

Using Long-Term Census Data to Inform Restoration Methods for Coastal Dune Vegetation

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Abstract Barrier islands are exposed to the wind and wave action from storms, which often disturbs both the geomorphology and vegetation. Conservation and restoration efforts for these important habitats could be improved with knowledge of how native plants respond to storms. We analyzed 10 years of annual data of vegetation of St. George Island, Florida, in the Gulf of Mexico, to quantify how the plant community responds to major storms and to predict which dune species might be appropriate for restoration after storm damage across dune zones. This prediction was tested with six plant species that differed in their storm response—from highly negative (local extinction in response to storms) to highly positive (increased abundance in response to storms). We measured transplant survival and growth (plant height and number of shoots) over 2 years in a restoration experiment across three major dune zones. We found that different species can be useful for restoration purposes in different dune zones, depending on both short- and longer-term management strategies. *Uniola paniculata* is a particularly strong restoration candidate across all dune zones, whereas *Muhlenbergia capillaris* and *Schizachyrium maritimum* would be beneficial for restoration in the interdune area. *Fimbristylis* spp. and *Sporobolus virginicus* demonstrate the strongest potential for restoration in the interdune and backdune areas. Restoration of disturbed areas often involves the seeding or transplanting of species to stabilize the landscape and initiate the return of the original vegetation. We show that the performance of native species, in response to storms, especially in conjunction with information on plant life history, can be useful for identifying the best species to use for restoration.

Keywords Barrier Island · Coastal ecology · Dune zone · Disturbance · Dune vegetation · Storm response

Introduction

Barrier Islands are a common landform along the eastern and Gulf coasts of North America (Hayes 1979) and account for almost 15 % of shorelines worldwide. They are important for buffering coastal areas from the effects of storms, but are not themselves impervious to disturbance, suffering degradation as a result of both coastal development (Funk et al. 2008) and tropical storms and hurricanes (Rodgers et al. 2009; Miller et al. 2010). Consequently, coastal restoration and management initiatives that attempt to rehabilitate damaged habitat have recently experienced a resurgence (Falk et al. 2006; Borja et al. 2010), with varied results. Restoration strategies can be difficult to implement successfully in coastal dune systems because dunes are dynamic habitats where multiple factors operate on different temporal and spatial scales to shape the environment (Boughey 1957; Fenster and Hayden 2007). For example, microsite differences in soil moisture can maintain distinct coastal plant communities at the local scale, while disturbances such as overwash from storms can damage vegetation across separate dune habitats (e.g., Stallins and Parker 2003).

Most undeveloped barrier islands are made up of three dune zones—foredune, interdune (or overwash), and backdune—that differ in geomorphology and vegetation (Lewis 1982; see also Otvos 2012). Plants in the high, regular sand dunes in the foredune area are typically stress- and salt-tolerant and have rapid vertical growth and extensive roots (Ehrenfeld 1990). Flat, low-lying interdune areas, behind the foredunes, are where overwash-tolerant dune plants can be found. These two zones generally protect the bay side of the island from climatic disturbances. The more protected backdune zone is lower and more stable and composed of old foredunes and swales that have migrated

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toward the mainland (Fagherazzi et al. 2003; Otvos 2012), harboring burial- and salt-intolerant dune species that are usually longer-lived (Ehrenfeld 1990; Dech and Anwar Maun 2006). Storm damage that denudes coastal areas of native vegetation often necessitates restoration, involving efforts to assist in the recovery of all three of these zones.

Recent criticisms of coastal restoration efforts have noted the absence of the application of ecological theory and data to restoration practices (Giardina et al. 2007; Palmer 2009). For example, coastal plant restoration has historically involved the installation of monocultures, often in degraded areas of the foredune zone only (Thom 2000), despite research which suggests that a broad variety of species should be considered across the entire damaged habitat (Palmer et al. 2008; Pries et al. 2008). In coastal dunes, successful restoration initiatives must take into account the relationships among geomorphology, ecology, and climate.

Identifying appropriate species for restoration remains problematic and is often driven by the availability of plant material rather than research. Ideally, plants used for restoration should be native species that can persist with minimal support and facilitate the reestablishment of other natives (Montalvo et al. 1997). Moreover, using a collection of species rather than a single one can maximize transplant success across dune zones (Stalter and Batson 1969; Camargo et al. 2002) while helping to restore diversity. Realistically, restoration candidates should have subsets of general characteristics that are noted as particularly likely to predict survival and establishment, tailored for the particular dune zone that is damaged and the goals of the restoration effort.

In this study, we used a unique long-term set of data on the vegetation of St. George Island, a microtidal barrier island 5 km off the NW coast of Florida, to quantify the abundance and storm response characteristics of various plant species in different dune zones. We then used these characteristics to predict which species had the highest potential for survival and growth in damaged dune areas. We expected that plant species less vulnerable to storms, as demonstrated by stable or increasing abundance after hurricanes, are more likely to have a positive influence on the succession that follows storms and may be useful for restoration purposes. We tested this novel method of identifying restoration species directly by transplanting selected species into degraded areas in all three coastal areas on St. George Island and comparing the survival and growth of different species within each zone, as well as the survival and growth of each species individually in all three zones.

Materials and Methods

St. George Island State Park (29°38' N, 84°54' W) occupies the eastern third of St. George Island and consists of the

fore-, inter-, and backdune zones common to most barrier islands. The soil is composed of a fine sand surface over a layer of sandy silt or clay and sits on top of a freshwater lens 0–10 m below the soil surface that is narrower and located farther below the soil surface in the backdune habitat (Schneider and Kruse 2006). A long-term census has documented vegetation dynamics on the island annually since 1999. The long-term data show that storms are the dominant drivers of species distribution and abundance on the island (Miller et al. 2010), suggesting that storm response could be a useful metric for the identification of restoration candidates.

Collection of Long-Term Data

In 1998, six permanent grids were established at the eastern tip of St. George Island for vegetation monitoring (Fig. 1): two grids in each dune zone (98 plots total). Vegetation within these grids has been censused annually in the fall when plant species are most easily identifiable. Each grid is 60×60 m and contains a 7×7 array of stakes. The 60-m scale was generally over twice the distance between dunes, allowing us to describe the broader spatial heterogeneity of the dunes. Each census, a 1-m² quadrat is placed over each stake and the number of individuals or number of clumps (depending on growth form) and percentage cover is recorded for each species. Most dune plants are relatively small such that the 1-m² plots were adequate for describing the plant community at any given elevation in this complex dune environment (for complete methods, see Miller et al. 2010).

Storm Response

Storms passed close to or directly over St. George Island several times between 1998 and 2008. The years 2004 and 2005 were marked by particularly intense storm activity, as indicated by precipitation (>31 cm of rain), wind (max speeds >140 mph), and surge data (up to 2 m from Hurricane Dennis in 2005) from the National Oceanic and Atmospheric Administration, during the summer and early fall, before the plant censuses were conducted for those years. The effects of these storms were highly variable among plots. Foredunes were more likely to be subject to blowouts and overwash, while interdunes are generally flooded by fresh water, sometimes for several weeks. Even backdunes were affected, with dune tops are eroding and troughs flooding. We quantified each species' storm response in each dune zone as its change in percentage of 1-m² plots occupied (P_S , hereafter referred to as occurrence) from 2003 to 2004 and from 2004 to 2005.

$$P_S = (P_{(t+1)} - P_{(t)}) / P_{(t)} \quad (1)$$

where $P_{(t)}$ is occurrence at time t and $P_{(t+1)}$ is occurrence at time $t+1$. These values for the two storm years used in Eq. 1 were averaged to yield a single P_S for each species in each dune habitat.

Restoration Candidates

We were interested in the restoration ability of species with different patterns of storm response in each dune zone. We therefore categorized the species by their responses to storms as being negative (species that decreased in abundance in storm years) or positive (species that increased in abundance in storm years). If a species' abundance experienced little change (P_S between -5 and $+5$ %), it was categorized as maintaining its abundance. We then selected six dune species that exemplified a range of responses to storms across the three zones (Table 1) for our restoration study.

These six species had different storm responses and were sufficiently abundant to supply source material for the study: *Centella asiatica* (Apiaceae), a perennial herbaceous dicot; *Fimbristylis* spp. (either *Fimbristylis spathacea* or *Fimbristylis caroliniana*—non-reproductive individuals cannot be easily identified in the field; Cyperaceae, a perennial graminoid); *Muhlenbergia capillaris* (Poaceae); *Schizachyrium maritimum* (Poaceae); *Sporobolus virginicus* (Poaceae); and *Uniola paniculata* (Poaceae), all perennial graminoids. For convenience, all six taxa are hereafter referred to only by genus. The long-term data suggest that on St. George Island, *Fimbristylis* and *Uniola* are characteristic foredune species, *Centella* and *Sporobolus* characteristic interdune species, and *Muhlenbergia* and *Schizachyrium* characteristic backdune species. These species are often found in similar areas around the Gulf Coast (Doing 1985; Moreno-Casasola and Espejel 1986), although they are not restricted to barrier islands (e.g., Blits and Gallagher 1991).

Transplanting

One hundred ramets of each of the six transplant species were collected from multiple source locations on St. George

Island in December 2007 to minimize negative effects on the extant vegetation. These ramets were then transplanted to a greenhouse at Florida State University in Tallahassee, FL. The plants were kept for 3 months in a 1:1 mixture of potting soil and sand, with a small amount of fertilizer (3:3:3; N/P/K), in individual 5×5-in. pots, watered twice a week. After 2 months, 300 similar-sized ramets of each species had been produced and were transplanted to field plots as plugs. Soil and fertilizer in the original plugs likely had only a small effect on the habitat as sand has a very low retention capacity and only a small amount of rain is sufficient to remove these sediments from the sand (Dahl et al. 1975).

Three 6×5-m quadrats were established in storm-damaged areas in each of the three experimental zones (fore-, inter-, and backdunes; Fig. 1). These areas were initially bare of any live vegetation due to sand movement following the storms of 2004 and 2005. Each of these nine quadrats contained thirty 1-m² plots into which one ramet of each species was transplanted, for a total of six transplants in each plot (180 transplants per quadrat). No water or fertilizer was applied after the plants were transplanted into the field to simulate realistic restoration conditions.

After transplanting in February 2008, the survival and growth of plants were monitored bimonthly for 2 years, for a total of 12 measurements. Survival was defined as the presence of green plant material aboveground. Growth was measured as the number and length (in centimeters) of the longest culms (for *Fimbristylis*, *Muhlenbergia*, and *Uniola*) or stolons (for *Centella*, *Schizachyrium*, and *Sporobolus*) of each transplant. Although leaf number was determined for *Centella*, because the growth of this species is primarily by rhizomes and only leaves appear aboveground, we did not measure stem length.

Analysis

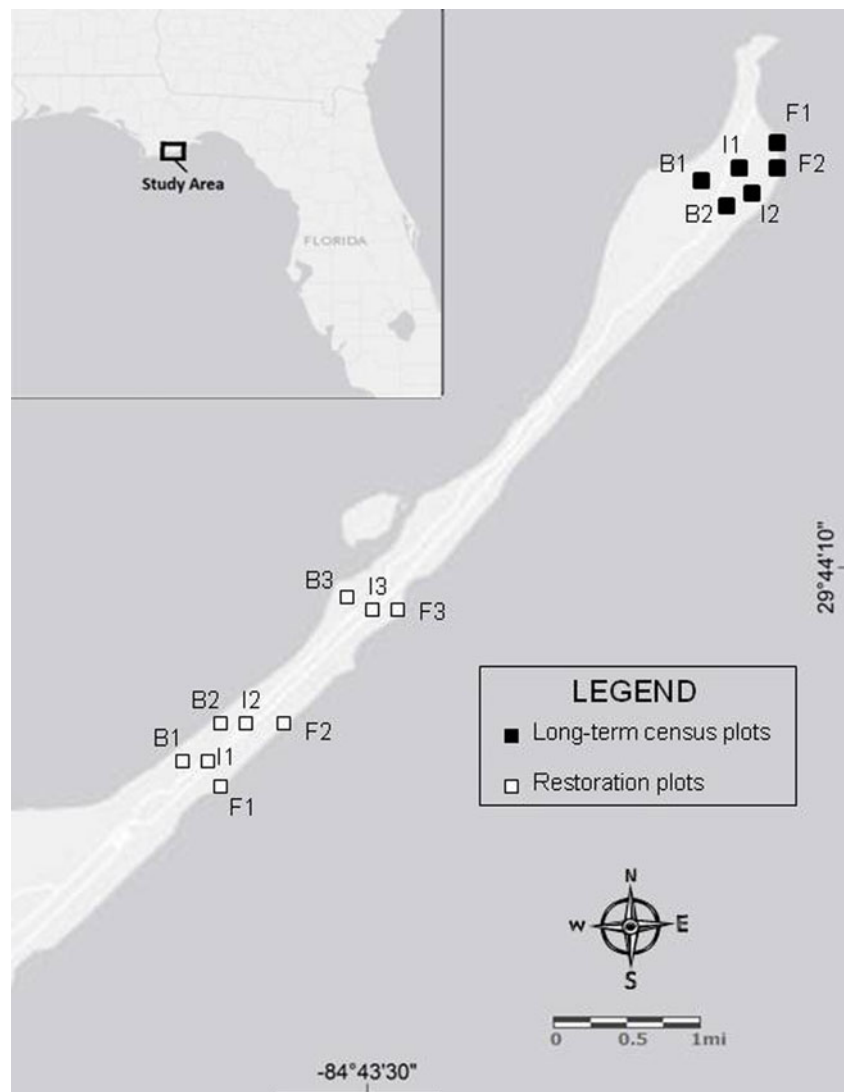
All analyses were conducted in R, version 2.12.2 (R Development Core Team 2007), with linear mixed models, with plots nested within quadrats, nested within dune zone (random factor, $n=3$). We analyzed the contribution of

Table 1 Direction and average size (in parentheses) of change in percentage occurrence in each of three dune zones of St. George Island, Florida, in response to storms between 2003 and 2004 and between 2004 and 2005 for each of the six transplant species chosen for the study

Species	Change in occurrence in response to storms		
	Foredune	Interdune	Backdune
<i>Centella asiatica</i>	Never present	Decrease (−55)	Decrease (−69)
<i>Schizachyrium maritimum</i>	Decrease (−17)	Decrease (−8)	Decrease (−7)
<i>Muhlenbergia capillaris</i>	Maintain (0)	Decrease (−20)	Maintain (+1)
<i>Uniola paniculata</i>	Maintain (0)	Maintain (+4)	Maintain (−4)
<i>Fimbristylis</i> spp.	Maintain (−4)	Increase (+7)	Increase (+75)
<i>Sporobolus virginicus</i>	Increase (+175)	Maintain (+4)	Increase (+200)

“Maintain” indicates little or no change

Fig. 1 Map of the study location of fordune (*F*), interdune (*I*), and backdune (*B*) long-term census plots and restoration plots on St. George Island State Park



independent variables to each of our response variables with two separate models. First, we created models that addressed the effects of dune zone and species identity (fixed factors) on the survival and growth of transplants. Second, we created models that addressed the effect of zone-specific response to storms (P_S , fixed factor) on transplant survival and growth. Models for survival and growth were analyzed separately for years 1 and 2.

For the first set of models (effects of dune zone and species identity), for both years, we conducted model selection using Akaike information criterion differences ($\Delta_i = AIC_i - AIC_{\min}$) and Akaike weights (likelihood of the model, given the data $w_i = \exp[-\frac{1}{2}\Delta_i] / \sum \exp[-\frac{1}{2}\Delta_i]$) to determine the best-fit models for inference (Burnham and Anderson 2002).

Survival

The contributions of dune zone, species identity, and zone-specific response to storms to survival (binary data) for the

proposed restoration species after 1 and 2 years were determined with linear mixed models (R package lme4; bernoulli distribution).

Growth

The contributions of dune zone, species identity, and storm response to stem number were analyzed with a linear mixed model (Poisson distribution). Finally, the contributions of dune zone, species identity, and storm response to log-transformed stem length were also analyzed with a linear mixed model (R package nlme; normal distribution).

We did not conduct a repeated-measures analysis because we did not find a direct effect of time in a within-subject correlation of the random effect for the intercept and the random effect of time for each of our response variables. Furthermore, models that did not explicitly include time had significantly better fit than models that did (survival: $P <$

0.001, $\chi^2=363.92$; stem number: $P<0.001$, $\chi^2=8,502.4$; stem length: $P<0.001$, $\chi^2=2,060.9$).

Results

Response of Natural Vegetation to Storms

From the census data, average change in species' occurrences in storm years was negative for all dune zones (−16 % in the foredune, −15 % in the interdune, and −13 % in the backdune). A positive response to storms was observed in some species, occurring least frequently in the foredune zone (6 of 34 species) and most frequently in the backdune zone (13 of 45). The six species selected for the transplant study occurred in all three dune zones and demonstrated a gradient of storm responses from strongly positive to strongly negative in different habitats (Table 1).

Restoration Trials with Transplants

Survival

Across all six species, the average overall transplant survival rates in the interdune and backdune zones were similar (57 and 54 % survival, respectively), and the average transplant survival in the foredune zone (26 % survival) was generally much lower than elsewhere ($\beta=-1.64$, $SE=0.48$, $z=-3.4$, $P=0.0006$). Survival of the transplants depended strongly on species and dune zones (Fig. 2).

The best-fit model for survival after 1 year was the full model, which included species identity, dune zone, and the interaction between the two ($\Delta_1=0$, $w_1=0.99$). After 1 year, *Centella* had the lowest total survival in all dune zones ($\beta=-1.74$, $SE=0.38$, $z=-4.54$, $P<0.0001$), a pattern especially apparent in the foredune and backdune zones, where the abundance of *Centella* transplants decreased precipitously after 6 months and remained low throughout the rest of the project (Fig. 2). *Sporobolus* maintained the highest overall average survival ($\beta=1.06$, $SE=0.36$, $z=2.96$, $P=0.003$) despite the significant decrease in its survival after the third census in the foredune zone (July 2008). *Fimbristylis* was the only species that demonstrated apparent seasonal variation in survival in the interdune and backdune zones, undergoing transient decreases in survival during the winter (February 2009 and January 2010 censuses). Storm response also significantly affected survival in the first year; higher transplant survival was documented for species that exhibited a positive ($\beta=0.71$, $SE=0.16$, $z=4.54$, $P<0.0001$) or maintenance ($\beta=1.09$, $SE=0.14$, $z=7.75$, $P<0.0001$) storm response (38 and 41 % survival, respectively) than for species that had a negative storm response (27 %).

The best-fit model for survival after 2 years was, again, the full model ($\Delta_1=0$, $w_1=0.99$). In year 2, survival was highest in the interdune zone ($\beta=0.47$, $SE=0.22$, $z=2.19$, $P=0.03$) and lowest in the foredune zone ($\beta=-1.39$, $SE=0.23$, $z=-6.14$, $P<0.0001$). *Sporobolus* ($\beta=0.89$, $SE=0.2$, $z=4.48$, $P<0.001$) and *Uniola* ($\beta=0.77$, $SE=0.2$, $z=3.96$, $P<0.001$) showed the highest overall survival. *Uniola* exhibited a relatively consistent survival (~65 %) across all dune zones, exhibiting its lowest survival, on average (50 %), in the interdune zone. *Muhlenbergia* and *Schizachyrium* showed similar patterns of survival (Fig. 2), with relatively low survival (<20 %) in the foredune zone but comparatively higher survival (60 % for *Muhlenbergia*, 35 % for *Schizachyrium*) in the interdune and backdune (~50 % for both) zones. *Centella* was documented as having the lowest overall survival of all the transplant species (16 %), mostly as a result of the high mortality experienced by this species in the foredune and backdune zones. In this second year, the dune species that responded to storms with a decrease in abundance (survival mean=34 %, $SE=2.2$ %) showed higher mortality than species that responses to storms with a maintenance (survival mean=47 %, $SE=2.5$ %) or an increase (survival mean=44 %, $SE=1.7$ %) in abundance ($\beta=-0.94$, $SE=0.42$, $z=-2.23$, $P=0.03$).

Stem number

After year 1, the best-fit model for stem number included only species identity ($\Delta_1=0$, $w_1=0.52$), as might be expected for plants with very different growth forms, but the model selection uncertainty is high as the evidence ratio (w_1/w_2-w_2 includes both species identity and dune zone) is 1.09, which is a relatively weak support for the best model. *Centella* showed the highest mean and variance in stem number in all three habitats ($\beta=0.46$, $SE=0.21$, $z=2.25$, $P=0.03$; Fig. 3), decreasing in stem number only slightly by the end of year 2. Interestingly, after 1 year, stem number was greater for species that responded to storms with a decrease in abundance (mean change in stem number=12 %, $SE=3.1$ %) than species that responded to storms with a maintenance (mean change in stem number mean=−4 %, $SE=2.1$ %) or an increase (mean change in stem number=−18 %, $SE=1.5$ %) in abundance ($\beta=1.29$, $SE=0.14$, $z=9.1$, $P<0.0001$).

After year 2, the best-fit model ($\Delta_1=0$, $w_1=0.81$) suggested that only species identity contributed to stem number of transplants as *Centella* exhibited the highest average stem number ($\beta=2.09$, $SE=0.15$, $z=14.16$, $P<0.0001$). In *Fimbristylis*, *Muhlenbergia*, and *Uniola*, culm number did not appear to change in any dune zone within years or from year to year, whereas stem number decreased by half for *Schizachyrium* between years (Fig. 3). The mean stem number for *Sporobolus* nearly doubled between year 1

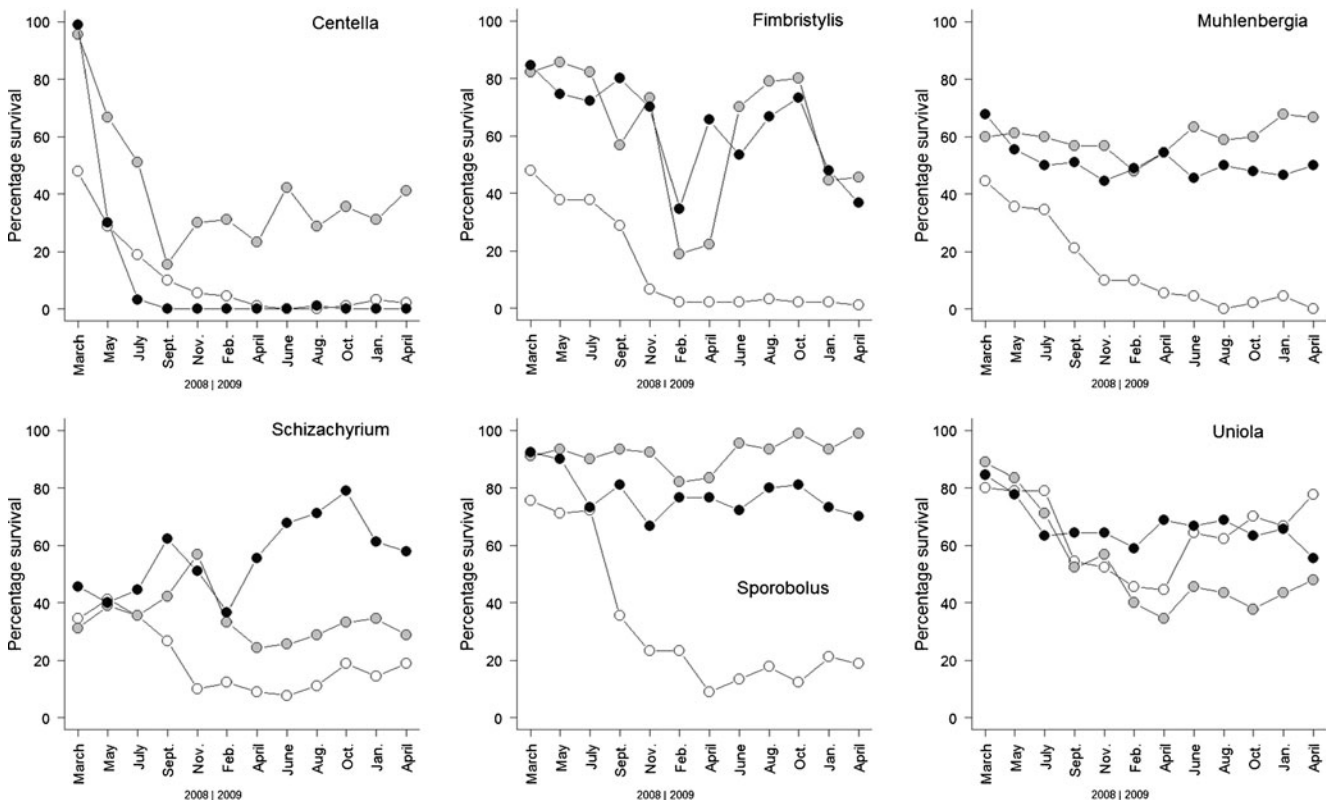


Fig. 2 Number of live individuals of each transplant species in foredune (white), interdune (gray), backdune (black) zones. An increase in the number of live transplants indicates a release from belowground dormancy

and year 2. Species that responded to storms with a decrease in abundance had higher numbers of stems than did species that maintained their abundances after storms ($\beta=1.56$, $SE=0.13$, $z=12.31$, $P<0.0001$).

Stem length

After year 1, the model that described stem length as a function of species identity only (as might be expected for plants with very different growth forms: $\Delta_1=0$, $w_1=0.625$) was not a convincingly better model than the model ($\Delta_2=1.12$, $w_2=0.35$) that included both species identity and dune zone (evidence ratio=1.8). Overall, *Uniola* had the longest stems of all the transplant species ($df=276$, t statistic=11.62, $P<0.0001$). The stem lengths of *Fimbristylis* ($df=274$, t statistic=-4.34, $P<0.0001$) and *Muhlenbergia* ($df=276$, t statistic=-2.67, $P=0.008$) were higher in the interdune zone than in either the fore- or the backdune zone after year 1, a distinction that was sustained during year 2 (Fig. 4). In contrast to stem number, after 1 year, species that responded to storms with a maintenance but not an increase in abundance yielded longer stems than those that responded to storms with a decrease in abundance ($df=286$, t statistic=5.03, $P<0.0001$).

After year 2, the best-fit model of stem length included species identity only ($\Delta_1=0$, $w_1=0.96$); under it,

Muhlenbergia increased overall in stem length ($df=350$, t statistic=15.76, $P<0.0001$), but *Sporobolus* and *Uniola* exhibited relatively little variation in stem length among dune zones after year 1. The role of storm response was slightly different in year 2 as species that responded to storms with an increase in abundance exhibited shorter stems than species that responded to storms with a maintenance or a decrease in abundance ($df=352$, t statistic=-13.13, $P<0.0001$).

Discussion

We used an existing set of long-term census-based data on vegetation dynamics to predict how well species would survive and grow in storm-damaged areas on St. George Island. We tested these predictions by transplanting six of these species into three disturbed dune zones and following the transplanted individuals for 2 years. Overall, the results suggested that (1) storm response can be an effective metric for choosing restoration species for coastal systems; (2) different dune zones are likely to require different restoration species; and (3) transplant success cannot be predicted from the dune zone with which the species is generally associated.

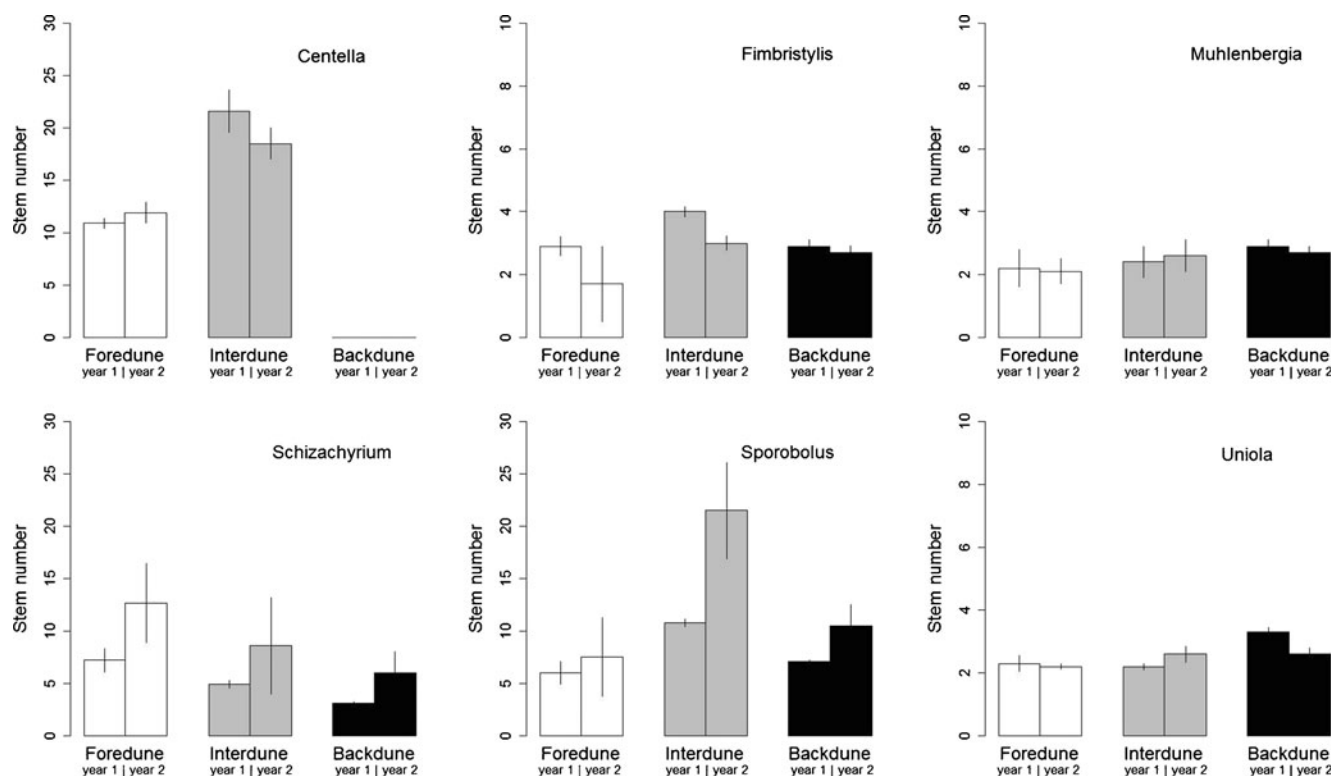


Fig. 3 Average stem number of each species in the foredune (white), interdune (gray), and backdune (black) zones after 1 and 2 years. Error bars, ± 1 SE. Note differences among panels in y-axis scale

Storm response appears to be a strong predictor of the survival of restoration candidates. *Fimbristylis* and *Sporobolus*, the two dune species that demonstrated the most consistent positive response to storms, were documented to have the highest overall transplant survival, while the lowest performing species in terms of average survival, *Centella* and *Schizachyrium*, had the most negative responses to storms. But, surprisingly, growth of restoration candidates had a negative relationship with storm response. These patterns could be explained by classic stress response syndrome theory (Chapin et al. 1993), which describes the trade-off between a plant's ability to survive a stressful environment and its growth capacity. Dune plants that are able to withstand the negative effects of a storm could be effective restoration species by *persisting* in storm-damaged areas, but may be less likely to grow and proliferate aggressively in those areas.

Of the six species we studied, the two species in our study that responded most negatively to storms, *Centella* and *Schizachyrium*, were predicted to have the lowest restoration potential of all species tested. Although *Centella* seemed to have high rates of growth in the interdune habitat, this result is probably an artifact of its growth form, which is highly rhizomatous. Indeed, *Centella* performed the most poorly overall, potentially because of reduced soil moisture availability or differences among zones in shading from surrounding

vegetation (Wankhar and Tripathi 1990). Similarly, in the first year after transplantation, *Schizachyrium* showed low growth and comparatively low survival in the backdune zone, where it is most commonly found, but performed well in other areas (Figs. 2 and 3). Perhaps *Schizachyrium* is more representative of a barrier-island climax community (Dahl et al. 1975; Johnson 1997) and therefore performed better, in the short term, in storm-degraded areas in the foredune and interdune zones, where stress could facilitate more rapid succession (Viejo 2009).

The two species that were documented as maintaining their abundances in response to storms in the long-term data, *Muhlenbergia* and *Uniola* (Table 1), exhibited different survival and growth capabilities in different dune zones. *Uniola* had relatively high, constant survival and growth in all three zones, but demonstrated its highest overall survival in the backdune area (Fig. 2), contrary to previous reports (Gormally and Donovan 2010). Our work supports the frequent use of *Uniola* as a restoration species, especially on foredunes (Hesp 1991), but we found that the restoration potential of this species extends beyond the foredunes. Alternatively, despite being common in the backdune areas of St. George Island, *Muhlenbergia* had only average transplant survival in this zone, suggesting that this species might not be a particularly robust transplant subject.

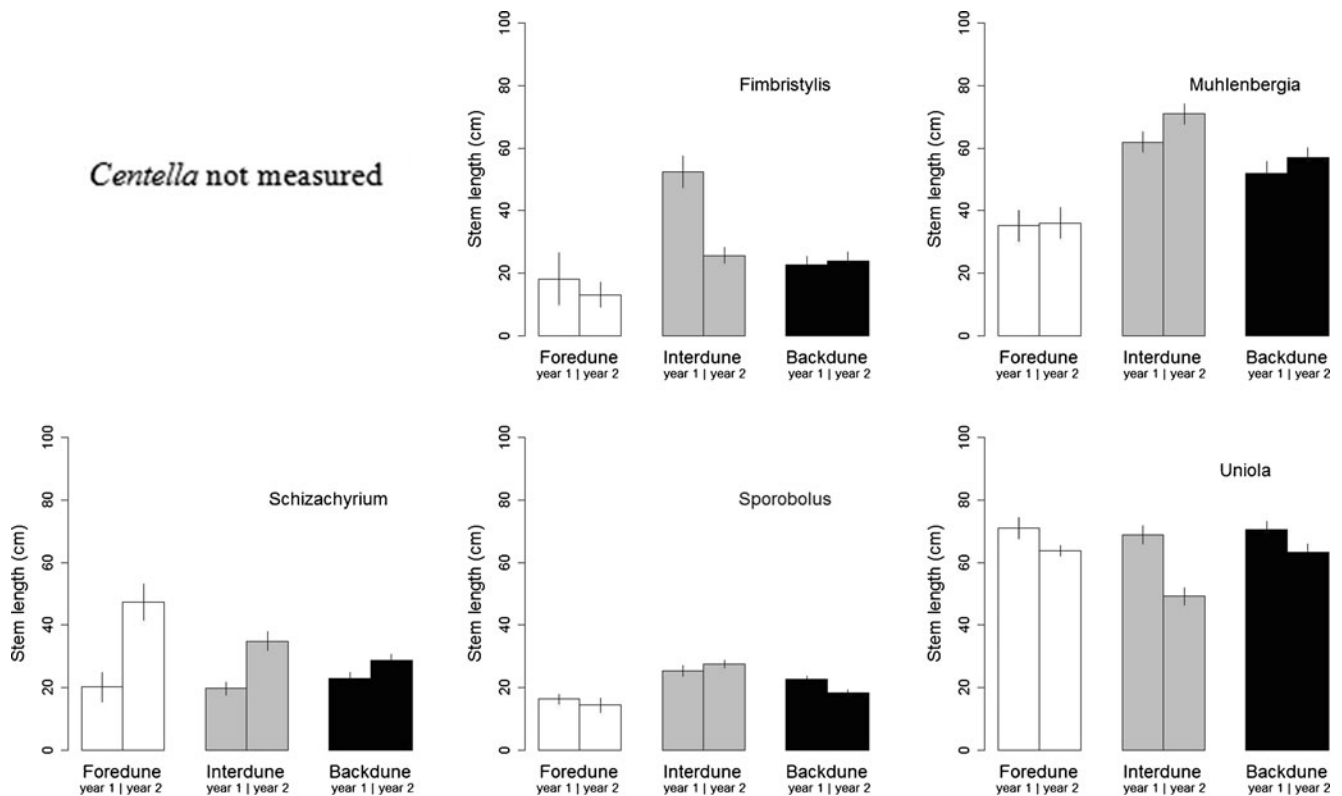


Fig. 4 Average stem length of each species in the foredune (white), interdune (gray), and backdune (black) zones after 1 and 2 years. Error bars, ± 1 SE

Finally, the two species that had some of the most consistent positive response to storms, *Fimbristylis* and *Sporobolus*, had relatively consistent high survival and growth in the inter- and backdune dune zones. Interestingly, *Fimbristylis* had its least robust storm response and its lowest transplant survival and growth in the foredune zone; perhaps because it is really a characteristic species of protected areas immediately behind foredunes (Miller et al. 2010; Johnson 1997). *Fimbristylis* may do well as a restoration species in the interdune and backdune zones because it acts as an early-succession species in these areas (Johnson 1997). These areas are also characterized by greater soil moisture and nutrient availability, which are known to be important for the survival and growth of *Fimbristylis* (Begum et al. 2006). *Sporobolus* had remarkably high relative survival and growth in all zones, potentially because of its salt tolerance (Blits and Gallagher 1991), while consistently doing best overall in the interdune and backdune zones, where it is found most often (Gornish 2009).

We conclude that robustness of storm response and transplant success are related, and our study did identify restoration candidates that would have high survival in specific dune areas. *Uniola* would be an effective restoration species in the short and long term in all dune zones. *Schizachyrium* and *Muhlenbergia* would perform best as restoration tools in

the interdune zone for both the long and short term. Finally, *Fimbristylis* and *Sporobolus* also have high potential as restoration species in the interdune and backdune zones, where, despite seasonal survival cycles, they exhibited high survival and growth in both years 1 and 2.

Interestingly, transplant success did not always match abundance or storm response across the three zones. For example, *Muhlenbergia* transplants had the highest survival and growth in interdunes, but its storm response was best in backdunes. This result illustrates the importance of choosing restoration species on the basis of disturbance-specific traits and restoration needs rather than storm responses or abundance patterns alone (Funk et al. 2008). Factors that influence the ability of a plant to survive immediately after a disturbance may differ from those that determine abundances much later (Bull et al. 2004). Clearly, dune plant species must be robust enough to survive the effects of storms, such as increased soil salinity and substrate destabilization (Miller et al. 2008), but other factors might be useful, in conjunction with storm response, for the identification of useful restoration candidates. For example, the method of reproduction (Harper 1967) or stress tolerance (Sarmiento et al. 2003) might be important factors determining success as a restoration species as these traits can affect both competitive ability and potential further spread.

Ecological data should be considered in applied restoration decisions. We incorporated a scientific approach into the design and implementation of a restoration effort and demonstrated the importance of considering past and present site conditions as well as drivers of large- and small-scale dynamic changes (Thom et al. 2005). Although using ecologically relevant traits to identify effective restoration candidates appears to be a useful restoration technique, it cannot completely replace trial studies of candidate species.

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