mass of the upstream load of sand before and after each experimental run, ($s_0 - s_1$). The proportion of sand captured (sand capture efficiency, CE) in the test box was the box's sand gain (in kg) divided by the amount of sand provided to the box:

$$CE = (b_1 - b_0)/s_{in} \qquad (1)$$

where b_0 is initial box mass, and b_1 is final box mass. Therefore, $1 - CE$ is the proportion of sand transported through the test box. We computed the volumetric sediment transport rate per unit tunnel width (including void spaces), q, by dividing sand mass, s_{in}, by the bulk density of sand ($\rho_s = \sim 1600$ kg/m^3) per experimental run time (1200 or 4800 s) per tunnel width (1.0 m).

We normalized the sand capture efficiency for each experimental run such that we could compare results across species and densities, but within a wind velocity. We normalized CE to CE_{norm} (CE/q^*), by the nondimensional volumetric sediment transport rate (q^*):

$$q^* = \frac{q}{D\sqrt{\dfrac{\rho_s - \rho_a}{\rho_a}gD}} \qquad (2)$$

where q is the dimensional volumetric sediment transport rate, ρ_a is the density of air (1.2 kg/m^3), D is the median grain size (2.4×10^{-4} m), and g is the acceleration of gravity (9.81 m/s).

We also investigated another response variable: highest sand deposition, H_{max} (cm). We measured this metric from vertical sand deposition around the tillers. At the start of the experiment, we marked the sand level on each grass tiller with black permanent marker at the box surface, re-leveled prior to the second wind velocity experimental run. Following each experimental run, we remarked each tiller with a colored marker at the final sand level. We gridded off the boxes into 100 10-cm² sections after both runs. Then we clipped the tillers below the sand, and measured the gain or loss in sand level on up to three tillers per 10-cm² section, and calculated H_{max}.

We determined grass morphological characteristics for each box by measuring the longest blade, blades per tiller, and tiller circumference at initial sand level, for the same three tillers per 10 cm² section. For each box, we tallied the total number of tillers, and obtained dry biomass for plant material above the initial sand level by drying grasses in a 38°C drying room for 24 hours. Further, we measured the average proportional flexure of vegetation in each box and velocity combination by measuring the vertical height of three random blades bent by the wind and dividing this value by the natural standing height of those random blades prior to turning on the fan.

Assessing the effects of sand deposition:

We assessed the growth response of the three grass species to different levels of sand deposition with a mesocosm experiment. In spring 2007 at Hatfield Marine Science Center (Newport, Oregon), we planted 41 permeable geotextile bags with grass mixtures (all three species) or monocultures in 30 cm of beach sand. Bags were 1 m² at the base, and were expandable vertically to 2 m tall. Each bag was planted with 15 adult plants from the Clatsop Plains foredunes in Northwest Oregon. We planted the mixture bags with five plants per species and the monoculture bags with 15 plants of the same species. We defined a plant as one rhizome with varying numbers of tillers (e.g., range of tillers/m² in monocultures: 28–51 for *A. arenaria*, 23–28 for *A. breviligulata*, and 16–21 for *E. mollis*). This planting density reflects observed lower densities of beach grasses on the foredune face (see Appendix A), and provided enough open sand space within the bag for above and below ground growth over the course of the experiment. We allowed the plants to establish for three months prior to sand deposition. Of the 41 bags, we subjected eight mixture replicates (32 bags) to one of the treatments of vertical beach sand deposition (0, 0.15, 2.20, and 4.20 cm) every two weeks for 1 year (0, 3.6, 52.8, 100.8 cm deposition per year). Three monocultures of each species (nine bags) were each subjected to the non-zero deposition treatments. We measured sand level in the bags on a biweekly basis. Natural sand settling occurred and this resulted in vertical sand accumulation (or loss) rates of −3.0 cm/yr, 9.4 cm/yr, 31.0 cm/yr, and 46.3 cm/yr. These rates reflect a range of vertical growth rates observed on dunes in the U.S. Pacific Northwest from 1997 to 2009 (Ruggiero et al. 2005, 2011).

We measured growth responses for each species in each bag at the start and end of the experiment. These included tillers/m², tiller growth form (determined by the tiller angle from the main rhizome; a right angle was deemed more lateral spreading growth, an acute angle was deemed more vertical growth), total plant dry biomass/m², and rhizome internode lengths (a proxy for growth response to deposition, measured on the first 16 internodes on the rhizomes of four random tillers per species–bag combination).

TABLE 1.   Top linear mixed-effects models (LME) from the wind tunnel experiment (using maximum likelihood, ML).

Fixed-effects model	Model results	Statistics
Model A: all wind tunnel densities, $\ln(CE_{norm})$ $\ln(CE_{norm}) = 13.110 - 0.677$**[velocity]**$+ 0.003$**[tiller density]**$- 1.0978$[blade flexure]$- 1.066$**[AMAR]**$- 0.441$**[AMBR]**	df = 47, AIC = 30.800, ΔAIC = 1.988, LR = 0.002, $P = 0.962$	velocity $F_{1,47} = 999.55$, $P < 0.0001$; tiller density $F_{1,47} = 160.34$, $P < 0.001$; blade flexure $F_{1,47} = 5.74$, $P = 0.021$; species $F_{2,47} = 50.68$, $P < 0.0001$
Model B: density blocks per species, $\ln(CE_{norm})$ $\ln(CE_{norm}) = 14.374 - 0.724$**[velocity]**$- 3.511$[tiller cross-sectional area]$- 2.207$[blade flexure]$+ 9.260$[tiller cross-sectional area $\times$ blade flexure]	df = 12, $AIC_c = 4.485$, $\Delta AIC_c = 4.587$, LR = 7.777, $P = 0.021$	velocity $F_{1,12} = 858.17$, $P < 0.0001$; tiller cross-sectional area $F_{1,12} = 0.20$, $P = 0.664$; blade flexure $F_{1,12} = 2.02$, $P = 0.180$; tiller cross-sectional area $\times$ blade flexure $F_{1,12} = 1.19$, $P = 0.297$
Model C: all wind tunnel densities, $\ln(H_{max})$ $\ln(H_{max}) = 0.692 + 0.074$**[velocity]**$+ 0.0005$**[tiller density]**	df = 50, AIC = -19.471, ΔAIC = 0, LR = 1.993, $P = 0.158$	velocity $F_{1,50} = 25.920$, $P < 0.001$; tiller density $F_{1,50} = 8.749$, $P = 0.005$
Model D: density blocks per species, $\ln(H_{max})$ $\ln(H_{max}) = 1.883 + 0.087$**[velocity]**$- 0.227$**[blades per tiller]**	df = 14, $AIC_c = 2.087$, $\Delta AIC_c = 2.591$, LR = 5.953, $P = 0.015$	velocity $F_{1,14} = 10.382$, $P = 0.006$; blades per tiller $F_{1,14} = 6.012$, $P = 0.028$

Notes: Response metrics are given with the model name. Variables were transformed based on residual vs. fitted plots and normal quantile plots. All models contain a Gaussian link function, and non-correlated explanatory variables ($|r| < 0.6$). For top model selection, we used Akaike's information criterion (AIC) or AIC for small sample sizes (AIC_c; for $n < 30$) and likelihood ratio (LR) tests. For competing models within $\Delta AIC < 2$, we chose the most parsimonious model. Significant explanatory variables are shown in boldface type in each fixed effects model. All wind tunnel densities are data from all experimental units ($n = 27$); density blocks per species are data from experiment density blocks reflecting field densities (*Ammophila arenaria* [AMAR] 500 tillers/m^2, $n = 3$; *Ammophila breviligulata* [AMBR] 250 tillers/m^2, $n = 3$; and *Elymus mollis* [ELMO], 125 tillers/m^2, $n = 3$). For density blocks per species, $\ln(CE_{norm})$ was almost equivalent among species (mean $\pm$ SE; AMAR 6 m/s, 9.316 $\pm$ 0.063; AMAR 9.5 m/s, 6.811 $\pm$ 0.103; AMBR 6 m/s, 9.210 $\pm$ 0.061; AMBR 9.5 m/s, 6.689 $\pm$ 0.193; ELMO 6 m/s, 9.191 $\pm$ 0.063; ELMO 9.5 m/s, 6.474 $\pm$ 0.047), as was $\ln(H_{max})$ (AMAR 6 m/s, 1.315 $\pm$ 0.107; AMAR 9.5 m/s, 1.678 $\pm$ 0.094; AMBR 6 m/s, 1.104 $\pm$ 0.203; AMBR 9.5 m/s, 1.587 $\pm$ 0.147; ELMO 6 m/s, 1.314 $\pm$ 0.084; ELMO 9.5 m/s, 1.358 $\pm$ 0.130).

Statistical analyses

We used R version 2.12.1 for all statistical analyses (R Development Core Team 2010). Natural-log transformations were applied to variables to conform to the assumptions of linear regression (e.g., $\ln(CE_{norm})$). Only non-correlated explanatory variables ($|r| < 0.6$) were used together within one model.

To assess the mechanism responsible for varying sand capture efficiency, we ran mixed-effects models in R package nlme with associated ANOVAs (Pinheiro and Bates 2000, R Development Core Team 2010) on the sand capture efficiency response vs. explanatory variables including species identity, morphology, and density. Each box was run at two wind velocities. We included run number (one or two) as a random effect to account for this repeated use of the same box. Fixed effects always included a velocity term (6 m/s or 9.5 m/s; an example R code was lme($\ln(CE_{norm})$~velocity + species, random = ~1 | run order), and additional factors including species identity and plant morphological characteristics (means per tiller, or per box, see Appendix C). We used likelihood ratio tests and Akaike's information criterion (AIC) for top model selection (Burnham and Anderson 2002, Zuur et al. 2009). To explore the sand capture results further, we applied top experimental models to foredune tiller

densities (tillers/m^2) in the field to predict $\ln(CE_{norm})$ and H_{max} for field densities (densities were measured in 2009 on the foredune face; see Appendix A for methods). For these predictions, we used mean blade flexure values per species–velocity combination (Appendix C).

To assess evidence for the growth response mechanism, we ran mixed-effects models in R package nlme with associated ANOVAs on the plant growth response variables vs. explanatory variables from the sand deposition experiment (sand deposition rate (cm/yr), mixture or monoculture, and species). We offset the sand deposition treatment rates by +0.01 to remove zero (0.01, 3.61, 52.81, and 100.81 cm/yr). We accounted for species nested within the mixture bags (by specifying a random effect as: random = ~1 | bag/species), and always included a fixed effect of the mixture or monoculture factor.

RESULTS

Sand capture efficiency among grass species

Across all wind tunnel experiment densities, higher $\ln(CE_{norm})$ was associated with lower wind velocity (6 m/s), higher tiller density, lower blade flexure (i.e., more rigid tillers), and species identity (Table 1, model A; Fig. 2a). Blade flexure and tiller density were somewhat
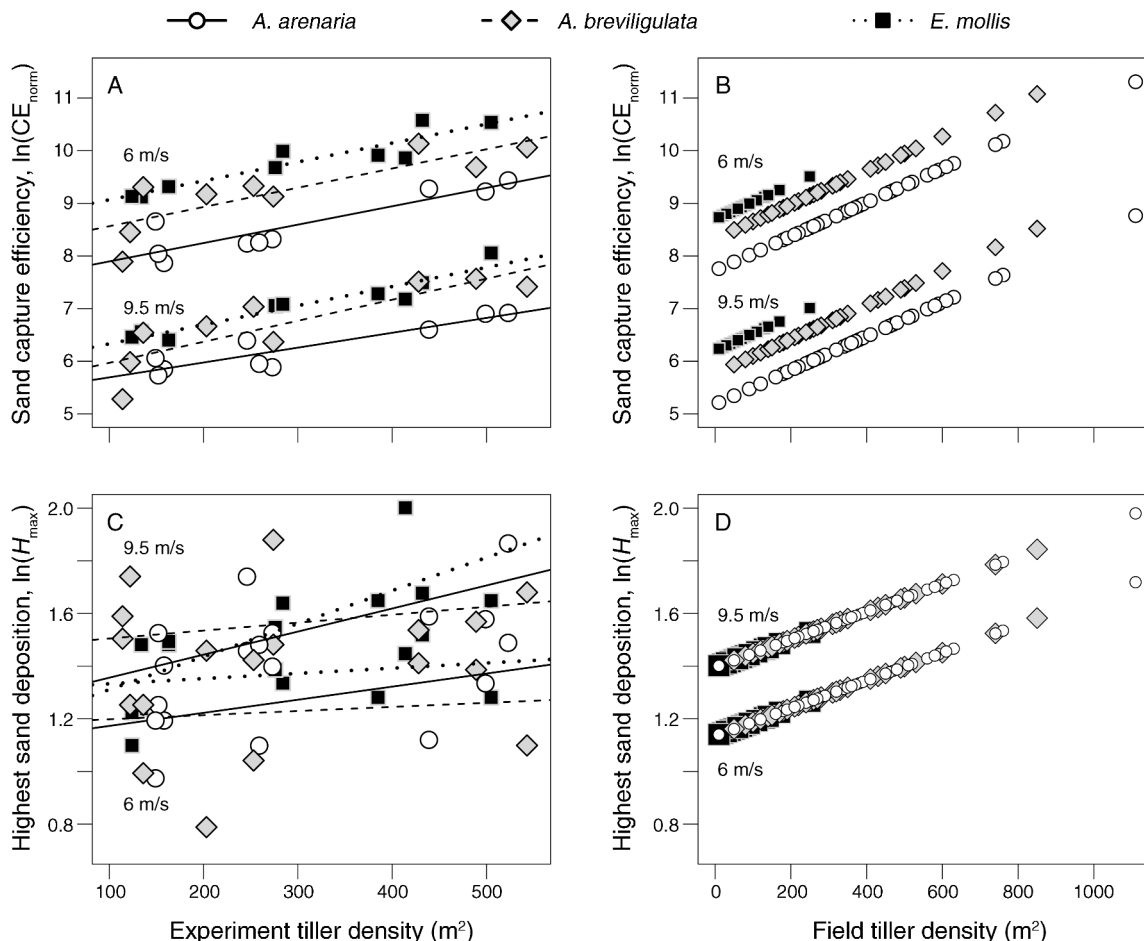
FIG. 2. For low (6 m/s) and high (9.5 m/s) wind velocity, (A) natural log of normalized sand capture efficiency, $\ln(CE_{norm})$, for grass species, across all experiment densities; (B) predictions of $\ln(CE_{norm})$ for maximum natural field tiller densities at 6 m/s and 9.5 m/s wind velocities, using Table 1, model A, applied to natural field densities on the foredune face (Appendix A), and mean blade flexure values from Appendix C; (C) maximum sand deposition level (cm), $\ln(H_{max})$, within each box, across all experiment densities (multiple regression lines are shown but species do not differ within velocity); (D) predictions of $\ln(H_{max})$ for maximum natural field tiller densities at 6 m/s and 9.5 m/s wind velocities, using Table 1, model C, applied to natural field densities on the foredune face (Appendix A). In panel B, the maximum CE_{norm} of A. arenaria is 0.27 and 0.28 times greater than A. breviligulata at 6 m/s and 9.5 m/s, respectively; and 5.1 and 4.8 times greater than E. mollis at 6 m/s and 9.5 m/s, respectively. In panel D, the maximum H_{max} of A. arenaria is 0.14 times greater than A. breviligulata at both velocities, and 0.57 times greater than E. mollis at both velocities.

negatively correlated at both wind velocities (6 m/s, $r = -0.488$, $P = 0.010$; 9.5 m/s, $r = -0.559$, $P = 0.002$). For a given density, $\ln(CE_{norm})$ was usually highest for E. mollis, followed by A. breviligulata and A. arenaria (Fig. 2a), but only differed between E. mollis and A. arenaria at each wind velocity (for the fixed effects models per wind velocity, R code $\ln(CE_{norm}) \sim$ species, the Tukey HSD test showed that only E. mollis and A. arenaria were different; $P = 0.001$ for 6m/s, $P = 0.024$ for 9.5m/s). Many of the plant structural characteristics differed by species (Appendix C) but did not explain the variation in $\ln(CE_{norm})$ across all experimental densities in mixed-effects models (Table 1). Tiller circumference, tiller cross-sectional area, biomass per tiller, overall above-sand biomass, blades per tiller, and tiller length were largest in E. mollis, moderate in A. breviligulata, and

smallest in A. arenaria (Appendix C). Blade flexure explained variation in $\ln(CE_{norm})$, even though it only differed between E. mollis and each Ammophila species at 6 m/s (Table 1, Appendix C). Predictions of $\ln(CE_{norm})$ from the top model of all wind tunnel experiment densities (Table 1, model A) applied to field tiller densities show that A. arenaria can achieve higher $\ln(CE_{norm})$ than the other species under the experimental time frames and velocities (Fig. 2b). For both wind velocities, the lowest vegetation density block (125 tillers/m²) for each species had substantially higher $\ln(CE_{norm})$ than the sand-only box (a Tukey HSD test on wind velocity showed that all sand–species comparisons had $P < 0.005$).

When we considered only wind tunnel experiment density blocks that represented field densities of species

(the density blocks per species are 125 tillers/m^2 for *E. mollis*, 250 tillers/m^2 for *A. breviligulata*, and 500 tillers/ m^2 for *A. arenaria*), ln(CE$_{norm}$) was almost equivalent, with *A. arenaria* slightly higher than *A. breviligulata* and *E. mollis* (Table 1). However, mixed-effects models for these densities showed that species identity did not explain ln(CE$_{norm}$) (for the fixed-effects model, R code ln(CE$_{norm}$)~velocity + species, ANOVA, species $F_{2,13}$ = 2.71, P = 0.108; a Tukey HSD test showed that all species comparisons had $P > 0.05$; $P = 0.085$ for *A. arenaria–E. mollis*; $P = 0.483$ for *A. breviligulata–E. mollis*; and $P = 0.502$ for *A. breviligulata–A. arenaria*). Instead, after accounting for velocity, blade flexure and tiller cross-sectional area were the most important (although not significant) variables (Table 1, model B).

Within the time frame of the experiment, the highest sand deposition (ln(H_{max})) was explained by higher wind velocity (9.5 m/s) and greater tiller density across all wind tunnel experiment densities (Table 1, model C; Fig. 2c). Predictions of ln(H_{max}) from the top model of all wind tunnel experiment densities (Table 1, model C) applied to field tiller densities show that *A. arenaria* can achieve higher ln(H_{max}) than the other species (Fig. 2d). For the density blocks per species, the ln(H_{max}) was slightly higher for *A. arenaria* compared to *A. breviligulata* and *E. mollis* (Table 1). However, ln(H_{max}) was not explained by species identity (for the fixed effects model: R code ln(H_{max})~velocity + species; ANOVA, species $F_{2,13}$ = 0.937, P = 0.417, the Tukey HSD test showed that all species comparisons had $P > 0.05$), but was explained by higher velocity and fewer blades per tiller (Table 1, model D). Blades per tiller were highest for *E. mollis*, then *A. arenaria* and *A. breviligulata*, and differed between *E. mollis* and each *Ammophila*, but not between the two *Ammophila* (Appendix C).

Growth response of grass species with different sand deposition regimes:

Growth habit and tiller density differed among species and sand deposition treatments, but not by mixture or monoculture (Table 2, Fig. 3). Final tiller density varied by species (Fig. 3a), with *A. arenaria* producing more tillers in response to higher sand deposition rates than *A. breviligulata* or *E. mollis*, both of which decreased tiller production with increasing sand deposition rate (Fig. 3a and b). Although all species increased biomass with increasing sand deposition rate, *A. arenaria* put on the most biomass at high sand deposition rates (Table 2, Fig. 3c). Vertical tiller growth was highest in *A. arenaria*, and increased relative to lateral tiller growth, especially as sand deposition rate increased (Table 2, Fig. 3d–f). Lateral tiller growth was greater than vertical tiller growth in both *A. breviligulata* and *E. mollis*, although lateral tiller density declined as sand deposition rate increased (Table 2, Fig. 3d–f). Finally, mean internode length (and maximum, not shown) increased for each species as sand deposition rate increased (Table 2, Fig. 3g).

DISCUSSION

Together, the wind tunnel and mesocosm experiment results provide evidence for a biophysical feedback between plant growth form and sand deposition, leading to the previously documented differences in the shapes of dunes dominated by the two grass invaders along the Pacific Northwest coast (Hacker et al. 2012). The dense, vertical growth habit of *A. arenaria* allows it to capture more sand, produce more vertical tillers, and build taller, narrower dunes, while the less dense, lateral growth habit of *A. breviligulata* is more suited for building shorter but wider dunes. Although *Ammophila arenaria* has been assumed to be a superior dune building species by coastal managers and engineers over the last century (as reflected in the widespread planting of *A. arenaria* around the world), this is the first study to directly measure the dune building capacities of multiple grass species exposed to similar environments. This is also the first study known to connect these mechanistic findings of species-specific sand capture and growth responses with observed gradients in sediment supply, vegetation, and dune geomorphology in the field (see Hacker et al. 2012).

Our wind tunnel experiment showed that the highest sand capture efficiencies (ln(CE$_{norm}$)) belong to the native *E. mollis* compared to the two invasive *Ammophila* species (Fig. 2a). Under these controlled tiller density manipulations, it appears that the tillers and biomass of *E. mollis* provide greater surface area, thus impacting the flow regime and impeding the movement of sand grains, resulting in greater sand deposition around the tillers (Appendix C). In support of this mechanism, *A. breviligulata* also has slightly thicker tillers and more biomass per tiller compared to *A. arenaria* (Appendix C) and it too has slightly higher ln(CE$_{norm}$) than its congener (Fig. 2a). However, these plant morphological characteristics did not explain differences in ln(CE$_{norm}$) as they were either not significant in top models, or did not appear in any competing top models (Table 1).

The effect of tiller morphology is greatly mitigated by tiller density. In fact, except for wind velocity (where decreased velocity resulted in greater ln(CE$_{norm}$)), tiller density was the most important explanatory variable influencing sand capture efficiency (Table 1, model A; Fig. 2a). Another important variable was blade flexure, with lower flexure (stiffer blades) resulting in greater overall capture efficiencies (Table 1, model A). This result makes sense because blade flexure is likely a consequence of tiller density, where surrounding blades provide increased structural support (Appendix A, Appendix B: Fig. B2). Our finding that higher vegetation density increases sediment capture and deposition agrees with other research (Hesp 1989, Arens et al. 2001, Murray et al. 2008, Burri et al. 2011). Nonetheless, for a given density used in the wind tunnel experiment, the native grass is slightly better at capturing sand than the two invasive species.

TABLE 2. Top linear mixed-effects models (LME) from the mesocosm experiment (using maximum likelihood, ML).

Fixed-effects model	Model results	Statistics
Model A: ln(final tiller density)		
M1: ln(tiller density) = 4.291 − 0.029[mono] + 1.143[AMAR] + 0.637[AMBR] − 0.002[sand]	df = 100, AIC = 154.09, ΔAIC = 0, LR = 2.309, P = 0.129	MixMono $F_{1,38}$ = 0.095, P = 0.758; species $F_{2,62}$ = 50.108, P < 0.001; sand $F_{1,38}$ = 2.223, P = 0.144
M2: ln(tiller density) = 4.224 − 0.052[mono] + 1.143[AMAR] + 0.637[AMBR]	df = 101, AIC = 154.40, ΔAIC = 0.31, LR = 2.309, P = 0.129	MixMono $F_{1,39}$ = 0.095, P = 0.759; species $F_{2,62}$ = 49.508, P < 0.001
Model B: ln(relative gain in tiller density)		
ln(tiller density) = 0.656 − 0.031[mono] + 0.485[AMAR] + 0.526[AMBR]	df = 101, AIC = 232.10, ΔAIC = 0, LR = 0.619, P = 0.432	MixMono $F_{1,39}$ = 0.016, P = 0.901; species $F_{2,62}$ = 6.170, P = 0.004
Model C: ln(relative gain in dry biomass)		
ln(biomass) = 3.420 + 0.045[mono] + 0.362[AMAR] + 0.320[AMBR] + 0.004[sand]	df = 100, AIC = 141.88, ΔAIC = 0, LR = 6.697, P = 0.010	MixMono $F_{1,38}$ = 0.304, P = 0.585; species $F_{2,62}$ = 8.961, P < 0.001; sand $F_{1,38}$ = 6.784, P = 0.013
Model D: ln(final lateral tiller density)		
ln(lateral tiller density) = 2.844 + 0.311[mono] − 1.741[AMAR] + 0.053[AMBR]	df = 101, AIC = 313.90, ΔAIC = 0, LR = 0.614, P = 0.433	MixMono $F_{1, 101}$ = 0.692, P = 0.411; species $F_{2, 101}$ = 41.869, P < 0.001
Model E: ln(final vertical tiller density)		
ln(vertical tiller density) = 3.527 + 0.056[mono] + 1.182[AMAR] + 1.094[AMBR]	df = 101, AIC = 269.54, ΔAIC = 0, LR = 0.815, P = 0.367	MixMono $F_{1,39}$ = 0.037, P = 0.849; species $F_{2,62}$ = 46.707, P < 0.001
Model F: ln(gain in no. vertical tillers/gain in no. lateral tillers)		
M1: ln(gain in verticals/gain in laterals) = 0.761 + 0.513[mono] + 0.970[AMAR] + 0.864[AMBR] − 0.002[sand] + 0.014[AMAR × sand] − 0.003 [AMBR × sand]	df = 98, AIC = 357.49, ΔAIC = 0 , LR = 6.863, P = 0.076	MixMono $F_{1,38}$ = 1.497, P = 0.229; species $F_{2,60}$ = 13.238, P < 0.001; sand $F_{1,38}$ = 0.265, P = 0.607; species × sand $F_{2,60}$ = 3.177, P = 0.049
M2: ln(gain in verticals/gain in laterals) = 0.675 + 0.533[mono] + 1.536[AMAR] + 0.737[AMBR]	df = 101, AIC = 358.36, ΔAIC = 0.87, LR = 6.863, P = 0.076	MixMono $F_{1,39}$ = 1.445, P = 0.232; species $F_{2,62}$ = 12.780, P < 0.001
Model G: mean internode length (cm)		
internode length = 3.920 + 0.287[mono] + 0.013[sand]	df = 99, AIC = 326.44, ΔAIC = 0, LR = 2.258, P = 0.323	MixMono $F_{1,38}$ = 1.342, P = 0.254; sand $F_{1,38}$ = 22.332, P < 0.001

Notes: Response metrics are given with the model name. The mesocosm bag was treated as a random effect, with species nested within bag (R code was random = ~1 | bag/species). We applied response or explanatory transformations based on residual investigations (residual vs. fitted plots, normal quantile plots). Models contain only non-correlated explanatory variables ($|r|$ < 0.6). For top model selection, we used AIC (AIC$_c$ for n < 30) and likelihood ratio (LR) tests. Significant explanatory variables are shown in boldface type in each fixed-effects model. Letters preceding response metrics align with Fig. 3 plot letters. Multiple top models are shown as M1 and M2. MixMono is a factor, where "mono" is a monoculture. In models, sand is the treatment deposition (cm/yr), where 0.01 was added to each deposition value (0.01, 3.61, 52.81 100.81 cm/yr).

Despite the differences in sand capture, our model predicts that the two invasive grasses are capable of much higher sand capture efficiencies (3.7–5.1 times at 6 m/s and 3.5–4.8 times at 9.5 m/s) compared to the native grass. This is because *A. arenaria* and *A. breviligulata* both have much higher tiller densities in the field than *E. mollis* (Fig. 2b). For example, *E. mollis* can reach as high as 250 tillers/m^2 on the foredune face, but lower tiller densities are more common (44.45 ± 5.04 [mean ± SE], Appendix A), suggesting that it never reaches densities in which it can capture as much sand as the two congeners (Fig. 2b). On the other hand, the field densities of *A. arenaria* tillers can be high, upward of 1110 tillers/m^2 (203.08 ± 27.26), and thus potentially allowing *A. arenaria* to capture more sand than the other species under natural conditions (Fig. 2b).

Moreover, our field data also suggest that the differences in natural growth form could play an important role in sand capture efficiencies being higher for *A. arenaria*. While random tiller placement in the wind tunnel allowed us to separate the effect of species from tiller density, this tiller arrangement does not necessarily reflect the natural growth form in the field. In nature, *A. arenaria* develops a high-density, tussock-like, tiller growth, where multiple vertical tillers grow from proximal rhizomes in a clumped manner (Appendix C; see also Greig-Smith et al. 1947, Gemmell et al. 1953, Huiskes 1979). Conversely, *A. breviligulata* has a lower density, lateral, and less-clumped tiller growth pattern, especially in regions of high sediment supply (Appendix C; see also Maun and Lapierre 1984, Baye 1990). Thus, these differences in growth form could create variability
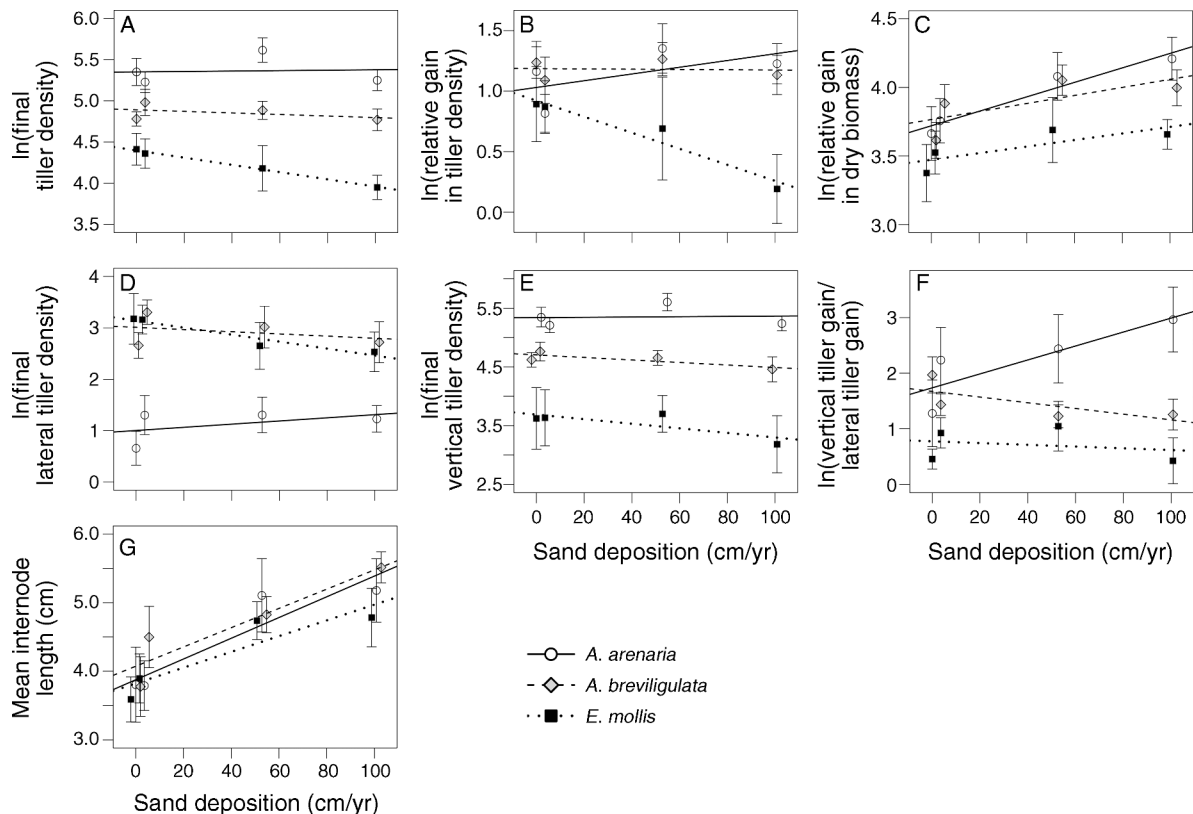
Fig. 3. Grass species growth responses from sediment deposition treatments in the mesocosm experiment (0, 3.6, 52.8, 100.8 cm deposition per year). Plant data from the experiment are scaled to 1 m^2. Data are ln-transformed; all data points are mean $\pm$ SE. (A) final tiller density; (B) relative gain in tiller density, measured as ([final tillers/m^2] − [initial tillers/m^2])/[initial tillers/m^2]); (C) relative gain in dry biomass, measured as ([final dry biomass/m^2] − [initial dry biomass/m^2])/[initial dry biomass/m^2]); (D) final lateral tiller density; (E) final vertical tiller density; (F) ratio of gain in number of vertical tillers to gain in number of lateral tillers, and (G) mean internode length. See Table 2 for model statistics matching these figures.

in capture efficiencies in the field that are not reflected in the wind tunnel. Further, wind tunnel studies with cylinder arrays (rather than living plants) support our hypothesis for larger differences in species-specific sand capture, based on differences in tiller morphology. Experiments with high cylinder aspect ratios (height/diameter), analogous to *A. arenaria* tillers, require lower densities to achieve the same sand capture as cylinders with lower aspect ratios. Within higher aspect ratio cylinder arrays, higher threshold wind velocities are necessary to mobilize sand (Musick et al. 1996). Conversely, an array with lower cylinder aspect ratios, analogous to *A. breviligulata* tillers or, with even lower aspect ratios, *E. mollis* tillers, requires higher densities to achieve the same sand capture. Thus at higher field densities, the greater tiller aspect ratio of *A. arenaria*, combined with its vertical growth, should yield more efficient sand capture than natural densities of *A. breviligulata* or *E. mollis*.

Sand capture is one measure of how the grasses may influence dune geomorphology, but growth response to sand deposition is potentially more important. The mesocosm experiment shows that species differ in their growth response to sand deposition rates. Across sand deposition rates, *A. arenaria* outpaced *A. breviligulata* and *E. mollis* in tiller growth (especially in vertical tiller growth) and in biomass (Table 2, Fig. 3). All species increased their internode lengths with increasing sand deposition rate (Table 2, Fig. 3g). However, while the increased internode length of *A. arenaria* contributes to vertical growth in tussock-like form, the increased internode lengths of *A. breviligulata* and *E. mollis*, combined with their lower tiller density and higher proportion of lateral tillers, shows that their growth strategy is distinctly horizontal and spreading (Table 2, Fig. 3).

The combination of species-specific growth response to sand deposition, differences in tiller density and arrangement in nature, and projected sand capture should all reinforce subtle differences in the dune growth biophysical feedback, leading to differences in dune shape (Fig. 1b). Specifically, taller, narrower dunes along the Pacific Northwest coast are dominated by high-density, vertical *A. arenaria* tillers and typically occur in regions of fairly neutral shoreline change rates (Hacker et al. 2012). Under these conditions, a relatively neutral overall beach sediment budget, combined with sediment available for transport to the foredune, leads

PLATE 1. A coastal foredune on South Beach, near Newport, Oregon, USA. The strong biophysical feedback between wind-blown sand and the growth of *Ammophila arenaria* leads to the formation of a small incipient dune seen in the foreground, and eventually a large foredune seen in the background. Photo credit: P. L. Zarnetske.

to long-term sand accumulation on the dune (Psuty 1993). Wind-blown sand is captured on the foredune face by high-density, vertical *A. arenaria* tillers, which increase the sand transport threshold wind velocity, thus promoting sand deposition (Bagnold 1941, Lancaster and Baas 1998). The dune elevation increases with the positive feedback of continued sand capture and deposition, and a growth response of more vertical, tussock-like tillers that result in higher tiller density per area (Fig. 1b: see also Baye 1990, Maun 1998, de M. Luna et al. 2011). Conversely, lower, wider dunes are dominated by lower-density, lateral *A. breviligulata* tillers and typically occur in regions of positive shoreline change rates. Under these conditions, the shoreline extends seaward as large amounts of sand deposit on the beach, and wind-blown sand is carried farther inland due to the relatively minor obstruction of a low elevation foredune (Psuty 1993). Sand that does deposit on the dune encounters lower density vegetation, with less efficient capture ability (Bagnold 1941, Lancaster and Baas 1998). This high sediment supply, in turn, promotes a positive feedback with *A. breviligulata* to send out lateral tillers (Fig. 3d and e), increasing the amount of sediment being captured on the front face of the foredunes, resulting in wide foredunes that are lower than those dominated by *A. arenaria* (Fig. 1b; see also

Baye 1990, Hacker et al. 2012). Foredunes dominated by *A. breviligulata* are also lower because *A. breviligulata* has a lower tiller density per area than *A. arenaria* (Fig. 3a), with the associated lower sand capture efficiency (Fig. 2b). Although no *E. mollis* dominant foredunes exist along the coast, our results show that its low density, lateral tiller growth would yield low, broad foredunes across sediment supply rates (Fig. 1b).

Our findings suggest that the growth response of *A. breviligulata* to sediment supply, and the resulting low and wide dunes, are causes for concern for dune restoration and coastal vulnerability. Its apparent constant growth across sediment supply gradients (Table 2, Fig. 3) suggests that it is more indifferent to the range of sediment supplies than *A. arenaria*, and thus may be more difficult to control. Further, our field data show that through time, *A. breviligulata* has displaced *A. arenaria* along the Pacific Northwest coast (Seabloom and Wiedemann 1994, Hacker et al. 2012, Zarnetske 2011). Thus, *A. breviligulata* could have negative effects on coastal protection because it grows consistently across multiple sediment supply regimes, it has the ability to generate shorter dunes, and has been overtaking *A. arenaria* as the dominant beach grass along the coast (Zarnetske 2011, Hacker et al. 2012). Further, it could have negative effects on native species

conservation as native richness is lower when *A. breviligulata* is dominant (Hacker et al. 2012).

Our study used sand capture and sand deposition experiments to characterize the ecological mechanisms responsible for variation in foredune shape along the Pacific Northwest coast. Our results suggest that a species-specific biophysical feedback occurs between sand deposition, growth habit, and growth-habit-mediated sand capture efficiency, resulting in distinctly different dune geomorphologies. This knowledge can be incorporated into dune-building models (Pattanapol et al. 2008, de M. Luna et al. 2011) that expand the plant-scale sediment capture mechanisms to ecosystem-scale dynamics. These models in turn, can assist in coastal management, restoration, and engineering decisions through the resulting dune geomorphology predictions. Given that vegetation plays an important role in foredune evolution, it will also be important to include vegetation parameters in models predicting risk to wave overtopping and coastal vulnerability, especially in light of the range of possible climate change influences on sea level rise (Bindoff et al. 2007) and storm frequency and intensity (Komar et al. 2009). More generally, understanding how dominant ecosystem engineers differ in their interactions with abiotic factors is necessary to make predictions of changes to physical environmental features, to guide ecosystem restoration efforts, and to inform decision-making that balances the need for ecosystem services and ecosystem conservation.

LITERATURE CITED

Aburto-Oropeza, O., E. Ezcurra, G. Danemann, V. c. Valdez, J. Murray, and E. Sala. 2008. Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences USA 105:10456–10459.

Arens, S. M., A. C. W. Baas, J. H. Van Boxel, and C. Kalkman. 2001. Influence of reed stem density on foredune development. Earth Surface Processes and Landforms 26:1161–1176.

Bagnold, R. A. 1941. The physics of blown sand and desert dunes. Methuen, London, UK.

Barbier, E., S. D. Hacker, C. Kennedy, E. Koch, B. Silliman, and A. D. Stier. 2011. The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193.

Barbier, E. B., et al. 2008. Coastal ecosystem-based management with nonlinear ecological functions and values. Science 319:321–323.

Baye, P. R. 1990. Comparative growth responses and population ecology of European and American beachgrasses (*Ammophila* spp.) in relation to sand accretion and salinity. The University of Western Ontario, London, Ontario, Canada.

Bindoff, N. L., et al. 2007. Observations: oceanic climate change and sea level. Pages 385–432 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Avery, M. Tignor, H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate. Cambridge University Press, Cambridge, UK.

Bouma, T. J., M. B. D. Vries, and P. M. J. Herman. 2010. Comparing ecosystem engineering efficiency of two plant species with contrasting growth strategies. Ecology 91:2696–2704.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burri, K., C. Gromke, M. Lehning, and F. Graf. 2011. Aeolian sediment transport over vegetation canopies: A wind tunnel study with live plants. Aeolian Research 3:205–213.

Cooper, W. S. 1958. Coastal sand dunes of Oregon and Washington. Geological Society of America, New York, New York, USA.

Corenblit, D., A. M. Gurnell, J. Steiger, and E. Tabacchi. 2008. Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights. Catena 73:261–273.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:95–117, 167–202, 281–308, 361–388.

Danielsen, F., M. K. Sorensen, M. F. Olwig, V. Selvam, F. Parish, N. D. Burgess, T. Hiraishi, V. M. Karunagaran, M. S. Rasmussen, L. B. Hansen, A. Quarto, and N. Suryadiputra. 2005. The Asian tsunami: a protective role for coastal vegetation. Science 310:643.

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

Duarte, C. M. 2000. Marine biodiversity and ecosystem services: an elusive link. Journal of Experimental Marine Biology and Ecology 250:117–131.

Fisher, S. G., J. B. Heffernan, R. A. Sponseller, and J. R. Welter. 2007. Functional ecomorphology: feedbacks between form and function in fluvial landscape ecosystems. Geomorphology 89:84–96.

Gemmell, A. R., P. Greig-Smith, and C. H. Gimingham. 1953. A note on the behaviour of *Ammophila arenaria* (L.) Link in relation to sand dune formation. Transactions and Proceedings of the Botanical Society of Edinburgh 36:132–136.

Greig-Smith, P., A. R. Gemmell, and C. H. Gimingham. 1947. Tussock formation in *Ammophila arenaria* (L.) Link. New Phytologist 46:262–268.

Gutierrez, J. L., et al. *In press.* Physical ecosystem engineers and the functioning of estuaries and coasts. *In* C. H. R. Heip, C. J. M. Philippart, and J. J. Middelburg, editors. Functioning of estuaries and coastal ecosystems. E. Wolanski and D. McLusky, series editors. Treatise on estuarine and coastal science. Elsevier, Amsterdam, The Netherlands.

Hacker, S. D., and M. N. Dethier. 2006. Community modification by a grass invader has differing impacts for marine habitats. Oikos 113:279–286.

Hacker, S. D., P. Zarnetske, E. Seabloom, P. Ruggiero, J. Mull, S. Gerrity, and C. Jones. 2012. Subtle differences in two non-native congeneric beach grasses significantly affect their colonization, spread, and impact. Oikos 120:138–148.

Hesp, P. A. 1989. A review of biological and geomorphological processes involved in the initiation and development of incipient foredunes. Proceedings of the Royal Society of Edinburgh 96:181–201.

Hesp, P. A. 1991. Ecological processes and plant adaptations on coastal dunes. Journal of Arid Environments 21:165–191.

Huiskes, A. H. L. 1979. *Ammophila arenaria* (L.) Link (*Psamma arenaria* (L.) Roem. et Schult.; *Calamgrostis arenaria* (L.) Roth. Journal of Ecology 67:363–382.

Jones, C. G., J. L. Gutierrez, J. E. Byers, J. A. Crooks, J. G. Lambrinos, and T. S. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862–1869.

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

Kaminsky, G. K., P. Ruggiero, M. C. Buijsman, and G. Gelfenbaum. 2010. Historical evolution of the Columbia River littoral cell. Marine Geology 273(1–4) (special issue):96–126.

Kirwan, M. L., and A. B. Murray. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. Proceedings of the National Academy of Sciences USA 104:6118–6122.

Koch, E. W., et al. 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. Frontiers in Ecology and the Environment 7:29–37.

Komar, P. D., J. C. Allan, and P. Ruggiero. 2009. Wave and nearshore-process climates: trends and variations due to Earth's changing climate. Pages 971–975 in Y. C. Kim, editor. Handbook of coastal and ocean engineering. World Scientific Publishing, Singapore.

Lancaster, N., and A. Baas. 1998. Influence of vegetation cover on sand transport by wind: field studies at Owens Lake, California. Earth Surface Processes and Landforms 23:69–82.

Langlois, E., A. Bonis, and J. B. Bouzillé. 2003. Sediment and plant dynamics in saltmarshes pioneer zone: *Puccinellia maritima* as a key species? Estuarine, Coastal and Shelf Science 56:239–249.

Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. Canadian Journal of Botany 76:713–738.

Maun, M. A., and J. Lapierre. 1984. The effects of burial by sand on *Ammophila* breviligulata. Journal of Ecology 72:827–839.

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

Murray, A. B., and C. Paola. 2003. Modelling the effect of vegetation on channel pattern in bedload rivers. Earth Surface Processes and Landforms 28:131–143.

Musick, H. B., S. M. Trujillo, and C. R. Truman. 1996. Wind-tunnel modelling of the influence of vegetation structure on saltation threshold. Earth Surface Processes and Landforms 21:589–605.

Pattanapol, W., S. J. Wakes, M. J. Hilton, and K. J. M. Dickinson. 2008. Modeling of surface roughness for flow over a complex vegetated surface. International Journal of Mathematical, Physical and Engineering Sciences 2:18–26.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed effects models in S and S-Plus. Springer, New York, New York, USA.

Psuty, N. P. 1992. Spatial variation in coastal foredune development. Pages 3–13 in R. W. G. Carter, editor. Coastal dunes: geomorphology, ecology and management for conservation: Proceedings of the Third European Dune Congress. Balkema, Rotterdam, The Netherlands.

Psuty, N. P. 1993. Foredune morphology and sediment budget, Perdido Key, Florida, USA. Geological Society, London, Special Publications 72:145–157.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ruggiero, P., G. Kaminsky, G. Gelfenbaum, and B. Voigt. 2005. Seasonal to interannual morphodynamics along a high-energy dissipative littoral cell. Journal of Coastal Research 21:553–578.

Ruggiero, P., J. Mull, P. L. Zarnetske, S. D. Hacker, and E. W. Seabloom. 2011. Interannual to decadal foredune evolution. In American Society of Civil Engineers, editor. Proceedings coastal sediments meeting, Miami, Florida, USA. World Scientific Publishing, Singapore.

Sallenger, A. H. 2000. Storm impact scale for barrier islands. Journal of Coastal Research 16:890–895.

Seabloom, E. W., and A. M. Wiedemann. 1994. Distribution and effects of *Ammophila breviligulata* Fern (American beachgrass) on the foredunes of the Washington coast. Journal of Coastal Research 10:178–188.

Snyder, R. A., and C. L. Boss. 2002. Recovery and stability in barrier island plant communities. Journal of Coastal Research 18:530–536.

Tal, M., and C. Paola. 2010. Effects of vegetation on channel morphodynamics: results and insights from laboratory experiments. Earth Surface Processes and Landforms 35:1014–1028.

Wiedemann, A. M., and A. Pickart. 1996. The *Ammophila* problem on the Northwest Coast of North America. Landscape and Urban Planning 34:287–299.

Zarnetske, P. L. 2011. The influence of biophysical feedbacks and species interactions on grass invasions and coastal dune morphology in the Pacific Northwest, USA. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Zarnetske, P. L., E. W. Seabloom, and S. D. Hacker. 2010. Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes. Ecosphere 1:art13.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. First edition. Springer Science + Business Media, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix A

Descriptions and photographs of morphological characteristics of beach grasses and their typical foredune shape, taken from field data across the Pacific Northwest coastal foredunes (for *Elymus mollis*, *Ammophila breviligulata*, and *Ammophila arenaria*) (*Ecological Archives* E093-126-A1).

Appendix B

Additional information about the wind tunnel experimental design, including the tunnel diagram, and photographs of one replicate set of beach grass species and density experimental units (*Ecological Archives* E093-126-A2).

Appendix C

Results from the wind tunnel experiment Tukey HSD post hoc multiple comparisons analysis of morphological characteristics of the three beach grass species: *Elymus mollis*, *Ammophila breviligulata*, and *Ammophila arenaria* (*Ecological Archives* E093-126-A3).