Use of Long-Term Vegetation Census Data to Inform Restoration Methods and Processes of Community Ecology on a Barrier Island

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USE OF LONG-TERM VEGETATION CENSUS DATA TO INFORM RESTORATION METHODS AND PROCESSES OF COMMUNITY ECOLOGY ON A BARRIER ISLAND

By

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A Thesis in press to the Department of Biological Science in partial fulfillment of the requirements for the degree of Master of Science

Degree Awarded: Summer Semester, 2009

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ACKNOWLEDGMENTS

I thank T. E. Miller for use of the long-term census data in addition to an overwhelming amount of lab, field and mental support and personal and professional encouragement. I thank A. A. Winn, N. Underwood, A. Mast and J. Chanton for facilitating an abrupt (and momentary) interruption of dissertation work to complete this tangential thesis, in addition to helpful comments and ideas on writing and project development. Special thanks to labmates C. terHorst for encouragement and guidance throughout this process and E. Simmons for uncountable hours of field assistantship on early Saturday mornings. J. Mola, J. Monge and M. Plastini provided consistently excellent field, lab and greenhouse help. Individuals at the Apalachicola National Estuarine Research Reserve have provided valuable data and field help, especially B. Dean, L. Edmiston, M. Lamb, L. Levy, N. Selly and J. Wanat. J. Donoghue provided guidance and lab space for particle analysis in addition to useful advice on all aspects of environmental sampling. M. Ye provided a TopCon Total Station for elevation measurements and S. Davis provided excellent instructions and guidance on its use in addition to help in the field. Volunteers past and present from the Florida State University Ecology and Evolutionary Biology program have been the reason the annual census has been so pleasant and fruitful. R. Wiedner provided wooden stakes for substrate movement measurement. H. Gamper and J. Sulik provided many hours of GIS explanation and sanity. J. Raymer at the Department of Environmental Protection in Pensacola provided valuable transplant and restoration advice. G. Bieniek, R. Davenport, A. Forde, L. Gabner, J. Grinath, F. Gruber, L. Haley, J. Hines, M. Hodgeson, K. Kox, K. Liane, P. Miller, E. Moran, A. Roman, M. Simon and M. Thairu volunteered many hours in the field. K. Milla supplied a spectrometer and GIS advice. A. Johnson, G. Nelson, T. Stallins, L. Dudly and J. Hines provided advice on methods and analysis for this project. Thanks to rangers and volunteers at St. George Island State Park for always being friendly and helpful. This study was funded by U.S. Fish and Wildlife, Florida State University’s Robert K. Godfrey Endowment Award for the Study of Botany and the National Oceanic and Atmospheric Administration’s National Estuarine Graduate Fellowship. Additional support was provided by the Florida Native Plant Society Travel Award.
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ABSTRACT

In the Gulf of Mexico, barrier islands absorb the majority of the wind and wave action from storms, resulting in modification of dune morphology and vegetation dynamics. Understanding changes in dune vegetation in response to storms can identify the ecological processes occurring in these areas as well as help predict future effects of tropical storms. Since 1999, T. Miller of Florida State University has been collecting data describing the dynamics of dune vegetation on St. George Island. These long-term census data provide an opportunity to investigate the ecology of dune ecosystems.

I analyzed this ten-year data set to quantify how vegetation responds to major storms and determine which dune species would be most useful for restoring damaged coastal areas. This approach was tested using six plant species that were identified by T. Miller as particularly robust to the effects of storms. I conducted a transplant experiment with these six species across dune microhabitats and quantified transplant survival and growth over time in each habitat. Results suggest that, while several of these species have significant potential for restoration use, the habitat from which a transplant species originates is not a good indicator of its success in different habitats. Further, it appears that transplants encourage succession on degraded habitat. I explored the potential to extrapolate this restoration technique to a broader group of landscapes using GIS and aerial images to characterize vegetation change over time on St. George Island and compared these data with long-term census data. Additionally, I investigated if remote sensing could be used to identify locations that were similar to St. George in the distribution of dune habitats and the effects of storms across these areas. Results suggest that remote sensing approaches can be useful for a subset of habitat and species types on barrier islands.

Lastly, I used estimates of plant growth in good and bad years from the long-term data to build a model that describes succession in dune habitats. The model can be used to identify how dune communities might respond to a change in storm frequency. The model predicts that an increasing frequency of storms will result in plant species turnover in each dune community with the foredune community expressing the most dramatic changes.
INTRODUCTION

Long-term data are important for understanding both the natural history of a habitat as well as for identifying the forces that sculpt the component species (Kroncke et al., 1998). This is especially important in dynamic habitats where multiple factors shaping the environment operate on different timescales and magnitudes. Barrier islands are a classic example of an ecosystem driven by dynamic abiotic and biotic components. Constant, normal wave action and rare but recurrent high frequency and intense storms (Fagherazzi et al., 2003) combine to create different unique habitats, each with a distinct geomorphology and plant community.

Quantifying the important ecological drivers has been the goal of a long-term census that has documented the vegetation dynamics on St. George Island in Apalachicola Bay since 1999. This data set, initiated by T. Miller (Florida State University), was created using an annual census conducted over ten years on the distribution and abundance of dune plant species over a 2.5 hectare area on a barrier island. This thesis consists of four projects that are related to this 10-year census.

Identifying long-term vegetation change in coastal regions allows a better understanding of the relationships among barrier island geomorphology, vegetation and climate and this, in turn, provides an opportunity to develop conservation techniques. In Chapter 1, I describe analyses of the long-term data with two goals: identifying temporal patterns in the vegetation across three major habitats (foreshore, interdune, and backdune) on St. George Island and then using this analysis to identify species that might be appropriate for restoration of these habitats following storm damage. Candidate species for restoration were identified based on dynamical response to storms and distribution and abundance patterns across the dune habitats.

In Chapter 2, I describe how I transplanted six of these candidate species into damaged areas on the island to test individual survival and growth across habitat types, as well as the effect of these transplants on natural dune plant succession. Using knowledge of the local community ecology to inform restoration design and implementation could improve conservation strategies along the Gulf Coast.

Long-term census data can only be used to identify good candidate species for restoration purposes if such data exists for the location of interest. In Chapter 3, aerial images (from remote sensing) are converted to vegetation maps to identify changes in vegetation communities through time on St. George Island and Little St. George, a similar nearby habitat. Ideally, future changes in vegetation distribution and abundance as a response to storms could then be identified without the use of ground-based long-term data by using remote sensing to compare vegetation maps at different times. The characterization of local dune habitats through remote sensing methods may allow this research to be generalized over a broader area, making more effective restoration techniques available to managers of critical coastal environments.

In Chapter 4, I describe a model that predicts how plant communities within dune habitats could change if storms increase in frequency, as expected by (among others) the Intergovernmental Panel on Climate Change (2007). The model uses the long-term census to predict how each species will grow in storm and non-storm years, and uses this information to predict vegetation composition over a range of storm frequencies. The model also predicts how community patterns such as diversity, richness, and average abundance will change with storm frequency.
CHAPTER 1

LONG-TERM CENSUS DATA

Introduction

Barrier islands are a common land form along the Eastern and Gulf coast of North America (de Jonge, & de Jong, 2002; da Silva et al., 2008; Houle, 2008) and account for almost 15% of the shorelines worldwide, despite their young geological age of about 4000-6000 years (Donoghue & Tanner, 1992). These coastal structures have been the focus of considerable research due, in large part, to the unique reciprocal relationship between the dune vegetation and the geomorphology of the dunes and islands themselves. Barrier islands are also important for buffering coastal areas from the effects of storms; tropical storms, such as hurricanes, can degrade barrier island habitat to flat, barren substrate (Walker & Willig, 1999). There has been a recent resurgence in interest in barrier islands with predictions that global change will cause an increase in the intensity and frequency of storms, especially in the Caribbean and the Gulf of Mexico (Parmesan et al., 2000).

Barrier islands can be partitioned into three habitat zones: foredune, interdune and backdune habitats, based on differences in geomorphology and vegetation (Lewis, 1982). Although processes perpetuating barrier island habitats can differ in type and magnitude (Boughey, 1957), many studies identify a common set of interactions that sculpt their basic shape (Stallins, 2005). Some of the most influential factors driving the zonation of barrier islands include the constant, normal wave and wind action and rare, but recurrent, high frequency and intense storms (Fagherazzi et al., 2003). Waves operate at the immediate shoreline, producing regular sand dunes and swales. Wind is also involved in the generation of the high, regular foredunes present at the ocean’s edge. The effects of storms can bring about a powerful overwash that breaches the foredunes, depositing sediments behind them and creating flat interdune areas. These two zones generally protect the bayside of the island from climatic elements, perpetuating a less dynamic, protected backdune habitat that consists of lower, stable dunes and swales.

Vegetation can play a large role in determining island geomorphology in a reciprocal relationship where the geomorphology also affects the vegetation (Baas, 2002; Stallins & Parker, 2003). Dune plants interact with sediment mobility and modify topography, and by doing so, shape the conditions under which they and other plants occur (Odum, 1988; Stallins, 2005). At least three general groups of dune plants have been identified as significant in geomorphologic development: (1) dune builders in foredune areas, (2) burial-tolerant stabilizers in interdune areas, and (3) burial-intolerant stabilizers in backdune areas (e.g., Ehrenfeld, 1990). These plants have growth forms that enable them to persist in and perpetuate these habitats. Dune builders are tall, are often clonal perennial grasses (Lewis, 1982), and typically have rapid vertical growth, enabling re-growth following burial. Their upright stems are important for slowing air movement, promoting the deposition of wind-born sand. Their extensive roots can efficiently trap and bind sand, encouraging dune growth. Burial-tolerant stabilizers can also withstand burial, but generally accomplish this through an extensive network of salt-tolerant lateral rhizomes, allowing them to persist in areas of overwash and perpetuating the flat interdune
habitat. Finally, burial-intolerant stabilizers are customarily longer-lived and woody (Dech & Maun, 2006).

Although dune habitats are a classic example of succession (e.g., Cowles, 1911), there are surprisingly few studies that have directly documented vegetation patterns over time on barrier islands (Johnson, 1997). To develop a better understanding of the distribution and abundance of vegetation across coastal dune habitats and the factors that can affect these communities, a long-term census was begun on St. George Island State Park in Apalachicola, FL to document vegetation dynamics through time.

With some of the largest dune structures in Florida, St. George Island (29°38’N; 84°54’W), a barrier island approximately 5 km off the NW coast of Florida, is a model system for the study of dune vegetation. St. George Island State Park, on the eastern third of the island, is largely composed of the fore-, inter-, and backdune habitats found on most barrier islands. Permanent plots were established across all three dune habitats in 1998 by T. Miller (Florida State University). Since that time (except for 2002), an annual census has been carried out to document dynamics of plant species across the island. Over 70 unique species have been identified. All data are publicly available at http://bio.fsu.edu/~miller/StGeorge and voucher specimens of most species are available from the R. Godfrey Herbarium at Florida State University.

An analysis of the first eight years of the long-term data using Principle Coordinate Analysis (PCoA) to correlate patterns of co-occurring dune species with environmental variables, suggests that precipitation and surge associated with major storms and temperatures in the summer are the major drivers of vegetation change across the dune habitats (Miller et al., in press). This demonstrates that quantifying how species abundances change through time, particularly in response to storms, can help to explain overall patterns of distribution and abundance. Additionally, this analysis indicates that, when disturbed, the plant communities in each habitat tend to undergo short-term succession back to their original constitution (also see Stallins, 2005). Thus, although there are longer-term successional patterns of foredunes becoming interdunes, then eventually backdunes that occur over 100-1000 year time periods (Berger et al., 2003), there are also shorter, relatively stable successional patterns that occur after storms over time scales of 2-4 years. It is these shorter term responses to storms that may help inform restoration practices

The identification of relatively stable community types from the long-term census provides an important, albeit partial, description of vegetation patterns on St. George Island. In this chapter, I have conducted new analyses on the data set to address questions about species patterns and potential for restoration. The goal of this chapter is to establish a collection of species that may be useful to rehabilitate storm damaged coastal areas, as well as to investigate a general methodology for identifying such species.

Restoration efforts generally involve the reestablishment of habitats to a state present before a damaging event (Falk et al., 2006). This ‘state’ of the habitat is difficult to define, it could be in regards to species composition or ecosystem services. Although restoration efforts can be plagued by unclear definitions of assessment (Michener, 1997) and, therefore, success (Zedler, 2007), success is often determined by the persistence of species used to initiate restoration and the resulting re-establishment of native species (Montalvo et al., 1997). Species used for restoration should therefore be chosen based on how well they facilitate achieving these goals, within local and regional limitations (Palmer et al., 1997). These include, but are not
limited to: size (Montalvo et al., 1997) and expense (Salmon et al., 1982; Holl & Howarth, 2000), location of the damaged area (Bell et al., 1997) and biological infeasibility (Falk et al., 2006). Characteristics noted as particularly beneficial for improved survival and establishment for species transplanted for restoration include genetic variation (Montalvo et al., 1997), local adaptation (Smith & Bradshaw, 1979) and rapid growth (Webb, 2000). Additionally, transplants collected locally might be more likely to conserve natural species richness (Gordon, 1994; Funk et al., 2008), while decreasing costs associated with the restoration effort. Lastly, using a collection instead of a single species for restoration can be beneficial as transplants can exhibit differential survival across habitat types (Stalter & Batson, 1969) and degrees of damage (Camargo et al., 2002). Ideally, restoration candidates would have all of these characteristics. More realistically, restoration candidates would have a subset of these general characteristics that are tailored for the particular habitat that is damaged and the goals of the restoration effort. In this chapter, I use long-term data to quantify storm response characteristics to identify effective restoration candidates for damaged dune habitats on St. George Island.

Since storms seem to be dominant drivers of species distribution and abundance on St. George Island (Miller et al., in press), storm response could be a useful metric to identify restoration candidates. The stress of a hurricane generally leads to a decrease in occurrence of most dune species on the island (see Results). This can exacerbate the damage and destabilization hurricanes inflict on the dunes themselves. It follows that plant species that exhibit a reduced vulnerability to storm effects by maintaining or increasing occurrence after a hurricane likely influence stabilization and regeneration of dunes in a disproportionate way and could be useful for restoration purposes. The long-term data make it possible to quantify storm response characteristics for all censused vegetation on the island.

Methods

Prior Research

In 1998, six permanent vegetation grids were established by T. Miller at the eastern tip of St. George Island (Fig. 1): two grids each in the foredune, interdune and backdune areas. Each grid is 60 x 60 m and contains a 7 x 7 array of smaller plots, for a total of 294 individual plots. The plots are censused annually in the fall when species are most easily identifiable. A 1-m² quadrat is placed over each plot and all vegetation is counted by # individuals or # clumps (depending on growth form) and % cover by species.

Analysis: Patterns of presence through time for individual species were quantified as percent species occurrences within plots in each year in each of the foredune, interdune, and backdune habitats (3 habitats x 98 plots/habitat). Percent occurrence (P) is determined as the proportion of plots in each habitat that contain a particular species. Change in percent occurrence per habitat over time in non storm years was determined by calculating the percent change in occurrence each year for each dune habitat:

Figure 1. (A) St. George Island is 48 km long and varies in width from 1-3 km. (B) The census grids in St. George Island State Park. (Source: Google Earth)
Change = (P_{t+1} - P_t)/P_t

$P_0$ is percent occurrence at time $t$ and $P_{t+1}$ is percent occurrence at time $t+1$. These values were averaged across years to get a single average change in percent occurrence ($P_C$) for each species in each dune habitat. Because I have used presence/absence on plots, a change in percent occurrence generally reflects the expansion of a species into additional plots via dispersal or recruitment and not growth of existing individuals into new plots, although this may not be true for some of the more ‘guerilla’ type growth forms of clonal species (Lovett Doust & Lovett Doust, 1982), such as *Hydrocotyle* and *Ipomea*.

Storms have passed close to or directly over St. George Island throughout the census period. The years of 2004 and 2005 were marked by particularly intense storm activity that directly affected the island, based on precipitation and surge data from the National Oceanic and Atmospheric Administration (NOAA: http://cdmo.baruch.sc.edu/). All storms in 2004 and 2005 that had effects on St. George Island occurred before the long-term census was conducted for that year. For this reason, the changes in occurrence in years 2004 and 2005 were quantified as above to generate a $P_S$, the magnitude of response of each species to storms in each habitat.

The top 25% most abundant species (presence in the most plots within a habitat), the middle 50% abundant species and the 25% least abundant species (presence in the least plots within a habitat) in each dune habitat are ranked as “common”, “average” and “rare”, respectively. Pearson’s product moment correlation was used to identify relationships between ranked abundance of species in each dune habitat and response to storms.

ANOVA was used to identify the contributions of habitat type, plant family, plant functional group (graminoid, forb, vine and shrub) and life cycle (annual, perennial, biennial) to the variance of the dependant variables, including the percent occurrence per habitat over time ($P$), magnitude of response to storms ($P_S$), average change in occurrence per habitat over time ($P_C$) and abundance ranking. Correlation analyses were also conducted to identify relationships between distribution and abundance across the dune habitats and response to storms.

**Restoration candidate species**

A dune species was considered as a restoration candidate using the following characteristics: the direction and magnitude of response to storms, prevalence (the number of dune habitats in which it was observed in the long-term census) and its ranked abundance in habitats for which it has a positive or unchanged storm response. Only species that were present in a habitat for at least one of the years used to compute storm response (2003, 2004 and 2005) were included. This ensured that species not present in plots in 2003, 2004 and 2005 (abundance values of 0) were not mistakenly identified as maintaining presence in response to storms because their $P_C = 0$.

**Results**

**Characterization of vegetation communities overall**

Occurrence in each dune habitat was determined for each species identified in the census (Table 2). Fifty-two species were observed in the census plots on St. George Island State Park between 1999 and 2008, the majority of which (68%) are perennials. The most common plant families are the Poaceae (33% of species observed in the census), the Cyperaceae (12% of species observed in the census) and the Asteraceae (9% of species observed in the census); each
family is found in similar proportions across the three dune habitats. Forbs were the most abundant plant type in each dune habitat, comprising 50% of the foredune plants, 47% of the interdune plants and 40% of the backdune plants. Since 1999, a total of 34 species have been identified in the foredune habitat, 36 species in the interdune habitat and 45 species in the backdune habitat. The largest average decline in average percent occurrence through time was observed in the backdune habitat (16% decline), followed by the foredune habitat (15% decline) and the interdune habitat (7% decline). Forty seven percent of species were found in all three dune habitats; 25% of species were found in only two dune habitats (four species in foredune and interdune, three species in foredune and backdune and six species in interdune and backdune); 28% of species were found in only one habitat (three species in the foredune habitat only, two species in the interdune habitat only and ten species in the backdune habitat only).

Table 1. List of species identified at least once in each dune habitat since 1999. The number following species names denotes average occurrence between 1999 and 2008. Number in parentheses denotes average change in occurrence of species within plots between 1999 and 2008. * = found in all three dune habitats, ‡ = found in only two dune habitats and † = found in only one dune habitat.

<table>
<thead>
<tr>
<th>Foredune</th>
<th>Interdune</th>
</tr>
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<tbody>
<tr>
<td>* Andropogon gyrans &lt; 1% (13)</td>
<td>* Andropogon gyrans &lt; 1% (0)</td>
</tr>
<tr>
<td>* Aristida purpurascens &lt; 1% (10)</td>
<td>* Aristida purpurascens &lt; 1% (0)</td>
</tr>
<tr>
<td>* Eragrostis lugens 12% (24)</td>
<td>* Eragrostis lugens 1% (0)</td>
</tr>
<tr>
<td>* Eustachys petraea 1% (0)</td>
<td>* Eustachys petraea 1% (0)</td>
</tr>
<tr>
<td>* Fimbristyli spp. 20% (63)</td>
<td>* Fimbristyli spp. 20% (63)</td>
</tr>
<tr>
<td>* Hedysotus uniflorus &lt; 1% (13)</td>
<td>* Hedysotus uniflorus &lt; 1% (0)</td>
</tr>
<tr>
<td>* Heterotheca subaxillaris 14% (47)</td>
<td>* Heterotheca subaxillaris 11% (14)</td>
</tr>
<tr>
<td>* Ipomoea imperati 18% (8)</td>
<td>* Ipomoea imperati 1% (42)</td>
</tr>
<tr>
<td>* Iva imbricata 4% (11)</td>
<td>* Iva imbricata 4% (11)</td>
</tr>
<tr>
<td>* Limonium carolinianum &gt;1% (0)</td>
<td>* Limonium carolinianum &gt;1% (0)</td>
</tr>
<tr>
<td>* Muhlenbergia capillaris &lt;1% (13)</td>
<td>* Muhlenbergia capillaris 2% (62)</td>
</tr>
<tr>
<td>* Oenothera humifusa 19% (120)</td>
<td>* Oenothera humifusa 6% (8)</td>
</tr>
<tr>
<td>* Panicum aciculare &lt;1% (13)</td>
<td>* Panicum aciculare &lt;1% (13)</td>
</tr>
<tr>
<td>* Panicum amarum 10% (12)</td>
<td>* Panicum amarum 9% (29)</td>
</tr>
<tr>
<td>* Panicum vaginatum 2% (22)</td>
<td>* Panicum vaginatum 2% (22)</td>
</tr>
<tr>
<td>* Physalis angustifolia 4% (36)</td>
<td>* Physalis angustifolia 4% (36)</td>
</tr>
<tr>
<td>* Polyprenum procumbens &lt;1% (13)</td>
<td>* Polyprenum procumbens &lt;1% (13)</td>
</tr>
<tr>
<td>* Sabatia stellaris &lt;1% (14)</td>
<td>* Sabatia stellaris &lt;1% (14)</td>
</tr>
<tr>
<td>* Schizachyrium maritimum 19% (137)</td>
<td>* Schizachyrium maritimum 19% (137)</td>
</tr>
<tr>
<td>* Sesuvium maritimum 2% (63)</td>
<td>* Sesuvium maritimum 2% (63)</td>
</tr>
<tr>
<td>* Spartina patens &lt;1% (0)</td>
<td>* Spartina patens &lt;1% (0)</td>
</tr>
<tr>
<td>* Sporobolus virginicus 4% (98)</td>
<td>* Sporobolus virginicus 4% (98)</td>
</tr>
<tr>
<td>* Uniola paniculata 52% (2)</td>
<td>* Uniola paniculata 52% (2)</td>
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Percent occurrence and change in percent occurrence for individual species were not significantly correlated within dune habitats. Common species did, however, show a smaller change in percent occurrence in all three dune habitats (see appendix). A multifactor ANOVA revealed that variance in overall percent occurrence is weakly explained by a plant’s life cycle (p = 0.04) and both plant family (p = 0.01) and the interaction between dune habitat type and plant family (p = 0.04) were significant for change in percent occurrence. The Aizoaceae and the Asteraceae were documented as experiencing large increases in percent occurrence in the foredune habitat and large decreases in the interdune habitat. Alternatively, the Gentianaceae experienced a large decrease in percent occurrence in the foredune habitat and a large increase in the interdune habitat. A species’ rank of abundance in a habitat was explained by its change in percent occurrence over time (p = 0.004) and by its growth type (p = 0.01).
All three dune habitats exhibit similar patterns of changes in species richness (Fig. 2, see appendix for detailed histograms). Changes in abundance were similar to patterns of diversity over time (Fig. 3), likely a direct result from the effects from hurricanes Ivan (2004) and Dennis and Katrina (2005). Change in percent occurrence between 2003 and 2004 and between 2004 and 2005 were determined for each species to establish storm response in each dune habitat. Average change in percent occurrence following storms in the foredune habitat was -16%, -15% in the interdune habitat, and -13% in the backdune habitat (Fig. 4). Positive storm response (increase in abundance after a storm event) was observed in the fewest species in the foredune habitat and in the most species in the backdune habitat.

**Response to Storms**

Considering dune species as potential candidates for restoration; six (17%) species in the foredune habitat exhibited a zero or positive change in percent occurrence after a major hurricane (Fig. 5a). These are (from largest to smallest storm response): Sporobolus virginicus, Cyperus croceus, Phyla nodiflora, Panicum amarum, Fimbristylis spp. and Uniola paniculata. Eight (22%) species in the interdune habitat exhibited a maintenance of or increase in percent occurrence after a major hurricane (Fig. 5b), including (from largest to smallest) Panicum amarum, Physalis angustifolia, Fimbristylis spp., Schizachyrium maritimum, Juncus megacephalus, Paspalum vaginatum, Muhlenbergia capillaris and Uniola paniculata. Lastly, thirteen (29%) species found in the backdune habitat increased in occurrence in response to a hurricane (Fig. 5c), including (from largest to smallest) Cynanchum angustifolium, Fimbristylis spp., Panicum aciculare, Cnidoscolus stimulosus, Eustachys petraea, Sabatia stellaris, Spartina patens, Muhlenbergia capillaris, Eragrostis lugens, Baccharis spp., Juncus megacephalus, Schizachyrium maritimum and Uniola paniculata.
Figure 5. Averages of 2004 and 2005 changes in percent abundance of species in the (A) foredune habitat, (B) interdune habitat and (C) backdune habitat. Filled circles indicate changes ≥ 0.
Table 2. Storm response indicates average percent change in occurrence in a dune habitat in response to 2004 and 2005 storms. Rank indicates where the occurrence of that species is located in the occurrence distribution for that habitat. Common = occurrence value in the top 25% of the distribution, rare = occurrence in the bottom 25% of the distribution, --- = occurrence is in middle 50% of the distribution. Prevalence indicates in how many dune habitats the species has been documented in the long-term census.

<table>
<thead>
<tr>
<th>Species</th>
<th>Storm response</th>
<th>Rank</th>
<th>Prevalence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baccharis spp.</td>
<td>backdune: 0%</td>
<td>---</td>
<td>1</td>
</tr>
<tr>
<td>Cnidoscolus stimulosus</td>
<td>backdune: 100%</td>
<td>---</td>
<td>1</td>
</tr>
<tr>
<td>Cynanchum angustifolium</td>
<td>backdune: 400%</td>
<td>rare</td>
<td>3</td>
</tr>
<tr>
<td>Cyperus croceus</td>
<td>foredune: 100%</td>
<td>rare</td>
<td>3</td>
</tr>
<tr>
<td>Eragrostis lugens</td>
<td>backdune: 4%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td>Eustachys petraea</td>
<td>backdune: 100%</td>
<td>rare</td>
<td>2</td>
</tr>
<tr>
<td>Fimbristylis spp.</td>
<td>foredune: 4%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>interdune: 37%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td></td>
<td>backdune: 200%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td>Juncus megacephalus</td>
<td>interdune: 20%</td>
<td>---</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>backdune: 0%</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>Muhlenbergia capillaris</td>
<td>interdune: 0%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>backdune: 13%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td>Panicum aciculare</td>
<td>backdune: 117%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td>Panicum amarum</td>
<td>foredune: 100%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>interdune: 130%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td>Paspalum vaginatum</td>
<td>interdune: 16%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td>Phyla nodiflora</td>
<td>foredune: 100%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td>Physalis angustifolia</td>
<td>interdune: 100%</td>
<td>rare</td>
<td>3</td>
</tr>
<tr>
<td>Sabatia stellaris</td>
<td>backdune: 100%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td>Schizachyrium maritimum</td>
<td>interdune: 21%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>backdune: 0%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td>Spartina patens</td>
<td>backdune: 100%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td>Sporobolus virginicus</td>
<td>foredune: 400%</td>
<td>common</td>
<td>2</td>
</tr>
<tr>
<td>Uniola paniculata</td>
<td>foredune: 4%</td>
<td>common</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>interdune: 0%</td>
<td>common</td>
<td></td>
</tr>
<tr>
<td></td>
<td>backdune: 0%</td>
<td>common</td>
<td></td>
</tr>
</tbody>
</table>

Of the final group of 19 restoration candidate species, six species have potential for foredune restoration, eight species have potential for interdune restoration and thirteen species have potential for backdune restoration. Nine plant families comprise this group. They are the: Asclepiadaceae, Asteraceae, Euphorbaceae, Cyperaceae, Gentianaceae, Juncaceae, Poaceae, Solanaceae and Verbenaceae. Grasses make up more than half of the restoration candidates (53%). Twenty one percent of the species are forbs, followed by graminoids (16%) and shrubs and vines (5% each). Only one (Sabatia stellaris) candidate is not a perennial.
Discussion

I have used long-term census data of vegetation dynamics to identify restoration candidate species in each habitat based on their growth response to storms. Most dune species respond to storms with a decrease in percent occurrence (Fig. 5). However, several responded well to storms (exhibit an increase in percent occurrence) or remain relatively unaffected by storms (exhibit 0 to 10% reduction in percent occurrence); it is these species that I suggest should be investigated for restoration potential.

Species with high potential for use in restoration should have a suite of desirable characteristics. It has also been proposed that good restoration species should have a net positive effect on community diversity (Funk et al., 2008) and be appropriate for the succession occurring in particular habitat (Montalovo et al., 1997). Using a group of species may also be more effective for restoration than using only one species per habitat for several reasons. A group of species may help to compressing the gradual process of succession into one phase by introducing several restoration species at once (Egler, 1954; Bradshaw, 1987). A group of species may also be better able to buffer further environmental disturbances than single species. The competitive effects resulting from an increase in the number of species used for restoration purposes has been shown to be overcome by the benefit these additional species supply (Bradshaw, 1987; Gomez-Aparicio et al., 2004). Restoration transplants have also been shown to accumulate more biomass when used in species-rich plantings to degraded areas (Callaway et al., 2003).

Prior studies show that different factors influence dune habitats in different ways (Ehenfeld, 1990; Hesp & Martinez, 2008; Miller et al., in press), making habitat-specific choices for restoration species necessary. The diversity and abundance patterns observed across the island, likely a result of environmental stress gradients (Hesp, 1991), result in differences between total abundance (Fig. 3) and average change in abundance (Fig. 4) of plant species in each dune habitat through time. This suggests that the way in which these abiotic factors affect each dune habitat is also different (Judd et al., 2008). Accordingly, dune species respond to storms with different changes in occurrence, depending on the habitat. Here, I suggest that species which exhibit a positive response following storms and (to a lesser extent) a high average percent occurrence in particular habitats can be useful for restoration purposes. This research was conducted with the assumption that maintaining or increasing percent occurrence after the stress of a storm will correlate with maintaining or increasing percent occurrence after the stress of transplantation for restoration purposes.

Of the six potential restoration species for the foredune habitat, *Cyperus croceus* is the only one considered rare, which suggests that this species may not remain abundant during longer periods between storms. Of the remaining species, *Sporobolus virginicus* is the superior candidate for restoration as it exhibited the largest increase in percent occurrence (400%) in response to storms and is known to be burial and saline flood tolerant (Breen et al., 1977). Moreover, the average change in percent occurrence for *S. virginicus* in the foredune habitat is over two times bigger than those of the other candidate species in this habitat. In the interdune habitat, *Juncus megacephalus* and *Physalis angustifolia* are not common, which again suggests that other factors may limit their percent occurrence during non-storm periods. Of the remaining species, *Paspalum vaginatum*, *Muhlenbergia capillaris* and *Schizachyrium maritimum* are found in the most dune habitats. Of these, *M. capillaris* has an almost ten times larger average percent positive change in percent occurrence in the interdune habitat than the other two species and has
been recoded as a final succession species in this area (Johnson, 1997); highlighting its strengths as a candidate for restoring the interdune habitat. In the backdune habitat, *Baccharis* spp., *Cnidoscolus stimulosus*, *Cynanchum angustifolium*, *Eustachys petraea* and *Juncus megacephelus* are rare and thus unlikely to be the best restoration species. Additionally, *Sebatia stellaris* is a relatively small annual that is unlikely to stabilize sand or change local conditions for later species. Of the remaining species, *Eragrostis lugens* and *S. maritimum* demonstrate the largest overall percent occurrence across dune habitats. *Schizachyrium maritimum* has both larger average percent occurrence and larger change in percent occurrence than *E. lugens*. *S. maritimum* has also been documented as a rapid primary and secondary succession species across the dune habitats (Snyder & Boss, 2002) and has been previously tested for restoration purposes (Thetford *et al.*, 2005), with successful results. This species is likely the best candidate for restoring the backdune habitat.

Only two species appear to have restoration potential in all three dune habitats: *Fimbristylis* spp. and *Uniola paniculata*. These two species are also common in all three dune habitats. *Fimbristylis* spp. is a characteristic foredune species and has been recorded as being a primary succession species in the interdune area (Johnson, 1997). *Fimbristylis* spp. also exhibits the unique characteristic of its taxonomy. It is a member of the Cyperaceae that represents only 10% of the families in the final group of restoration candidates. Moreover, *U. paniculata* is frequently used as a restoration species, especially on foredunes, because of its rapid establishment of fragments (Snyder & Boss, 2002; Miller *et al.*, 2003) and its adaptation to various stresses (Hesp, 1991).

The final group of restoration species for St. George Island State Park is: *Fimbristylis* spp. and *Uniola paniculata* (characteristic foredune species), *Sporobolus virginicus* (characteristic interdune species) and *Muhlenbergia capillaris* and *Schizachyrium maritimum* (characteristic backdune species). This final group of restoration species exhibits important features of the barrier island itself; species characteristic of all dune habitats are represented, and the group demonstrates potential to restore the coastal system both specifically (within each dune habitat) and comprehensively (across all dune habitats).

Coastal regions worldwide provide important ecological services, such as unique habitat for an array of wildlife and protection of inland landscapes from storm surges. These systems are vulnerable to the effects of hurricanes and tropical storms and the vast majority of coastal degradation in the U.S. this century was in the Gulf of Mexico (Turner, 2001). Documenting the ecology of these habitats is necessary for understanding the factors driving system dynamics and for the development of protective management practices. Although it is generally recognized that restoration species should be well matched to their environment (Olafson, 1997), plant species chosen for restoration on barrier islands are often based on convenience (van der Putten, 1990; Gordon & Rice, 1998) or abundance in the foredune environment only (Reis & Freitas, 2002). There has been a call for a more science-based approach to restoration (Giardina *et al.*, 2007; Funk *et al.*, 2008) such as applied here. When available, long-term data can facilitate the design and implementation of a restoration effort, tailored to a specific habitat.
CHAPTER 2
RESTORATION

Introduction

Coastal restoration and management initiatives have a long history but have more recently experienced a resurgence in activity (Knutson, 1980; Young, 2000; Falk et al., 2006). This is mostly due to increased coastal development combined with increasing damage from storms related to climate change (Salmon et al., 1982; Funk et al., 2008). Long-term success in restoration, generally defined as the reestablishment of habitats to a state that was present before a disturbance event, has been frequently criticized (Williams & Zedler, 1999; de Jonge & de Jong, 2002). Much of the criticism is related to the absence of ecological theory and data application to restoration practices (Millar & Libby, 1989; Giardina et al., 2007). Understandably, restoration design and implementation are limited by both local and regional factors (Palmer et al., 1997). These include, but are not limited to: size (Montalvo et al., 1997) and expense (Salmon et al., 1982; Holl & Howarth, 2000), location of the damaged area (Bell et al., 1997) and biological infeasibility (Falk et al., 2006). Nevertheless, while the importance of using science to inform design and implementation of restoration initiatives is widely appreciated (Allen et al., 1997; Allen et al., 2002), projects that integrate this type of approach are still uncommon (for examples see Willems, 2001; Bull et al., 2004; van Cleve et al., 2006).

In coastal dune habitats, restoration initiatives would best be designed with a consideration of the relationships among geomorphology, vegetation and climate. Although difficult to quantify (Ruiz-Jaen & Aide, 2005; Zedler, 2007), the success of many coastal restoration efforts have been characterized as less than ideal. There are various reasons for this. The creation of vegetative monocultures in degraded areas (Thorn, 2000; Gomez-Pina et al., 2002; Reis & Freitas, 2002) can limit efforts as research suggests that diversity can encourage restoration (Auclair, 1983; Tilman et al., 2001; Fornara & Tilman, 2009). In addition, coastal restoration efforts still generally focus on the foredune habitat only (Salmon et al., 1982; Thorn, 2000). Studies have highlighted the importance of comprehensive approaches where restoration efforts are applied to the entire damaged habitat, instead of simply a portion (Kim et al., 2008; Palmer et al., 2008; Pries et al. 2008).

Long-term census data can identify factors that may improve applied conservation techniques. Principle Coordinate Analysis (PCoA) of the long-term census data from St. George Island demonstrated that climatic factors best correlated with vegetation changes vary among habitats (Miller et al., in press). In Chapter 1, I used these census data to determine which dune species might be most effective for restoration in foredune, interdune and backdune habitats. Their potential for maintaining stable percent occurrence, even after storms like Ivan (2004) and Dennis and Katrina (2005). Alternatively, O. humifusa rapidly declines in numbers. ○ = foredune, x = interdune and □ = backdune.
restoration use was based primarily on their growth following storms and their overall relative abundance. As might be expected (Erasmus et al. 2002), most dune plants respond to storms and hurricanes with a decrease in percent occurrence across the three dune habitats (forendunes, interdune and backdunes; e.g, Fig. 6; Box, 1981; Ellenberg, 1988). There are, however, several species that demonstrate either an increase in percent occurrence following storm events or remain relatively unaffected by these events.

Based on a preliminary analysis, T. Miller (Florida State University) identified two dune species characteristic of each of three common dune habitats for use in restoration based on storm response data from the long-term census (Table 3; for more comparisons between all species in long-term data and restoration species, see appendix). From the foredune habitat, *Fimbristylis* spp. Cyperaceae (hereafter *Fimbristylis*) and *Uniola paniculata* Poaceae (hereafter *Uniola*), both perennial graminoids were chosen. *Fimbristylis* species is either *spathacea* or *caroliniana*; nonreproductive individuals cannot easily be identified in the field. The range of *Fimbristylis* extends from eastern Canada to the Virgin Islands while *Uniola* is documented as existing along the eastern U.S. from Virginia to Mexico. From the interdune habitat, *Centella asiatica* Mackinlayaceae (hereafter *Centella*), an herbaceous dicot and *Sporobolus virginicus* Poaceae (hereafter *Sporobolus*), a C4 graminoid, both perennials were chosen. From the backdune habitat *Muhlenbergia capillaris* and *Schizachyrium maritimum* Poaceae (hereafter *Muhlenbergia* and *Schizachyrium*, respectively), both perennial graminoids were selected. These species, in addition to *Centella* and *Sporobolus* occur within the south eastern U.S. and all but Puerto Rico. All restoration candidates are thought to be non-invasive in north Florida.

Table 3. Average change in percent occurrence in each dune habitat in response to storms for each transplant species chosen for the study and an average value for all species censused (excluding transplant species). Values are an average of change in occurrence between 2003-2004 and 2004-2005. A value of 0% indicates no change in occurrence between storm and non storm years.

<table>
<thead>
<tr>
<th></th>
<th>Foredune</th>
<th>Interdune</th>
<th>Backdune</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Centella asiatica</em></td>
<td>0%</td>
<td>-30%</td>
<td>-40%</td>
</tr>
<tr>
<td><em>Fimbristylis</em> spp.</td>
<td>+4%</td>
<td>+40%</td>
<td>+75%</td>
</tr>
<tr>
<td><em>Muhlenbergia capillaris</em></td>
<td>0%</td>
<td>0%</td>
<td>+13%</td>
</tr>
<tr>
<td><em>Schizachyrium maritimum</em></td>
<td>-7%</td>
<td>+21%</td>
<td>-9%</td>
</tr>
<tr>
<td><em>Sporobolus virginicus</em></td>
<td>+175%</td>
<td>+2%</td>
<td>+200%</td>
</tr>
<tr>
<td><em>Uniola paniculata</em></td>
<td>0%</td>
<td>+4%</td>
<td>-4%</td>
</tr>
<tr>
<td>Average</td>
<td>-29%</td>
<td>-52%</td>
<td>-53%</td>
</tr>
</tbody>
</table>
three habitats. Restoration goals span a variety of scales (Montalvo et al., 1997; Falk et al., 2006) and the investigation described here was conducted at a relatively small scale. In this trial of potential restoration species, the restoration capabilities of each species were evaluated based on survival and growth of individuals in each dune habitat. I also considered how well the transplants collectively encouraged the degraded habitat to return to a pre-storm state by quantifying the response of extant vegetation and changes in environmental conditions.

**Methods**

**Transplanting**

One hundred ramets of each of the six transplant species were collected from multiple source locations in St. George Island State Park during their dormant season in December 2007 and transplanted to a greenhouse at Florida State University in Tallahassee, FL. The plants were kept for three months in a 1:1 soil:sand mixture, with a small amount of fertilizer (3:3:3) in individual 5 x 5 inch pots and watered twice a week. Vegetative shoots were regularly broken off and replanted to generate more individuals. Once 300 ramets of each species were obtained, the plants were transplanted to field plots as ‘plugs’ (including soil from the pots). Soil and fertilizer in the original plots are believed to have 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 x 5 m quadrats were installed in storm damaged areas in each of the three dominant dune habitats (fore-, inter- and backdune) on St. George Island State Park, for a total of nine experimental quadrats. Each quadrat is composed of thirty 1 m$^2$ plots in which one of each transplant species is planted, for a total of six unique transplants in each plot (Fig. 7). No water or fertilizer was used after the plants were installed in the field. Each experimental quadrat was paired with a control quadrat, erected in a nearby location, in which no transplants were provided.

After transplanting in February 2008, the plants were monitored bi-monthly for survival and growth, for a total of six measurements over a period of a year (in 2008: March, May, July, September and November and in 2009: January). Survival was determined by the presence of green plant material above ground. For live plants, growth was quantified in two ways. First, new growth was quantified by counting the number of stems coming out of the ground for each transplant. Different morphologies of the transplant species necessitated the delineation of different definitions for this measurement for each species. Culm number was counted for *Fimbristylis*, *Muhlenbergia* and *Uniola* while stem number was counted for *Schizachyrium* and *Sporobolus*. Second, the longest stem or leaf of each transplant was measured to the nearest cm. Stem length was not determined for *Centella* because the growth of this species is primarily by underground rhizomes with no upright stems.
To document effects of transplants on sand accumulation and movement, three wooden stakes (2 m in length, buried 1 m) were installed in a N-S transect across each experimental and control quadrat in July 2008. Sand height at each stake was measured bimonthly to the nearest cm. Gravimetric percent soil moistures were documented in February 2008 by collecting a 2 cm diameter x 7 cm column of sand from the center of each plot and placing the soil into an airtight bag. The samples were brought back to Florida State University and weighed, dried at 60°C, and re-weighed to determine percent soil moisture. Temperature was also collected from ten random plots per quadrat by placing a thermometer 5 cm into the soil and recording the temperature after 30 seconds. To document effects of transplants on the growth of naturally occurring species, percent cover was visually estimates for each species (excluding transplanted individuals) on ten randomly selected plots in each experimental quadrat, and in the same ten plots in each associated control quadrat.

**Analysis**

**Species Level:** Average overall survival was determined for each species by averaging survival values at each census (n=6) in each habitat. These values were compared within species across habitats using ANOVA. Percent change in survival through time was calculated for each habitat using the formula:

\[
\text{Change in survival} = \frac{S(t+1) - S(t)}{S(t)}
\]

where \(S(t)\) is average survival in time \([t]\) and \(S(t+1)\) is average survival in time \([t+1]\). Percent change in survival was normally distributed for the fore and backdune habitats. Analysis of contributions of independent factors (dune habitat type and time) to survival (binary data) for the proposed restoration species were conducted using a repeated measures generalized linear model (family = binomial, link function = logit) using the GENMOD procedure in SAS (SAS Version 9.1). GENMOD facilitates partitioning categorical (dune habitat) and continuous (time) variables in the model. Comparisons between percent change in survival within species across habitats and between species in the same habitat were conducted using ANOVA using the mean percent change of each species at each site.

Stem length and stem number of transplants were analyzed in a method similar to survival analysis. Both dependent variables were analyzed overall and through time. Differences in plant morphologies prevent comparisons of stem length and number among species. Only percent changes in these variables through time were compared among species, within dune habitats. Contributions of independent factors to patterns of growth were conducted using a repeated measures ANOVA. Stem length data was normally distributed for all species in all habitats and stem number data was log transformed to a normal distribution for each species in each dune habitat. ANOVAs were conducted using freeware R version 2.5.1 (R Development Core Team, 2007).

Mauchly tests for sphericity were conducted to validate repeated measures ANOVA. Tests demonstrated that assumptions of sphericity were not violated for survival or growth.

**Habitat Level:** Total percent cover data and alpha diversity were not normally distributed within habitats. These data were log transformed (variance homogeneity assumptions were met) and analyzed across and within habitats with a paired t test.

Sand accumulation, percent moisture and surface temperatures were also compared between experimental and control plots within dune habitats. Because sand accumulation measurements were made repeatedly (five times since initial transplanting) these values were analyzed in a repeated measures ANOVA to determine contributions of dune habitat, time and
plot type (experimental vs. control) on percent changes in sand height. Percent moisture and temperature data were normally distributed among habitats and were analyzed using a paired one tailed t-test.

Results

Species Level Results

Survival Overall: Survival over the first year significantly varied among species and habitats. Average survival was lowest on the foredunes (37%). In this habitat, *Fimbristylis* and *Muhlenbergia* exhibited significantly lower overall survival (p = 0.005 and p < 0.001, respectively), compared to their survival in the interdune and backdune habitats. The highest overall survival (56%) was found on interdunes, with similar survival in the backdunes (54%) where *Schizachyrium* had the highest survival (p = 0.02). *Sporobolus* exhibited the highest overall survival (74%) followed by *Uniola* (66%) and *Fimbristylis* (54%). Alternatively, *Centella* showed the lowest (30%) overall survival followed by *Schizachyrium* (38%) and *Muhlenbergia* (45%). *Centella, Sporobolus* and *Uniola* did not differ significantly in their survival across the dune habitats (Fig. 8).

Survival through Time: Few species were able to maintain high (> 80%) survival through time (Fig. 9; note that species can “increase” in survival when previously dormant plants begin to grow). The amount of change in percent survival of transplants decreased through time for all habitats. The single significant difference in changes in survival through time was documented in the backdune habitat (p = 0.03) for *Centella*. GLM results revealed that survival for foredune species *Fimbristylis* and *Uniola* is explained by time (p < 0.001) and by habitat (p = 0.02 and p = 0.05, respectively). For interdune species *Centella*, survival is explained by time and habitat (p < 0.001 for both). This species exhibited an immediate exponential decrease in survival through time in the interdune and backdune habitats. *Sporobolus* demonstrated this dynamic in the foredune habitat a short period after transplanting. The survival of this species is only explained significantly by habitat (p = 0.001) and marginally by time (p = 0.08). Survival patterns of the two backdune species, *Muhlenbergia* and *Schizachyrium*, were explained by habitat only (p < 0.001 for both). These species were recorded as having relatively stable survival in the interdune and backdune habitats.

![Figure 8. Overall survival of transplants in each dune habitat. FS = Fimbristylis, UP = Uniola, CA = Centella, SV = Sporobolus, MC = Muhlenbergia and SM = Schizachyrium.](image-url)
Stem Length Overall: Stem length for all species in one year of growth was normally distributed. Transplants showed highest overall stem length in the interdune habitat (p = 0.001). *Fimbristylis* had larger stems in the interdune habitat than any other habitat with about equal stem lengths in the fore and backdune habitats. *Muhlenbergia* and *Sporobolus* had their longest stems in the interdune habitat and second longest stems in the backdune habitat. *Schizachyrium* showed no difference in stem length between habitats while *Uniola* exhibited slightly longer stems in the interdune habitat than the foredune habitat.

**Stem Length through Time:** Each transplant species exhibited similar growth patterns for stem length among dune habitats (Fig. 10). *Uniola* was the only species that exhibited increased stem length in the foredunes while also exhibiting the largest average decrease in stem length through time in the interdune habitat. ANOVA results indicate that stem length of *Uniola* was explained by time (p < 0.001) and marginally by habitat (p = 0.08). Alternatively, *Fimbristylis* exhibited the largest average decrease in stem length in the foredune habitat and was one of the only species to exhibit stem length increase in the interdune habitat through time. Stem length of *Fimbristylis* was explained by habitat, time and the interaction between the two (p < 0.001 for all factors). Stem length for *Muhlenbergia* increased in the interdune and the backdune habitat and was explained by habitat and time (p < 0.001 for both) and less so by the interaction between the two (p = 0.04). *Sporobolus* exhibited the largest average decrease in stem length through time in the backdune habitat. Stem length for *Sporobolus* is explained by habitat, time and the interaction between the two (p < 0.001 for each). Interestingly, stem length for *Schizachyrium* was not explained by time or dune habitat type. The amount of change documented in stem length of transplants decreased over time in all habitats.
<table>
<thead>
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<th>Backdune</th>
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<td><em>Sporobolus</em></td>
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<td><img src="image11" alt="Graph" /></td>
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</tbody>
</table>

*Height (cm) vs. time*
Figure 10 - Continued

<table>
<thead>
<tr>
<th>Foredune</th>
<th>Interdune</th>
<th>Backdune</th>
</tr>
</thead>
</table>

| Uniola height (cm) | time | time | time |

Figure 10. Average length of longest stem for each transplant species (excluding Centella) in each dune habitat over time. Each time value represents a census of restoration species, which occurred every two months following the initial transplanting.

**Stem Number Overall:** The distribution of stem number was skewed in each dune habitat for each species and was log transformed for all analyses. Transplants in the interdune habitat exhibited the overall largest number of stems per plant (p < 0.001) and stem number per plant was similar between the fore and backdune habitats (Fig. 11). All but two transplant species were documented as having their largest number of stems overall in the interdune habitat. Stem number of Schizachyrium was highest in the foredune habitat while Uniola had the largest number in the backdune habitat.

**Stem Number through Time:** The transplants exhibited similar patterns of stem number between the dune habitats, but the effects of habitat and time on stem number differed between transplant species, as might be expected for species with very different morphologies. Stem number of both Centella and Sporobolus is explained by habitat, time and the interaction between the two (p < 0.001 for each). Stem number of Fimbristylis is explained by time (p < 0.001) and less so by the interaction between habitat and time (p = 0.03). Stem number of Muhlenbergia is explained by habitat and time (p < 0.001 for both) and the interaction between the two (p = 0.04). Stem number of Schizachyrium is explained by habitat (p < 0.001), time and the interaction between the two (p = 0.04 for both). Stem number of Uniola was explained only by time (p < 0.001). The amount of change in number of stems for transplants in each dune habitat decreased through time.
<table>
<thead>
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<td><img src="image" alt="Graph" /></td>
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<tr>
<td><strong>Muhlenbergia</strong></td>
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<tr>
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</tr>
</tbody>
</table>
Figure 11. Average number of stems/leaves/culms for each transplant species in each dune habitat over time. Each time value represents a census of restoration species, which occurred every two months following the initial transplanting.
In the foredune habitat, stem length and number of stems are negatively correlated (p = 0.06) and in the backdune habitat the change in stem length and number of stems are positively correlated (p = 0.02).

**Habitat Level Results**

Total percent cover of the natural (non-transplant) vegetation was larger in restoration plots compared to associated controls across dune habitats (Fig. 12). This relationship was significant in the interdune habitat (p = 0.001). Alpha diversity (not including transplant individuals) was also higher in restoration plots compared to controls in every habitat (p < 0.001 for all habitats).

Soil moisture was marginally higher on restoration plots compared to controls in the foredune habitat (p = 0.07) and significantly higher in the restoration plots in the backdune habitat (p < 0.001). In the interdune habitat, the opposite pattern was observed, with higher soil moisture on control plots. Surface temperatures were significantly higher in the backdune restoration plots compared to control plots (p = 0.002); no difference was detected between surface temperatures of restoration and control plots in the foredune or interdune habitats (Table 4). Both time (p = 0.005) and habitat type (p < 0.001) had significant effects on sand accumulation. The foredune habitat experienced the greatest sand accumulation while the inter and backdune habitats similarly experienced very small changes in sand accumulation. Sand accumulation was not significantly different between restoration and control plots.

**Table 4.** Average temperature and percent moisture of surface soil in restoration and control plots in each of the three dune habitats.

<table>
<thead>
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<th>Interdune</th>
<th></th>
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</thead>
<tbody>
<tr>
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<td>Temperature</td>
<td>Moisture</td>
<td>Temperature</td>
<td>Moisture</td>
<td>Temperature</td>
</tr>
<tr>
<td>Restoration</td>
<td>16.1°</td>
<td>2.4%</td>
<td>19.1°</td>
<td>1.2%</td>
<td>22°</td>
</tr>
<tr>
<td>Control</td>
<td>16°</td>
<td>1.8%</td>
<td>18.8°</td>
<td>1.5%</td>
<td>20.3°</td>
</tr>
</tbody>
</table>

**Discussion**

This research documents the survival and growth of six native plants in three dune habitats test the efficacy of using long-term census data to identify species for restoration. The
transplant species in this study exhibited different individual survival and growth characteristics across the dune habitats through time and, collectively, facilitated the growth of native plants. Overall, the results suggest (1) transplant success cannot be predicted based on the habitat with which the species is generally associated and (2) transplanted species demonstrate different capabilities for restoration use, depending on the temporal goals of the restoration effort.

This study suggests that the foredune species, *Fimbristylis* and *Uniola* have high potential as possible restoration species in storm degraded habitats. Transplanted individuals of both species exhibited relatively high survival and growth in the interdune and backdune habitats. Survival and growth characteristics of *Uniola*, were particularly high and constant across the three habitats. Despite the dominance of *Uniola* in more xeric, higher elevation environments and the distribution of *Fimbristylis* localized in generally lower elevation environments, both species are naturally found with higher than average percent occurrence across all three dune habitats (Chapter 1).

*Centella* and *Sporobolus* displayed their highest survival and growth in the interdune habitat from which they were derived. Across dune habitats, *Sporobolus* exhibited relatively higher overall survival and growth than *Centella*, which displayed low survival in the foredune and backdune habitats. Overall, *Centella* was the poorest performing transplant species and was disproportionately affected by dune habitat and time. It appears that *Centella* would not be an effective restoration candidate in any dune habitat. However, the morphology and taxonomy of this species is unique among the species tested and the added value of diversity that *Centella* could contribute should not be overlooked. Alternatively, *Sporobolus* showed remarkable robustness in survival and growth across all habitats while consistently doing best overall in the interdune and backdune habitats where it is found most often (Chapter 1). This species could be useful for restoration in any dune habitat, especially the interdune and backdune habitats.

The backdune species *Muhlenbergia* and *Schizachyrium* displayed the most similar patterns of success through time across the dune habitats. Both species had their highest survival in the backdune habitat, despite having relatively low survival in this habitat when compared to the other transplant species. But, both species exhibited lowest growth in their habitat of origin. Dynamics of these backdune transplant species suggest that they would perform best as restoration tools in any habitat, excluding the one from which they are generally found. This might make sense when considered within a successional framework. The backdune habitat can be considered a successional climax community on a barrier island (Gleason, 1927; Dahl et al., 1975), and species characteristic of this habitat could also be considered climax or equilibrium species. A backdune habitat degraded by storms often consists of bare sand that more closely resembles a primary succession habitat and, perhaps, species that are characteristic of the climax community in this habitat (like *Muhlenbergia* and *Schizachyrium*) are likely to not do as well under these environmental conditions.

The facilitation of extant vegetation by the transplants (Fig. 12) was particularly encouraging. Facilitation was observed almost immediately after transplants were installed, a much more rapid result than generally documented for restoration efforts (Reis & Freitas, 2002). Clearly, transplant practices that encourage the growth of native vegetation are desirable. At this point, the mechanisms by which this facilitation occurred are unclear. While it may be related to soil moisture or temperature changes caused by the transplants, it may also be related to soil disturbance or changes to other microhabitat variables. However, whatever the cause, this facilitation occurred at varying degrees in all three dune habitat and is worthy of further study.
There appears to be only a loose relationship between magnitude of storm response (an increase of percent occurrence following a storm compared to a maintenance of percent occurrence) and transplant survival and growth. *Uniola* decreased in percent occurrence in the backdune habitat following storms (Table 3) but, when transplanted, had its highest overall survival in this habitat (Fig. 8). *Muhlenbergia* maintained a constant percent occurrence in the interdunes and increase in the backdunes following storms, but was documented as having highest survival and growth in the interdune habitat (Table 3); *Centella* exhibited a similar dynamic. No relationship was observed for the remaining restoration candidate species.

Documenting higher success for transplant species in dune habitats with which they are generally not associated highlights the importance of choosing restoration species based on disturbance specific traits (here, storm response) and restoration needs, as opposed to simply presence and abundance within a particular habitat (Funk, *et al.*, 2008). Previous studies have found that many species can disperse across seemingly inhospitable environments (Stetter *et al.*, 1993) and dune transplants can tolerate conditions not generally found in their usual habitat (Stalter & Batson, 1969). This is also relevant to the lack of a consistent relationship observed between survival and growth of the transplant species in this experiment, a phenomenon documented elsewhere (e.g., Bull *et al.*, 2004). The ability of a plant to survive in a novel habitat is likely influenced by a set of factors that differ in type and magnitude from those that influence growth characteristics. In some habitats, *Centella* and *Sporobolus* maintained high initial survival, but survival rates decreased sharply soon thereafter. These species might be more appropriate for projects with short term restoration goals. Alternatively, some species maintain their survival and growth dynamics through time (e.g., *Muhlenberia* in interdunes and backdunes), a characteristic more beneficial for long-term restoration projects.

Despite the fact that some species from this experiment appear to have significant restoration potential, using storm response and distribution across dune habitats as guides to identify restoration candidate species is not a flawless approach. There are a multitude of factors operating across the barrier island which drive dune vegetation dynamics (Ehrenfeld, 1990). Choosing one factor to determine candidate species might limit a comprehensive restoration of damaged habitat. Nonetheless, the approach described here is a useful way to reconsider restoration design and implementation.

Although there is still debate over the usefulness of scientific approaches to restoration (Cabin, 2007; Giardina, 2007), the added value of considering ecological data in conservation management is well known (Jackson, *et al.*, 2001; Thorrold *et al.*, 2001). This work incorporated a scientific approach to designing and implementing a restoration effort. Using an ecologically relevant trait to identify effective restoration candidates appears to be a useful restoration technique, demonstrating the importance of considering past and present site conditions as well as drivers of large and small scale dynamic changes (Thom, *et al.*, 2005). Both the success of the transplants in all three dune habitats and the facilitation of a native plant community across the barrier island can be considered high when compared to other studies (Roze & Lemauviel, 1995; Grootjans *et al.*, 2002). Future work should include ecological considerations not currently integrated into this study, including herbivory on transplants (Hester *et al.*, 1994), geographic distance between habitats where transplants are acquired and habitats where transplants are installed (Montalvo & Ellstrand, 2000) and invasion resistance (Funk *et al.*, 2008). Because of the habitat- and species-specific features of this method, this technique should be amenable to other coastal areas where restoration efforts might fail to meet their goals (Thorn, 2000).
CHAPTER 3
REMOTE SENSING

Introduction

Chapter 1 describes identifying potential restoration species for St. George Island based on changes in vegetation occurrence following major tropical storms in the area. This method could be applied to other coastal environments, especially in north Florida. However, extrapolating predictions determined using this approach over a wider scale will only be appropriate if comparable habitats with similar storm damage can be identified. Additionally, implementing a long-term census program in these other areas to establish how particular dune species respond to storms is impractical. One possible approach that might overcome these problems would be the use of remote sensing. I explored the possibility of using remotely sensed images to (1) identify similar coastal areas and storm damage in these areas (2) establish clear patterns of vegetation change through time and (3) investigate if this approach could be useful to identify potential restoration species. Concordance between the census data and the remote sensing analysis would confirm the value of using remote sensing approaches in restoration.

Historically, remote sensing and geographic information systems (GIS) were used almost exclusively in the geological sciences. Recently, improvements in spatial and spectral resolution of remotely sensed images have resulted in the more frequent application of these tools in a broader group of fields. Remote sensing techniques are now used whenever acquiring data for large spatial scales is feasible by analyzing aerial or satellite imagery (Field et al., 1995). Aerial and satellite imagery have been used in dune systems to determine geomorphic ages (e.g., Johnson, 1997; Jones et al., 2008) and tectonic and landform characteristics (e.g., Hanamgond & Mitra, 2008), to quantify vegetation recovery (e.g., Zaremba & Leatherman, 1986) and to model habitat processes (e.g., Sellars & Jolls, 2007).

In ecology, remote sensing approaches are often used to indirectly identify characteristics of vegetation, including percent cover, chlorophyll content and leaf-area-index (Jensen, 2007) in addition to investigating changes in these characteristics (Running et al., 1994). Remote sensing can be particularly useful when attempting to distinguish patterns of vegetation change through time because (1) appropriate collection of imagery results in precisely located, repeatable measurements and (2) discriminating between the cover of different vegetation types can be feasible with high resolution imagery (O’Neill et al., 1997). Change detection involves the comparison of high resolution images of a particular location at different times (Arroyo-Moya et al., 2005). Using remote sensing to detect vegetation change is relatively simple but the interpretation of the results is not, as multiple control points for ground truthing and a strong knowledge of the ecology of the system of interest are necessary (Jano et al., 1998). Additionally, remote sensing methods can be highly subjective and susceptible to bias. Despite the difficulty in using change detection to identify ecological patterns, it is used in a variety of capacities, including investigating change in anthropogenic (e.g., Ridd & Liu, 1998) and faunal (e.g., Jano et al., 1998) land use and land use planning (e.g., Estreguil & Lambin, 1996).
Using remote sensing to quantify changes in vegetation has also been useful for conservation purposes (e.g., Cayuela et al., 2006), as it can quantify degradation and fragmentation rates. This method enables not only the identification of transitions in vegetation types, but also the change in bare ground cover through time. This can also be useful for documenting succession and habitat rehabilitation after damaging events, like fires and hurricanes.

Extrapolating the restoration methods described in Chapter 1 beyond St. George Island requires identifying habitats that are similar to St. George in geomorphology and vegetation, in addition to quantifying storm damage in these areas. Remote sensing might be a reasonable approach for determining the distributions of plant species and gradients of vegetation change to identify habitat similarity (Stallins & Parker, 2003). Moreover, remote sensing could be useful to assess changes in bare sand cover and vegetation occurrence to quantify storm damage through time.

Once a habitat has been established as suitable for the application of restoration efforts, remote sensing can be used in the absence of long-term census data to identify potential restoration species. Remote sensing can be used to quantify vegetation or landform change before and after storms, while considering each unique location independently. Using storm response as a restoration value throughout the Gulf of Mexico is reasonable because the abiotic factors that drive sand dune development and dune vegetation communities in the region are likely similar to those at St. George Island (Snyder & Boss, 2002; Miller et al., in press).

To explore how the restoration methods described in Chapter 1 can be applied to other areas in north Florida, I used remote sensing to describe vegetation patterns over time for St. George Island State Park. The vegetation patterns from remote sensing were then compared to similar values determined from a long-term census of vegetation on St. George Island to see if there is a concurrence between the two methods. The remote sensing analysis was then applied to include Little (or Cape) St. George Island. Little St. George is a 9 mile long, barrier island to the west of St. George Island that is managed by the Apalachicola National Estuarine Research Reserve. Preliminary field surveys of the island reveal vegetation that is similar in type and distribution to St. George Island (Gornish, unpublished data). Remote sensing was used to compare the habitats and vegetation of Little St. George and St. George Island as well as to determine if storm damage is of similar magnitude in each dune habitat on the two islands. Finally, restoration candidate species, suggested by remote sensing approaches, were considered for Little St. George.

The remote sensing analysis presented here was limited by several constraints including the accessibility of aerial imagery and species’ growth form. Nonetheless, this is a useful exploration of how remotely sensed data can be used to identify storm damaged areas in coastal ecosystems and how this data might also be used to identify potential species for restoration.

**Methods**

**Images**

Aerial images of St. George Island and Little St. George were obtained from two publically available sources: the Department of Environmental Protection, Florida LABINS DOQQ (http://data.labins.org/) for 2004 and the Department of Transportation, Florida (http://www2.dot.state.fl.us) for 2007. Images for both locations were taken in May of both
years. The images were 1m resolution MrSID (multiresolution seamless image database) graphics in true color (three reflective bands). A textural layer was added to each image to increase differences between vegetation types. Images were analyzed using ERDAS Imagine (Leica Geosystems GIS & Mapping group/ERDAS IMAGINE 9.X). Geometric corrections were applied to images to reduce distortions caused by relief displacement and earth curvature using ground control points.

**Habitat Analysis**

Fore-, inter- and backdune habitats were identified from the 2004 aerial imagery based on qualitative ground cover analysis and textural differences. The area encompassed by each habitat in both locations was conducted using the measurement tool in ERDAS (area coverage for St. George was measured from the entry gate at the west most portion of St. George Island State Park to the eastern tip of the island and the entire island of Little St. George was measured).

**Field Data**

*In situ* global positioning system (GPS) coordinates (datum: WGS 1984) were recorded for patches of abundant dune species and bare sand cover within St. George Island State Park using a Trimble Nomad (Trimble Navigation Limited). GPS coordinates were collected for monoculture stands of major species at least 2m in area and for patches of bare sand of the same size (Fig. 13). Digital photos of stands at each GPS point were also collected. GPS coordinates were differentially corrected in Pathfinder Office and exported as a shape file into the image classification software for data analysis.

![Figure 13. Aerial photo of St. George Island State Park from 2007. Inset highlights GPS points taken at the center of the island.](image)

It was not feasible to collect GPS coordinates for every dune species on St. George Island. Growth form (species that do not grow in large monocultures, species that grow to a small size, etc.) or characteristics of abundance (rare species, transient species) restricted the collection of GPS coordinates to a subset (16) of the plant species (about 57% of total cover of
dune vegetation) found on the island. Attempts were made to collect GPS points for species in each of the three dune habitats: foredune, interdune and backdune habitats. GPS points were collected for the following species:

<table>
<thead>
<tr>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Andropogon glomeratus</td>
</tr>
<tr>
<td>Croton punctatus</td>
</tr>
<tr>
<td>Cyperus esculentus</td>
</tr>
<tr>
<td>Eragrostis lugens</td>
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<tr>
<td>Heterotheca subaxillaris</td>
</tr>
<tr>
<td>Hydrocotyle bonariensis</td>
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<td>Iva mbricate</td>
</tr>
<tr>
<td>Juncus megacephalus</td>
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<tr>
<td>Muhlenberia capillaris</td>
</tr>
<tr>
<td>Panicum amarum</td>
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<tr>
<td>Schizachyrium maritimum</td>
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<td>Sesuvium maritimum</td>
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<tr>
<td>Sesuvium portulacastrum</td>
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<tr>
<td>Smilax auriculata</td>
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<tr>
<td>Sporobolus virginicus</td>
</tr>
<tr>
<td>Uniola paniculata</td>
</tr>
<tr>
<td>Hydrocotyle bonariensis</td>
</tr>
</tbody>
</table>

**Image Classification**

GPS coordinates were mapped onto aerial images of St. George Island State Park. Two of the nine census years (2004 and 2005) were characterized by extreme tropical storms and hurricanes that caused the loss of foredunes and severe flooding on St. George Island (see Chapter 1). Because of this, identifying storm response would ideally be conducted by comparing species’ abundance in pre-storm 2004 to post-storm 2006. However, images for St. George Island were not available for 2006; therefore images of the island in 2007 were used. Each GPS point was described by one pixel in the image. The pixel value (brightness value in each color band) for that GPS point was established as a spectral signature for the species the point represented (e.g., Coops et al., 2004; Zaady et al., 2007). Through supervised classification (an approach that uses location and direct visual identification of vegetation types a priori through aerial photography, map analysis or a combination of both), vegetation types and bare sand with a known spectral reflectance were used to train a classification algorithm to create a pixel by pixel signature for the whole image. Every pixel within the image was assigned to the species for which it has 95% likelihood of being a member, classified as sand or remained unclassified; pixels cannot have more than one classification.

Changes of vegetation cover through time were analyzed using pixel differencing in the spatial modeler tool in ERDAS. This process uses classified maps of the same region at two different points in time. A vegetation map of an image acquired at a later time is ‘subtracted’ pixel by pixel, from an earlier vegetation map, resulting in a map that exhibits differences in the distribution and abundance of vegetation cover between the two time periods. Quantitative data is then retrieved from this map in the form of change in classified pixel values, which I converted to a percent change from 2004 to 2007 (% CPV).

Images of Little St. George were also transformed into vegetation maps using the spectral signature data from St. George by unsupervised classification. An analysis of the changes in vegetation cover through time was then conducted using these maps. The change data were not normally distributed. Spearman rank-order correlation analyses were conducted between change detection results on St. George Island and vegetation change documented in the long-term census over the same period of time in addition to between change detection results of St. George Island and Little St. George.

**Long-Term Census**

In 1998, six permanent vegetation grids were established by T. Miller at the eastern tip of St. George Island: 2 grids each in the foredune, interdune and backdune areas (see methods in Miller et al., in press). Each grid is 60 x 60 m and contains a 7 x 7 array of plots, for a total of 294 individual plots. The plots are censused annually in the fall when species are most easily
identifiable. A 1-m² quadrat is placed over each plot and all vegetation is counted by # individuals or # clumps (depending on growth form) and % cover by species.

Patterns of presence through time for individual species were quantified as percent species occurrences within plots in each year (n = 98) in each of the foredune, interdune, and backdune habitats. Percent occurrence (P) is the number of census plots occupied by a species out of the total number of census plots in a given habitat. Percent occurrence values from 2004 and 2007 for each species in each habitat documented in the long-term census were compared against remote sensing results from St. George Island. There is not a complete overlap of the plant species used in the remote sensing and those in the long-term census, so these methods could not be compared for all species in all habitats.

Results

Habitat Analysis

The entire area of St. George Island State Park in 2004, including wetlands, anthropogenic landmarks such as roads and buildings and flat beach areas adjacent to the waters edge was 772 hectares. The area of St. George that can be considered as part of one of the three dune habitats was approximately 537 hectares. The entire area of Little St. George was 886 hectares, and the three dune habitats cover an area of approximately 534 hectares. Table 5 describes the percentage each dune habitat represents in both locations.

Table 5. Percentage of total area comprised by the three dune habitats of each dune habitat in both St. George Island State Park and Little St. George Island.

<table>
<thead>
<tr>
<th></th>
<th>Foredune</th>
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<th>Backdune</th>
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<tr>
<td>St. George Island</td>
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<tr>
<td>Little St. George</td>
<td>2.4</td>
<td>10.4</td>
<td>47.2</td>
</tr>
</tbody>
</table>

Table 6. Percent sand cover of each dune habitat in St. George Island State Park and Little St. George between 2004 and 2007.

<table>
<thead>
<tr>
<th>Sand Cover</th>
<th>2004</th>
<th>2007</th>
<th>% change</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Fore</td>
<td>Inter</td>
<td>Back</td>
</tr>
<tr>
<td>St. George Island</td>
<td>65</td>
<td>55</td>
<td>14</td>
</tr>
<tr>
<td>Little St. George</td>
<td>69</td>
<td>40</td>
<td>2</td>
</tr>
</tbody>
</table>

The overall percent cover of bare sand in both locations increased from 2004 to 2007, consistent with the occurrence of storm damage (Table 6). The remote sensing analysis is summarized in table 7 as the percent change in pixel values between 2004 and 2007 in each dune habitat for each species. During this period of three years, substantial changes in the abundance of the 16 species analyzed occurred. Overall, there was similar average change across the three habitats (-25%, -29%, and -26%, in the foredune, interdune, and backdune, respectively). Remote sensing identified only one species that responded favorably to the effects of storms: *Panicum amarum* increased in all three habitats. *Heterotheca subaxillaris* showed the greatest
decline of all foredune species, *Juncus megacephalus* was the most affected in interdunes, and *Andropogon glomeratus* in the backdunes. Graminoids exhibited an average decrease in abundance of 34% between 2004 and 2007 while forbs exhibited an average decrease of 45% during the same time period.

**Species Analysis**

The percent of pixels that remained unclassified in each dune habitat were disproportionately larger than the percent of those that were classified. In the foredune habitat, 91% of pixels remained unclassified, in the interdune habitat, 86% of pixels remained unclassified, in the backdune habitat, 88% of pixels remained unclassified.

<table>
<thead>
<tr>
<th>% CPV</th>
<th>Remote Sensing</th>
<th>Long-Term Census</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Andropogon glomeratus</em></td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Croton punctatus</em></td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Cyperus esculentus</em></td>
<td>-17</td>
<td>-53</td>
</tr>
<tr>
<td><em>Eragrostis lugens</em></td>
<td>-4</td>
<td>NA</td>
</tr>
<tr>
<td><em>Heterotheca subaxillaris</em></td>
<td>-70</td>
<td>-62</td>
</tr>
<tr>
<td><em>Hydrocotyle bonariensis</em></td>
<td>-22</td>
<td>NA</td>
</tr>
<tr>
<td><em>Iva imbricata</em></td>
<td>-53</td>
<td>NA</td>
</tr>
<tr>
<td><em>Juncus megacephalus</em></td>
<td>-12</td>
<td>-78</td>
</tr>
<tr>
<td><em>Muhlenbergia capillaris</em></td>
<td>+17</td>
<td>+46</td>
</tr>
<tr>
<td><em>Panicum amarum</em></td>
<td>-32</td>
<td>-19</td>
</tr>
<tr>
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<td>-50</td>
<td>-48</td>
</tr>
<tr>
<td><em>Sesuvium portulacastrum</em></td>
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</tr>
<tr>
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<td>-7</td>
</tr>
<tr>
<td><em>Sporobolus virginicus</em></td>
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<td>-8</td>
</tr>
<tr>
<td><em>Ulinola paniculata</em></td>
<td>-78</td>
<td>-70</td>
</tr>
</tbody>
</table>

Table 7. Percent change in cover of dune species on St. George Island between 2004 and 2007 as identified by remote sensing and percent change in occurrence documented in the long-term census. NA indicates that the species was not observed in either 2004 or 2007, as opposed to an indication of no change.

The long-term census showed somewhat different patterns than the remote sensing, with 4 of 10 species increasing in the foredunes, 1 of 10 in the interdune, and 4 of 12 species in the backdune. The average total change in cover between 2004 and 2007 as identified by remote sensing was -40%, compared to an average of -23% observed in the long-term census during the same time period. In the foredune and backdune habitats, there was no correlation between the percent change observed by the two methods (Spearman rank correlations; foredune: $P = 0.84$; backdune: $P = 0.95$). However, in the interdune, the two methods gave similar results (Spearman rank correlation, $P = 0.012$).

The average change in cover for species on Little St. George Island varied widely between the three habitats (Table 8). Between 2004 and 2007, there was an average change of -3% in the foredune habitat, +10% in the interdune habitat and +26% in the backdune habitat.
Several species were identified as restoration candidates because they increased in cover in all three habitats as a response to storms: *Eragrostis lugens, Hydrocotyle bonariensis, Juncus megacephalus, Panicum amarum, Schizachyrium maritimum, Smilax auriculata* and *Uniola paniculata*. *Sesuvium maritimum* exhibited the greatest decrease in cover in the foredune habitat, *Iva imbricata* was most affected in the interdune and in the backdune habitat *Muhlenbergia capillaris* had the largest percent decrease in cover. Graminoids exhibited an average increase in cover of 47% between 2004 and 2007 while forbs exhibited an average decrease of 26% during the same time period.

### Table 8. Percent change in cover of dune species on Little St. George between 2004 and 2007 as identified by change detection.

Percent change in cover for species on St. George Island using similar methods (Table 4) is presented for comparison. NA indicates that the species was not observed in either 2004 or 2007, as opposed to an indication of no change.

<table>
<thead>
<tr>
<th>% CPV</th>
<th>Little St. George</th>
<th>St. George Island</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fore</td>
<td>Inter</td>
</tr>
<tr>
<td><em>Andropogon glomeratus</em></td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Croton punctatus</em></td>
<td>NA</td>
<td>-25</td>
</tr>
<tr>
<td><em>Cyperus esculentus</em></td>
<td>-17</td>
<td>-18</td>
</tr>
<tr>
<td><em>Eragrostis lugens</em></td>
<td>+21</td>
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</tr>
<tr>
<td><em>Heterotheca subaxillaris</em></td>
<td>-16</td>
<td>-41</td>
</tr>
<tr>
<td><em>Hydrocotyle bonariensis</em></td>
<td>+10</td>
<td>+31</td>
</tr>
<tr>
<td><em>Iva imbricata</em></td>
<td>-30</td>
<td>-72</td>
</tr>
<tr>
<td><em>Juncus megacephalus</em></td>
<td>NA</td>
<td>+9</td>
</tr>
<tr>
<td><em>Muhlenbergia capillaris</em></td>
<td>-27</td>
<td>-29</td>
</tr>
<tr>
<td><em>Panicum amarum</em></td>
<td>+4</td>
<td>+40</td>
</tr>
<tr>
<td><em>Schizachyrium maritimum</em></td>
<td>NA</td>
<td>+12</td>
</tr>
<tr>
<td><em>Sesuvium maritimum</em></td>
<td>-40</td>
<td>NA</td>
</tr>
<tr>
<td><em>Sesuvium portulacastrum</em></td>
<td>NA</td>
<td>-11</td>
</tr>
<tr>
<td><em>Smilax auriculata</em></td>
<td>NA</td>
<td>+124</td>
</tr>
<tr>
<td><em>Sporobolus virginicus</em></td>
<td>-1</td>
<td>-10</td>
</tr>
<tr>
<td><em>Uniola paniculata</em></td>
<td>+70</td>
<td>+39</td>
</tr>
</tbody>
</table>

The one restoration candidate identified by remote sensing for St. George Island (*Panicum amarum*) was also identified as useful for restoration in Little St. George using the same method. Remote sensing identified 37% of the species on Little St. George as exhibiting a directionally opposite (increase) change in cover than what was documented for St. George Island using the same method. In the foredune and backdune habitats, there was no correlation between the percent change observed on the two islands (Spearman rank correlations; foredune: $P = 0.29$; backdune: $P = 0.19$). The two islands had marginally similar results in the interdune habitat (Spearman rank correlation, $P = 0.09$).
Discussion

Results from this exploratory analysis suggest that remote sensing might be a useful approach to successfully extrapolating restoration methods tested in Chapter 2 to areas beyond St. George Island. The approach seems to be particularly helpful for the identification of areas to consider for restoration. However, it does not appear that a remote sensing approach would be appropriate for use as a singular method to establish candidate restoration species.

Remote sensing methods allowed for the comparison of dune habitats between St. George Island and Little St. George to reveal similarities in how the habitats were partitioned across each island. Furthermore, storm damage appears to be comparable between the islands based on change detection of bare sand and vegetation cover between 2004 and 2007. These results suggest that remote sensing can be a useful way to determine if a location is suitable for the application of the restoration methods described in Chapter 1, based on how analogous the geomorphology and the basic effects of storms at a particular location are to those found on St. George Island.

Ideally, using remote sensing to quantify change in species abundances through time should produce results that are similar to the ground-based long-term census data. There appeared to be congruency between results of the two approaches only for species in the interdune habitat. Perhaps, the group of species used in this analysis is somewhat different than those from the 50+ species that have been documented in the long-term census (Miller et al., in press). The long-term census has been conducted on the prograding eastern tip of St. George Island and may contain slightly different habitats and species. Graminoids made up the majority (56%) of the 16 species analyzed here, contrary to the species group described in the long-term census data set, of which, the majority are forbs. It appears that, at the simple spectral level used here, remote sensing methods were not able to capture an adequate representation of all vegetation types found across the island. Instead, the types of vegetation that were best represented were clonal grasses, which often grow in large, monoculture stands. These kinds of plants also happen to make up a majority of the species present in the interdune habitat.

The general agreement of vegetation changes within the interdune habitat between remote sensing results and the long-term census data suggest remote sensing may be substituted for the more labor intensive census work in some habitats. However, an accuracy assessment (used to quantify misclassification of pixels) was not conducted for this work. A large time lapse existed between most current imagery (2007) and GPS collection (2009) and unequal numbers of GPS points were collected for each of the 16 species analyzed, two factors that may have contributed bias or imprecision to the estimates.

Error reduction and accuracy assessments could be accomplished using hyperspectral images collected at the same time as field data collection. Hyperspectral images would facilitate the identification of a larger number of dune species more precisely by reducing unclassified pixel number and overall variance associated with pixel classification. Mixed vegetation stands can also be classified using hyperspectral imagery, making it possible to classify groups of species that are more reflective of the actual vegetation. The identification of a more diverse group of species would potentially broaden the types of habitats for which remote sensing could be used as an approach to restoration.

One species, *Panicum amarum* was identified as a potential restoration candidate by both the long-term census and remote sensing (see Chapter 1). However, there were five species
(Juncus megacephalus, Muhlenbergia capillaris, Schizachyrium maritimum, Sporobolus virginicus and Uniola paniculata) included in this analysis that were found to be potential restoration candidates using the long-term census data, but not using the remote sensing. A potential reason for this contrast is differences in sizes of sampled areas. Discord between patterns observed at different scales is common in ecology (Levin, 1992) and conservation biology (Lewis et al., 1996). The remote sensing analysis was applied to vegetation cover of the entire state park (772 hectares) while the long-term census documents vegetation occurrence on a much smaller scale (2.5 hectares). It is likely that patterns emerging at the more detailed scale at which the long-term census is conducted become obscured at the larger scale at which the remote sensing is conducted. Neither approach is ‘better’, but the smaller scaled long-term census data are likely more appropriate when precision is of important than generality and the larger scaled remote sensing data are better suited for instances when comprehensive analysis is required.

Similarities between vegetation response to storms on St. George Island and Little St. George were also strongest in the interdune habitat, suggesting that remote sensing may work for identifying restoration species in particular habitats. The inequality of restoration species identified by remote sensing methods on St. George and Little St. George, however, highlights the importance of individually assessing restoration candidates at a particular location. The difference in potential restoration candidates between the islands could be due to a variety of factors, including abiotic differences, such as dissimilarities in soil moisture and soil chemistry or unique characteristics of the freshwater lens underneath each island. The single biggest difference between the two locations, however, is anthropogenic influence. St. George is connected to the mainland by a causeway that was built in 1965, making it an easily accessible site for recreation. No road connects Little St. George to the mainland, significantly reducing the number and influence of people on this island. Many of the species that exhibited differential response to storms between the two islands are found near the waters edge (Eragrostis lugens, Schizachyrium maritimum and Uniola paniculata in the foredune area, on the ocean side of barrier islands). These areas are more frequently used by individuals in St. George Island State Park and could result in a decreased abundance and vigor of the species that exist in these areas. This decrease could manifest in reduced cover as a response to storms.

Prior studies have discussed the usefulness of using a remote sensing approach to investigate response of vegetation to damaging events (Zaremba & Leatherman, 1986; Jano et al., 1998; Sanchez-Azofeifa et al., 2001) and as a method of conservation and restoration design and management (Franklin, 2001; Schman & Ambrose, 2003; Cayuela et al., 2006). The analysis presented here describes a way in which to coalesce these two themes to explore the potential use of a remote sensing approach to identify habitats experiencing the negative effects of storms and species in these habitats that are resilient to these effects.

This suggests that remote sensing may be helpful to identify habitats that would benefit from restoration, but that it was less than ideal for identifying candidate restoration species in these areas. It is clear that the remote sensing methods used here need refinement for broader application. Field data can be used to elucidate patterns observed with remote sensing methods (Osborne et al., 2001) and advancements that enhance resolution can increase the precision of imagery analysis. With the advent of more sophisticated tools, remote sensing methods are becoming better at elucidating patterns at scales that are particularly relevant to conservation and restoration (Turner et al., 2003), which may result in restoration efforts that more frequently involve a remote sensing component (Westman, 1991).
CHAPTER 4

MODELING THE EFFECTS OF HURRICANE FREQUENCY ON DUNE VEGETATION

Introduction

Changes in tropical cyclone and hurricane activity are an increasingly important component of global climate change (Emanuel, 2007). Despite intense debate concerning the mechanisms responsible (Elsner et al., 2006; Vecchi & Soden, 2007), most models describe relatively similar relationships between climate change and hurricane activity. The frequency (Webster et al., 2005; IPCC, 2007) and intensity (Emanuel, 2005; Trenberth, 2005) of tropical storms and hurricanes is increasing and is projected to continue doing so for at least the next 50-100 years as a result of climate change. Coastal systems in tropical and subtropical climates are especially vulnerable to the effects of storms, yet there is surprisingly little information on how climate change may affect these areas (Alley et al., 2003; Fagherazzi et al., 2003; Harley et al., 2006; Prato, in press). This is due, in part, to a lack of long-term studies (Johnson, 1997) that directly measure recovery within coastal vegetation communities after damaging events (but see Grootjans et al., 1991).

Predicting vegetation response to storms is difficult as the habitats that make up coastal systems are regulated by different types and gradients of stress (Houle, 2008; da Silva et al., 2008), resulting in both disturbance and recovery that can vary significantly among habitats (Helmer et al., 2000). Storms also vary in intensity, making recovery hard to predict (Sousa, 1984; Pickett & White, 1985). The differential response of dune species to storms has been identified as an important characteristic driving vegetation dynamics and succession across barrier islands (see Chapter 1, Miller et al., in press) but it is not well understood how the predicted increase in frequency of hurricane events might change the composition of coastal plant communities.

Using a successional framework to understand the effects of storms could be useful because individual species, suites of species, and habitats can be isolated to investigate storm response. Studies that investigate succession after severe damaging events in long-term plots (Hibbs, 1983) or reconstructions (Henry & Swan, 1974) highlight the importance of considering both the response of individual species to these events and how the behavior of a species contributes to changes in community structure.

The fore-, inter- and backdune habitats that characterize a barrier island represent gradually older stages of long-term (500+ year) succession across the island (Gleason, 1927; Dahl et al., 1975). Primary succession occurs on newly exposed bare sand immediate to the shoreline, that gradually builds to form foredunes. Wind moves these dunes inland while winds and waves create newer dunes on the generally progressing shores. The foredunes eventually degrade and the vegetation found there slowly gives way to secondary succession in flatter interdune areas (Johnson, 1997). These interdune areas are particularly subject to saltwater flooding from storm surge and freshwater flooding from heavy rains, creating very different conditions for vegetation. Finally, the interdune habitat shifts to low dunes and troughs in the backdunes where a higher diversity of longer lived species stabilize the habitat.
At a much shorter time scale of months to a few years, these habitats also undergo succession when they recover from climatic disturbances. The plant communities within each dune habitat change in response to environmental stresses like sand movement, drought, and, particularly, heavy precipitation and storm surge resulting from hurricanes (Miller et al., in press). It is these short term responses from hurricane events that can be used to make predictions about the effects of increasing storm frequency within each dune habitat. Hurricanes can denude large swaths of habitat across a barrier island in a single event and succession may then be re-started within each dune habitat. On average, every four years a named tropical storm passes within 125 nautical miles of St. George Island, in Apalachicola, FL, and approximately every third storm is a category 3-5 hurricane (about every 11 years) (National Hurricane Center: http://www.nhc.noaa.gov/).

Because dune species that are found in more than one habitat often exhibit habitat-specific growth patterns (including storm response; Chapter 1, Miller et al., in press), I expected species to respond differently to increasing storm frequency in each dune habitat. Dune habitats would then exhibit different recovery pathways in response to an increase in the frequency of hurricanes. The largest number of species that increase or maintain abundance following storms are found in the backdune habitat, while the fewest are found in the foredune habitat. This makes it likely that the foredune plant community will exhibit the greatest overall change in response to increasing hurricane frequency while the backdune community will quickly become dominated by a collection of storm resilient species.

I used the long-term data from St. George Island to quantify vegetation dynamics in storm and non-storm years. I then used this information to create a model of vegetation dynamics on St. George Island under different storm frequencies. This is a first-order model that predicts the patterns of species occurrence and plant communities that might be created by the disturbance and subsequent recovery that occurs in each dune habitat (Feagin et al., 2005). To my knowledge, this is the first model of how Gulf coastal plant communities may be expected to change with storm frequency.

**Methods**

Species percent occurrence and changes in occurrence through time in each dune habitat can be determined from the ten-year data collected by T. Miller (http://bio.fsu.edu/~miller/stgeorge). Percent occurrence was quantified as the number of plots occupied by each species out of the 98 1-m² plots in each of three habitats (foredunes, interdunes, and backdunes) censused each year since 1999 (see Miller et al., in press for a more complete description of the census methods). Species occurrences were used to parameterize a vegetation model in which each species is started at their ambient non-storm occurrence, then allowed to increase or decrease through time based on the frequency of storms and the species-specific changes in occurrence in storm and non-storm years. Separate models were created for foredune, interdune and backdune habitats. The model was built using the freeware R version 2.5.1 (R Development Core Team, 2007).

The model simulates the percent occurrence of each species within a particular dune habitat through time. Models for each dune habitat include only those species that were observed in that particular habitat at least three times during the period of 1999-2008. Species were
defined as ‘common’ if present in a particular dune habitat more than three times since the first census. Distributions of percent occurrence and growth for common species were described as either normal (Gaussian), uniform (unimodal) or skewed (beta), based on patterns exhibited by each species in the census. Species were defined as ‘rare’ if present in a particular dune habitat only three times since the first census. Distributions in percent occurrence and growth for rare species were defined as uniform, bounded by minimum and maximum percent occurrence values from the long-term data set. The initial percent occurrence value of each common species was randomly chosen from the species-specific distribution of percent occurrence within that habitat in non-storm years, but only using values > 1%. Initial percent occurrence of all rare species was 0. Non-absorbing percent occurrence boundaries for the model were 0 and 100%.

Percent occurrence values in each time step are derived from growth rates in either non-storm years \( R_n \) or storm years \( R_s \). For common species, \( R_n \) is chosen at random from a species and habitat-specific distribution of change in percent occurrence in non-storm years. For storm years, the \( R_s \) of each common species is taken from a uniform distribution bounded by the values of the change in percent occurrence observed after the two most destructive storm years for St. George Island, 2004 and 2005. The percent occurrence \( P_t \) of a common species in time step \( t \) is:

\[
P_t = P_{t-1} + (P_{t-1} \times R)
\]

\( R = R_n \) if a hurricane does not occur in time step \( t \) or \( R = R_s \) if a hurricane does occur in time step \( t \).

The percent occurrence of a rare species is a value chosen at random from a uniform distribution, bounded by 0 and the maximum percent occurrence value. Rare species that were documented in the long-term census only after a storm event become extinct in non-storm time steps, but have the chance to recolonize in storm time steps. Rare species documented as extinct in the long term data after storm events have a chance to recolonize in non-storm time steps and become extinct in storm time steps. At every time step, common species with percent occurrence values of 0 are given a random chance to colonize the habitat with a percent occurrence between 0 and 5%. There is no density dependant regulation in the model.

The model for each habitat was run for 100 years, with 100 replicate runs for each of the following hurricane probabilities: 0.16, 0.20, 0.25, 0.33, 0.5 and 1 per year (respectively, hurricanes approximately every 6, 5, 4, 3, 2, and 1 years). Percent occurrences of each species were determined for every run of the model and then averaged across the 100 replicates for each species to get a single percent occurrence value for each species at each combination of time step, habitat, and level of hurricane frequency. Model predicted percent occurrence changes for individual species were compared across hurricane frequencies in two ways: direction of change and magnitude of change. First, the directional change of occurrence can be positive (increase in percent occurrence), negative (decrease in percent occurrence) or zero (no change in percent occurrence). Second, response to increasing hurricane frequency with an increasing rate of percent occurrence change is considered a response of high magnitude. Otherwise, the response is considered low magnitude. Model results were compared to current storm response values identified from the long-term census data.

At the community level, effects of changing hurricane frequency were quantified by comparing species richness (number of species), alpha diversity, determined by the Shannon-Weiner diversity index \( H' = \sum \text{proportion of species in the habitat} \times \ln[\text{proportion of species in habitat}] \) and average species percent occurrence at each storm frequency. Biotic similarity
between dune habitats was also determined with the Classic Jaccard similarity index using EstimateS version 8 (Colwell, 1999). The strength of relationships between resulting habitat characteristics and hurricanes were tested using Pearson product moment correlations for normally distributed data; otherwise, Spearman rank-order correlation analyses were used.

Non-metric multidimensional scaling (NMDS) was used to identify species that contribute most to changes in vegetation as hurricane frequency increases (Clark, 1993). NMDS is a robust, non-parametric ordination approach for similarity analysis that uses occurrence values of each species, time step and habitat to calculate a community score (Torgerson, 1958). This analysis takes into account the independent vegetation dynamics occurring within each dune habitat, as described in Chapters 1 and 2 and facilitates making comparisons within and among dune habitats across all hurricane frequencies. NMDS analysis was conducted in R (Vegan package) and a final solution for two dimensions was reached after 20 iterations. Community scores for the last ten time steps of each model simulation were averaged, resulting in a centroid value that represented the equilibrium community of that habitat in a particular hurricane frequency. Communities were compared within and among dune habitats at different hurricane frequencies. Dune species also receive a score at each time step for each parameter value in each habitat. This score is a function of the individual species’ occurrence, compared to the occurrence of all other species in that habitat in that time step.

**Results**

**Species Patterns**

Model results predicted 67% of foredune species will decrease in percent occurrence as hurricane frequency increases, consistent with the results of the long-term census (Table 9). Species that are negatively affected by increasing storms include some common species (e.g., *Phyla nodiflora* and *Eragrostis lugens*), but the negative effects in foredune species are most pronounced for relatively rare species (e.g., *Heterotheca subaxillaris*, *Hydrocotyle bonariensis* and *Ipomea imperati*). A small number of the more common species are expected to increase with storm frequency (*Fimbristylis* spp., *Sesuvium maritimum* and *Sporobolus virginicus*), but the overall result is lower species diversity and average percent occurrence in the foredunes (Fig. 14).

Eighty percent of the species in the interdune habitat are predicted to decline with increasing storm frequency, resulting in an overall decrease in average percent occurrence and species diversity in this habitat (Fig. 14). The model predicted that species with both lower (e.g., *Eragrostis lugens*, *Ipomea imperati* and *Oenothera humifusa*) and higher than average percent occurrence (e.g., *Cyperus croceus*, *Juncus megacephalus* and *Paspalum vaginatum*) will decline as hurricanes increase in frequency. Many of the species that are predicted to decrease in percent occurrence in the interdune area are not specialists in this habitat and can be found across the island (Table 9). A small group of more common species are predicted by the model to increase in percent occurrence (e.g., *Panicum amarum*, *Physalis angustifolia* and *Uniola paniculata*).

Sixty-seven percent of plant species in the backdune habitat were predicted to decline in percent occurrence in response to increasing hurricane frequency. Over half of the common species in this habitat were predicted to greatly decrease in percent occurrence (e.g., *Ipomea imperati*, *Physalis angustifolia*, *Schizachyrium maritimum* and *Smilax auriculata*) as storms...
increase in frequency. A few common species were predicted to respond positively to increased storm frequency (Aristida purpurascens, Cynanchum angustifolium and Sporobolus virginicus), but the model generally predicts a change in dominance in the backdune habitat to species that are usually occur infrequently (e.g., Andropogon gyrans, Cenchrus incertus, Panicum amarum and Paronychia erecta), resulting in a relatively small effect of increasing storm frequency on average percent occurrence and diversity (Fig. 14).

There is no significant difference in the percentage of species that are predicted to exhibit negative responses to storms among the three dune habitats. Rare species are more likely to decline as storms increase (p = 0.04). This trend is strongest in the backdune habitat and weakest in the foredune habitat.

Table 9. Comparisons between current response to storms from long-term census data (‘census’) and predictions of response rate to increasing hurricane frequency from the succession model (‘model’) in each dune habitat. 0 = no change in percent occurrence, + = linear rate of increasing percent occurrence, ++ = increasing rate of increasing percent occurrence, - = linear rate of decreasing percent occurrence, - - = increasing rate of decreasing percent occurrence. Empty cells indicate that model predictions for this species = percent occurrence < 1% or the species was not included in the model for the particular habitat.
Table 9 – Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Foredune</th>
<th>Interdune</th>
<th>Backdune</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sesuvium maritimum</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Smilax auriculata</td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sporobolus virginicus</td>
<td>++</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Uniola paniculata</td>
<td>0</td>
<td>-</td>
<td>+</td>
</tr>
</tbody>
</table>

Community Patterns

Species richness in the foredune (p = 0.02) interdune (p = 0.01) and backdune (p = 0.03) habitats were negatively correlated with hurricane frequency (Fig. 14A; Spearman rank correlations; foredune: $\rho_s = -0.88$; backdune: $\rho_s = -0.84$ and Pearson’s product moment correlations; interdune: $r = -0.91$). Alpha diversity was strongly ($p < 0.001$ for all habitats) negatively correlated with storm frequency in all habitats (Fig. 14B; Pearson’s product moment correlations; foredune: $r = -0.99$; interdune: $r = -0.98$ and backdune: $r = -0.99$). However, the effect of increasing frequency on diversity is relatively small, except at the highest storm frequency. For all dune habitats average occurrence was also negatively correlated ($p = 0.08$ for foredune and $p < 0.001$ for interdune and backdune) with hurricane frequency (Fig. 14C; Spearman rank correlation; foredune: $\rho_s = -0.75$ and Pearson’s product moment correlations; interdune: $r = -0.99$ and backdune: $r = -0.98$). An increase in storm frequency resulted in the foredune and interdune habitats ($p = 0.003$) becoming more similar (Fig. 14D; Spearman rank correlations: $\rho_s = 0.96$), while the similarities between the other habitat pairs decreased (Spearman rank correlations; interdune and backdune $\rho_s = -0.52$ and Pearson’s product moment correlations; foredune and backdune: $r = -0.67$).
NMDS illustrates that the plant communities in the foredune habitat experience continuous change as a result of increased hurricane frequency (Fig. 15A). The responses of these communities are influenced most by relatively rare species that respond to an increase in storm frequency with declines in occurrence. At high storm frequencies, more common species that respond positively to an increased frequency of storms contribute the most, leading to significant changes in community structure. The patterns observed for plant communities in the foredune habitat are in contrast with those observed in the interdune and backdune habitats (Fig. 15B, C). In these habitats, plant communities remain relatively similar at any hurricane frequency lower than a storm per year but there are differences in the characteristics of species maintaining these dynamics. In the interdune habitat, there does not appear to be any clear pattern of the types of species contributing most to the community that exists at the highest storm frequency. Half of these species have higher than average occurrence and respond negatively to increased storm frequency and the other half has lower than average occurrence and respond positively to an increase in storm frequency. Many of the species that contribute most to the plant communities in the interdune habitat at lower storm frequencies respond negatively to storms and occur less often than average. The vegetation communities in the backdune habitat exhibit yet a third pattern. All the species that contribute most to the community observed at high storm frequencies have lower than average occurrence and respond favorably to increasing storm frequency. The species that maintain the plant communities of the backdune habitat at smaller hurricane frequencies are a mixture of those with lower and higher than average occurrence and positive and negative response to increasing storm frequency.
Discussion

The St. George Island long-term data quantified the significant effects of storms on dune vegetation (Miller et al., in press). I have used these species- and habitat- specific effects of storms to make first-order predictions of how changing storm frequencies may affect the vegetation in different dune habitats. The model predicts that, with increasing hurricane frequency, the occurrence of many individual species will change, with each dune habitat predicted to exhibit turnover in different dominant species. The model also predicts only slight declines in dune plant diversity in all habitats, except at the highest storm frequencies. In addition, the foredune and interdune habitats are predicted to become more similar to one another, while both will become more dissimilar to the backdunes.

The foredune habitat is expected to be most affected by increasing storms (Fig. 14), with declines in species richness and average occurrence. Interestingly, species diversity is expected to peak at low to intermediate storm frequencies. Increasing storm frequency seems to have more of a continuous effect on plant communities in the foredunes than in the other two habitats. The species that come to dominate when hurricanes occur frequently (e.g., Fimbristylis spp., Sesuvium maritimum and Sporobolus virginicus) appear integral to the primary succession that occurs in the foredune habitat after storms. Species documented in the long-term census as having average occurrence in this habitat are predicted to become less dominant when hurricanes are more frequent (e.g., Eragrostis lugens, Hydrocotyle bonariensis, Ipomea imperati and Schizachyrium maritimum). These species are likely secondary or climatic succession species that are more prevalent in years following storms.

In the interdune habitat, the model predicts that alpha diversity and average occurrence will decrease primarily at high storm frequencies, while species richness is predicted to decline in a more continuous manner. The lack of a consistent pattern describing how species will change their percent occurrence in response to increasing storm frequency might be a result of the intermediate characteristics of the interdune habitat itself. The interdune habitat can be

![Figure 15. Community NMDS scores for each habitat in blue (A = foredune, B= interdune, C=backdune) for each hurricane frequency (1 = every year, 0.5 = ~ every 2 year, 0.33 = ~ every 3 years, 0.25 ~ every 4 years, 0.2 ~ every 5 years, 0.16 ~ every 6 years). Species codes are plotted in red.]
considered as the secondary stage of succession in the chronosequence from foredunes to backdunes (Gleason, 1927; Dahl et al., 1975). As such, this habitat may include species from a variety of successional stages. The interdune habitat has the smallest number of endemic species and shares the most species with other dune habitats (Chapter 1). Species found in the interdune habitat are likely to have a greater variance in morphological, life history and stress tolerant traits.

The model predicts that the backdune habitat will be least affected by increasing storm frequency, with minimal declines in species richness, comparatively smaller declines in alpha diversity and average occurrence, except at very high storm frequency. A possible explanation for this predicted pattern is related to competition: the backdunes have higher percent cover of older, potentially more competitive species (see Chapter 1). Competition in this habitat most likely occurs for water, which is limiting in all three habitats (Ehrenfeld, 1990), and storms are almost always accompanied by significant, sometimes extreme, precipitation. The increased moisture in the backdune habitat might be releasing the backdune species from competitive stress by making water more available. A reduction in competitive stress could mitigate the negative effects of hurricanes, minimizing changes in the backdune habitat as a result of increasing hurricane frequency.

The model predicts that increased storm frequency will result in an increase of similarity between the vegetation communities in foredune and interdune habitats. Species that appear to be responsible for the composition of the plant communities within these two habitats at high storm frequencies (Fig. 15) are similar (i.e. Phyla nodiflora and Sporobolus virginicus). Alternatively, it appears that many of the backdune species that decrease in abundance in response to storms are being replaced with rare species. This maintenance of backdune diversity (Fig. 14A) is likely responsible for the backdune community decreasing in similarity from both the foredune and interdune habitats. Species responsible for backdune community characteristics at high storm frequencies, like Cenchrus incertus, Eragrostis lugens and Paronychia erecta (Fig. 15), are not important for the remaining habitats at these frequencies.

Overall, species with higher percent occurrence within dune habitats are more likely to respond positively to an increase in the frequency of storms. However, species that are more generalist types (occur in more habitats) are more likely to respond with a decrease in occurrence, a seemingly confounding result as prevalent species on St. George Island often have the largest average occurrence in each dune habitat (Chapter 1). Perhaps, among the common species, generalists are less well equipped to deal with the hurricane effects that are unique to each habitat.

Developing this model of vegetation dynamics on St. George Island is beneficial both for elucidating potentially obscured patterns in the large data set, as well as using predictions to inform management approaches. Despite its simplicity, the model provides insight into some non-linear, unexpected patterns that might otherwise have remained unrecognized. Establishing a preliminary understanding of how organisms will respond to damaging events as a result of climate change can be useful for estimating extinction risk for species of concern (Thomas et al., 2003), designing restoration methods (Prach & Pysek, 2001), and targeting conservation approaches (Palmer et al., 2008).

Interpreting these simulations is limited by simplifying assumptions inherent in the model. Storm behavior in the model was simplified by assuming only additive effects for increasing storm frequency and the use of a single hurricane intensity. These assumptions likely
reduced variance associated with individual species storm response and minimized stochasticity associated with model results. The absence of density dependence and competition in the model could obscure the occurrence of species that can take advantage of empty niche space in lieu of adequate storm response; some annuals such as *Sabatia stellaris* and short-lived perennials such as *Heterotheca subaxillaris* may use such a strategy. Lastly, the two years of storm response data used in the model may not be representative of an average response; storms can clearly vary in intensity, amount of precipitation accompanying them, time of year, etc. This limitation is associated with most models where more complete datasets with which to develop models don’t yet exist. This concern should encourage more researchers to initiate and continue long-term analyses of vegetation response to damaging events. With these considerations in mind, the model predictions can be used to development a general understanding of dune vegetation response to storms.

Model results suggest predictions of vegetation change within each dune habitat that could not have been learned from simply extrapolating the analyses presented in Chapter 1. Data from the long-term census is not sufficient to derive information of how the balance between storm years and non-storm years affects individual species and entire communities. Species that respond well to storms at low hurricane frequency (0.25 or, about every 4 years as documented in the long-term census) do not necessarily do well when exposed to more frequent storm events. Moreover, the types of dune species that are disproportionately responsible for community level response patterns to increasing storm frequency are only accessible from model simulations.

Despite the unique way that each habitat responds to an increasing frequency of storms, implications of these changes are not restricted to an individual habitat. The three habitats are inextricably linked and changes that occur in the vegetative community of any one dune habitat will affect all other habitats and ultimately, the succession of the entire coastal system.
CONCLUSION

Most studies of coastal vegetation focus on a small subset of species (Ehrenfeld, 1990), not necessarily representative of the entire plant community or of the different habitats that occur on coasts. Development of a comprehensive understanding of the vegetation on coastal dunes, however, requires investigating entire plant communities at scales that cover the range of available habitats. A long-term census of ten years of vegetation dynamics across the major dune habitats in St. George Island State Park has been used previously to demonstrate how the plant communities are affected by climate, primarily summer temperatures and precipitation, as well as surge associated with major storms (Miller et al., in press). This thesis further uses this long-term data set to develop restoration approaches, specific species for restoration, extensions to remote sensing methods and models of the effects of climate change.

Storms, especially hurricanes, can bury or remove vegetation, and cause flooding by saltwater (storm surge) and freshwater (precipitation), all of which can be destructive to vegetation and the dunes themselves. I identified candidate species for dune restoration following storm disturbance by using the long-term census to identify species that were either little affected by or exhibited positive growth following storms (Chapter 1). The species identified by this method were habitat-specific and should provide an appropriate set of species for managers to consider.

Six species identified previously from a preliminary analysis of the long-term data were transplanted into storm-damaged foredune, interdune, and backdune areas in St. George State Park. After one-year, the survival and growth of the transplants suggest which of these species may actually be useful for restoration, and in which habitats. The differential survival and growth of transplant species between dune habitats highlights the complex relationship between dune species and the habitats in which they are found. Dynamic changes observed through time underscore the need to consider candidate species based on long and short-term restoration goals.

Using long-term census data to inform restoration may serve as a model for determining species to use in future restoration. Remote sensing and GIS based methods may enable this method to be applied in similar locations where long-term census data is often not available. Similarities (and dissimilarities) between the habitats and storm damage on St. George Island State Park and Little St. George were demonstrated using remote sensing approaches. The identification of restoration candidate species using aerial imagery, however, was not fully successful. Vegetation response to storms as determined by remote sensing methods and long-term data on St. George Island and Little St. George were in agreement only in the interdune habitat. This pattern was also seen in comparisons between changes in the cover of dune vegetation on St. George Island and Little St. George using remote sensing. While the remote sensing method demonstrated some habitat- and species-specific potential for identifying possible restoration species, it is also clear that this approach has, at present, some technological limitations.

Lastly, the long-term census data was used to create a simulation of how vegetation on coastal areas will respond to changing (especially increasing) frequency of storm events. The first-order model highlighted the short-term succession to be expected from an increase in storm frequency within dune habitats. Not surprisingly, the model demonstrates that species diversity and richness, as well the occurrence of most individual species, will generally decline if storm frequency increases. More importantly, the model suggests how species occurrence patterns will shift within each habitat, resulting in different assemblages. The model results, although
speculative, are the first of their kind (but see Houser et al., 2008).

The long-term census data has proved to be valuable not only for a range of applications for St. George Island State Park, but potentially for the 2000 miles of Florida coastline, in addition to similar habitats along the Gulf and eastern US coasts. These data will become more informative through time: they are essential input for developing theories on the role of geology, vegetation, and disturbance in coastal areas, as well as for documenting and predicting effects of climate change in this critical habitat.
Table 10. Description of all major species mentioned in thesis.

<table>
<thead>
<tr>
<th>Species Name</th>
<th>Family</th>
<th>Common Name</th>
<th>Species Name</th>
<th>Family</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Baccharis</em> spp.</td>
<td>Asteraceae</td>
<td></td>
<td><em>Panicum aciculare</em></td>
<td>Poaceae</td>
<td></td>
</tr>
<tr>
<td><em>Centella asiatica</em></td>
<td>Mackinlayaceae</td>
<td>Asiatic pennywort</td>
<td><em>Panicum amarum</em></td>
<td>Poaceae</td>
<td>Switchgrass or beachgrass</td>
</tr>
<tr>
<td><em>Cnidoscolus stimulosus</em></td>
<td>Euphorbiaceae</td>
<td>Spurge nettle</td>
<td><em>Paspalum vaginatum</em></td>
<td>Poaceae</td>
<td>Stiltgrass</td>
</tr>
<tr>
<td><em>Cynanchum angustifolium</em></td>
<td>Asclepiadaceae</td>
<td>Gulf coast swallow wart</td>
<td><em>Phyla nodiflora</em></td>
<td>Verbenaceae</td>
<td>Frogfruit</td>
</tr>
<tr>
<td><em>Cyperus croceus</em></td>
<td>Cyperaceae</td>
<td>Baldwin’s flatsedge</td>
<td><em>Phy sac chargetia</em></td>
<td>Solanaceae</td>
<td>Coastal groundcherry</td>
</tr>
<tr>
<td><em>Eragrostis lugens</em></td>
<td>Poaceae</td>
<td>Mourning lovegrass</td>
<td><em>Sabatia stellaris</em></td>
<td>Gentianaceae</td>
<td>Marsh pink</td>
</tr>
<tr>
<td><em>Eustachys petraea</em></td>
<td>Poaceae</td>
<td>Pinewoods fingergrass</td>
<td><em>Schizachyrium maritimun</em></td>
<td>Poaceae</td>
<td>Gulf blue stem</td>
</tr>
<tr>
<td><em>Fimbristylis spp.</em></td>
<td>Cyperaceae</td>
<td>Hurricane grass</td>
<td><em>Spartina patens</em></td>
<td>Poaceae</td>
<td>Saltmeadow cordgrass</td>
</tr>
<tr>
<td><em>Juncus megacephalous</em></td>
<td>Juncaceae</td>
<td>Bighead rush</td>
<td><em>Sporobolus virginicus</em></td>
<td>Poaceae</td>
<td>Seashore dropseed</td>
</tr>
<tr>
<td><em>Muhlenbergia capillaris</em></td>
<td>Poaceae</td>
<td>Gulf or pink muhlygrass</td>
<td><em>Uniola paniculata</em></td>
<td>Poaceae</td>
<td>Sea oats</td>
</tr>
<tr>
<td><em>Oenothera humifusa</em></td>
<td>Onagraceae</td>
<td>Seabeach evening primrose</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 16. Soil characteristics of the three dune habitats on St. George Island State Park.

Figure 17. (A) Average percent abundance plotted against average percent change in abundance in each habitat. Each point represents a single species. (B) Restoration species highlighted.
Figure 18. Detailed histograms of the composition of the ten most abundant dune species in each dune habitat by year.
BIBLIOGRAPHY


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BIOGRAPHICAL SKETCH

Education

PhD  Present  Florida State University, Ecology
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BS  2006  Hunter College, Conservation Biology
BS  2003  University at Buffalo, Business
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Research

Patterns in Competitive Hierarchies
Part of a group conducting a meta-analysis of diallel competition experiments to test historical niche concepts. January 2008 – Present

Allee Effects on Invasion Dynamics
Part of a group constructing reasonable and relevant parameters of an allee effect, applicable for any taxa, for general models of invasion speed. January 2008 - Present

Investigating Relationships Between Climate Change and Response
Testing the differential effects of global change across the colonization pathway to identify mechanisms driving response to climate change. December 2007 - Present

Use of Census Data to Inform Restoration of Gulf Coast Dune Vegetation, St. George Island, Florida
Utilized a long-term database of vegetation change in different coastal habitats on St. George to identify 6 candidate species for restoration and conservation work across dune habitats. Currently testing these predictions by restoring sections of the shoreline in St. George State Park through transplant experiments. August 2007 – Present

Community Effects of Habitat Degredation, Hudson Bay, Canada
Investigations of the interacting biotic and abiotic factors that lead to the initiation and spread of habitat degradation and rapid ecological change (trophic cascades) that adversely affect most of the species sharing this coastal habitat. September 2005 – September 2008
Manuscripts

Teaching Experience
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Florida Native Plant Society Conference Travel Award May 2008
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