1    **Investigating dune-building feedback at the plant level: insights from a multispecies field**

2    **experiment**

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14   **Abstract**
15   Coastal foredunes provide the first line of defense against rising sea levels and storm surge and

16   for this reason there is increasing interest in understanding and modeling foredune formation and

17   post-storm recovery. However, there is limited observational data available to provide empirical

18   guidance for the development of model parameterizations. To provide guidance for improved

19   representation of dune grass growth in models, we conducted a two-year multi-species transplant

20   experiment on Hog Island, VA, U.S.A. and measured the dependence of plant growth on

21   elevation and distance from the shoreline, as well as the relationship between plant growth and

22   sand accumulation. We tracked total leaf growth (length) and aboveground leaf length and found

23   that *Ammophila breviligulata* (American beachgrass) and *Uniola paniculata* (sea oats) grew

24   more than *Spartina patens* (saltmeadow cordgrass) by a factor of 15% (though not statistically

25  significant) and 45%, respectively. Our results also suggest a range of basal/frontal area ratios

26  (an important model parameter) from 0.5-1 and a strong correlation between transplant growth

27  and total sand deposition for all species at the scale of two years, but not over shorter temporal

28  scales. Distance from the shoreline and elevation had no effect on transplant growth rate but did

29  have an effect on survival. Based on transplant survival, the seaward limit of vegetation at the

30  end of the experiment was approximately 30 m from the MHWL and at an elevation of 1.43 m,

31  corresponding to inundation less than 7.5% of the time according to total water level

32  calculations. Results from this experiment provide evidence for the dune-building capacity of all

33  three species, suggesting *S. patens* is not a maintainer species, as previously thought, but rather a

34  moderate dune builder even though its growth is less stimulated by sand deposition than *A.*

35  *breviligulata* and *U. paniculata.*

36

37  Introduction
38      Barrier islands are low-lying, sandy landforms and comprise approximately 10% of the

39  world's coastline (Stutz and Pilkey, 2011). Coastal foredunes (the first dunes landward of the

40  beach) line the seaward side of many barrier islands and are the first line of defense against

41  elevated water levels, protecting the landward side of an island, back-barrier marshes, and bays

42  from inundation during storms. The height of foredunes relative to the maximum water level is a

43  key factor in determining the impact of storms and along with storm surge controls whether or

44  not overwash will occur (Sallenger, 2000; Ruggiero et al., 2001; Houser et al., 2008).

45      Coastal foredunes often form via a feedback between dune grasses and sand transport

46  processes. Plants act as surface roughness elements that reduce the shear stress imparted to the

47   sand surface by wind (e.g., Bressolier and Thomas, 1977; Raupach et al., 1993; Arens, 1996;

48   Durán and Herrmann, 2006), causing sand to be deposited on and around plants (e.g., Hesp,

49   1981, 2002); dune-building vegetation increases deposition of sand on timescales as short as

50   weeks (e.g. Arens, 1996). In turn, a moderate amount of sand deposition enhances the growth of

51   aboveground biomass of dune-building grasses (e.g., Disraeli, 1984; Ehrenfeld, 1990; Maun,

52   1998; Maun and Perumal, 1999; Gilbert and Ripley, 2010). The balance between the rate of

53   burial and the rate of plant growth determines aboveground plant biomass (i.e., the aboveground

54   volume of the plant) and therefore the degree to which a plant reduces wind flow. If a plant can

55   grow vertically at a rate that is greater than the rate of sand deposition, then the stimulation of

56   growth by burial will increase the area of the plant that interacts with the wind, further enhancing

57   dune growth.

58        Although the distance from the shoreline that dune-building vegetation becomes

59   established exerts a first-order control on dune height (Durán and Moore, 2013), species type and

60   vegetation density affect dune width, height, growth rate, and alongshore continuity by

61   influencing the rate of sand deposition (e.g., Godfrey, 1977; Hesp, 1984a;  Seabloom and

62   Wiedemann, 1994; Arens, 1996; Stallins and Parker, 2003; Hacker et al., 2012; Zarnetske et al.,

63   2012; Wolner et al., 2013.). For example, on the U.S. West Coast, the invasive *Ammophila*

64   *arenaria,* a relatively tall and dense grass that has an upright growth form which results in

65   coastal dunes that are tall and narrow compared to dunes dominated by grasses that exhibit a

66   more lateral growth pattern (Hacker et al., 2012; Zarnetske et al., 2012).  Similarly, on the U.S.

67   east coast, *Ammophila breviligulata* tends to be associated with tall, continuous dunes whereas

68   *Uniola paniculata*, which grows more slowly in the lateral direction, tends to be associated with

69   dunes that are discontinuous or hummocky (e.g., Godfrey, 1977; Godfrey et al., 1979; Stallins

and Parker, 2003; Stallins, 2005). Recent numerical work by Goldstein et al. (2017) builds on previous conceptual work from Godfrey (1977), suggesting that differences in the lateral growth rates between these two species, combined with physical processes that tend to reset dune-building in low areas, explain the observed relationships between alongshore dune morphology and grass species dominance on the U.S.A. East Coast.

Additionally, some researchers have suggested that although certain species build dunes, others, such as *Spartina patens* (i.e., "maintainer species"; Wolner et al., 2013), may suppress dune formation, leading to maintenance of low areas (Stallins, 2002, 2005; Wolner et al., 2013; Brantley et al., 2014). Stallins (2002, 2005) posits that *S. patens* binds sand acting as part of a weak positive feedback cycle that prevents dune growth, suggesting an additional way in which the type of vegetation present may be important in determining dune morphology. However, recent modeling work by Durán Vinent and Moore (2015) and Goldstein and Moore (2016), which demonstrated the evolution of low and high areas in the presence of only a single dune-building grass, suggests that the presence of maintainer species is not necessary for low dunes to form and persist for long periods.

Because vegetation influences patterns of dune growth and the ultimate shape of coastal foredunes, understanding how the growth rate of vegetation varies across the beach environment is important to improving predictions of dune growth rate and form. Many studies of dune-building grasses have demonstrated that sand deposition is an important factor controlling dune grass growth (e.g., van der Valk, 1974; Maun, 1998; Maun and Perumal, 1999; Dech and Maun, 2005). Moderate amounts of deposition can have a positive effect by stimulating growth, but large amounts of burial can cause mortality (Selisker, 1994; Maun, 1998; Maun and Perumal, 1999; Dech and Maun, 2005; Lonard et al., 2011). Other factors include salinity and water

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93   availability, for which Young et al. (2011) use distance from shoreline and elevation as proxies.

94   Young et al. (2011) found that forbs tend to occupy the beach area closest to the shoreline, dune

95   grasses tend to occupy the foredune area at a higher elevation and close to shore, and shrubs

96   occupy habitats farther from shore, behind the dune line. Previous work also demonstrates the

97   effects of salt spray, soil salinity, soil moisture, and sand deposition on plant growth (Oosting

98   and Billings, 1942; Disraeli, 1984; Ehrenfeld, 1990; Young et al., 1994; Wilson and Sykes,

99   1999), but the relative importance of each factor can be difficult to isolate and varies from one

100  geographic area to another (Greig-Smith, 1961; Wilson and Sykes, 1999). Other factors that can

101  influence plant growth are management actions (beach raking, scraping, and driving) (Kelly,

102  2014) as well as organic input from seagrass or wrack deposition on the shoreline (which can

103  change soil texture) (Cardona and García, 2008; Del Vicchio et al., 2017).  Though the effects of

104  all of these different factors can be difficult to identify, we hypothesize that their integrated

105  effect on plant growth may result in measurable differences in growth rate as a function of

106  distance from the shoreline and elevation.

107       In addition, the cross-shore location and elevation at which plants grow appears to be

108  partially determined by short-term fluctuations in sea level and wave run-up. For example,

109  Kuriyama et al. (2005) and Hesp (2013) report that the seaward limit of vegetation corresponds

110  with the elevation reached by wave run-up only a few times a year. This seaward limit of

111  vegetation affects the width of the beach, the sand flux from the beach to dune, and the dune

112  elevation (Arens, 1996; Hesp et al., 2005; Durán and Moore, 2013).  A large supply of sand to

113  the beach from the nearshore also widens the beach, enhancing sand flux from the beach to

114  dunes (e.g. Psuty, 1988; Aargaard et al., 2004; Anthony et al., 2006; Houser and Mathew, 2011).

115  In contrast, shell lag and soil moisture limit the beach area across which sand is available for

116 transport (e.g., Delgado-Fernández et al., 2012; Wolner et al., 2013; Hoonhout and de Vries,

117 2016). Wind intensity, as well as gustiness, are also important controls on how often and in what

118 quantities sand is transported across the beach to the dune (Davidson-Arnott et al., 2005; Walker

119 et al., 2009; Bauer et al., 2009; Davidson-Arnott and Bauer, 2009;).

120        Numerical models of coastal dune formation provide insights into the relative importance

121 of the different mechanisms involved in dune-building, yet parameterizations of plant growth

122 rates and growth form, especially species-specific rates, are currently limited by a lack of

123 sufficient observational data. In addition, efforts are needed to determine whether, or not, certain

124 species, such as *Spartina patens*, prevent dunes from growing (i.e. interrupt the positive feedback

125 between deposition and growth), as previously hypothesized (e.g., Stallins, 2002; Stallins, 2005;

126 Wolner et al., 2013; Brantley et al., 2014). In their review, Gilbert and Ripley (2010) also argue

127 that field experiments to measure plant response to burial for adult dune grasses are necessary, as

128 many of the studies thus far have focused on laboratory experiments and seedlings. Related to

129 these needs, the most relevant timescale for modeling the response of dune grasses to sand

130 deposition, and the influence of vegetation on sediment transport, also remain unclear.

131        To address these gaps in understanding and with the hope of identifying simple

132 relationships between plant location and plant growth as we hypothesize above, we conducted a

133 multi-species transplant experiment, which we monitored for two growing seasons, and in which

134 we assess 1) plant growth rate as a function of elevation and distance from the shoreline for three

135 different species of dune grass common on the U.S. East Coast; 2) sand accumulation and its

136 influence on each of the three grass species; and 3) the evolution of the seaward limit of

137 vegetation. Our findings, presented below, provide observational guidance for vegetation-related

138    parameters used in coastal dune models and general insights that can inform future dune

139    modeling experiments.


140    **Approach**

141    *Study Site and Meteorological Conditions*
142            We performed our field work at the southern end of Hog Island, VA, which is located

143    within the Virginia Barrier Islands in the mid-Atlantic Bight on the East Coast of the U.S.A.

144    (Figure 1). Hog Island is an undeveloped, mixed-energy rotational drumstick island (Hayes,

145    1979; Harris, 1992) with a tidal range of ~2 m. It is owned by The Nature Conservancy and is

146    part of the Virginia Coast Reserve Long-term Ecological Research site. Since 1972, the south

147    end of the island has been accreting (Fenster and Hayden, 2007; Fenster and Dolan, 1994);

148    currently the beach along the southern end of the island is ~50 m wide and populated by embryo

149    dunes, with the density of natural vegetation ranging from about 0 to 5 plants/m$^2$. The soil is

150    made up of fine to medium sand with very little organic matter. Shell lag covered an average of

151    10% of the study area. The main foredune has a slope of 25-35 degrees, and the beach from the

152    foredune to the shoreline varies in elevation from 1.5 to 2.5 meters in elevation (Figure 1). The

153    erosion and deposition of sand within the experimental area varied between plant sites and within

154    plant sites. Most sites showed erosion and deposition, depending on the season. During high

155    water events, most of the low sites were scoured. During the winter, the beach narrowed and

156    deposition increased in some areas. Because the study site is quite variable in topography, there

157    is no clear pattern of deposition in relation to distance from shore.

158            Hog Island lies in the habitat range of several important dune grasses, making it an ideal

159    place for a multi-species transplant experiment. *Ammophila breviligulata*, also known as

160    American beach grass, dominates many of the dunes from Hog Island northward and grows (and

161  is planted) as far south as Cape Fear, NC (Woodhouse et al., 1977; Goldstein et al 2018). A $C_3$

162  (cool season) grass, *A. breviligulata* propagates using rhizomes and thrives in depositional

163  environments (Disraeli, 1984; Ehrenfeld, 1990; Selisker, 1994). *Uniola paniculata* (sea oats)

164  dominates dunes south of Cape Hatteras and has been found growing on the Virginia Barrier

165  Islands (Tatnall, 1946; Harris et al. 2017; Mullins and Moore, 2017.) and as far north as

166  Assateague Island, Maryland (Stalter and Lamont, 1990; Goldstein et al., 2018). *U.paniculata*

167  also propagates via rhizomes but is a $C_4$ (warm season) grass (Wagner 1964, Lonard et al, 2011).

168  *Spartina patens* (saltmeadow cordgrass), grows along the entire U.S. Atlantic coast, propagates

169  via rhizomes, has a high salinity tolerance (it can survive up from 1 to 27 ppt; Lonard, Judd, and

170  Stalter, 2010), and grows in marshes as well as on beaches and dunes. The leaves of *S. patens* are

171  narrower and more upright than those of *A.breviligulata* and *U.paniculata* (Figure 2). In addition

172  to these perennial dune grasses, Hog Island is also inhabited by numerous annual native beach

173  and dune plants including *Panicum amarum* (bitter panicgrass), *Cakile endentula* (sea rocket),

174  and *Salsola kali* (Russian thistle).

175      We retrieved meteorological data from the Hog Island weather station (Porter et al.,

176  2016) and compared monthly averages for mean, maximum, and minimum temperature as well

177  as mean, maximum, minimum precipitation and wind speed (Figure 3). We compare values from

178  2000-2013 to 2014 and 2015 to determine if conditions during the experiment deviated from

179  typical conditions. The highest wind speed recorded was from Hurricane Arthur in July 2014,

180  and the extreme precipitation event in September of 2014 delivered a record rainfall relative to

181  the remainder of the available record. The average temperature was typical, and the maximum

182  and minimum were usually less extreme than the monthly maximum and minimum temperatures

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183    recorded between 2000 and 2013. Average precipitation throughout the experiment was higher

184    than the average for the comparative period, as was wind speed.

185

186    *Experimental design and data collection*

187    In May of 2014 we planted 2 individuals each (to improve likelihood of retaining one

188    healthy individual) of *A. breviligulata* (Figure 2A)*, S. patens* (Figure 2B)*,* and *U. paniculata*

189    (Figure 2C) at 60 sites in two cross-shore swaths (A and B; for a total of 360 plants at 180 sites)

190    extending from a distance of 21.3 m from the mean high water line (MHWL) to the dune crest

191    (103.5 m from the MHWL) and in elevation from 1.25 m to 3.78 m (Jass 2015; Figure 1). Plants

192    were spread evenly, though randomly, throughout the swaths, with each species experiencing

193    roughly the same range of conditions overall. The minimum distance between plant sites was

194    1.06 meters, and most sites were between 1.4 and 3.4 meters away from the next nearest plant.

195    We planted some of the transplants closer to the water than the natural perennial grasses were

196    found. After 4 weeks, we also removed the plant at each site that had fewer or weaker leaves,

197    leaving a single individual plant at each site. (Jass, 2015). The crest of mature foredunes on Hog

198    Island is on average ~50 meters from the shoreline (Yousefi Lamini et al., 2017). The beach is

199    wider in our study area than along the majority of the island because the southern end of the

200    island has been accreting seaward in recent years, making this an ideal location to study plant

201    growth across a range of elevations and distances from shore.

202    We sorted and selected intermediate-sized seedlings, grown from seed, by a nursery, and,

203    prior to planting, trimmed the leaves of *A. breviligulata* and *U. paniculata* seedlings to 25 cm

204    and leaves of *S. patens* to 20 cm (not all the *S. patens* plants had leaves longer than 20 cm,

205    preventing us from trimming at 25 cm) to reduce variation in seedlings (Jass, 2015). We marked

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206  each plant site with a fiberglass stake and attached a label recording species and swath A or B

207  (Jass, 2015). Each pair of seedlings (root plugs of ~5 cm) was planted approximately 5 cm away

208  from the stake, 10 cm away from each other, and 2 cm below the sand surface (Jass, 2015).

209  During the first 4 weeks of the experiment we watered the plants 8 times (120 mL each) and

210  replaced any plants that died with an individual from a reserve garden (which was cared for in

211  the same way as the transplants) to reduce any effects of transplant shock on the experiment

212  (Jass, 2015). To reduce competition, we clipped vegetation within 1 m of each plant site prior to

213  planting and then clipped as necessary to maintain a 1 m-wide perimeter for the first growing

214  season (May- October 2014; Jass, 2015). At the end of the 4 weeks, we removed the smaller

215  plant at each site, leaving just one individual at each site. Although this resulted in just one plant

216  per site, multiple replicate plants at a single site would impact growth (Franks, 2003) as these

217  plants grow quickly.  Additionally, the dune environment is highly variable and even nearby

218  plants may experience different environmental conditions (Greig-Smith, 1961; Wilson and

219  Sykes, 1999; Young et al., 2011).

220      To establish monuments from which to measure elevation over the course of the

221  experiment, we installed 2 GPS benchmarks using PVC pipe filled with concrete on a secondary

222  dune ridge (Jass, 2015). We measured the UTM coordinates and NAVD88 (North American

223  Vertical Datum of 1988) elevation of each benchmark using a Trimble R-6 GPS antenna and

224  post processed the points using the National Geodetic Survey's Online Positioning User Service

225  (NGS-OPUS) (XY error = 0.008 cm, Z error = 0.022 cm).  (Jass, 2015).

226

227  *Measurement methods*
228      At each month during the growing seasons of 2014 and 2015 (May – October), we

229  measured the longest leaf of each transplant from the surface of the sand, hereafter referred to as

230  "longest aboveground leaf length" or "LagLL."  We found the longest leaf by gathering the

231  primary clump of leaves and straightening them. We then measured the distance from the sand

232  surface to the tip of the longest leaf as it was straightened. We also recorded plant state as

233  healthy (green and upright), stressed (yellow and/or horizontal), missing, or dead (completely

234  brown), and photographed each plant to document our plant state observation. In June and

235  October of 2014, and in June of 2015, we photographed the plan view (from the top) and frontal

236  view of healthy plants and used the image-processing package, ImageJ (Schneider et al., 2012),

237  to measure frontal and basal area (Jass, 2015). In October of 2016, we also photographed 8

238  natural plants of both *A. breviligulata* and *S. patens* and measured their basal and frontal areas.

239  An extreme high water event between the September and October 2015 collection dates

240  deposited large amounts of wrack on the plants within our experiment making observations

241  difficult. For this reason, we have not used data from the October 2015 collection (our last) in

242  our analyses. Additionally, in the months of March 2015 and April 2016, we measured elevation

243  at each plant site and recorded plant absence, presence, or death (plant was completely brown

244  and did not recover during the growing season), but did not measure leaf length because many

245  leaves were still senesced. We exclude these data from the analyses of plant growth. Taking

246  these omissions into account, we had a total of 11 sets of measurements of longest aboveground

247  leaf and elevation — May (planting height, initial elevation), June, July, August, September,

248  October 2014 and May, June, July, August, September 2015.

249      We used a Nikon DTM-322 total station (angle error = 5 arc seconds) to measure the

250  elevation of the sand surface at each plant site (measured on the landward side of the plant stake)

251    monthly through the growing season (Jass, 2015). In some cases, the plant grew enough to

252    surround the stake and our measurement was in the middle of the plant clump, while in other

253    cases, the plant did not grow around the stake and the measurement site was bare and

254    immediately adjacent to the edge of the plant. Elevations measured in the middle of the clump

255    were usually higher than those measured adjacent to the clump, as sand deposition was greater in

256    and around the plants than distant from the plants. The difference between elevation in the clump

257    and beside the clump was always less than 10 cm, and there was no pattern among the plants in

258    terms of which plants grew around the stake. Initial elevation of plant site is hereafter referred to

259    as "$z_i$". Since the elevation of the ground surface changed at each plant site with each

260    observation and we measured longest aboveground leaf length from the ground surface, we

261    clarify notation here and in Figure 4: We determined total leaf growth ($dl_{tot}$) by calculating the

262    difference between the initial and final ground surface elevation ($dz_{tot} = z_f - z_i$), adding this

263    quantity to the final longest aboveground leaf length measurement ($LagLL_f$) and then subtracting

264    the initial final longest aboveground leaf length measurement ($LagLL_i$) (Eq. 1).

265
$$dl_{tot} = \left((z_f - z_i) + LagLL_f\right) - LagLL_i \qquad \text{Eq. 1}$$

266         This results in $dl_{tot}$ values less than zero for some individuals because their final

267    aboveground leaf length ($LagLL_f$) was very short (due to leaf senescence) and, in some cases, the

268    ground surface was eroded during the experiment. In September of 2015, we measured the

269    location of the planted, as well as the naturally occurring, seaward-most perennial and annual

270    plants, associated with each of our experimental swaths. We use total leaf growth as a proxy for

271    total plant growth, which we assume to be an integrated measure of how a plant responds to

272    different environmental factors—both the etiolation response and biomass growth. We chose to

273    focus on leaf length because it can be collected quickly and easily, and because it is less

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274    disruptive to the field site than the collection of basal area measurements. As such, we collected

275    leaf length measurements every month of the growing season (and at the end of the experiment,

276    which is important for assessing total growth).  We only collected basal area measurements 3

277    times throughout the experiment (June 2015, October 2014, and June 2015) and these are

278    therefore lower in temporal resolution and cover a shorter time period. We use aboveground leaf

279    growth to determine how the combination of plant growth and sand deposition affect the

280    aboveground size of the plant that is available to slow the wind causing sand deposition.

281        We calculated the NAVD88 elevation of the mean high water line (MHWL) at the

282    location of the experiment (0.46 m) using VDATUM (NOAA), and then measured the shore

283    perpendicular distance between each plant site and the MHWL to measure distance from shore

284    (Jass, 2015).

285

286    **Results**

287    *Plant mortality*

288        We began our experiment (after retaining the healthiest individual at each plant site) with

289    60 individuals of each species. Plants from each species died during the course of the experiment

290    (May 2014 - September 2015).  Specifically, we lost 16 (27%) of the *A. breviligulata* plants, 36

291    (60%) of the *S. patens* plants, and 40 (66.7%) of the *U. paniculata* plants. We found that of the

292    plants that died in June, July, and August (of 2014 and 2015), 65% were planted at initial

293    elevations greater than 2.5 m (Figure 5B). In addition, all plants died that experienced more than

294    20 cm of net erosion, defined as the difference between initial elevation and the elevation at the

295    time mortality was recorded.  We observed that low elevation plant sites were prone to scouring

296    associated with high water events (Figure 5C). We also found that none of the *S. patens*

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297    transplants survived at elevations above 3 m (Figure 5B). In addition to these trends related to

298    the vertical dimension, we found a multidimensional trend worth mentioning as it relates to the

299    seaward limit of vegetation. All plants within 30 m of the shoreline that were also below 1.47 m

300    died during the experiment (Figure 5, A and B).  Beyond these results, we found no other

301    discernable species-specific patterns in plant death.

302

303    *Leaf growth differences and basal area differences*

304        For the analysis presented here we used data for transplants that were recorded as healthy

305    during the entire course of the experiment from May 2014 to September 2015 (*A. breviligulata*: n

306    = 44, *S. patens:* n = 24, *U. paniculata:* n = 20). We compared the total leaf lengths, longest

307    aboveground leaf lengths, and basal/frontal areas for each species and used the ANOVA, aov,

308    and TukeyHSD functions in the statistical package R (R Core Team, 2013) for each comparison.

309    Results are reported as the mean ($\bar{x}$) ± one standard deviation and significance is determined at

310    the p < 0.05 level—hereafter we use the term 'significant' to describe only those relationships for

311    which p < 0.05.

312        Total leaf growth lengths ($dl_{tot}$) for *A. breviligulata* and *S. patens* individuals were

313    significantly shorter than for *U. paniculata* individuals, and *S. patens* exhibited almost half the

314    range of measurement of the other species (Figure 6A, Tables 2 and 3). Considering just

315    aboveground leaf length at the end of the experiment ($L_{ag}LL_f$), an ANOVA test indicates that *A.*

316    *breviligulata* exhibited significantly longer mean $L_{ag}LL_f$ than the mean of *S. patens* individuals

317    and significantly shorter $L_{ag}LL_f$ than the mean of the *U. paniculata* individuals (Fig 6B, Table 2

318    and 3). As in total leaf growth lengths, the range of $L_{ag}LL_f$ for *S. patens* was half the range of the

319    other species.

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320     *S. patens* transplants had a significantly lower basal/frontal area than transplants of *A.*

321     *breviligulata* and *U. paniculata* (Fig 6C) as evidenced by the ANOVA and Tukey post-hoc tests.

322     The natural *A. breviligulata* and *S. patens* plants had a smaller range of values than their

323     transplant counterparts (Tables 2 and 3).


324     *Individual factors that influence plant growth—Linear regression*
325           We used the linear model (lm) function in R to analyze, for each of the three species, the

326     relationship between plant growth and the factors of elevation, distance from shore, and sand

327     deposition (at the monthly, seasonal, and two-growing seasons time scale). We acknowledge that

328     elevation and distance from shore are proxies for environmental conditions (i.e., soil salinity,

329     groundwater availability, etc.). We performed an F-test to determine significance for all of the

330     linear regressions. When considering the relationship between only two variables none of the

331     species showed a correlation between total leaf growth and distance from shore (Figure 7A) or

332     between total leaf growth and initial elevation (Figure 7B).

333           To investigate the effects of burial on overall plant growth, we analyzed total leaf growth

334     for experimental (2- growing seasons) and seasonal time periods. For all three species, the total

335     change in elevation at each plant site measured over the course of the two-experiment which

336     spanned two growing seasons (May 2014-Sept 2015) ($z_f$ - $z_i$) is positively correlated with total

337     leaf growth ($dl_{tot}$) (Figure 8) and statistically significant (AB slope = 1.48, SP and UP slopes =

338     1.89). However, this positive correlation was not statistically significant at the annual time scale

339     for any of the species (May 2014- Oct 2014 or May 2015-Sept 2015), even when considering the

340     combined data from each year (May 2014- Oct 2014 and May 2015-Sept 2015).

341           To investigate the effects of burial on *aboveground* leaf length at different timescales

342     (which was of interest because we hoped to determine at what time scale vegetation response to

343    sand deposition occurs), we analyzed longest aboveground leaf length (LagLL) change and

344    elevation change at the experimental (2-growing season), seasonal, and monthly time scales. To

345    do this, we performed a linear regression on the relationship between the final aboveground leaf

346    length (LagLL$_f$) and total elevation change (dz$_{tot}$) over 2 seasons which results in a statistically

347    significant positive correlation for *A. breviligulata* and *U. paniculata* and a positive correlation

348    (though not statistically significant) for *S. patens* (Figure 9). However, analyzing data from 2014

349    and 2015 separately, none of the species showed a significant correlation between longest

350    aboveground leaf length and total elevation change at the scale of one year.  When the data from

351    both years are combined, *A. breviligulata* showed a significant positive correlation between

352    above ground leaf length and elevation change (Figure 8B). The monthly change in above-

353    ground leaf length (dagldt) and the monthly change in elevation (dzdt) are significantly

354    (positively) correlated only for *S. patens* (Figure 8C).

355

356    *Combination of factors that influence plant growth—Multiple linear regression*
357            To determine the best-fit equation to describe the growth of each species over the course

358    of our experiment, we performed a multiple linear regression for the following variables: initial

359    elevation, change in elevation, and distance from shoreline. Because our site was quite variable

360    in topography, elevation and distance from shoreline are not tightly correlated—there are some

361    low areas close to the foredune, and some high areas close to the shore on embryo dunes.

362    Erosion and deposition patterns were also variable across the site.  Because none of these

363    variables were tightly correlated with each other we included all of them in the analysis. We

364    normalized the variables by subtracting the mean and dividing by the standard deviation, and

365    created linear models using all possible combinations of the variables. We chose the best linear

366  model using a method similar to the stepwise method (Draper and Smith, 1966; Table 4) — we

367  eliminated the models for which the F statistic was not statistically significant, and then we

368  further narrowed down the number of linear models by choosing only those with an $R^2$ adjusted

369  value was more than 0.1 higher than other models (similar to a step-wise analysis of models).

370  Finally, we chose the models that had the lowest AIC (Akaike Information Criterion) score

371  (Akaike, 1973), which can be considered as the optimal model (Table 4).

372       The results of the multiple linear regression analysis are as follows (coefficients are

373  dimensionless and represent the relative importance of each variable):

374  $$A.\,breviligulata:\,dl_{tot} = -23.17x + 255.4dz_{tot} - 127.5zi + 530.6$$

375  $$S.\,patens:\,dl_{tot} = 106.9dz_{tot} + 451.5$$

376  $$U.\,paniculata:\,dl_{tot} = 206.2dz_{tot} - 41.64zi + 872.7$$

377  Where $dl_{tot}$ is the total change in leaf length across the entire experiment, $x$ is the distance from

378  the shoreline, $dz_{tot}$ is the total change in elevation across the time period of the experiment, and

379  $z_i$ is the initial elevation. For all of the species, $dz_{tot}$ had the largest coefficient. For *S. patens*,

380  leaf growth is best explained by elevation change. The same is true for *U. paniculata*, with the

381  addition of initial elevation. All parameters are significant for *A. breviligulata* – elevation

382  change, initial elevation, and distance from the shoreline.  Growth of *A. breviligulata* is

383  significantly positively correlated with change in elevation, but negatively correlated with initial

384  elevation and distance from shoreline (Table 4).

385  *Seaward limit of vegetation and total water level calculation*
386       All of the transplants emplaced below 1.43 m in elevation that are within 30 m of the

387  MHWL died (Figure 5), yielding a seaward limit to transplant vitality. As a follow-up to the

388  experiment, we recorded mortality in April of 2016 and display it in figure 10, which shows no

389  clear pattern in plant mortality within each swath (Figure 10). The transplants at elevations

390  below 1.43 m but very close to the dune (where we observed ponding of fresh water following

391  heavy rainstorms) grew well and survived throughout the entire experiment. We also measured

392  the elevation of the seaward limit of perennial (*A. breviligulata, S.patens*) (dark green triangles;

393  mean of 1.37 m) and annual (*C. edentula* (sea rocket), *S.Kali* (Russian thistle)(light green

394  triangles; mean of 1.54 m) vegetation in September 2015 (Figure 10).

395      We computed a total water level (TWL) time series for the site for May 2014-April 2016

396  using hourly tide gauge data from the Hog Island (VCR_LTER data set, Porter et al., 2016), and

397  hourly wave buoy data (Buoy 44014, http://www.ndbc.noaa.gov/). The TWL series is an

398  estimate of the height reached by water on the beach through time (e.g., Ruggiero et al., 2001).

399  We calculated wave runup using the predictor of Stockdon et al. (2006) and a beach slope of

400  0.05 as measured for our cross-shore transects measured using the total station. From this record,

401  74 days of data were missing, mostly from the end of 2014, resulting in a total of 626 days and

402  89% coverage of this time period. Because the missing data encompassed approximately 6 days

403  of elevated water levels (as indicated by the tide gauge at the Chesapeake Bay Bridge Tunnel,

404  which has a continuous record during this period), it is likely that our analysis slightly

405  underestimates the actual TWL during the study period. Using the TWL time series, we summed

406  the cumulative hours at each elevation using 0.1 cm bins, shown in Figure 11.

407      The average elevation of the seaward-most extent of vegetation was highest for the

408  perennial vegetation (dark green, average elevation = 1.54 m), lowest for the annual vegetation

409  (light green, average elevation = 1.37 m), and the elevation of the seaward-most limit for our

410  transplants (black, lowest elevation = 1.43 m) was in between (Figure 11). We calculated the

411  number of inundation hours (NIH) for each elevation using the TWL for 1) the total time of the

412    experiment, 2) the growing season months (May-Sept) and 3) all winter season months (Oct-

413    April), and found that the seaward-most elevation at which plants survived corresponded to the

414    elevation above which the water rose for 425 hours (i.e., underwater 5.5 % of the time) and 500

415    hours (i.e., underwater 8.7% of the time) for perennials (non-growing season levels) and annuals

416    (growing season levels), respectively.


417    **Discussion**

418    *Potential Effects of Experimental Design*
419          There were several aspects of our experimental design that could have affected transplant

420    growth and sand deposition in the dune environment. By trimming the transplants to reduce

421    variation in initial size we may have stimulated growth early on in the experiment. However, we

422    trimmed all of the transplants, and the trimming only reduced transplant height by a maximum of

423    20%, so we expect any effects of trimming to be consistent across the experiment and minimal.

424    We also planted our transplants as plugs, which were composed of more organic matter than the

425    existing sandy substrate. While this may have contributed to plant growth at the beginning of the

426    experiment by providing nutrients and organic matter to the transplant roots, the transplants

427    looked similar to the surrounding natural plants by the end of the first growing season, and we

428    expect that any effects of potential additional nutrients would be limited to the first couple of

429    months and consistent across the transplants. The removal (by clipping) of surrounding

430    vegetation may also have influenced sediment transport by increasing the amount of exposed

431    nearby sand available for transport. The initial density of surrounding vegetation ranged from ~0

432    to 5 plant clumps/m$^2$, so the effect of clearing vegetation on pre-existing nearby sand availability

433    may have been greater in areas with initially higher densities than those with lower densities.

434    However, our transplants were spread evenly throughout the swaths and all were centered within

435     a 1-m radius circle from which vegetation had been removed by clipping, so the effect of

436     different surrounding plant densities would not have affected some plants (or species) more than

437     others.  Despite the potential effect of these aspects of our experimental design, our consistency

438     in applying treatments equally to all transplants and the similarity between our transplants and

439     natural plants by the end of the first growing season suggests that these effects, if present, were

440     consistent across transplants and short-lived.

441     *Plant Mortality*

442           We recorded widespread plant mortality during the experiment. Loss of all three species

443     at elevations above 2.5 m in June, July and August may have been the result of the short root

444     systems of our transplants (~10 cm) and the extremely low soil moisture at shallow depths at

445     these elevations during summer months.  We hypothesize that the plants that died in association

446     with greater than 20 cm of net erosion either washed away or likely suffered from more extreme

447     root exposure during scouring events than other plants.  Specific measurement of root exposure

448     following high water events would be required to more fully determine plant survival thresholds

449     during extreme conditions. Future studies could also investigate the role of freshwater

450     availability and transplant root plug length as controls on plant mortality.

451           Because of widespread transplant mortality, our data density is different for each species.

452     However, we did find that *A. breviligulata* survived the best of the three species (only 16%

453     mortality vs >60%). This may be because it is naturally the most dominant dune species at the

454     site. The reduction in sample size arising from mortality may explain the lack of a relationship

455     between total leaf growth and distance from shore or elevation.  Alternatively, such simple

456     relationships may be undetectable regardless of sample size, or they may simply not exist.

457     Additionally, because our analysis of plant growth did not include unhealthy or dead plants, we

458    may overestimate transplant growth in the dune environment (because unhealthy or dying plants

459    will likely grow more slowly).

460    *Species-specific Insights*
461             Each of the three dune grass species responded differently to environmental conditions

462    throughout our experiment, as reflected in differences in leaf growth rates and basal/frontal area

463    ratios, suggesting that each species may influence dune growth in a different way. Although this

464    is not surprising because we expect variation in plant shape for different species, this difference

465    in overall plant shape is consistent with the greater potential for *A. breviligulata* and *U.*

466    *paniculata* to trap sediment (and build dunes more quickly) in three dimensions relative to *S.*

467    *patens*. Previous authors have attributed differences in dune width and height to differences in

468    the morphology of dominant dune grass species (e.g., Godfrey, 1977; Woodhouse et al., 1977;

469    Godfrey et al., 1979; Hesp, 1984a; Hacker et al., 2012; Zarnetske et al, 2012, 2015).  Our results

470    add to this growing body of evidence and suggest that the same phenomenon may be true for the

471    three U.S. East coast dune-grass species, especially when considering the effects of *S. patens*

472    relative to the other two species.

473             Consistent with previous studies of *A. breviligulata* (e.g. Disraeli, 1984; Ehrenfeld,1990;

474    Maun, 1998), *U. paniculata* (Wagner, 1964;  Miller et al., 2010; Ehrenfeld, 1990;  Harris et al.,

475    2017) and *S. patens* (Godfrey and Godfrey, 1976; Godfrey et al., 1979; Ehrenfeld, 1990; Stallins,

476    2002), our results suggest that all three species are significantly stimulated by sand deposition

477    (Figure 6). Though part of the strength of this positive correlation admittedly arises from the

478    need to include the change in elevation in the determination of total change in leaf length,

479    investigating the relationship between these two quantities is the only way to assess how well

480    plants keep up with burial. However, keeping up with burial is not the entire story as our results

481    also reveal a significant positive correlation between aboveground leaf length (which was not

482    calculated using change in elevation) with the change in elevation for *A. breviligulata* and *U.*

483    *paniculata.* Importantly, in our transplant experiment neither the effect of deposition on total

484    leaf length nor the effect of deposition on aboveground leaf length was apparent except when

485    analyzing data at the temporal scale of two years. The lack of consistent correlation between

486    sand deposition and plant growth at the shorter, monthly (and annual) timescale suggests there is

487    a lag of at least more than a year between sand deposition and measurable effects of subsequent

488    stimulation of plant growth. It is not clear whether this is because of a lag in effect or because the

489    annual signal is so small that it is swamped by noise in the signal. Interestingly, Keijsers et al.

490    (2016) found no correlation between percent cover of vegetation and sand accumulation on the

491    order of a decade, suggesting that the feedback between plant growth and sand deposition

492    operates most successfully on the order of a few years.

493         Although we found that plant growth is positively correlated with sand deposition for

494    each species after a period of two years, that our analysis does not reveal a clear correlation

495    between plant growth and distance from shore  is consistent with the findings of studies of

496    lacustrine dunes that indicate distance from shore was not an important influence on plant growth

497    (Maun and Perumal, 1999; Dech and Maun, 2005; Forey et al. 2008). It is also consistent with

498    previous studies that suggest a single environmental factor cannot determine where plants grow

499    (Maun and Perumal 1999, Young et al. 2011). Thus, it appears that biotic and abiotic factors are

500    not operating in a sufficiently comprehensive or consistent fashion to alter plant growth. This

501    lack of correlation could be due to the nature of our study (we used transplants and did not

502    measure natural grasses), the small sample size of plants that survived for the entire course of the

503    experiment, or the variability in water table level and soil moisture, but it could also indicate that

504    plant growth it not strongly influenced by the variables that change with distance from shore and

505    elevation alone.

506         The multiple linear regression analysis provides more insight into the combination of

507    factors that influence plant growth for each species. The weak negative correlation between *A.*

508    *breviligulata* growth and the combination of distance from shore and elevation (when both

509    factors are considered along with total change in elevation) is surprising because other authors

510    have found *A. breviligulata* growth to be densest at some distance from the shoreline where sand

511    burial is greatest, which tends to be around the peak of the foredune (Cheplick, 2005; Young et

512    al., 2011; Yousefi Lalimi et al., 2017). Our use of transplants, which necessarily had shallow root

513    systems and therefore did not have access to groundwater when planted on the foredune, may at

514    least partially explain why the transplants grew more slowly farther from shore.

515         The multilinear regression analysis for *U. paniculata* and *S. patens* suggests that fewer

516    factors are correlated with growth than in the case of *A. breviligulata*, though all results included

517    the change in elevation variable. The negative correlation between *U. paniculata* growth and

518    elevation, agrees well with results of previous studies that note the influence of elevation on *U.*

519    *paniculata* growth; Oosting and Billings (1942) found this species grew best at a maximum

520    distance from the water table, and Hester and Mendelssohn (1989) found that *U. paniculata*

521    plants were water logged at a distance of 0.3 m above the water table but did well above 0.9 m

522    above the water table.  Neither elevation nor distance from shore were included in the best

523    equation for *S. patens,* which emphasizes the ability of *S. patens* to survive in a wide range of

524    environmental conditions—this species grows well in marshes as well as on beaches and dunes

525    (Ehrenfeld, 1990; Lonard, Judd, and Stalter, 2010). It is not as adapted to the environment of

526    shifting sand (Woodhouse et al., 1977), which may explain why it exhibited, on average, the

527     least amount of the total leaf growth, aboveground leaf growth, and basal/frontal area ratio at the

528     end of the experiment out of the three species in our experiment.

*Support for reclassification of S. patens as a dune builder*
530          Whereas previous work has documented the ability of *S. patens* to recover from burial

531     (Godfrey and Godfrey, 1976; Ehrenfeld, 1990), some researchers have emphasized the ability of

532     this species to grow in overwash areas more readily than other species found in the beach

533     environment (Ritchie and Penland, 1988), suggesting that its presence in these areas may prevent

534     dunes from growing (Godfrey et al., 1979; Stallins, 2005; Wolner et al., 2013). We favor an

535     alternative (though not new, see Woodhouse, 1982) interpretation: *S. patens* is frequently found

536     in overwash flats because it has a relatively high salinity tolerance (Oosting and Billings, 1942;

537     Ehrenfeld, 1990; Lonard et al., 2010).  Because it grows more slowly, is less stimulated by

538     burial, and has a smaller basal area than *A. breviligulata* and *U. paniculata,* it will tend to be less

539     effective at causing sand deposition and therefore will accumulate sand less quickly than the

540     other two recognized dune-building grasses. This interpretation is supported by our finding that

541     the positive correlation between aboveground leaf length and sand deposition for *S. patens* was

542     not statistically significant (as it was for the other species) and our finding that the longest leaves

543     of *S. patens* transplants exhibited the least amount of growth and the smallest basal/frontal area

544     of the three dune grasses. Even with slower rates of aboveground leaf growth, *S. patens*

545     effectively builds elevation, creating higher topography, which then provides potential sites for

546     other dune grass species to become established, as recognized by Woodhouse (1982). Thus, not

547     only are the results of our experiment inconsistent with the hypothesis that *S. patens* prevents

548     dune growth (as posited by the maintainer hypothesis), they also suggest that *S. patens* is

549     effective at causing sand deposition, just less so than *A. breviligulata* and *U. paniculata*. Given

550    our findings and these arguments, combined with model results from Durán and Moore (2015)

551    and Goldstein and Moore (2016), which indicate that a vegetative maintainer feedback is not

552    necessary for low-lying areas to persist, we propose that in the overwash, beach, and dune

553    environments, *S. patens* is a moderate 'dune-builder' rather than a 'maintainer' species.


554    *Empirical guidance for modeling dune formation*
555        Taken together, our findings also yield insights into the vegetative dynamics of dune-

556    building grasses for both ecology and coastal dune modeling. Results from our linear and

557    multilinear regression analyses confirm the importance of including burial effects in plant growth

558    equations.  They also suggest that a combination of other factors (i.e., distance from shore,

559    elevation) are important as well, but in different ways for different species. For example, when

560    representing the growth of *S. patens*, the relative influence of sand deposition on growth rate

561    should be 10-20% less than for representations of *A. breviligulata* and *U. paniculata* (Table 2).

562    Incorporating the details of these results into dune growth models in a quantitative way will

563    require relating changes in longest leaf length (the measure of plant growth studied here) to

564    changes in percent cover (the quantity used to represent plant growth in dune models), for a large

565    number of natural plants and is the subject of ongoing work.

566        Additionally, our results indicate that basal/frontal area ratios are species-specific. Our

567    observational data provides some guidance on the appropriate ratio to use for the three East

568    Coast dune species; 0.7-1 for *A. breviligulata*, ~1 for *U. paniculata,* and a value of 0.5-0.6 for *S.*

569    *patens*, though our sample size was small and more observations are needed, especially of

570    natural plants.

571        The seaward limit of vegetation is also an important parameter for inclusion in numerical

572    models of dune growth. Though perennial and annual plants are different in their persistence in

573    the beach environment, it seems reasonable to expect that if TWL is important in determining the

574    seaward extent of perennials, it would also be important in determining the extent of annuals. If

575    TWL determines extent, the seaward limit of perennials would be determined by the highest total

576    water levels throughout the year (which usually occurs in the winter).  Similarly, the seaward

577    limit of annuals would be affected by water levels during the growing season (which are usually

578    lower than the winter levels, unless there is a hurricane). Our results, which indicate that the NIH

579    for annuals and perennials (5.5 % vs. 8.7%, resp.) and the elevation of the seaward extent (1.54

580    m vs. 1.37 m, resp.) are similar, suggests that the same process—TWL—determines the seaward

581    extent of both types of vegetation. The time of inundation we report is slightly greater than

582    findings from Kuriyama et al. (2005), which may be because our TWL record was computed

583    from observational data at nearby locations rather than observed on the beach locally through

584    time. Regardless, both Hesp (2013) and Kuriyama et al. (2005) indicate that the seaward limit of

585    vegetation occurs at an elevation where wave run-up only occurs a few times a year. If this

586    analysis, is generalizable, then it should be possible to approximate the seaward limit of annual

587    and perennial vegetation (and potential changes in this limit with changes in sea level and

588    storms) by computing a TWL, instead of making direct observations of the seaward extent of

589    vegetation. Additional comparisons between TWL, NIH and the seaward extent of vegetation

590    will be helpful in determining the extent to which this finding applies to other locations.


591    *Conclusions*
592         Results from our multi-species transplant experiment highlight the differences in growth

593    among different dune grass species, the importance of sand burial in determining plant growth,

594    and the complexity of factors that influence plant growth. We found that of the three dune

595    grasses we planted, *S. patens*, on average, grew less than the *A. breviligulata* and *U. paniculata.*

596 However, leaf growth was positively correlated with sand deposition for all species. Although *S.*

597 *patens* may not build dunes as quickly as *A. breviligulata* or *U. paniculata*, and has a small

598 basal/frontal area which results in less total sand accumulation, it does grow in response to burial

599 and thus is more appropriately classified as a dune-building species rather than as a maintainer.

600       We found that the influence of burial on plant growth is to reduce aboveground area

601 initially as a plant is buried, but that moderate amounts of sand burial increase overall plant

602 growth at the two year timescale. The balance between burial and growth should be considered

603 when modeling vegetation response to burial — it is a non-linear and species-specific response,

604 as noted in previous studies (e.g. Maun, 1998; Gilbert and Ripley, 2010). Also relevant to

605 modeling efforts, we found plant basal/frontal area (important in parameterizing surface

606 roughness) to be between 0.5 and 1, and that the seaward limit of vegetation corresponded to an

607 elevation which was inundated for a total of only 50 days (7.5% of the time) over the course of

608 our experiment.

609       This work provides insight into factors affecting the growth of *A. breviligulata, S. patens,*

610 and *U. paniculata* transplants in the beach and dune environment and highlights species-specific

611 differences that are important to include in modeling efforts if dune growth is to be accurately

612 portrayed. Improved model parameterizations will aid in increasing our understanding of the

613 vegetation-sediment transport feedback that causes dunes to grow and will enhance our ability to

614 explore the effects of changing future conditions on the dune-building process.

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Tables

Table 1. Abbreviation and variables.

| Abbreviation or Variable | Meaning |
|---|---|
| AB | *Ammophila breviligulata* |
| B/F | Basal/frontal |
| dagl years | Difference in aboveground leaf length for each season, analyzed together |
| dagldt | Monthly change in aboveground leaf length |
| $dl_{tot}$ | Total leaf growth |
| dz years | Change in elevation for each season, analyzed together |
| dz14 | Change in elevation from beginning to end of 2014 season |
| dz15 | Change in elevation from beginning to end of 2015 season |
| dzdt | Monthly change in elevation |
| $dz_{tot}$, dz | Total change in elevation |
| LagLL | Longest aboveground leaf length |
| $LagLL_f$ | Final longest aboveground leaf length |
| $LagLL_i$ | Initial longest aboveground leaf length |
| NatAB | Natural *Ammophila breviligulata* |
| NatSP | Natural *Spartina Patens* |
| NIH | Number of inundation hours |
| SP | *Spartina patens* |
| TWL | Total water level |
| UP | *Uniola paniculata* |
| x, dist | Distance from shoreline |
| $z_f$ | Final elevation |
| $z_i$, el, zi | Initial elevation |

Table 2. Averages, standard deviations, and ranges of total leaf growth(dltot ), longest aboveground leaf length (LagLL), and basal/frontal (B/F) area ratios for each species**.**

| | $dl_{tot}$ (mm) | | | $L_{ag}LL_f$ (mm) | | | B/F area | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD | range | $\bar{x}$ | SD | range | $\bar{x}$ | SD | range |
| *Ammophila breviligulata* | 531 | 295 | 1286 | 760 | 219 | 922 | 1.08 | 0.50 | 2.53 |
| *Spartina patens* | 452 | 162 | 664 | 595 | 132 | 536 | 0.5 | 0.43 | 1.58 |
| *Uniola paniculata* | 873 | 261 | 1178 | 1035 | 186 | 899 | 1.07 | 0.22 | 0.83 |
| Natural *A. breviligulata* | | | | | | | 0.68 | 0.23 | 0.75 |
| Natural *S. patens* | | | | | | | 0.59 | 0.16 | 0.46 |

Table 3. Analysis of variance and TukeyHSD values for differences in means and variances of total leaf growth ($dl_{tot}$ ), longest aboveground leaf length (LagLL), and basal/frontal (B/F) area ratio (p<0.05 in bold).

| ANOVA | F value | Pr(>F) | |
|---|---|---|---|
| $dl_{tot}$ plant (Figure 3,A) | 17.4 | 5.1e-7 | |
| TukeyHSD comparison | Difference (mm) | p adj | |
| SP-AB | -79 | 0.47 | |
| **UP-AB** | **342** | **1.5e-4** | |
| **UP-SP** | **421** | **2.4e-6** | |
| ANOVA | Fvalue | Pr(>F) | |
| LagLL plant (Figure 3,B) | 28.6 | 3.7e-10 | |
| TukeyHSD comparison | Difference (mm) | p adj | |
| **Sp-AB** | **-164** | **0.0038** | |
| **UP-AB** | **274** | **3.1e-6** | |
| **UP-SP** | **439** | **0.00e-6** | |
| ANOVA | F value | Pr(>F) | |
| B/Farea (Figure 3, C) | 5.0 | 4e-4 | |
| TukeyHSD comparison | Difference | p adj | |
| **SP-AB** | | **-0.37** | **0.01** |
| UP-AB | | -0.01 | 0.10 |
| NatAB-AB | | -0.40 | 0.12 |
| **NatSP-AB** | | **-0.50** | **0.03** |
| DM-AB | | 0.42 | 0.91 |
| UN-SP | | 0.36 | 0.06 |
| NatAB-SP | | -0.40 | 0.10 |
| NatSP-SP | | -0.13 | 0.98 |
| DM-SP | | 0.79 | 0.42 |
| NatAB-UP | | -0.40 | 0.21 |
| NatSP-UP | | -0.49 | 0.07 |
| DM-UP | | 0.42 | 0.91 |
| NatSP-NatAB | | -0.09 | 0.10 |
| DM-NatAB | | 0.82 | 0.41 |
| DM-NatSP | | 0.92 | 0.29 |

Table 4: The results of the multilinear regression pseudo-stepwise selection of best variables to use for each species. The variables are "dist" for distance from shoreline, "dz" for change in elevation, and "zi" for initial elevation. For each combination of variables, we calculated the F statistic, $R^2$ value, $R^2$ adjusted value, and AIC statistic for each model. We eliminated the models whose F statistic was not statistically significant, and then further narrowed down the number of models by choosing only those whose R2 adjusted value was more than 0.1 higher than other models (those which are bolded). Finally, we chose the models that had the lowest AIC score, which can be considered optimal. Bolded values are significant, shaded values are the final selection.

| Ammophila | dist | **dz** | zi | dist, dz | dist, zi | **dz,zi** | **dist, dz, zi** |
|---|---|---|---|---|---|---|---|
| F stat | 0.16 | **40.69** | 2.23 | **31.21** | 1.41 | **48.9** | **32.26** |
| $R^2$ | 0.004 | 0.50 | 0.052 | 0.62 | 0.07 | 0.71 | 0.72 |
| $R^2_{adj}$ | -0.02 | 0.49 | 0.029 | 0.56 | 0.019 | **0.7** | **0.69** |
| AIC | 3387.86 | 3130.41 | 3369.34 | 3038.72 | 3365.62 | 2928.4 | 2926.16 |
| Spartina | dist | **dz** | zi | dist, dz | dist, zi | **dz,zi** | dist, dz, zi |
| F stat | 2.95 | **16.08** | 1.074 | **11.23** | 1.42 | **8.83** | **7.13** |
| $R^2$ | 0.12 | 0.43 | 0.049 | 0.53 | 0.12 | 0.47 | 0.53 |
| $R^2_{adj}$ | 0.08 | **0.41** | 0.003 | **0.48** | 0.04 | **0.42** | **0.46** |
| AIC | 15.14 | 14.70 | 15.22 | 16.52 | 17.14 | 16.64 | 18.52 |
| Uniola | dist | dz | zi | dist, dz | dist, zi | **dz,zi** | dist, dz, zi |
| F stat | 0.13 | **30.97** | 0.7 | **15.4** | 0.81 | **16.33** | **10.28** |
| $R^2$ | 0.007 | 0.63 | 0.038 | 0.64 | 0.09 | 0.66 | 0.66 |
| $R^2_{adj}$ | -0.05 | **0.61** | -0.016 | **0.60** | -0.02 | **0.62** | **0.59** |
| AIC | 1740.9 | 1544.23 | 1734.81 | 1539.75 | 1726.4 | 1532.12 | 1533.79 |