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Invasion of Hurricane-Disturbed Scrub Communities on Barrier Islands in Mississippi: a Battle Between Native and Non-Native Ecosystem Engineers

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INVASION OF HURRICANE-DISTURBED SCRUB COMMUNITIES ON BARRIER

ISLANDS IN MISSISSIPPI: A BATTLE BETWEEN NATIVE AND NON-NATIVE

ECOSYSTEM ENGINEERS

A Dissertation
presented in partial fulfillment of requirements
for the degree of Doctor of Philosophy
in the Department of Biology
The University of Mississippi

by

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ABSTRACT

Some communities may resist invasion because they are dominated by ecosystem

engineers. If these dominant species are removed by some catastrophic disturbance, they can be

replaced by invasive species that will dramatically alter the ecosystem in a way that may prevent

its recovery. I tested several hypotheses related to this idea within barrier island scrub

communities dominated by Florida rosemary (*Ceratiola ericoides* Michx.). Hurricanes represent

a major source of disturbance to coastal Florida rosemary communities, and individual rosemary

shrubs in three populations recently impacted by major hurricanes were not protected from the

storm surge at higher elevation. Unlike inland populations of rosemary more likely to be

affected by fire, some individuals in coastal populations resprouted following hurricane damage

and may reproduce at an earlier age. After Hurricane Katrina, which caused widespread

mortality of rosemary and other dune species on Horn and Petit Bois Islands, Mississippi, an

invasive grass, *Panicum repens* L. (torpedograss), began encroaching upon the dunes from its

previous habitat in adjacent swards. Previous studies have shown that rosemary inhibits the

growth of native bunchgrasses via allelopathy, and I demonstrated in two greenhouse

experiments that rosemary may be capable of mild alleopathic inhibition of torpedograss

aboveground growth. Comparing pre-storm data to torpedograss abundance and Florida

rosemary recruitment after the hurricane revealed that after an initial increase, torpedograss

density on the dunes declined as the native community recovered. Torpedograss did not threaten

rosemary seedling recruitment, perhaps due to persistent soil effects associated with the pre-

ii

storm presence of adult rosemary shrubs; therefore it appears that Florida rosemary's removal by the hurricane contributed to encroachment by torpedograss, but that torpedograss did not sufficiently alter the dune habitat to prevent community recovery. An increase in hurricane frequency or intensity could change the outcome of this interaction. Although it is an aggressive wetland invader, torpedograss may play a more opportunistic role in xeric systems. During a fourteen-month study at Archbold Biological Station, populations of torpedograss adjacent to pasture were increasing, while those adjacent to scrub were declining. Roadside populations of torpedograss therefore represented propagule sinks rather than sources at this location.

LIST OF ABBREVIATIONS AND SYMBOLS

ABS   Archbold Biological Station

HCA   Hydrocinnamic acid

IS   Site adjacent to interior scrub

MHW   Mean high water

MSL   Mean sea level

P   Site adjacent to pasture

r   Exponential growth rate constant

RGR   Relative growth rate

RS   Site adjacent to boundary with Archbold Reserve

YSH   Year(s) since hurricane

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The invasion and alteration of native ecosystems by non-native species is an important type of global environmental change (Sax et al. 2005). Non-native species that alter ecosystem processes change the rules dictating persistence of all resident species within the invaded portion of a community (Vitousek 1990), and could therefore be a threat to biodiversity. An emerging consensus among ecologists is that, given an adequate supply of propagules, most communities are likely to become invaded (Levine et al. 2003). Some questions that remain, however, are: 1) What makes some communities very resistant to invasion even when the availability of propagules of non-resident species is high? 2) What can make communities once resistant to invasion vulnerable to invasion? 3) What are the impacts of invasion? I addressed these three crucial questions in invasive species biology by considering a situation that has not received much attention: The inhibition or promotion of invasion through the activities of ecosystem engineers. Specifically, I examined the allelopathic effects of a native shrub, Florida rosemary (*Ceratiola ericoides* Michx.), upon invasion by a non-native species, torpedograss (*Panicum repens* L.), in the wake of a catastrophic disturbance, Hurricane Katrina, which drastically altered community composition and local topography in its wake.

Florida rosemary is a dioecious evergreen shrub of the family Empetraceae. Native to the southeastern United States, it has long been recognized as a member of a community of plants occupying deep, extremely well-drained, sandy coastal and inland soils and commonly termed Florida scrub, the rosemary phase of sand pine scrub (Abrahamson 1984), or more simply,

rosemary scrub (Nash 1895, Mulvania 1931, Webber 1935). The rosemary scrub community resists fire and burns infrequently, as vegetation within the scrub is relatively sparse compared to surrounding areas. New Florida rosemary seedlings do not reach reproductive age for ten to fifteen years according to studies of rosemary scrub located in the relic dunes of Florida, so a fire cycle of greater frequency than ten years is likely to result in a gradual population decline as seed bank stores are depleted and never replenished (Johnson 1982). Some authors have suggested that allelopathy in Florida rosemary (Fischer et al. 1994, Menges and Kimmich 1996, Richardson and Williamson 1988) inhibits community invasion by highly flammable species, especially native bunch grasses, and thus effectively reduces fire frequency in the community and maintains favorable conditions for fire-intolerant plants.

Panicum repens, variously known as torpedograss, couch panicum, creeping panic, or wainaku panic, is a rhizomatous perennial C_4 grass that is common in marshy areas along the Gulf Coast, California, and Hawaii. Although its origins are uncertain as it is now found worldwide, it is believed to have been introduced to North America in ballast water or as forage for cattle (Tabor 1952); the first recorded collection of torpedograss in the United States occurred in 1876. The grass is currently listed as a noxious weed in four states (USDA NRCS 2007). When introduced into an area, torpedograss spreads rapidly, primarily through clonal growth, and is capable of creating thick, highly flammable mats of ground cover in a short period of time. Accounts of torpedograss in proximity to rosemary scrub (Penfound and O'Neill 1934) began to appear in the literature in the early 1900s.

Prior to Hurricane Katrina, a Category 3 storm, torpedograss was common on Horn and Petit Bois Islands, but was only occasionally observed on the dunes (Eleuterius 1979). However, following the 2005 hurricane season, preliminary observations by Brewer (personal

communication) indicated catastrophic mortality of Florida rosemary and increases in torpedograss abundance within the dune community, as well as changes in the abundances of other species. In addition to the reduction in abundance of scrub dominants, the storm surge associated with Hurricane Katrina dramatically shifted the distribution of sand, thereby significantly altering the microtopography of the scrub habitat. As a result, several dunes within the rosemary scrub habitat were flattened, potentially changing patterns of drainage within the scrub.

Storm surge from hurricanes may be a more important source of environmental disturbance than fire for coastal populations of Florida rosemary (Conner et al. 1989, Myers 1990, Gibson and Menges 1994). I examined the impact of hurricanes on Florida rosemary populations by comparing rosemary survival within five coastal populations along the Gulf of Mexico: Horn and Petit Bois Islands, Mississippi and Santa Rosa Island, St. George Island, and Cape San Blas, Florida. Using ratios of live-to-dead rosemary at various elevations and information on historic hurricane tracks (NOAA 2011), I examined the effects of the storm surge associated with several major hurricanes on Florida rosemary in order to test the hypothesis that individual rosemary shrubs at sufficiently high elevation enjoy protection from storm surge.

I explored two alternative hypotheses to explain the invasion of island scrub habitat by *Panicum repens*: First, that a reduction in competition (e.g., via a reduction in soil allelopathic agents, itself the result of Florida rosemary's decline) allowed the spread of torpedograss into these areas, and alternatively, that the flattening of dunes associated with the storm surge reduced the depth of drainage, thereby enabling torpedograss, a facultative wetland species, to invade the scrub community. An ecological footrace between Florida rosemary and torpedograss may determine the fate of these island scrub communities. Both torpedograss and Florida rosemary

3

exhibit the properties of ecosystem engineers; that is, they are capable of having large-scale impacts upon ecosystem structure and function through modification of their habitat (Jones et al. 1994). Torpedograss has the potential to increase flammability of the scrub habitat, whereas Florida rosemary has the potential to reduce invasion by torpedograss and thus flammability, perhaps through allelopathy or perhaps by restoring dune structure and pre-storm moisture regimes. Therefore, the outcome of this race has the potential for far-reaching implications within the community. I used a series of three experiments to examine the potential allelopathic effects of Florida rosemary on torpedograss growth, and addressed other factors (such as differences in soil moisture) which may have previously hindered invasion by torpedograss. Over three years' time, I observed the recovery of Florida rosemary and the growth of torpedograss on Horn and Petit Bois Islands, Mississippi, and considered the mechanisms likely to be responsible for the community changes I observed.

Finally, I examined the importance of propagule pressure (Levine 2000, Von Holle and Simberloff 2005) on the growth rate of torpedograss in proximity to undisturbed inland Florida scrub at Archbold Biological Station on the Lake Wales Ridge, Florida. I tested the hypothesis that roads represent pathways of invasion for this aggressive exotic grass. Because torpedograss spreads primarily or exclusively by rhizomatous growth and is frequently observed in disturbed areas such as roadsides at Archbold (and perhaps elsewhere in the southeastern U. S.), determining whether roadsides are corridors for invasion or merely convenient sinks for opportunistic propagules has important implications for management strategies.

My goal was to address several specific questions: Is Florida rosemary recovering from Hurricane Katrina, and what is the impact of the current hurricane regime on coastal populations of rosemary? What factor or factors have allowed invasion of rosemary scrub communities by

4

torpedograss? Will that invasion continue, resulting in dense swards around emerging seedlings of Florida rosemary and interfering with their establishment? Do allelopathic chemicals from Florida rosemary inhibit the growth of torpedograss, and if so, to what extent? Are undisturbed inland populations of Florida scrub made more vulnerable to invasion by torpedograss by the presence of roadsides, or is torpedograss merely an opportunist utilizing the disturbed roadside habitat without spreading beyond its verges? The answers to these community-specific questions have the potential to offer insights into several broader issues in the field of invasion ecology.

I: HURRICANE IMPACTS ON FLORIDA ROSEMARY ACROSS THE EASTERN REGION OF THE GULF COAST

Abstract

Periodic hurricanes represent a major source of stochastic disturbance to coastal plant communities, with the potential to temporarily alter species composition as well as local topography, soil salinity, and resource availability. *Ceratiola ericoides* Michx. (Florida rosemary), a dominant member of a unique association of xeric, deep-sand species known collectively as rosemary scrub, is present on barrier islands along the Gulf Coast of Mississippi, Alabama, and Florida as well as a number of inland relic dunes. Unlike interior populations of Florida rosemary, which are periodically reduced by fire and must recover from a seed bank, island populations of rosemary are likely to be influenced by hurricanes more than fires. These disturbances may have different effects on adult mortality. I quantified the impact of major hurricanes on island populations of Florida rosemary along the Gulf Coast and examined the impact of storm surge, elevation, and time-since-hurricane on Florida rosemary survival and resprouting in five populations on the Mississippi and Florida coasts. Ratio of living-to-dead rosemary shrubs was higher on two barrier islands not struck by a major hurricane since 1985 than on three barrier islands impacted in 2004-2005 by Hurricanes Ivan and Katrina. There was also a trend toward greater mortality on the Mississippi barrier islands than on Santa Rosa Island in west Florida, but the difference was not statistically significant. This result probably reflected similar impacts of Hurricanes Ivan and Katrina and the fact that they occurred in consecutive

years. In contrast to previous observations of infrequently disturbed inland populations of

Florida rosemary, which exhibited an obligate seeder strategy, the coastal populations of Florida

rosemary showed the capacity to resprout following moderate to severe hurricane damage and

may begin to reproduce at an earlier age than inland Florida rosemary, adaptations that would

benefit the post-hurricane recovery of these populations.

<u>Introduction</u>

Coastal regions in the tropics and subtropics have developed under the influence of a

regime of tropical cyclones, which have the potential to impact geomorphology, hydrology,

productivity, nutrient cycling, and community composition (Conner et al. 1989, Michener et al.

1997, Doyle 2009). These normal aperiodic events (Conner et al. 1989) may be an important

source of environmental disturbance in these systems (Lugo et al. 1983, Johnson and Barbour

1990). Major hurricanes sometimes completely submerge barrier islands (Stoneburner 1978),

altering topography and severely damaging vegetation. Barrier island communities are strongly

affected by sand movement (Eleuterius 1979, Johnson and Barbour 1990), and are heavily

impacted by both erosion and flooding due to hurricanes (Eleuterius 1979). The occasional

destruction, separation, or re-joining of barrier islands that can occur due to hurricanes (Otvos

1979) is an emphatic reminder of the power of wind and water, but less dramatic changes still

have significant impacts upon coastal plant communities. In 1960, Hurricane Donna heavily

altered beaches in southern Florida, shifting sediments and leading to near-total mortality of

some plant species (Craighead & Gilbert 1962). In 1969, Hurricane Camille reduced vegetative

cover in Mississippi river delta marshes by 25%, completely scoured aquatic macrophytes from

ponds and lakes in the area, and altered water salinity and organic content in areas reached by the

storm surge (Chabreck & Palmisano 1973). On barrier islands, Camille's storm surge uprooted oaks and leveled sand dunes on Cat Island, removed over one-third of the vegetation on Ship Island, and divided the island itself into three pieces (Gunter and Eleuterius 1971). Hurricane Allen leveled dunes, removed or buried vegetation, and changed the relative abundance of plant species on South Padre Island, Texas in 1980 (Judd & Sides 1983). Dunes on Santa Rosa Island were leveled by a 2-4m storm surge from Hurricane Opal in 1995 (Bush et al. 1996, Miller et al. 2001). In 1996, the eye of Hurricane Lili struck the Bahamas, and the resultant storm surge reduced vegetation on unprotected islands by 42%, scouring even high-elevation areas (Spiller et al. 1998). Most recently, the storm surge associated with Hurricane Katrina greatly impacted Horn and Petit Bois Islands, Mississippi when it made landfall in August 2005. Many dunes were flattened and vegetation was uprooted, buried, or killed by the storm surge.

The interior dune communities of Horn and Petit Bois Islands deserve special attention because they are examples of an unusual native plant association. The dominant species of this association is a dioecious evergreen shrub of the family Empetraceae, Florida rosemary (*Ceratiola ericoides* Michx.). Also known as sand heath, Florida rosemary is native to the southeastern United States, and has long been recognized as a member of a community of xerophytic plants occupying deep, extremely well-drained, sandy coastal and inland soils, and commonly termed Florida scrub, or more specifically, rosemary scrub (Nash 1895, Mulvania 1931, Webber 1935). The rosemary scrub community is frequently restricted to high ridges (Abrahamson et al. 1984), resists fire, and burns infrequently: Every ten to one hundred years (Myers 1990), at which time individual rosemary shrubs are completely killed, and species recovery occurs through germination from within a seed bank accumulated over several years beneath parent plants. According to studies of inland rosemary scrub in south-central Florida,

new Florida rosemary seedlings do not reach reproductive age for ten to fifteen years, so a fire cycle or disturbance regime of greater frequency than ten years is likely to result in a gradual population decline as seed bank stores are depleted and never replenished (Johnson 1982).

Although rosemary scrub is maintained by infrequent fires in inland areas (Abrahamson 1984), in coastal systems hurricanes, tropical storms, and wind-driven shifts in sand distribution between storm events may be more important sources of disturbance than fire (Conner et al. 1989, Myers 1990, Gibson and Menges 1994). In the aggregate, these disturbances may result in an overall higher frequency of disturbance than is observed in inland populations. Accordingly, such high disturbance frequency has the potential to select for earlier onset of reproduction (Gibson and Menges 1994, Parker et al. 1997) and/or a greater reliance on resprouting by adults that survive the disturbance (Givnish 1981, Zammit and Westoby 1987).

To examine the role of hurricane activity in disturbance of coastal rosemary scrub communities and determine the relative importance of storm surge and topographic elevation in survival, I collected data on five coastal populations of Florida rosemary located along the Gulf Coast of Mississippi and northwestern Florida and the major hurricanes that have struck them in the past 25 years. I tested three hypotheses: First, that hurricanes represent a major source of stand-wide mortality to these populations, and that abundance of live rosemary would increase with time-since-hurricane; second, that shrubs growing at higher elevation would enjoy greater protection from hurricane-induced storm surges and would be more likely to survive them, such that more live rosemary shrubs are present at higher elevation; and third, that in contrast to inland populations of Florida rosemary, where infrequent fires are the primary source of disturbance, resprouting contributes significantly to recovery of coastal populations after hurricanes.

Materials and Methods

Sampling and Measurements

I visited four barrier islands and one coastal peninsula (cape) along the northern Gulf Coast between 2008 and 2010 (hereafter generalized as barrier islands). The sites chosen represent a range of topographic variation and frequency of hurricane incidence. Presented from west to east, they are Horn and Petit Bois Islands in Mississippi and Santa Rosa Island, Cape San Blas, and St. George Island in Florida. At Horn and Petit Bois Islands I used 1.5m radius plots of varying elevation established to quantify recovery from Hurricane Katrina. At the Florida sites, I established 10-15 1.5m radius plots along a transect of varying elevation. For each of these sites I counted the number of live and dead Florida rosemary shrubs, and calculated relative elevation by using the angle of incline (measured with a Suunto PM-5 Clinometer) and the distance between plots (measured with a Sonin Combo Pro distance meter). On barrier islands where I was able to relate plots to the mean high water line (MHW), I standardized elevation among barrier islands relative to mean sea level (MSL) using elevation records from the nearest tidal datum station (NOAA 2010). This technique was successful on St. George Island and Cape San Blas. On islands where I could not relate plots to MHW (Horn Island, Petit Bois Island, and Santa Rosa Island), I estimated elevation relative to MSL for the coordinates of one plot on Google Earth (Ver. 6.0.1.2032, beta), and used this value as a baseline for translating relative elevation to absolute elevation across the other plots on that island. Elevation resolution presented on Google Earth is not ideal, and so I interpret the accuracy of absolute elevation for three of the five barrier islands with caution, but relative elevation data for plots on individual barrier islands remain relatively accurate.

Using NOAA's Historical Hurricane Tracks database (National Oceanic and

Atmospheric Administration), I researched all major (Category 3-5) hurricanes that passed

within 80 nautical miles of these five sites and collected the best records of the sustained wind

speed and storm surge associated with each of these hurricanes at or near the island of interest.

Sustained wind speed for all of these hurricanes was 105-110 knots at the time of impact and was

omitted from analysis since it did not vary much from island to island. In addition, wind may be

less important than storm surge as a source of hurricane-related disturbance; the majority of

damage to Santa Rosa Island by Hurricane Opal were attributed to water action rather than to

wind (Bush et al. 1996).

Hurricane Intensity and Elevation Differences among Islands

I quantified differences among the islands with respect to hurricane impact by calculating

a storm surge index for each of the three regions: Mississippi barrier islands (Horn and Petit

Bois Islands), West Florida (Santa Rosa Island), and the Big Bend region of Florida (Cape San

Blas and St. George Island). The storm surge index for each hurricane and the barrier island it

impacted was obtained by dividing the local storm surge associated with that storm by *YSH*, the

number of years elapsed between the hurricane's landfall and my sampling date:

$$surge\ index = \frac{storm\ surge\ (m)}{YSH}$$

According to this formula, the potential impact of a hurricane on a barrier island was assumed to

be greatest when storm surge was high and little time for recovery had occurred. For each

barrier island, I chose the highest storm surge index for statistical analysis, since it was likely to

represent the hurricane associated with the greatest damage. I tested my assumption that there

were topographic differences among these five barrier islands by comparing mean elevation of the points on the five islands by one-way analysis of variance (ANOVA).

Quantifying Hurricane-Caused Mortality

For each plot where rosemary shrubs were observed, I estimated island differences in rosemary survivorship by calculating a ratio of living to dead shrubs (*ln [abundance living + 1] – ln [abundance dead + 1]*) in 2008. Plots containing no Florida rosemary were excluded from analysis. The validity of this approach was assessed by comparing the calculated live-to-dead ratio on Horn Island to the rate of survival on Horn Island before and after Hurricane Katrina. Horn Island was the only island for which I had pre- and post-storm data. Using data collected by Stephen Brewer from a 10m x 100m belt transect in June 2002, May 2004, October 2004, and October 2005, I calculated survival rates of rosemary shrubs during a time period in which no major hurricanes affected Horn Island (from June 2002 to May 2004), during a time period in which Hurricane Ivan occurred (from May 2004 to October 2004), and during a time period in which Hurricane Katrina occurred (from October 2004 to October 2005). Survival rates were quantified by marking 20 plants and calculating the proportion that survived until the next census. Live-to-dead ratios were quantified by counting all live shrubs and snags within the transect at each of the censuses.

To quantify the potential for hurricanes and elevation to influence the ratio of live to dead shrubs on each of the islands, I used analysis of covariance (ANCOVA), which examined the effects of island, elevation, and the island x elevation interaction. Differences in live-to-dead ratio between and within regions were tested using planned orthogonal contrasts among islands. One contrast was done to see if the live-to-dead ratio was higher on Cape San Blas and St.

George Island (which had the lowest storm surge index) than on the remaining islands. A second contrast was done to see if live-to-dead ratio on Santa Rosa Island was higher than that on the Mississippi barrier islands, the latter of which had the highest storm surge index. A third contrast examined the difference between Cape San Blas and St. George Island, and a fourth contrast examined the difference between Horn Island and Petit Bois Island.

Resprouting on Horn, Petit Bois, and Santa Rosa Islands

To quantify resprouting following hurricane damage, I calculated proportions of severely damaged shrubs with resprouting stems on Horn and Petit Bois Islands in 2010 and Santa Rosa Island in 2008. I considered a severely damaged shrub to be one in which at least ¾ (but not all) of the leaves were brown at the time of observation. Resprouting stems were readily identifiable as orthotropic (vertical and not decumbent) epicormic branches originating from older, typically decumbent, branches.

In addition, to estimate the degree and speed of resprouting, I marked seven damaged rosemary shrubs on Horn and Petit Bois Island after Hurricane Katrina and visually assessed them (percent damage = volume of area occupied solely by brown leaves or leafless stems relative to total shrub size) from 2008 to 2010.

Results

Major hurricanes and storm surge indices:

Five major hurricanes have passed within 80 nautical miles of the barrier islands in this study in the past 25 years (Table 1-1): Elena, Opal, Ivan, Katrina, and Dennis. Although all five hurricanes were Category 3 at landfall, with maximum sustained winds of 105-110 knots when

they struck the island in question, they varied greatly in storm surge magnitude. Hurricane

Katrina had the greatest storm surge by far in the area of interest.

Table 1-1: Major hurricanes in study area from 1985 to 2010.

Hurricane	Year	Category at Landfall	Storm Surge Range (m)
Dennis	2005	3	0.8 - 2.1
Katrina	2005	3	5.2 - 6.7
Ivan	2004	3	1.0 - 4.6
Opal	1995	3	1.5 - 4.3
Elena	1985	3	1.8 - 3.0

The magnitude of the storm surge associated with each hurricane also decreased with

greater distance from the eye; for example, Hurricane Ivan had a strong impact at Santa Rosa

Island but passed at a greater distance from Horn and Petit Bois Island. This variation was

captured in the storm surge index calculated for each hurricane/barrier island combination (Table

1-2). Katrina and Ivan, both recent hurricanes with large storm surges, had the greatest surge

indices. Hurricane Elena is unusual in having passed from east to west along the shoreline and

impacting all five sites; it is also the only major hurricane in recent years to have struck Cape

San Blas and St. George Island.

Table 1-2: Impact of hurricanes on five barrier islands from 1985 to 2010. The hurricane chosen as the most likely to impact vegetation on each barrier island, and thus the index used for analysis, is indicated by an asterisk.

Island	Hurricanes within 80 nm	Storm Surge (m)	Time since hurricane (years)	Storm Surge Index
Horn	Katrina*	6.71	5	1.34
	Ivan	0.98	6	0.16
	Elena	2.44	25	0.10
Petit Bois	Dennis	0.76	5	0.15
	Katrina*	6.71	5	1.34
	Ivan	0.98	6	0.16
	Opal	0.00	15	0.00
	Elena	2.44	25	0.10
Santa Rosa	Dennis	2.13	5	0.71
	Ivan*	4.57	6	1.14
	Opal	3.05	15	0.23
	Elena	2.44	25	0.11
Cape San Blas	Elena*	3.05	25	0.13
St. George	Elena*	3.05	25	0.13

Rosemary scrub on barrier islands in Mississippi was generally lower in elevation and had less topographic variation than that on islands in Florida (Figure 1-1). Mean elevation differed significantly among the sites by ANOVA ($F_{4,108} = 15.88$, $p < 0.01$), with Horn and Petit Bois Island sites being lower in elevation than transects on Cape San Blas, St. George Island, and Santa Rosa Island (Tukey's HSD, $p < 0.05$).

Variation in elevation among barrier islands
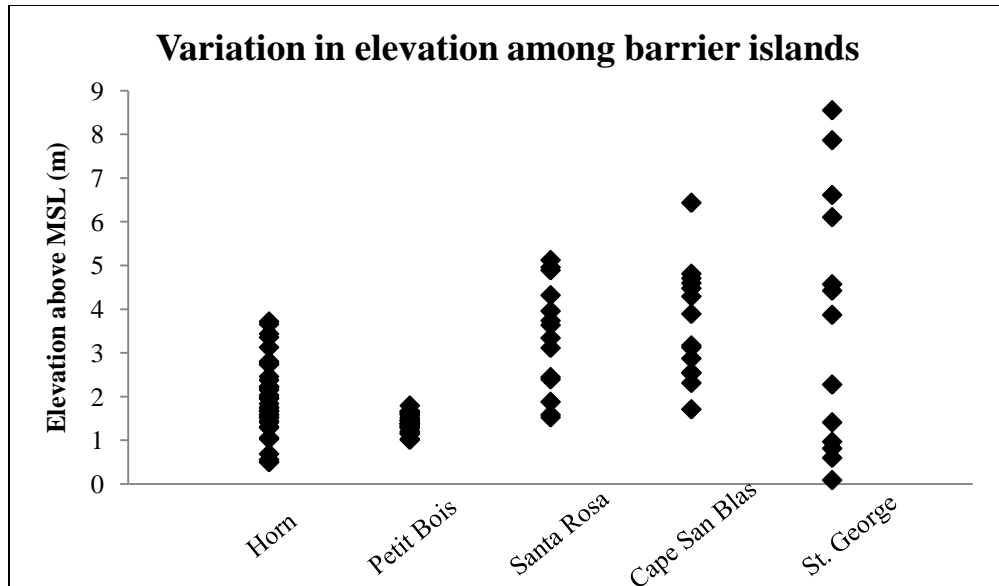
Figure 1-1: Mean elevation and topographic range of five Gulf Coast barrier islands.

Relationships between mortality and storm surge

The ratio of live shrubs to snags at a given time (live-to-dead ratio) appeared to be a reasonably good proxy for survival rates in this species. A chi-square test revealed a reasonably good fit between observed live-to-dead ratios and those expected from measured survival rates, although the ratio slightly overestimated survival through Hurricane Katrina (Table 1-3). Survival rate between June 2002 and May 2004 and live-to-dead ratios at these times were relatively high on Horn Island (Table 1-3). Survival rate on Horn Island between May 2004 and October 2004 (during which Hurricane Ivan made landfall in Alabama) and live-to-dead ratio in October 2004 were lower (Table 1-3). Both the survival rate between October 2004 and October 2005 and the live-to-dead ratio in October 2005 (two months after Hurricane Katrina) were substantially lower than in the previous censuses (Table 1-3).

Table 1-3: Live-to-dead ratios and survival rates of Florida rosemary on Horn Island based on data collected in June 2002, before and after Hurricane Ivan (May and October 2004) and before and after Hurricane Katrina (October 2004 and October 2005). Observed survival rate is plant per plant since the previous census.

Census Date	Observed Number Alive	Observed Number Dead	Observed Survival Rate	Expected Number Alive	Expected Number Dead	χ^2
June 2002	155	4				
May 2004	145	9	0.9	138.6	15.4	$\chi^2 = 2.95$ df = 1 $p = 0.09$
October 2004	81	68	0.6	89.4	59.6	$\chi^2 = 1.97$ df = 1 $p = 0.16$
October 2005	14	67	0.1	8.1	72.9	$\chi^2 = 4.78$ df = 1 $p = 0.03$

Consistent with a hypothesis of significant hurricane-caused mortality, live-to-dead ratios were greatest on those islands with the lowest storm surge index (Cape San Blas and St. George Island) and lowest on the islands with the highest storm surge index (Horn and Petit Bois Islands). Analysis of covariance revealed a highly significant effect of island on live-to-dead ratio ($F_{4,55} = 11.2$, $p < 0.01$). Planned contrasts revealed that most of the differences among islands was due to differences between the Big Bend region and the remaining two regions ($F_{1,55} = 13.3$, $p < 0.01$). Although there was a slight trend toward higher live-to-dead ratios on Santa Rosa Island than on the Mississippi barrier islands (Figure 1-2), the difference was not statistically significant ($F_{1,55} = 1.5$, $p = 0.22$). None of the contrasts between islands within regions was statistically significant ($p > 0.61$). The main effect of elevation on live-to-dead ratio was not statistically significant ($F_{1,59} = 0.73$, $p = 0.4$). Contrary to the hypothesis that plants at higher elevations would be less vulnerable to hurricane damage, I found no evidence that island interacted with elevation to influence live-to-dead ratios ($F_{4,55} = 0.44$, $p = 0.8$).

Ratio of live-to-dead rosemary
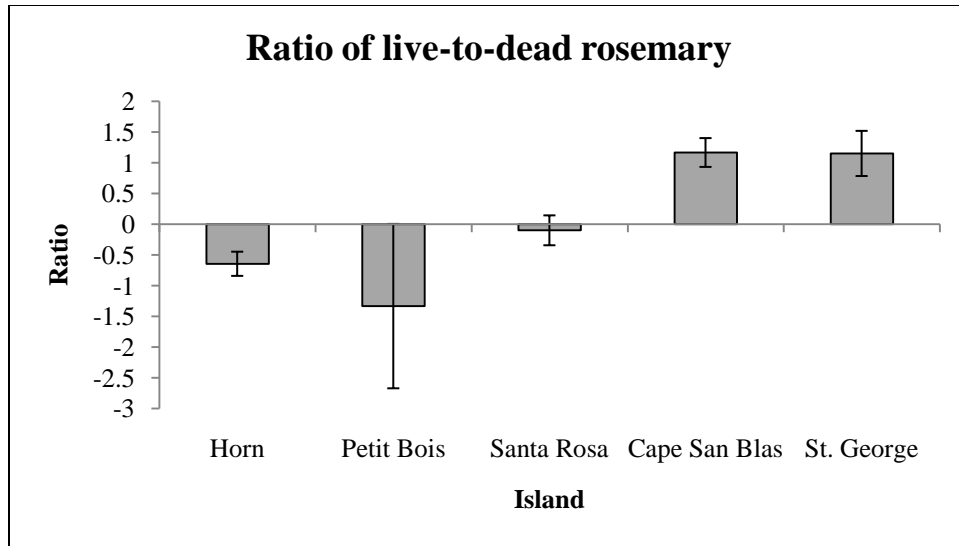
Figure 1-2: Ratio of living to dead rosemary shrubs at sites surveyed on five barrier islands on the Gulf Coast in 2008. Error bars are ±1 standard error.

Resprouting From Hurricane Damage

Resprouting of damaged shrubs was observed on all three islands recently impacted by hurricanes. The proportion of severely damaged shrubs that resprouted was 0.74 (79/134) on Santa Rosa Island, 0.58 (22/38) on Petit Bois Island, and 0.38 (5/13) on Horn Island. A chi square test of independence of resprouting and island was not statistically significant ($\chi^2 = 2.04$; $p = 0.36$). The counts of resprouting shrubs represented 18%, 17%, and 6% of all live and dead shrubs observed after Hurricanes Ivan and Katrina on Santa Rosa Island, Petit Bois Island, and Horn Island, respectively.

Each of the monitored shrubs exhibited resprouting during the study. Estimates of recovery of photosynthetic area ranged from 15 – 60% over a three-year period (Table 1-4).

Table 1-4: Estimates of recovery in seven hurricane-damaged Florida rosemary shrubs on Horn (H) and Petit Bois (PB) Islands from 2008 to 2010.

Shrub ID	Estimated percent damage remaining			
	May 2008	July 2008	July 2009	June/September 2010
H1	80	40	20	20
H2	50	40	5	5
H3	50	70	20	30
H4	95	90	80	80
PB1	70	60	60	60
PB2	50	35	50	15
PB3	95	95	80	70

Discussion

Hurricanes can have a powerful impact on island populations of Florida rosemary. The

populations of Florida rosemary on Cape San Blas and St. George Island in Florida, which have

not been struck by a major hurricane since Elena in 1985, exhibited a far greater proportion of

living rosemary shrubs when compared to Santa Rosa Island, Horn Island, and Petit Bois Island,

which experienced high storm surge from Ivan and Katrina in 2004 and 2005. However, given a

strong enough storm surge, there may be few differences in the magnitude of observable damage

in Florida rosemary populations, at least not in the short-term of the recovery period. I was

unable to distinguish between damage to rosemary populations on Santa Rosa Island and the

Mississippi barrier islands. Storm surge index was higher and elevation was lower on the

Mississippi barrier islands than at Santa Rosa Island, which suggests that Hurricane Katrina

could have had a greater impact on Horn and Petit Bois Islands than Hurricane Ivan did at Santa

Rosa Island. Despite this difference, I did not observe an increase in ratio of living-to-dead

rosemary shrubs on Santa Rosa Island.

Although logic suggests that rosemary shrubs at higher elevation might be protected from

moderate storm surge, I was unable to find evidence to support this hypothesis. Therefore, in

contrast to what is commonly observed following fires in inland populations (Gibson and

Menges 1994), I found little evidence of spatial heterogeneity in hurricane-caused mortality within an island. I hypothesize that high elevations on interior dunes do not provide refugia from storm surges of the magnitude associated with Hurricanes Ivan or Katrina. Although Santa Rosa Island has a higher average interior dune elevation than do the Mississippi barrier islands, ratios of live-to-dead plants were not significantly greater on Santa Rosa Island than on the Mississippi barrier islands.

Another notable difference in rosemary scrub composition that may be associated with the longer hurricane return interval on St. George Island and Cape San Blas was the dense presence of reindeer lichen (*Cladonia* spp.) in the scrub on St. George Island and Cape San Blas. Lichen abundance may be impacted by hurricane overwash (Buckley and Henderson 1986 in USFWS 1999), and if they are swept away or buried by widespread storm surge and must recover from intact lichen patches (USFWS 1999) recolonization could take many years. Lichens were observed at the sampling site on Santa Rosa Island in 2008 (three years after Hurricane Dennis and four years after Hurricane Ivan), but only on high ridges. Lichens on Horn Island were present during a 2002 survey (Brewer 2007), but no lichens were observed in the scrub on Horn or Petit Bois Island in a post-Katrina assessment in October 2005. As of fall 2010, five years after Hurricane Katrina, there were still no lichens observed in the scrub on Horn or Petit Bois Island. Lichens may alter rates of seed germination (Hawkes and Menges 1996, Hawkes and Menges 2003), so their abundance has the potential to impact recovery of these communities.

Coastal and inland populations of Florida rosemary appear to exhibit differing patterns of damage and recruitment following natural disturbances, with coastal stands more heavily impacted by sand movement and hurricanes and inland stands structured more by fire (Gibson

and Menges 1994). I observed a number of rosemary shrubs on Santa Rosa, Horn, and Petit Bois Island that were heavily damaged by Hurricanes Ivan or Katrina, but resprouted in the years following the storms. Some plants produced new leaves on defoliated branches, and some sprouted new stems from the base of the plant. In contrast, fire kills shrubs or individual branches of Florida rosemary completely, and resprouting has not been reported in inland populations (Myers 1985). Damaged rosemary shrubs in coastal populations may be capable of recovering from hurricane damage if the stress associated with storm surge (and perhaps a short-term increase in soil salinity) causes leaf abscission without killing stem tissue.

Effective resprouting of damaged shrubs (observed in the current study) and early seed production (Gibson and Menges 1994, Brewer, unpublished data) may allow coastal populations to recover more rapidly from disturbances, thereby making them better adapted for frequent disturbances than inland populations of Florida rosemary. Limited fuel accumulation within rosemary scrub can reduce fire frequency, but Florida rosemary has no adaptation to reduce hurricane frequency. Doyle (2009) estimates a return interval of Category 1 hurricanes ranging from every 6-7 years at Mobile Bay, Alabama, to less than 15 years along the Mississippi Coast and northwestern Florida, with at least one major hurricane (Category 3 or higher) occurring along the Mississippi coastline every 13 years. As with inland populations (Abrahamson 1984), seedling recruitment was not observed on Horn and Petit Bois Islands until two years after Hurricane Katrina killed most of the adult shrubs. A seedling cohort that was produced on Horn Island after a patchy fire in 2002 was completely eliminated by Hurricane Katrina in 2005 (Brewer, unpublished data). Given the combination of frequent hurricanes, disturbances from sand movement during years between hurricanes, and delayed seedling recruitment that depends on adult mortality, complete reliance on recruitment from seed for population recovery could be

21

a very risky strategy in coastal areas. Resprouting of severely damaged adults and early seed

production may be crucial for the long-term viability of coastal populations of Florida rosemary.

Studies debate the relative importance of natural cycles and climate change in the

greater number of hurricanes observed in the North Atlantic basin since 1995 (Pielke et al.

2005). Regardless of the ultimate causes, most studies agree that the available data suggest we

are in a phase of the Atlantic Multi-decadal Oscillation (Schlesinger & Ramankutty 1994)

associated with warmer sea surface temperatures and greater hurricane activity in the North

Atlantic region (Goldenberg et al. 2001, Webster et al. 2005, Hoyos et al. 2006, Knight et al.

2006, Black et al. 2007, Saunders and Lea 2008, Trenberth 2005; but see also Landsea et al.

2006, Knutson et al. 2008, Vecchi et al. 2008). Coastal ecosystems bordering the Gulf of

Mexico are shaped by certain patterns of hurricane frequency and intensity (Michener et al.

1997). In the current study, the sites that had experienced the longest recovery period between

major hurricanes (St. George Island and Cape San Blas) were both located near the Big Bend

region of Florida, an area with an unusually long return period between hurricanes (Doyle 2009)

because it is rare for hurricanes to turn northeast after entering the Gulf and make landfall in the

northern region of peninsular Florida (Davis and Barnard 2003). Such spatial variation in

hurricane frequency along the Gulf of Mexico could be used to understand current and future

temporal variation in hurricane impact. Given that Florida rosemary is a keystone species and

ecosystem engineer in island scrub communities, even a modest shift in hurricane frequency or

intensity may have a strong impact upon the ecosystem processes delineated by a tropical storm

regime. If this is so, the coming years may hold changes in store for barrier island plant

communities such as the rosemary scrub.

II: HURRICANE KATRINA'S IMPACT ON ABUNDANCE AND RECOVERY OF TWO

SPECIES IN THE ROSEMARY SCRUB ON HORN AND PETIT BOIS ISLANDS,

MISSISSIPPI

Abstract

Although storm surge associated with hurricanes can have a great impact on coastal plant communities, few studies identify the specific effects of hurricanes and the recovery of impacted communities because it is rare to have pre-storm community data. The predicted increase in major tropical cyclones in the North Atlantic basin and the growing catalogue of invasive species that may take advantage of such catastrophic disturbances make observational studies of coastal community recovery particularly relevant to present concerns. In 2005, Hurricane Katrina swept over Horn and Petit Bois Islands, Mississippi, bringing with it a storm surge that caused topographic changes to the interior dunes and heavy mortality to species in the rosemary scrub community, including the dominant species, *Ceratiola ericoides* Michx. Following the storm, an invasive grass, *Panicum repens* L., began encroaching upon the dunes from the low-elevation swards where it existed prior to the storm. Invasion by torpedograss could interfere with seedling recruitment through resource competition or alter ecosystem function by increasing fuel load and thus fire frequency in the rosemary scrub community. Because most individuals of Florida rosemary typically do not survive fire, must re-establish from a seed bank, and take years to reach maturity, populations are potentially threatened by frequent fires. I established plots on these two barrier islands and monitored recruitment of Florida rosemary seedlings and invasion

23

of torpedograss from 2003 to 2010 on Horn Island and from 2006 to 2010 on Petit Bois Island, and measured potential environmental covariables such as soil moisture, elevation, and organic matter in 2008 and 2010 to determine the importance of these factors in determining abundance of torpedograss and Florida rosemary seedlings. Torpedograss density on the dunes was greater after the storm than before the storm on Horn Island and increased in the first two years after the storm on both islands. However, density decreased between 2008 and 2010 on the dunes on both islands, remaining high only in low-lying swards. I found no evidence that torpedograss interfered with rosemary seedling recruitment, which began two years after the hurricane and was particularly high around large Florida rosemary snags. Rosemary seedling abundance was positively correlated with soil organic matter, probably indicating greater recruitment around the remnants of larger adult shrubs. Torpedograss abundance was negatively correlated with factors associated with large rosemary shrubs such as soil organic material and rosemary seedlings within the dune community, suggesting a negative effect of Florida rosemary on torpedograss recruitment that persists after death. It appears that torpedograss benefitted in the first two years following Hurricane Katrina but then declined and retreated to more mesic adjacent areas thereafter. In addition, there appeared to be a negative effect of large, reproductive rosemary adults on torpedograss, which could offer rosemary seedlings protection from competition with torpedograss following the mortality of adults.

Introduction

Over the last decade, the impact of strong tropical cyclones has received great attention. Studies fiercely debate the relative importance of natural cycles and climate change in the greater number of hurricanes observed in the North Atlantic basin since 1995 (Pielke et al. 2005).

Regardless of the ultimate causes, most results agree that we are in a phase of the Atlantic Multi-decadal Oscillation (Schlesinger & Ramankutty 1994) associated with warmer sea surface temperatures and greater hurricane activity in the North Atlantic region (Goldenberg et al. 2001, Webster et al. 2005, Hoyos et al. 2006, Knight et al. 2006, Black et al. 2007, Saunders & Lea 2008, Trenberth 2005).

The predicted pattern of more frequent intense hurricanes has the potential to impact plant communities on barrier islands bordering the Gulf Coast (see Chapter 1). Some of these communities are strongly affected by sand movement (Eleuterius 1979, Johnson and Barbour 1990), and are heavily impacted by both erosion and flooding due to hurricanes (Eleuterius 1979). Overwash may be the most important of a myriad of hurricane-generated effects, and it is not uncommon for major hurricanes to completely submerge barrier islands (Stoneburner 1978), altering topography and severely damaging vegetation. Hurricanes frequently shift sand (Craighead and Gilbert 1962, Gunter and Eleuterius 1971, Spiller et al. 1998) and flatten dunes (Gunter and Eleuterius 1971, Chabreck and Palmisano 1973, Judd and Sides 1983, Bush et al. 1995, Miller et al. 2001), altering elevation and perhaps local species composition as a result. In some ecosystems silt and debris may fertilize the areas in which they are deposited, temporarily increasing nutrient availability (Craighead and Gilbert 1962, Conner et al. 1989, Michener et al. 1997). Salt spray and soil salinity (Barbour & De Jong 1977) have long been recognized as important environmental factors to which coastal plants must adapt, and salinity can increase in the wake of hurricanes (Alexander 1967, Chabreck & Palmisano 1973, Valentine 1977, Lin and Kleiss 2006), although heavy rainfall associated with the storm may alleviate this effect (Craighead and Gilbert 1962). Rainfall associated with hurricanes can also have a lasting impact upon plant communities, potentially alleviating seasonal water stress (Cry 1967), and heavy

precipitation from tropical storms has been tracked in thicker tree rings of slash pines on the barrier islands of Mississippi (Stoneburner 1978).

The storm surge associated with Hurricane Katrina, estimated to be between 5.2 and 6.7 meters (National Oceanic and Atmospheric Administration), greatly impacted Horn and Petit Bois Islands, Mississippi, when it made landfall in August 2005. The interior dune community of these islands experienced extreme disturbance: Many dunes were flattened and vegetation was uprooted, buried, or killed by the storm surge. This community, an example of an unusual native plant association, deserves special attention. The dominant species of this association, which experienced 65 to 85% mortality during the hurricane, is a dioecious evergreen shrub of the family Empetraceae, Florida rosemary (*Ceratiola ericoides* Michx.). Also known as sand heath, Florida rosemary is native to the southeastern United States, and long-recognized as a member of a community of fire-intolerant plants occupying deep, extremely well-drained, sandy coastal and inland soils and commonly termed Florida scrub, or more specifically, rosemary scrub (Nash 1895, Mulvania 1931, Webber 1935). The rosemary scrub community resists fire and burns every ten to every one hundred years (Myers 1990). During these infrequent fires, individual rosemary shrubs are completely killed, and species recovery occurs through germination from within a seed bank, which occurs after approximately a two-year delay (Abrahamson 1984). According to studies of rosemary scrub located in the relic dunes of Florida, rosemary seedlings do not reach reproductive age for ten to fifteen years, so a fire cycle of greater frequency than ten years is likely to result in a gradual population decline as seed bank stores are depleted and never replenished (Johnson 1982).

Rosemary scrub is considered unique among xeric Florida scrub associations. Because the community tends toward a lower percentage of vegetation cover (Givens et al. 1984, Johnson

and Abrahamson 1990) and retains vegetation-free gaps for a longer period of time than other scrub communities, sometimes indefinitely (Hawkes and Menges 1995), gaps in rosemary scrub communities may offer refugia for endemic and other native species between fires (Hawkes and Menges 1996, Menges and Hawkes 1998). Although coastal rosemary scrub in Mississippi lacks many of the notable species found in analogous communities in Florida, scrub on the barrier islands of Mississippi provides habitat for gulf rock-rose (*Helianthemum arenicola*), beach sand-squares (*Paronychia erecta*), and seaside balm (*Conradina canescens*), all state listed and sensitive plant species in Mississippi.

Individual rosemary shrubs are frequently surrounded by patches of bare sand, contributing to the gaps so characteristic of the rosemary scrub community. These bare patches may be a result of a combination of factors, including competition, the formation of cryptobiotic soil crusts, infrequent intense fires, and allelopathy (Fischer et al. 1988, Richardson and Williamson 1988, Fischer et al. 1994, Hunter and Menges 2002). Studies have demonstrated Florida rosemary's ability to inhibit germination of Florida sandhill bunch grasses (Richardson and Williamson 1988, Fischer et al. 1994) and native scrub and gap specialists (Hunter and Menges 2002) via leaf and litter leachates, and survival of at least one species increases in the absence of Florida rosemary (Menges and Kimmich 1996).

In 1895, Nash noted that rosemary scrub on relic dunes in peninsular Florida contained no grasses whatsoever, save the occasional ephemeral appearance of a few bunch grasses. However, accounts of the non-native, rhizomatous, perennial species torpedograss (*Panicum repens* L.) along the Mississippi coast (Lloyd and Tracy 1901), on Horn Island (Pessin and Burleigh 1941), and specifically in proximity to rosemary scrub (Penfound and O'Neill 1934), began to appear in the literature in the early 1900s. The species has also become a troublesome

invader in parts of Florida, and is listed as a Category I invasive species throughout the state by the Florida Exotic Pest Plant Council (FLEPPC 2009). Using the U. S. Geological Survey's Alien Plants Ranking System (USGS APRS Implementation Team 2000), Hutchinson and Menges (2006) recently assigned torpedograss the highest potential for invasiveness (encompassing impact to natural communities, likelihood of becoming a pest, and difficulty to control) among sixty-six non-native plants in peninsular Florida. Prior to Hurricane Katrina, torpedograss on Horn and Petit Bois Island persisted primarily in the low-lying swales surrounding the interior dunes and on the fringes of the rosemary scrub community on these islands (Penfound and O'Neill 1941, Eleuterius 1979). Reduction of competition from native species, removal of the dominant Florida rosemary and its potential allelopathic effects, increased availability of rainfall and nutrients, or some combination of these hurricane-induced factors could provide torpedograss with an opportunity to expand its range into formerly unoccupied areas in the rosemary scrub.

Both torpedograss and Florida rosemary exhibit the properties of ecosystem engineers; that is, they are capable of having large-scale impacts upon ecosystem structure and function through modification of their habitat (Jones et al. 1994). Torpedograss has the potential to increase flammability of the scrub habitat, a community not adapted for frequent fires, whereas Florida rosemary has the potential to reduce invasion by torpedograss and thus flammability, perhaps through allelopathy, competition, or by restoring dune structure and pre-storm moisture regimes. Rosemary scrub on the barrier islands seems to have resisted permanent invasion after hurricanes in the century since torpedograss was observed there, but the mechanisms responsible for this recovery are unknown, as are the effects of a storm as powerful as Katrina on interactions with an aggressive non-native species. The invasion of rosemary scrub by torpedograss has the

28

potential to decrease species diversity, eliminate rare species, and alter the composition of neighboring habitats by reducing or eliminating the availability of refugia from fire. If torpedograss encroaches upon the dunes it may also impede the recovery of Florida rosemary by surrounding emerging seedlings and rendering them vulnerable to mortality by fire. Monitoring changes in the interior dune plant community on Horn and Petit Bois Islands in the years following Hurricane Katrina may offer answers as to whether the community will recover completely, how quickly it will do so, and what the fate of these barrier island communities will be if the frequency of major hurricanes increases in the next few decades.

The importance of environmental factors may be particularly relevant in coastal systems, which exhibit a high degree of heterogeneity (Ievinsh 2006). Environmental qualities such as topography and soil characteristics of the interior dune community and the adjacent swales may also play a role in dictating the distribution of torpedograss, and if so, hurricane-caused changes in these characteristics could allow torpedograss to expand its range following the storm. I test the hypothesis that elevation, along with soil characteristics potentially related to elevation such as moisture, nutrient content, and salinity, influence the abundance of torpedograss and that changes in those characteristics may have contributed to post-Katrina community shifts.

This study also addresses important questions regarding exotic species, which often pose a serious threat to biodiversity. We are still uncertain what makes some non-native species invasive and others merely alien. A better understanding of processes that may facilitate invasion, as well as the ways in which native systems can defend themselves from invaders, may help us to predict, monitor, and combat future invasions. Grasses are considered particularly potent as invaders, with the potential to alter ecosystem function (D'Antonio and Vitousek 1992), and Crooks (2002) emphasizes the impact of invasive ecosystem engineers, including those with

the ability to impact fire regime. Davis et al. (2000) introduced the idea that invasibility

fluctuates in space and time with resource availability, which may be increased through

disturbance-related removal of competitors or inflow of resources. Exploring the issue of

invasion through the study of the response of a species such as torpedograss, which has the

potential to dynamically alter habitat, to catastrophic disturbance is an approach with far-

reaching implications.

Finally, this research investigates a potential ecosystem-level effect of hurricane activity.

Such studies are particularly relevant as we move into what many climatologists expect to be an

active hurricane cycle. In recent years the incidence of hurricanes along the Gulf Coast

(Trenberth 2005), and in particular the number of major storms of Category 3 or higher

(Goldenberg et al. 2001, Pielke et al. 2005, Trenberth 2005, Hoyos et al. 2006) has increased

dramatically. Barrier islands and their associated communities are likely to weather many more

in the years to come. The coming years may be our first indication of the fate that awaits these

communities.

Materials & Methods

Study Sites:

Horn and Petit Bois Islands are part of a chain of white sand islands that separate the

Mississippi Sound and the Gulf of Mexico, located approximately 19 kilometers from the

mainland (Penfound & O'Neill 1934). Both are located within Gulf Islands National Seashore,

and fieldwork took place with the permission and assistance of the National Park Service. Plant

community type on these barrier islands is strongly dependent on elevation, with relic (interior)

dune communities among those highest in elevation (Eleuterius 1979). The vegetation of these

islands was thoroughly surveyed and community maps prepared by Eleuterius (1979), and community composition of the relic dunes was more recently assessed by Brewer (2007).

Changes in Torpedograss and Florida Rosemary Seedling Abundance:

To assess the rate of torpedograss invasion and Florida rosemary recovery, I first examined abundance of torpedograss in 2006 and 2007. These data were estimates of total tiller (upright stem) densities obtained by Brewer within a 10m x 100m belt transect on interior dunes on Petit Bois Island and two 10m x 100m transects on dunes on Horn Island. Brewer also obtained pre-storm estimates of tiller densities in 2003 on Horn Island, and these estimates are presented here. I then examined changes in abundance of torpedograss between 2008 and 2010 within these transects and the adjacent torpedograss swards using a more precise sampling procedure. I established a total of 89 1.5 meter radius plots on Horn and Petit Bois Islands in 2008. Plots were established in torpedograss swards and on four locations on the dunes: Beneath living rosemary shrubs, beneath rosemary snags (dead shrubs) where torpedograss was invading, rosemary snags with rosemary seedlings, and on dunes without rosemary where torpedograss was invading (Table 2-1). During each of four visits between 2008 and 2010, I counted torpedograss tillers, dead and damaged Florida rosemary adult shrubs, and Florida rosemary seedlings within each of these circular plots, and estimated recovery or decline of damaged rosemary shrubs. Changes in the log-transformed relative abundance of torpedograss and Florida rosemary were analyzed by repeated-measures analysis of variance and overall differences from 2008 to 2010 were analyzed by factorial ANOVA. Because there were not enough living rosemary shrubs to establish a sufficient number of plots for data analysis, this plot type was excluded from statistical analysis, and trends from live rosemary plots are reported

31

separately in Chapter 1. I compared the number of torpedograss tillers, the number of living

adult rosemary plants, and the number of rosemary seedlings within all other plots types in 2008,

2009, and 2010. Count data were log-transformed to meet assumptions of normality.

Table 2-1: Description of plot criteria

Plot type	Location	Characteristics
Snag with *Panicum repens*	Dunes	Rosemary snag, vicinity being invaded by torpedograss
Snag with seedlings	Dunes	Rosemary snag with minimal or no torpedograss; rosemary seedlings recruiting
Live rosemary	Dunes	Damaged rosemary shrub(s) survived the hurricane, with or without torpedograss and/or seedlings
Dune with *Panicum repens*	Dunes or lower dunes	Scrub habitat where rosemary was not present in the vicinity prior to the hurricane; torpedograss present
Torpedograss sward	Swale	Low-lying, more vegetated, and immediately adjacent to the scrub; torpedograss abundant; other non-scrub species may be present

Environmental Variation:

To assess environmental characteristics, samples of the top 4 inches of soil were collected

from each plot on Horn Island ($n = 52$) and Petit Bois Island ($n = 37$) in May 2008 and again in

June (Horn Island) and September (Petit Bois Island) 2010. Several plots were lost in the

intervening years, reducing 2010 sample size (Horn Island, $n = 32$; Petit Bois Island, $n = 34$).

Deeper samples were not taken, as the soil was too sandy in most cases to be collected with a soil

auger; sampling at depths greater than 4 inches would have required considerable environmental

disturbance to dislocate surface sand. Soil samples were sealed in watertight bags and returned

to the laboratory for analysis.

A portion of each sample was assessed for wet weight, dried, and weighed again. Soil

moisture for 2008 and 2010 samples were calculated as the proportion of soil composed of water.

I attempted to analyze 2008 soil samples from the interior dune communities of Horn and Petit

Bois Island for salinity by mixing soil with distilled water at a known ratio and determining

salinity of the resultant solution with a hand refractometer (A366ATC). However, soil salinity

was so low as to be immeasurable. Samples collected in 2010 were analyzed to determine the

proportion of organic content. Available soil nitrate was so scant that it was immeasurable

through direct analysis. Instead, I incinerated soil samples in a muffle furnace at 400°C to

determine the proportion of organic material in soil collected at different locations. Soil nitrogen

and organic content were highly correlated in a previous study of a dune scrub community

(Holton and Johnson 1979).

Relative elevation data were collected at each plot in 2010. I assumed that, barring the

impact of another hurricane, these measurements were unlikely to change substantially over a

three-year period. Relative elevation for each plot was calculated using the angle of incline

(measured with a Suunto PM-5 Clinometer) and the distance (measured with a Sonin Combo Pro

distance meter) between plots. Plots were referenced to the mean high water line (MHW), and

then related from MHW to local sea level measurements based on benchmark data from tidal

stations (NOAA). Elevations used in data analysis therefore represent the elevation of each plot

relative to local sea level.

Soil moisture and organic content were arcsine-square root transformed and elevation

data were log-transformed to meet assumptions of normality prior to comparison of each of these

factors among the different plot types by ANOVA. To test for a relationship between the three

factors (soil moisture, soil organic content, and plot elevation) and torpedograss distribution 1)

within torpedograss swards; and 2) on the dunes, I included the factors as predictor variables in a

multiple linear regression using log-transformed tiller counts in each plot as the response

variable. I performed the same analysis within dune plots only using rosemary seedling abundance as the response variable. Since some of these environmental variables might be correlated with plot type or island, I also performed analysis of covariance of the plot type x island model, including the effect of the three potentially significant environmental variables on abundance of each species. Finally, I performed analysis of covariance of the three environmental variables and rosemary seedling abundance with the main effect of island upon torpedograss abundance in the dune plots. In all cases, I used 2008 soil moisture values since, unlike 2010 values, they were collected in the same season. Also, a brief rain shower during collection of soil samples on Horn Island in 2010 is likely to have altered soil moisture values.

Results

Torpedograss:

Torpedograss density was greater after Hurricane Katrina in 2006 than before the hurricane in 2003 on Horn Island (Table 2-2). Density increased between 2006 and 2007 on both Horn and Petit Bois Islands (Table 2-2). In contrast to these initial increases, torpedograss density did not increase in study plots on the barrier islands between 2008 and 2010, and some locations exhibited a significant decrease. Factorial ANOVA indicated that the difference in 2008 and 2010 abundance was not statistically significant, but there was a significant plot type x island interaction ($F_{3,61} = 3.70$, $p = 0.02$). Between 2008 and 2010 it appeared that torpedgrass abundance decreased on the dunes of Horn Island and everywhere on Petit Bois Island, where it was not as plentiful in 2008, and results supported this observation statistically. Torpedograss abundance significantly decreased between 2008 and 2010 in all plot types on both barrier islands except in swards on Horn Island (planned contrasts, $F_{1,61} = 6.18$, $p = 0.02$; Figure 2-1).

Table 2-2: Increases in torpedograss within 10m x 100m dune transects of Horn Island (two transects) and Petit Bois Island (one transect) following Hurricane Katrina.

Island	Date				
	September 2003	**October 2005**	**May 2006**	**October 2006**	**July 2007**
Horn	1150	--	3073	--	14747
Petit Bois	--	200	236	600	--
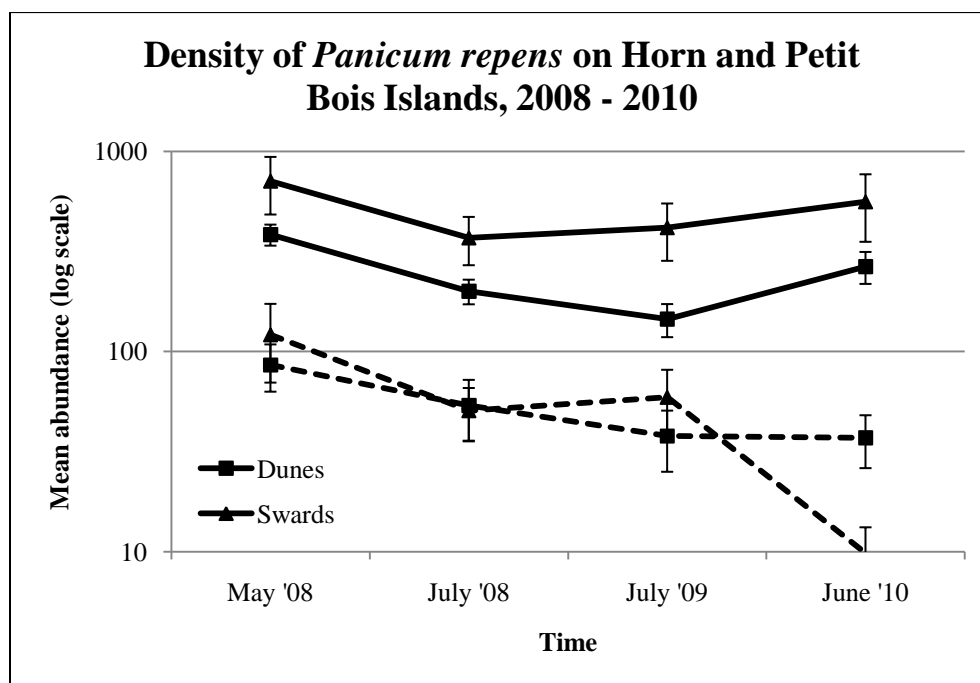
Figure 2-1: Torpedograss abundance within sward and dune sampling plots on Horn (solid lines) and Petit Bois (dashed lines) Islands from 2008 to 2010. Error bars are ±1 standard error.

Torpedograss density was consistently highest over time in torpedograss swards and lowest near rosemary snags where seedlings were abundant. Repeated-measures ANOVA indicated a significant effect of plot type on abundance ($F_{9,134} = 2.28$, $p = 0.02$). Torpedograss swards had the highest tiller counts and rosemary snags with seedlings the lowest by planned contrast ($F_{3,55} = 3.43$, $p = 0.02$). Torpedograss growing on the dunes and surrounding rosemary

snags without seedlings maintained intermediate densities and were not significantly different

from one another (Figure 2-2).
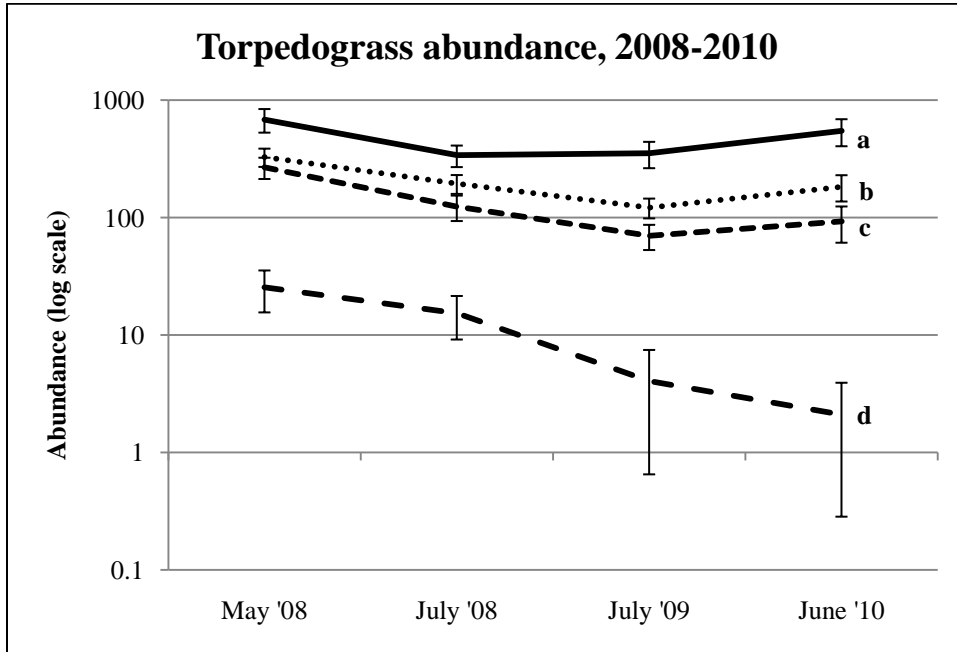
Figure 2-2: Torpedograss density associated with four plot types: (a) torpedograss swards, (b) dunes, (c) snags with torpedograss, and (d) snags with rosemary seedlings. Error bars are ±1 standard error.

Rosemary seedlings:

Florida rosemary seedlings began emerging two years after Hurricane Katrina. No

seedlings were observed within any of the transects in July 2007, but in May 2008, 67% of

observed rosemary snags had at least one seedling within 1.5 meters of the parent plant, and most

had more than one. By July 2010, 75% of observed snags had nearby seedlings. Of the six plots

marked that contained damaged adult shrubs, one-half contained seedlings in 2008, and seedlings

germinated in another plot by fall 2010. Few seedlings were observed on bare dunes without an

obvious adult snag nearby (0.13% of the 23 dune plots), and no seedlings were present in

torpedograss swards.

The highest seedling density observed was around one large snag with 90 seedlings within a 1.5m radius in 2008. Generally, however, density was much lower, with a mean of 7.7 seedlings per 1.5m radius plot in 2008 increasing to 9.8 in 2010 (mean for all plots containing rosemary snags, regardless of the presence of torpedograss), with maximum counts of 20-27 seedlings. Some seedling mortality was observed in late 2008 and 2009, particularly around the large matriarch.

Factorial ANOVA on changes in seedling density indicated a significant effect of plot type ($F_{3,58} = 6.87$, $p < 0.01$). Plots with snags contained significantly more seedlings than bare dunes or torpedograss swards (planned contrasts, $F_{1,58} = 19.84$, $p < 0.01$), but there was no difference in seedling increase over time based on the presence or absence of torpedograss (Figure 2-3). Although there were fewer seedlings within plots categorized as snags containing torpedograss, the rate of rosemary seedling recruitment was not significantly different between plot types over the three-year period, suggesting that torpedograss did not have a negative impact on seedling recruitment.
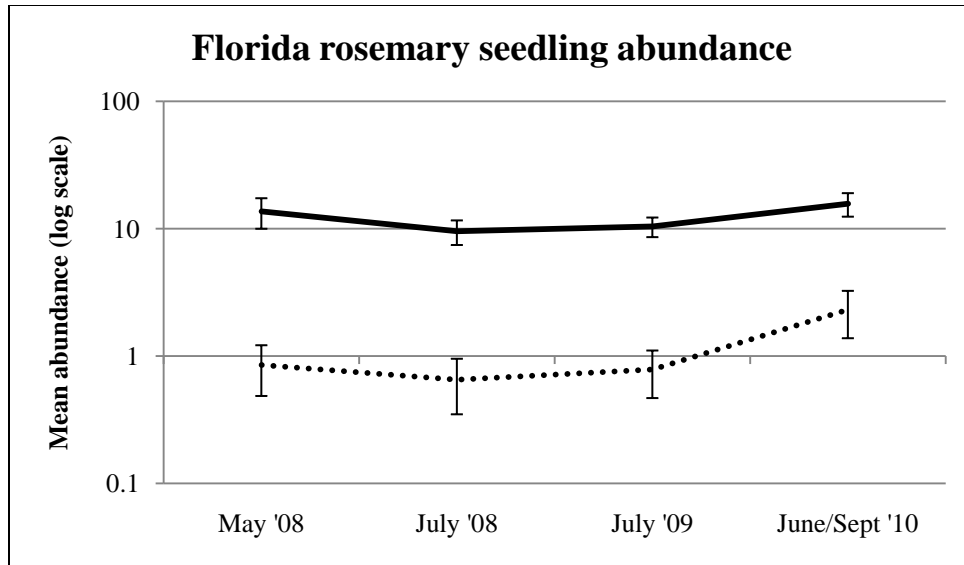
Figure 2-3: Change in Florida rosemary seedlings in plots that began with torpedograss (dotted line) versus plots that began with seedlings (solid line). Error bars are ±1 standard error.

Environmental Variation:

Torpedograss swards on Petit Bois Island, but not Horn Island, were significantly higher in moisture than other plot types in 2008 according to post-hoc tests on a significant interaction of island and soil type ($F_{3,60} = 10.09$, $p < 0.01$; Tukey's HSD, p < 0.05; Figures 2-4 and 2-5). In both 2008 and 2010, there was a significant association between location type and soil moisture (2008: $F_{3,79} = 45.79$, $p < 0.01$; 2010: $F_{3,63} = 4.33$, $p < 0.01$; Figure 2-6), with soil in torpedograss swards containing more moisture than soil collected from dunes or beneath rosemary snags (Tukey's HSD, $p < 0.05$).
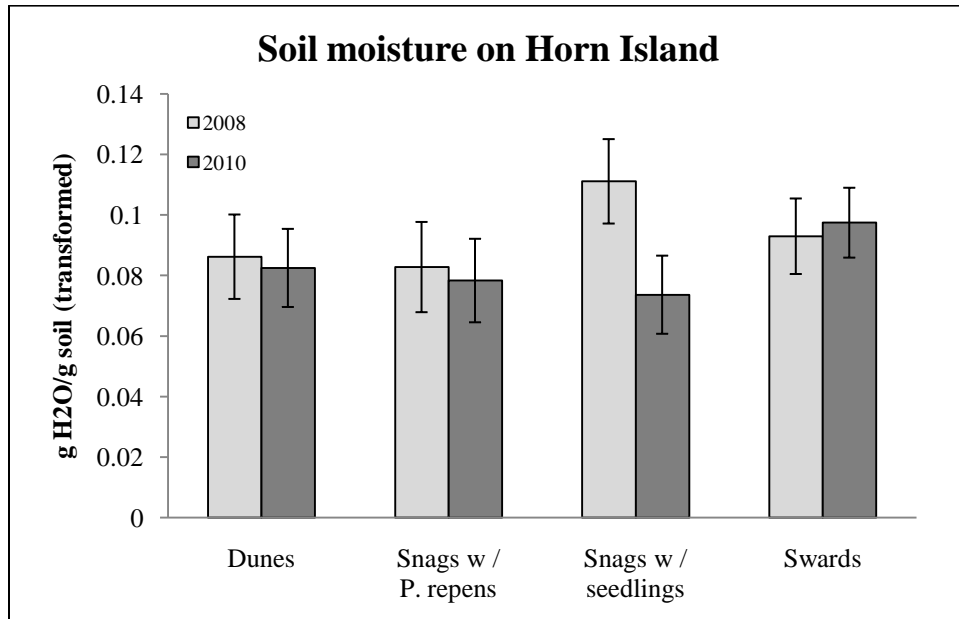
Figure 2-4: Soil moisture on Horn Island in 2008 ($n = 52$) and 2010 ($n = 32$). Error bars are ±1 standard error.
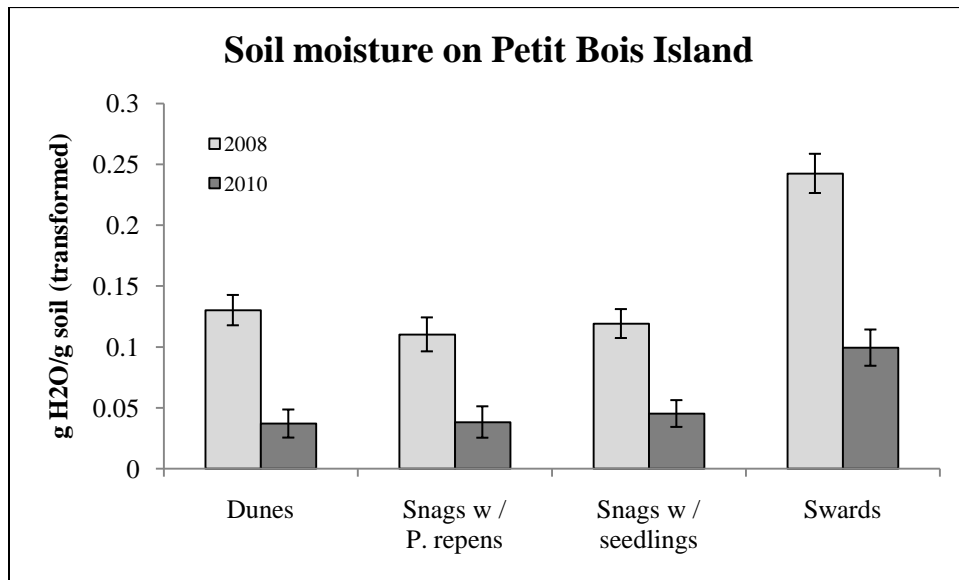
Figure 2-5: Soil moisture on Petit Bois Island in 2008 ($n = 37$) and 2010 ($n = 34$). Error bars are ±1 standard error.
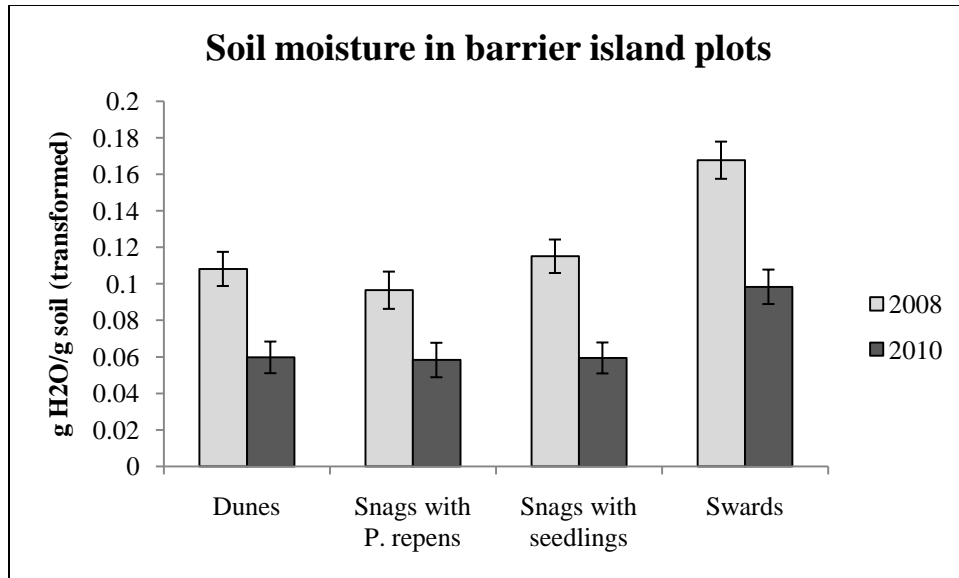
Figure 2-6: Soil moisture in four different plot types in 2008 and 2010. Error bars are ±1 standard error.

Torpedograss swards contained a mean of 2.6% organic material, significantly more than any other plot type ($F_{3,63} = 9.70$, $p < 0.01$; Tukey's HSD, $p < 0.05$; Figure 2-7). Rosemary snags with seedlings contained the next highest organic content (1.1%), followed by rosemary snags invaded by torpedograss (0.6%) and dunes invaded by torpedograss (0.4%). There was no difference in soil organic matter between barrier islands and no significant interaction term.
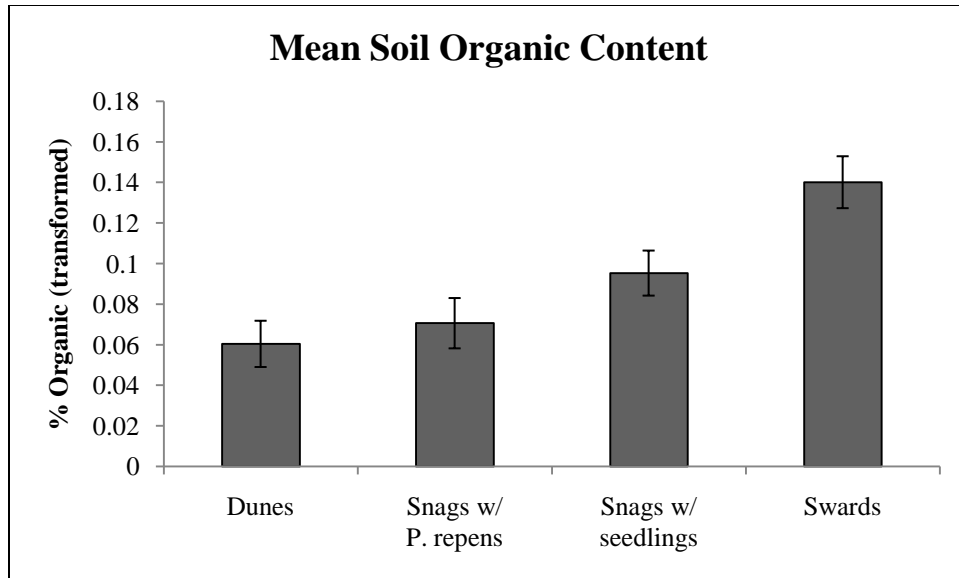
Figure 2-7: Percent organic content in four different plot types. Error bars are ± standard error.

Torpedograss swards were found at lower elevation than any other plot type (Figure 2-8). On Petit Bois Island, where mean plot elevation was lower than on Horn Island, torpedograss swards were not significantly lower in elevation than the dune-type plots. ANOVA indicated a significant main effect of plot type on elevation, with swards associated with lower elevation than the other three plot types ($F_{3,60} = 7.09$, $p < 0.01$; Tukey's HSD, $p < 0.05$), a significant main effect of island on elevation ($F_{1,60} = 11.22$, $p = 0.01$), and a significant interaction term ($F_{3,60} = 2.75$, $p = 0.05$) attributable to lower elevation of dune plots on Petit Bois Island (planned contrasts, $F_{1,60} = 18.69$, $p < 0.01$).
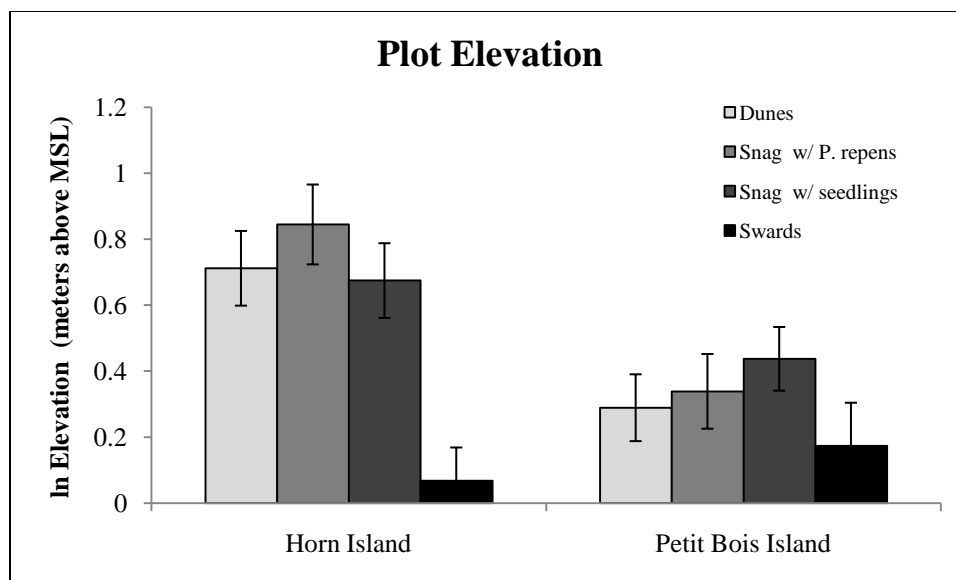
Figure 2-8: Mean elevation of plots on Horn and Petit Bois Islands. Error bars are ±1 standard error.

Predictors of Torpedograss Abundance

When data from within torpedograss swards alone were considered in a multiple linear regression, torpedograss density was negatively correlated with soil moisture (t_{13} = -4.05, $p <$ 0.01) and positively correlated with elevation (t_{13} = 2.58, $p <$ 0.03) and organic content (t_{13} = 2.56, p = 0.03). The best model in a backward stepwise multiple linear regression included all three factors (Table 2-3), and was over nine times as likely the next best model, which did not include elevation.

Within torpedograss swards, abundance increased with elevation and perhaps with soil organic matter, even when differences between Horn and Petit Bois Islands were taken into account. With island as a main effect in analysis of covariance, torpedograss abundance was still significantly positively correlated with elevation (t_{13} = 2.33, p = 0.04), and the positive correlation with soil organic matter approached significance (t_{13} = 2.14, p = 0.06), but soil moisture was no longer a significant covariate. Including island in the model eliminated the

42

significant negative correlation with soil moisture because torpedograss density was greater in the drier Horn Island swards than in the wetter Petit Bois swards (Horn Island: 6.57 ± 0.33; Petit Bois Island: 5.06 ± 0.48; $F_{1,13} = 6.61$, $p = 0.02$).

Table 2-3: Linear regression models predicting torpedograss abundance within swards. M represents soil moisture, O represents soil organic content, and E represents plot elevation. An asterisk designates the best model.

Model	R^2_{adj}	AIC_a	Δi	w
M + O + E*	0.53	0.05	0	0.86
M + O	0.31	4.47	4.42	0.09
M	0.19	5.82	5.77	0.05

On the dunes, torpedograss density was negatively correlated (rather than positively correlated) with soil organic matter ($t_{50} = -2.15$, $p = 0.04$), positively correlated with elevation ($t_{50} = 2.19$, $p = 0.03$), and not significantly correlated with soil moisture ($p = 0.39$). The best model in a backward stepwise multiple linear regression included soil organic matter and elevation, but not soil moisture (Table 2-4); however, the best model still explained less than fifteen percent of the torpedograss density on the dunes.

Because soil organic matter varied among plot types ($F_{2,44} = 30.78$, $p < 0.01$) and the elevation of dune plots was greater on Horn Island than on Petit Bois Island ($F_{1,44} = 9.31$, $p < 0.01$), inclusion of plot type and island in the model eliminated the significant relationships between density and organic matter and between density and elevation (organic matter: $p = 0.67$; elevation: $p = 0.44$). Upon replacing plot type with Florida rosemary seedling density in the ANCOVA model, I found that torpedograss density was highly negatively correlated with the abundance of Florida rosemary seedlings ($t_{50} = -5.79$, $p < 0.01$). As with the ANCOVA model that included plot type, none of the continuous environmental variables were a significant

predictor of torpedograss density. Hence, by far the best predictor of torpedograss density was

Florida rosemary seedling density.

Table 2-4: Linear regression models predicting torpedograss abundance on dunes. M represents soil moisture, O represents soil organic content, and E represents plot elevation. An asterisk designates the best model.

Model	R^2_{adj}	AIC_a	Δi	w
O + E*	0.13	87.89	0.00	0.57
M + O + E	0.13	89.21	1.32	0.29
E	0.07	90.68	2.79	0.14

Predictors of Florida Rosemary Seedling Abundance:

Rosemary seedling abundance was positively correlated with soil organic matter ($t_{50} = 3.75$, $p < 0.01$), but was not significantly correlated with any other environmental variable ($p > 0.50$). The best multiple regression model predicting seedling abundance included soil organic matter alone (Table 2-5). An ANCOVA revealed that both soil organic matter and plot type were significant predictors of abundance of rosemary seedlings on the dunes (organic matter: $t_{50} = 2.11$, $p = 0.04$; plot type: $F_{3,58} = 85.10$, $p < 0.01$). When plot type was removed from the ANCOVA model, the strength of the relationship between Florida rosemary density and organic matter increased ($t_{50} = 3.86$, $p < 0.01$).

Table 2-5: Linear regression models predicting Florida rosemary seedling abundance on dunes. M represents soil moisture, O represents soil organic content, and E represents plot elevation. An asterisk designates the best model.

Model	R^2_{adj}	AIC_a	Δi	w
O*	0.20	14.27	0.00	0.58
O + E	0.20	15.60	1.33	0.30
M + O + E	0.18	17.31	3.04	0.13

Discussion

Prior to Hurricane Katrina, which made landfall as a Category 3 storm on the Saffir-Simpson scale, torpedograss was common on Horn and Petit Bois islands, but was predominantly confined to the margins of rosemary scrub patches. However, following the 2005 hurricane season, plant community composition on these three islands changed dramatically: Each island experienced extensive mortality in certain woody and herbaceous plant species, including 65-85% mortality in Florida rosemary. Torpedograss rhizomes may be anchored up to 7m deep (Bodle and Hanlon 2001) and the species is capable of extending tillers up to the soil surface from considerable depths, making it highly resilient to tropical storms. Torpedograss was not greatly affected by the hurricane, which supports an observation by Judd and Sides (1983) that low-growing, more shallowly rooted species are more likely to be dislodged or buried in sediment by storm surge. Torpedograss densities on the dunes increased in 2006 and 2007, but from 2008 to 2010, dune torpedograss generally decreased, although overall torpedograss density during this period was variable across both time and space. Density remained extremely high in torpedograss swards on Horn Island, with as many as 2600 tillers occupying a 1.5m radius plot. Mean density fluctuated from year to year but showed little change in torpedograss swards on Horn Island from 2008 to 2010, although it decreased on the dunes, particularly in proximity to rosemary seedlings. On Petit Bois Island, both density and robustness of torpedograss tillers were much lower, and density decreased during the study period in swards as well as upon the dunes.

Torpedograss appears to be negatively affected by some factor positively associated with proximity to rosemary snags that were reproductive prior to being killed by the hurricane. Torpedograss showed the greatest densities in swards, intermediate densities on bare dunes and

near rosemary snags with few or no seedlings, and steadily decreasing densities near rosemary snags with seedlings present. Within plots containing rosemary snags with seedlings, torpedograss density decreased at a greater rate on Horn Island than on Petit Bois Island; original torpedograss density in these plots was higher on the former island than on the latter. Snags with seedlings nearby were generally larger and older at the time of death than were snags with no seedlings nearby (Brewer, unpublished data), suggesting that larger, older adults had the opportunity to accumulate a larger seed bank. When seedling densities of Florida rosemary were included in the multiple regression examining the relationship between torpedograss density and all measured environmental variables, none of the environmental variables was significant. Hence, competition between Florida rosemary and torpedograss may in large part be responsible for the negative association between snags with seedlings and torpedograss density. The precise mechanism of competition that might give rise to this association remains unclear. One possibility is allelopathy, although it is unlikely that the seedlings themselves exerted an allopathic effect on torpedograss. The rosemary seedlings observed were three years old at maximum, still extremely small (< 15 cm in height) and dropping little or no litter. Seedlings could possibly have exhibited an allelopathic effect via the production of root exudates. This is a possibility with some support (Quintana-Ascencio and Menges 2000, Hunter and Menges 2002, Hewitt and Menges 2008), but seedlings, and probably seedling root surface area available for leaching allelochemicals, were both still very small during the study period. A more likely explanation is that the negative association is a legacy of allelopathy that occurred before the storm. My experimental investigations of allelopathy revealed no consistent negative effect of soil from beneath large snags with live seedlings on the growth of torpedograss (see Chapter 3). I did, however, find evidence of an allelopathic effect of soil from beneath large living plants

46

(Chapter 3). If large adults were more effective than small plants at producing larger halos of ground free of torpedograss prior to the storm, the lower densities of torpedograss in the vicinity of large snags may simply indicate a colonization lag by torpedograss in these areas. Adults could, in effect, "protect" their offspring from competition and/or increased fire risk from flammable grasses even after their death.

Torpedograss swards were consistently associated with low elevation and relatively high soil moisture and organic content, although there was some variation in magnitude between barrier islands and sampling years. On the dunes, two of the three environmental factors examined, elevation and soil organic content, were weak predictors of torpedograss density; but the positive relationship between torpedograss density and elevation was associated with sampling location. Horn Island, with generally higher elevation, also had higher torpedograss density, and elevation could be removed as a significant factor impacting density when island was included as a factor in analysis of covariance. Torpedograss abundance was negatively correlated with soil organic matter on the dunes and positively correlated with soil organic matter in the low-lying swales surrounding them. Soil organic matter was a significant covariate associated with torpedograss abundance in analysis of covariance with island as the main effect, but not when plot type was included as a main effect or when rosemary seedling abundance was included as a covariate, suggesting that the negative correlation with organic matter is more accurately attributed to the proximity to rosemary snags that were reproductive prior to being killed by the hurricane. The scrub soil of inland Florida is nutrient-poor (Kalisz and Stone 1984, Myers 1990) and it is likely that nutrients are similarly scant within the scrub on the barrier islands, so in the absence of other factors I expected torpedograss abundance to be consistently positively correlated with organic matter. In the sward areas, the positive correlation between

47

organic content and torpedograss density may indicate a positive response of torpedograss to higher nutrient content. Detritus from upslope would be expected to wash down the dunes into surrounding low-lying areas during rainfall events, and Mulvania (1931) observed that dry organic matter is easily blown away from bare areas in the scrub. The mean elevation of torpedograss swards was the lowest of any plot type for both barrier islands, making them a likely sink for organic material. If organic material is accepted as a proxy for nutrient concentration then torpedograss swards are richer in nutrients than the dune ridges they surround. (The decline of torpedograss growth after six weeks in soil collected from all locations except for torpedograss swards (Chapter 3) also lends support to the conclusion that sward soil is higher in nutrient content than soil from the dunes.) It is also possible that the high density of torpedograss within the swards is, in itself, a factor contributing to the greater organic material there. Grasses have the capacity to alter many ecosystem processes (D'Antonio and Vitousek 1992), and in the case of torpedograss this should surely include the capacity to rapidly produce large amounts of biomass, potentially increasing the soil organic content. If so, it is possible that torpedograss is also one among a number of exotic species that have already demonstrated the ability to alter soil properties due to differences in litter quality or quantity. Invasive species tend to have faster growth rates than the native species with which they compete, in turn affecting nutrient cycling (Ehrenfeld 1993). However, to test this possibility a more in-depth analysis of the effects of torpedograss upon soil nutrients would be necessary.

Torpedograss swards contained more soil moisture than any other plot type, but within the swards there was not a significant association between soil moisture and torpedograss abundance once island-specific differences in soil moisture were considered. Torpedograss sward plots on Petit Bois Island contained much greater soil moisture than any of the dune plots,

but not on Horn Island, and this may be due to a profound difference in the vegetative composition in torpedograss sward plots on the two islands. On Petit Bois Island, topography was less varied than on Horn Island, and torpedograss maintained a modest presence in low-lying areas surrounding the rosemary-dominated dunes along with several taller and more numerous species (e.g., *Spartina patens, Physalis angustifolia, Opuntia humifusa, Ilex vomitoria*). By contrast, although other species were sometimes observed in areas of moderate torpedograss density on Horn Island, the grass frequently formed dense monocultures in which it had few competitors and no taller, overshading shrubs. A combination of much higher torpedograss density and less shade on Horn Island probably contributed to reduced soil moisture in torpedograss swards on that island. The positive correlation between torpedograss density and elevation in torpedograss swards was unexpected, but may also be related to shading if torpedograss tillers at higher elevation received greater light, a parameter that was not examined in this study. It is also possible that torpedograss is more prone to sand burial at low elevation.

Despite the negative association of torpedograss tillers and dead rosemary, torpedograss tillers and other native grasses that were present around dead rosemary snags sometimes grew thickly among the fallen branches and appeared to attain greater height than on bare dunes. This could be because remnants of the root ball provide better water retention and/or a nutrient source as they decay, or the grasses may have simply exhibited taller growth to escape the shading effect of the snag branches. Torpedograss was also sometimes observed growing sparsely beneath adult Florida rosemary shrubs.

Mortality was observed among both torpedograss tillers and rosemary seedlings in summer 2008 and 2009, probably as a result of drought: A weather station in Pascagoula, MS (the most proximate to the barrier islands) recorded rainfall below normal 9 of the 12 months

between July 2008 and 2009. There was no rainfall recorded in May or June 2009, ranking precipitation for these two months 12 – 15cm below normal (National Climatic Data Center).

It has been suggested that some native species of the inland Florida scrub may take advantage of seed dormancy induced by rosemary litter leachates to avoid competition with adult Florida rosemary shrubs until they are killed by fire (Hunter and Menges 2002). Florida rosemary may also avoid competing with its own seedlings by preventing seed bank germination until such time as the parent is killed. Johnson (1986) raised the possibility that rosemary leaf litter may inhibit germination of its own seeds. Inland rosemary seedling establishment occurs principally or exclusively post-fire (Johnson 1982, Johnson et al. 1986, Menges and Kohfeldt 1995), although all-aged stands of Florida rosemary indicate more constant recruitment in response to more frequent localized disturbance and perhaps enhanced seed scarification (Johnson 1986) in some coastal populations (Gibson and Menges 1994). I observed heavy recruitment beginning two years after Hurricane Katrina in the vicinity of large adults killed by the storm on Horn and Petit Bois Islands and continuing for at least three years.

Seedling recruitment of Florida rosemary began in the fall of 2007, two years after Hurricane Katrina. This concurs with reports of seedling emergence no earlier than two years post-fire in relic dune populations in Florida (Abrahamson 1984). Recruitment continued throughout the three-year study period. The longevity of seed bank viability in Florida rosemary scrub is uncertain (Johnson 1982, Gibson and Menges 1994), so further observation will be necessary to determine how long the high rates of recruitment observed in this study will continue. I also observed resprouting of adult rosemary shrubs that were heavily damaged but not completely defoliated by the hurricane (see Chapter 1); this may represent an important method of post-disturbance recovery for island populations of Florida rosemary, since recovering

adults have the potential to begin rebuilding the seed bank immediately without the multiple-year lag seedlings require for germination and maturation.

Although some recruitment of rosemary seedlings was observed on bare dunes, the overwhelming majority of seedlings were located within close proximity to damaged or dead adult shrubs. This observation supports the suggestion by Gibson and Menges (1994) that dispersal of Florida rosemary seeds is limited, as most juvenile rosemary seedlings are associated with adult females, despite potential avian seed vectors. Rosemary seedling abundance was positively correlated with soil organic matter as well as the snag-with-seedlings plot type on the dunes. This is probably a reflection of the size of the parent shrub, as larger, older adults had the opportunity to accumulate a larger seed bank as well as providing more organic material during decay. Another possibility is that the organic material provided by decay may itself provide some advantage to emerging seedlings, such as increasing nutrient availability, water retention, or both. Based on pre- and post-hurricane observations of barrier island topography (Brewer, personal communication) Hurricane Katrina shifted a great deal of sand on Horn Island, and presumably had the potential to shift the seed bank contained therein, yet seedlings were still confined primarily to the area surrounding dead adult shrubs. The fibrous root ball of the adult shrub, combined with the windbreak provided by the dead snag, may also have an anchoring effect on local microtopography, reducing seed dispersal to unsuitable off-dune areas and facilitating more closely-growing stands of rosemary easily fertilized by wind-dispersed pollen. In addition, the higher density of the seed bank accumulated beneath adult shrubs (200-1000/m^2, Johnson 1982) could contribute to a concommitant higher density of seedling emergence in areas around adult shrubs despite some sand movement.

Despite the possibility that these dune systems receive periodic salt spray and are inundated with salt water during tropical storm events, soil salinity was below the threshold of measurement using a refractometer. I was therefore unable to associate soil salinity with the abundance of either of the two species studied here. The highly permeable, sandy soil of the interior dunes receives relatively frequent rainfall and probably does not retain enough salt to create particularly saline soil water, although I cannot discount the possibility that salinity varies seasonally with rainfall events and may increase during droughts. There may be a temporary increase in soil salinity in these systems following hurricanes, but in most cases when salinity has been examined following a hurricane, salt concentrations have soon declined to pre-storm levels, possibly due in part to the heavy rainfall associated with the storm. It is therefore unsurprising that two and a half years after Hurricane Katrina there was no evidence of a hurricane-associated increase in soil salinity on Horn and Petit Bois Islands.

Underlying environmental factors on these barrier islands distinguish coastal rosemary scrub from the surrounding swales. Soil moisture and soil organic content may differ both as a result of variation in elevation and as a result of ecosystem engineering in plant communities occupying, and potentially altering, those areas. However, although environmental factors affect torpedograss distribution within the low-lying swales surrounding the scrub, within the rosemary scrub the presence of dead rosemary shrubs was the most significant determinant of torpedograss abundance measured in this study.

Torpedograss density increased on the dunes from 2005-2008, immediately after Hurricane Katrina, but then declined during the study period from 2008-2010. If the hurricane increased resource availability temporarily after the storm, simultaneously removing the majority of the native shrubs present in the scrub, then higher invasibility of the rosemary scrub during

this period is in accordance with the theory of fluctuating resource availability (Davis et al. 2000). Barrier island communities such as these are subject to periodic catastrophic disturbance from hurricanes, which have the potential to simultaneously remove competition from native vegetation while increasing resources available to invaders. Although coastal communities are adapted to a certain pattern of hurricane disturbance and may even benefit from the associated resource influxes (Conner et al. 1989, Michener et al. 1997), invasive species have the potential to alter ecosystem-level processes (Vitousek 1990), including recovery from disturbance. If invaders instead of native species take advantage of increased resource availability following hurricanes, then an advantageous natural disturbance may instead become an opportunity for non-native species to gain a foothold in the community.

Panicum repens, an invasive facultative wetland plant, appears to have benefitted in the two or three years following Hurricane Katrina from topographic changes, an influx of nutrients during the storm surge, a reduction in competition and perhaps associated allelopathy from Florida rosemary (see Chapter 3), and the species' innate ability to spread quickly and opportunistically. As native dune species more adapted to xeric conditions have begun recovering from the hurricane, torpedograss is beginning to die back to pre-storm abundance and distribution, persisting only in more mesic, low-lying areas. This process may be exacerbated by rhizome decay belowground, leaving torpedograss tillers on the dunes without a supply of shared resources from ramets located in these richer areas.

Eleuterius (1979) reported that torpedograss occurred in 21.2% of relic dune plots during a survey of species occurrence. Although present for at least three decades, this invasive grass has not yet dominated the scrub community, but torpedograss does appear to have temporarily benefitted from the hurricane, and thus changes in hurricane intensity and frequency predicted by

some models could alter the balance between native and non-native engineers in this ecosystem. Future observation of barrier island communities could answer several questions about the rosemary scrub, including differences in coastal and inland populations of Florida rosemary, the ability of barrier island communities to recover from tropical storms during a more active hurricane season, and the ability of torpedograss in particular and invasive species in general to affect ecosystem-level processes in the face of catastrophic disturbance. One potential change, an increase in fire frequency within the rosemary scrub that might inhibit the ability of Florida rosemary seedlings to reach reproductive age, was not supported by these data, since the retreat of torpedograss from the dunes coincided with seedling recruitment. Conner et al. (1989) suggest that hurricanes represent a natural process to which coastal systems are well-adapted, and that detrimental effects such as vegetation loss are seldom lasting when human influence (e.g., anthropogenically altered marshes) is not a factor. Non-native species invasions represent another impact to which local ecosystems are not necessarily adapted, and we should seize available opportunities to further study the effect of hurricanes upon interactions between native and non-native species.

III: ALLELOPATHY AND INVASION: CAN A NATIVE DEFENSE INHIBIT A NON-NATIVE SPECIES?

Abstract

Recent studies have suggested that species may become invasive because they use a novel weapon, allelopathy, to inhibit the growth of naïve plants in their introduced range. Can native species also restrict the growth of an invader through the same mechanism? I explore this possibility in the context of two ecosystem engineers exposed to catastrophic disturbance by Hurricane Katrina within the interior dune communities of barrier islands in Mississippi. *Ceratiola ericoides* Michx. (Florida rosemary), a native xeric shrub adapted to infrequent fires, is believed to inhibit the growth of native bunchgrasses via allelopathy, thus reducing fuel load and fire frequency. *Panicum repens* L. (torpedograss), a non-native, drought-tolerant, facultative wetland grass, was present at the margins of the scrub prior to Hurricane Katrina but began invading the scrub after the storm surge led to widespread mortality of Florida rosemary. I used three experiments to test the hypothesis that Florida rosemary previously inhibited the spread of torpedograss via allelopathy. My results indicate that the soil associated with living rosemary shrubs has a mild inhibitory effect on torpedograss aboveground (but not belowground) growth, and this effect was ameliorated by the addition of activated carbon. Direct hydrocinnamic acid addition also inhibited aboveground torpedograss growth, even at low concentrations. However, a field study of torpedograss performance in areas where it is abundant showed no effect of litter addition in a natural setting. The tendency of North American populations of torpedograss to

reproduce rhizomatously rather than via seeds may render it less vulnerable than native bunch

grasses to allelopathy from Florida rosemary, but mild allelopathic effects may be sufficient to

put torpedograss at a disadvantage when combined with resource competition from scrub

residents under undisturbed conditions.

Introduction

Recent studies have suggested that exotic species may invade a community because they

bring a novel mechanism of interaction, allelopathy, to bear upon competitors with which they

did not co-evolve and which thus have no ready defense (e.g., Callaway and Aschehoug 2000,

Bais et al. 2003, Callaway and Ridenour 2004, Prati and Bossdorf 2004; others reviewed in

Hierro and Callaway 2003). In a few cases, allelopathy has also been proposed as a method by

which native communities can deter invasion. Weidenhamer and Romeo (2005) provide support

for the hypothesis that a native Florida scrub plant, *Polygonella myriophylla* (Small) Horton,

inhibits the growth of bahiagrass (*Paspalum notatum* Fluegga), an exotic, perennial grass that

reproduces by seed and rhizomatous growth.

Another scrub species that has exhibited alleopathic characteristics is *Ceratiola ericoides*

Michx., Florida rosemary. Also known as sand heath, Florida rosemary is a dioecious evergreen

shrub of the family Empetraceae. Native to the southeastern United States, it has long been

recognized as a member of a community of fire-intolerant plants occupying deep, extremely

well-drained sandy soils and commonly termed Florida scrub, or more specifically, rosemary

scrub (Nash 1895, Mulvania 1931, Webber 1935). The rosemary scrub community resists fire

and burns at intervals of ten to one hundred years (Myers 1990). These infrequent fires

completely kill individual rosemary shrubs, and local population recovery occurs through

germination from within a seed bank accumulated over the preceding years beneath parent plants. Rosemary scrub occurs upon relic dunes located many miles from the coastline (interior rosemary scrub) as well as in coastal areas and on sandy barrier islands (coastal rosemary scrub). According to studies of interior rosemary scrub on the Lake Wales Ridge, Florida, new rosemary seedlings do not reach reproductive age for ten to fifteen years, so a fire cycle of greater frequency than ten years is likely to result in a gradual population decline as seed bank stores are depleted and never replenished (Johnson 1982). Some authors have suggested that allelopathy in certain species of the Florida scrub (Williamson 1990, Williamson et al. 1992, Weidenhamer et al. 1994), including Florida rosemary (Richardson and Williamson 1988, Fischer et al. 1994, Menges and Kimmich 1996, Hunter and Menges 2002), inhibits community invasion by highly flammable species, thus effectively reducing fire frequency in the community and maintaining favorable conditions for plants adapted to infrequent fires. The allelochemical of interest, ceratiolin, degrades when exposed to water and sunlight to form hydrocinnamic acid; the latter is thought to be the more inhibitory compound (Fischer 1994). Litter and, to a lesser extent, leaf washes of Florida rosemary containing these compounds have shown inhibitory effects on several native grasses (Richardson and Williamson 1988, Hunter and Menges 2002), as have specific tests of analytical-grade hydrocinnamic acid when applied to weed species (Williams and Hoagland 1982).

Panicum repens L., variously known as torpedograss, couch panicum, creeping panic, or wainaku panic, is a rhizomatous perennial grass common in marshy areas along the Gulf Coast, California, and Hawaii. Although its origins are uncertain as it is now found worldwide, it is believed to be an introduced species in North America; the first recorded collection of torpedograss in the United States occurred in 1876. When introduced into an area, torpedograss

spreads rapidly, primarily through clonal growth. Although it also produces wind-dispersed

seeds, these appear have extremely low to zero viability (Wilcut et al. 1988b, Smith 1995 in

Sutton 1996). The species is capable of creating thick mats of ground cover in a short period of

time, potentially increasing local flammability as grasses are particularly well suited to do

(D'Antonio and Vitousek 1992). Torpedograss is currently listed as a noxious weed in four

states (USDA NRCS 2011), is recognized as an agricultural weed in tropical and subtropical

regions worldwide (Holm 1977), and has become a troublesome invader in parts of Florida,

where it is listed as a Category I invasive species throughout the state (FLEPPC 2009). Using

the U. S. Geological Survey's Alien Plants Ranking System (USGS APRS Implementation Team

2000), Hutchinson and Menges (2006) recently assigned torpedograss the highest potential for

invasiveness (encompassing impact to natural communities, likelihood of becoming a pest, and

difficulty to control) among sixty-six non-native plants at Archbold Biological Station in south-

central Florida.

In 1895, Nash noted that a population of inland rosemary scrub contained no grasses

whatsoever, save the occasional ephemeral appearance of a few bunch grasses. However,

accounts of torpedograss along the Mississippi shoreline (Lloyd and Tracy 1901, Pessin and

Burleigh 1941), and specifically in proximity to rosemary scrub (Penfound and O'Neill 1934),

began to appear in the literature in the early 1900s. Menges (1999) observed that exotic species

seldom invaded the scrub without an opportunity created by some form of disturbance. On Horn

and Petit Bois Islands, Mississippi, where the interior relic dunes support a community of coastal

rosemary scrub, recent catastrophic disturbance by Hurricane Katrina (a Category 3 storm that

made landfall in late 2005) dramatically changed plant community composition. Prior to the

storm, torpedograss was common on Horn and Petit Bois Islands but was primarily confined to

the low-lying margins of rosemary scrub patches. However, the hurricane produced a storm surge that washed over the islands, uprooted or buried many plants, and shifted the distribution of sand, altering community composition and topography simultaneously. In addition to extensive mortality in certain other woody and herbaceous plant species, Florida rosemary suffered approximately 95% mortality, and in the year following Hurricane Katrina, torpedograss began to extend ramets into areas formerly dominated by Florida rosemary (see Chapter 1).

Invasion of rosemary scrub by torpedograss following mortality of Florida rosemary caused by Hurricane Katrina suggests that allelopathy from Florida rosemary may have previously prevented invasion by torpedograss. If Florida rosemary inhibits the growth of torpedograss, then as new rosemary seedlings reach an age to produce sufficient litter, this native species has the potential to reduce the competitive ability of torpedograss and perhaps return the scrub community to pre-storm composition. Alternately, torpedograss may be resistant to allelopathic inhibition. Unlike some native bunch grasses, torpedograss relies almost exclusively on vegetative reproduction through rhizomatous growth. If growth and vegetative reproduction of established adults are less sensitive to allelopathy than are germination and seedling establishment, then torpedograss may be less sensitive than native bunch grasses to allelopathy. If so, resistance of undisturbed rosemary scrub community to invasion by torpedograss may simply reflect more intense resource competition or apparent competition.

Regardless of the mechanism of resistance of undisturbed rosemary scrub to invasion by torpedograss, each species exhibits the properties of an ecosystem engineer and as such disproportionately affects ecosystem processes in such a way as to benefit itself (Jones et al. 1994). Hence, a modest increase in one species could lead to a subsequent dramatic increase in that species at the expense of the other, producing an ecosystem with alternative stable states

(Holling 1973). If Florida rosemary is competitively superior to torpedograss, recovery of Florida rosemary following disturbance has the potential to halt and reverse invasion by torpedograss and thus maintain the natural firebreak that makes rosemary scrub a "fire-fighting association" (Webber 1935). On the other hand, invasion of rosemary scrub by torpedograss following catastrophic disturbance has the potential to increase fuel load, putting seedlings of Florida rosemary at risk of mortality by fire, which in turn could jeopardize recovery of the population. Such a positive feedback could lead to a torpedograss-dominated assemblage that resists further change. The outcome of interactions between Florida rosemary and torpedograss therefore has far-reaching implications within this community.

I designed three complementary experiments to test my hypothesis that Florida rosemary inhibits growth of torpedograss via allelopathy: 1) a 3-month shadehouse study of torpedograss collected from several locations and planted in soil collected from different locations on the barrier islands, with and without the addition of rosemary litter and activated carbon; 2) a 3-month bioassay to assess the effects of hydrocinnamic acid application at low, medium, and high concentration upon the growth of torpedograss from rhizome nodes; and 3) a 14-month field study of the effects of litter addition to torpedograss plots established along the edges of firelanes where torpedograss is abundant and soil, light, and temperature conditions are similar to those on the Mississippi barrier islands. My goals were to determine if growth in soil exposed to living or dead Florida rosemary, its litter, or the allelochemical hydrocinnamic acid could inhibit the rhizomatous growth of torpedograss in laboratory or field studies, and if this inhibition could be traced to allelopathy.

Materials and Methods

Shadehouse experiment:

In summer 2009, I grew torpedograss tillers in the shadehouse at Archbold Biological Station (Venus, Florida, USA) in a factorial design encompassing soil type, carbon treatment, and torpedograss source population. Archbold Biological Station is located on the Lake Wales Ridge in south-central Florida, and is an area where both torpedograss and inland rosemary scrub are abundant, so although torpedograss was exposed to local environmental fluctuations, they were biologically realistic (with the exception of moisture: sprinklers were used to irrigate pots when rain was sparse). I collected soil from five location types representative of the coastal rosemary scrub community and the adjacent swale community on the barrier islands: 1) bare dunes within the rosemary scrub; 2) near torpedograss swards (at the ecotone between scrub and swale); 3) within torpedograss swards in the swale community; 4) beneath dead rosemary shrubs (containing fragments of rosemary skeleton); and 5) beneath live rosemary shrubs. A sixth soil treatment also contained soil from beneath live rosemary shrubs, but received a supplement of approximately 5 grams of dry rosemary litter once a week, mimicking the presence of a living adult rosemary shrub and intended to provide a way to separate the effects of soil characteristics from the effect of litter addition. To account for the physical effects of added litter to the soil surface (e.g., reduced evaporation from the soil surface, physical obstruction of torpedograss tiller emergence), fragmented plastic chips were added to the surface of the other soil treatments. Soil was obtained from Horn Island, MS, Santa Rosa Island, FL, and St. George Island, FL. Plant community, not the island of soil origin, was the factor of interest in this experiment; the Florida islands were used as additional soil sources for logistic reasons.

Activated carbon adsorbs many organic compounds (Cheremisinoff & Ellerbusch 1978) and is frequently used experimentally to reduce inhibitory effects of one plant on another and thus demonstrate allelopathy (Mahall and Callaway 1992, Prati and Bossdorf 2004, Callaway et al. 2005, Abhilasha et al. 2008), including at least one case in which the allelopathic species was a shrub of the family Empetraceae (Nilsson 1994). I hand-mixed finely ground Black Magic Super Activated Carbon (Mars Fishcare North America, Inc., Chalfont, PA) at a concentration of 20 ml per liter of soil (Callaway and Aschehoug 2000) into one third of the pots of each soil treatment. As a control for the addition of activated carbon, one third of the pots were supplemented at the same concentration with a source of non-activated carbon: Ground Cowboy Brand 100% All-natural Lump Charcoal (Cowboy Charcoal Co., Brentwood, TN). Finally, one-third of the pots were filled with untreated soil.

To account for potential differences among populations, torpedograss was collected from Horn Island, Petit Bois Island, and Archbold Biological Station (ABS). Ramets were separated into individual tillers (here defined as an upright stem) and planted in ¼ liter pots of soil. Tillers that had swollen, knotty "ginger-like" nodes were avoided to reduce error variance, as these swollen nodes are likely to represent a source of stored resources (Hossain et al. 1999). For each treatment combination (6 soil types x 3 carbon treatments x 3 source populations), five torpedograss tillers were planted, providing a total of 270 tillers. Before potting, maximum root length was measured, and immediately after planting tiller height was recorded. For three months, torpedograss performance was assessed weekly by per-pot counts of tiller number and tiller height. At the end of the study, the contents of each pot were separated and dried to assess aboveground (stem and blade) biomass, panicle biomass, root biomass, and rhizome biomass. Panicle production was negligible during the course of the experiment and panicle biomass was

included in aboveground biomass rather than being analyzed separately. Rhizome fragments retrieved at the end of the experiment were visibly withered and decaying, and no new rhizomes were produced from the central node during the course of the experiment. Rhizome biomass was therefore excluded from analysis, and belowground biomass is represented by fine root dry weight. All biomass data were log-transformed to meet assumptions of normality.

Six cases were excluded from data analysis (pots #48, 94, 192, 193, 194, and 213) because these ramets did not survive transplantation to individual pots. Two basic comparisons of torpedograss growth were made: Analysis of torpedograss performance in the five soil types (5 x 3 x 3 factorial analysis), which explores the impact of soil source upon torpedograss, and analysis of torpedograss growth in the same soil type with and without rosemary litter addition (2 x 3 x 3 factorial analysis), which addresses the specific effect of litter addition upon torpedograss performance. Growth was represented in several different ways: 1) tiller growth rate (*ln* final green tissue – *ln* initial green tissue) over the duration of the study; 2) final biomass; and 3) weekly measurements of tiller number and height. Initial tiller height was positively correlated with tiller growth rate ($t_{173} = 3.67$, $p < 0.01$) in the soil type tests, as well as with aboveground ($t_{173} = 10.72$, $p < 0.01$), belowground ($t_{173} = 7.21$, $p < 0.01$), and total ($t_{173} = 9.57$, $p < 0.01$) biomass in the soil type comparison and in both the soil ($F_{11,160} = 3.58$, $p < 0.01$) and litter ($F_{11,56} = 3.11$, $p < 0.01$) repeated-measures analyses of variance of changes in tiller height. Initial tiller height was therefore included as a covariate in these tests.

HCA bioassay:

In 2010, I tested the effect of hydrocinnamic acid (HCA) application on torpedograss growth. Although it is less biologically realistic than litter application, HCA application

represents the most direct way to test for inhibition of torpedograss growth by Florida rosemary. Jordan (1990) reported that HCA is found in soil near live rosemary shrubs at concentrations of 15-418 ppm, and several studies have observed significant inhibition of *S. scoparium* germination with direct application of HCA at concentrations as low as 60-63 ppm and inhibition of radicle growth at 125 ppm (Tanrisever et al. 1987, Fischer et al. 1988, Williamson et al. 1992). I used these ranges as a guideline and adapted a method described by Williamson et al. (1992). One torpedograss node, collected from either Horn Island or Archbold Biological Station, was weighed and planted within each of 120 ¼ liter pots filled with clean dune sand. Torpedograss rhizomes are capable of sprouting into new tillers with a high rate of success (Wilcut et al. 1988, Wilcut et al. 1988b, Sutton 1996, Hossain et al. 1999, Hossain et al. 2001, Hossain et al. 2004), and transplanting rhizomes alone eliminates variation in preexisting photosynthetic material at time of planting. I preferentially selected swollen ginger-like nodes for planting, as these structures were associated with increased culm emergence from buried rhizome clippings in a previous study (Hossain et al. 1999). Wet weights were collected from all nodes before planting, and nodes were randomly assigned to one of four treatments. Hydrocinnamic acid, which is soluble in water to a concentration of 3490 ppm (Weidenhamer et al. 1993), was dissolved in aqueous solution at a concentration of 0, 25, 200, or 500 ppm. Pots were watered with 25ml of the treatment concentration twice weekly.

I assessed torpedograss performance over time through monthly observation of tiller abundance and maximum green tissue height. At the end of the three-month study, I collected above- and belowground wet and dry weights. I compared treatments using repeated-measures analysis of variance to examine changes over time and factorial ANOVA to compare differences in growth resulting from HCA concentration and torpedograss source.

Litter addition field study:

In June 2009, I chose ten sites at Archbold Biological Station along the edges of firelanes where torpedograss was abundant. At each site, six 25cm radius plots were randomly established along a 20 or 30 meter transect, with at least 1 meter between plot edges, for a total of sixty plots. One half of the plots at each site were assigned randomly to either a control (no litter addition) or treatment (litter addition) group. Approximately ¾ cup of Florida rosemary litter was applied to the soil surface of plots in the treatment group every other month. Tiller number, maximum tiller height, and panicle production were assessed at the beginning of the experiment and every other month through August 2010. Tiller persistence was also estimated by marking five tillers per plot with colored plastic ties, and then recording survival of these tillers over time. When a tiller died, another tiller was chosen randomly.

Torpedograss growth indicators were examined as a cumulative result of fourteen months of litter application (factorial ANOVA on log-transformed final data) and as they changed over time (repeated-measures ANOVA on log-transformed bimonthly data). A Survival/Reliability test (JMP 5.0.1a, SAS Institute Inc.) was used to analyze the persistence of tillers recorded from month to month, accounting for censored data (e.g., the unknown fate of tillers that were still living when data collection ended).

Results

Shadehouse experiment:

Tiller growth rate

There was no main effect of soil type, carbon addition, or source population on tiller growth rate of torpedograss grown in different soil types. However, in the study examining the

effect of litter addition to live rosemary soil, adding activated carbon improved torpedograss

growth rate, and there was a trend toward decreased growth rate with litter addition (Figure 3-1).

Three-way ANOVA of the main effects of litter addition, carbon addition, and source population

indicated a lower growth rate with litter addition that approached significance ($F_{1,68} = 2.89$, $p =$

0.09), a significant effect of carbon addition ($F_{2,68} = 3.68$, $p = 0.03$), and no effect of source

population. The highest tiller growth rate was in soil augmented with activated carbon, the

lowest in soil without carbon, and tillers grown with non-activated carbon had an intermediate

growth rate (planned contrasts, $F_{1,68} = 6.03$, $p = 0.02$).
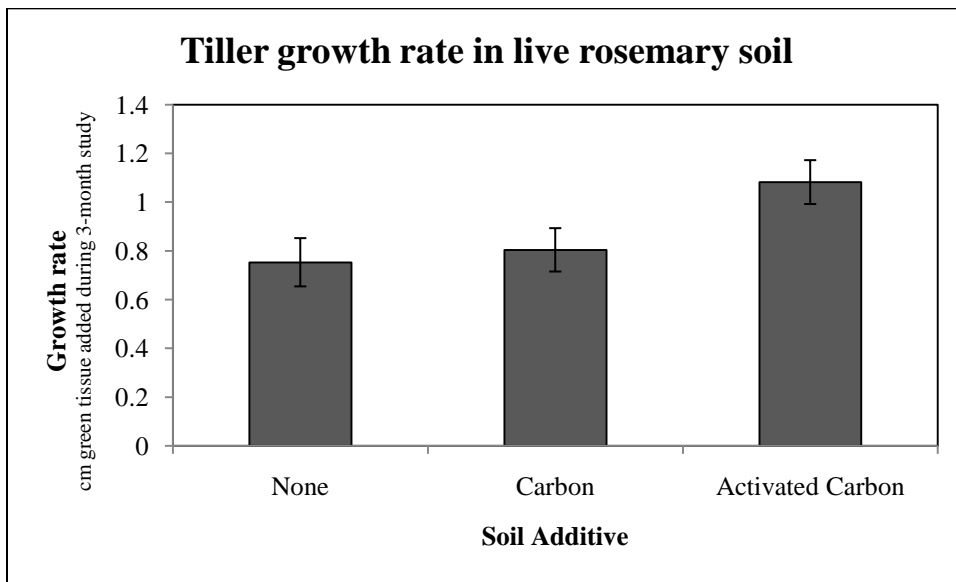
Figure 3-1: Torpedograss tiller growth rate in live rosemary soil. Error bars are ±1 standard error.

Aboveground biomass

In tests of torpedograss performance within different soil treatments, 3-way analysis of

covariance indicated a significant effect of source population ($F_{2,173} = 4.40$, $p = 0.01$) on

aboveground biomass. Torpedograss from ABS performed significantly better than torpedograss

from Petit Bois Island (Tukey's HSD, $p < 0.05$). There was also a significant interaction

between soil type and carbon addition ($F_{8,173} = 1.98$, $p = 0.05$). Planned contrasts within this interaction indicated that while carbon addition (regardless of activation) had no significant effect on aboveground biomass in torpedograss sward soil, aboveground biomass in soil from beneath live rosemary shrubs was significantly increased by carbon addition when compared to all other soil types ($F_{1,173} = 4.88$, $p = 0.03$), including torpedograss swards ($F_{1,173} = 6.87$, $p = 0.01$).

Soil from beneath live rosemary shrubs appeared to cause a persistent reduction in aboveground biomass consistent with allelopathy. With initial height as a covariate, three-way analysis of variance on aboveground biomass indicated a positive main effect of carbon addition ($F_{2,67} = 7.02$, $p < 0.01$; Figure 3-2), but no effect of litter addition or source population on torpedograss grown in live rosemary soil ($p > 0.50$). Unaugmented soil produced the least biomass and activated carbon the most, with non-activated carbon having an intermediate effect ($F_{1,173} = 8.91$, $p < 0.01$).

Figure 3-2: Effect of carbon addition on aboveground torpedograss biomass. Error bars are ±1 standard error.

Belowground biomass

Unlike aboveground biomass, belowground biomass was not impeded by live rosemary soil. There was a main effect of soil type ($F_{4,173} = 6.07$, $p < 0.01$), with the highest root biomass occurring in torpedograss sward soil (planned contrasts, $F_{1,173} = 11.64$, $p < 0.01$), but tillers planted in soil from beneath live rosemary also produced high belowground biomass (Figure 3-3). Belowground biomass was also affected by source population ($F_{2,173} = 8.30$, $p < 0.01$), with torpedograss from ABS outperforming that from the two barrier islands (Tukey's HSD, $p < 0.05$).

I found no evidence of an allelopathic effect on root biomass, and in fact the addition of carbon to soil from torpedograss swards decreased root biomass. Planned contrasts on the soil type x carbon interaction showed that while carbon addition had different effects on root biomass in torpedograss sward soil and live rosemary soil ($F_{1,173} = 5.94$, $p = 0.02$), there was not a trend of improved performance in live rosemary soil with carbon addition. Instead, root biomass decreased in torpedograss sward soil when any type of carbon was added ($F_{1,173} = 7.50$, $p < 0.01$) (Figure 3-3).
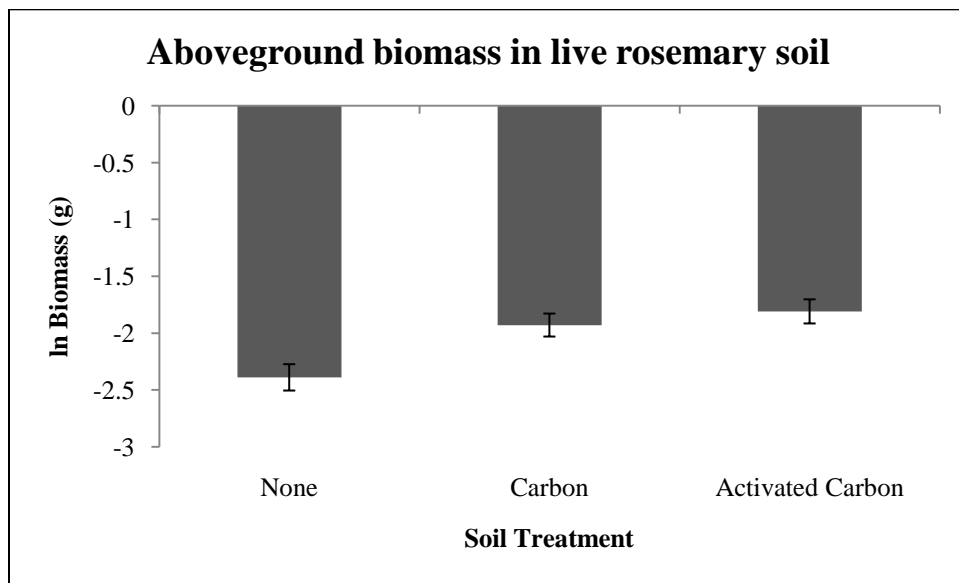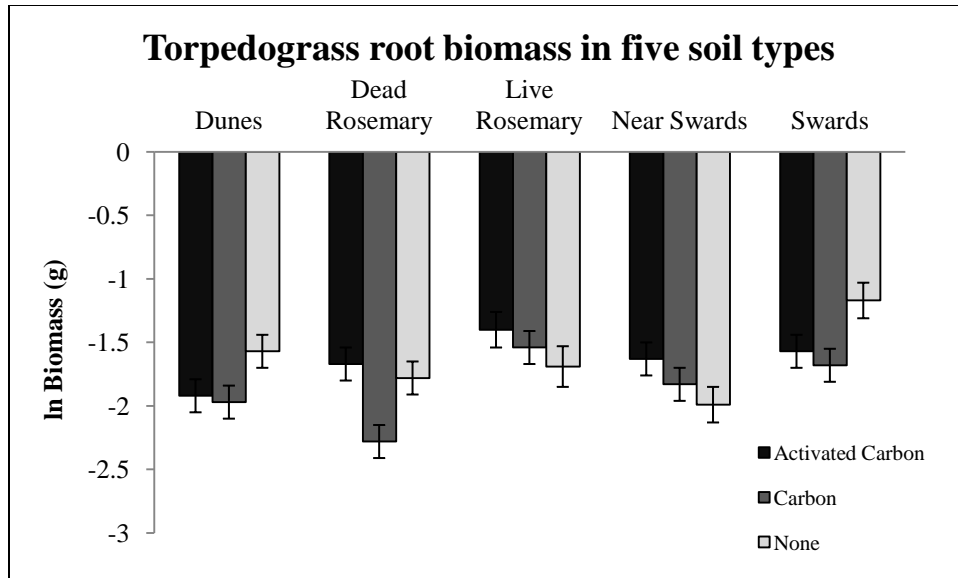
Figure 3-3: Effect of carbon addition on belowground torpedograss biomass. Error bars are ±1 standard error.

Root biomass in the litter addition analysis was significantly impacted by source population ($F_{2,67} = 4.00$, $p = 0.02$), with ABS torpedograss producing more biomass than torpedograss from Petit Bois Island (Tukey's HSD, $p < 0.05$). Litter addition significantly decreased root biomass ($F_{1,67} = 5.54$, $p = 0.02$) relative to live rosemary soil without litter added (Figure 3-4). Although the main effect of carbon addition approached statistical significance ($F_{2,67} = 2.59$, $p = 0.08$), the lack of an interaction with litter addition suggests that some mechanism other than allelopathy is responsible for the observed reduction in root biomass.
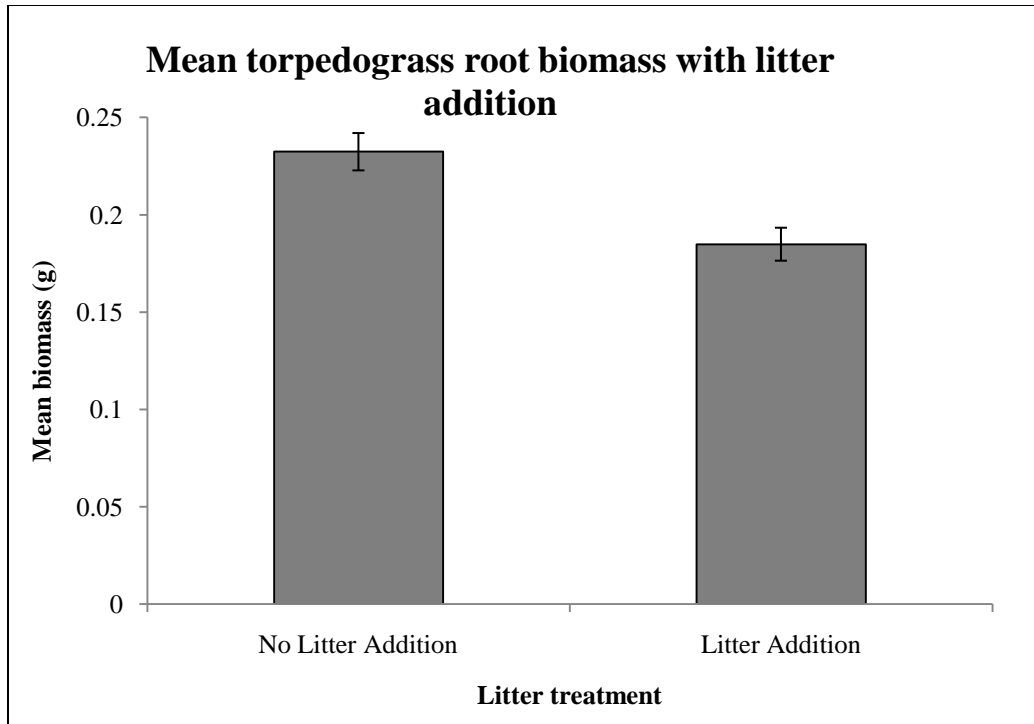
Figure 3-4: Mean root biomass of torpedograss grown in Florida rosemary soil, with and without the weekly addition of rosemary litter. Error bars are ±1 standard error.

Total Biomass

Total biomass varied among source populations and soil types. Analysis of covariance on total biomass (stems + panicles + roots) showed a significant main effect of soil type ($F_{4,173} = 3.27$, $p = 0.01$). The greatest biomass was produced when torpedograss was grown in soil from torpedograss swards (planned contrasts, $F_{1,173} = 3.96$, $p = 0.05$), but live rosemary soil also produced significantly more biomass than the other three treatments (planned contrasts, $F_{1,173} = 4.20$, $p = 0.04$). There was also a significant main effect of population of origin ($F_{2,173} = 6.74$, $p < 0.01$), with ABS tillers producing more than the barrier islands (Tukey's HSD, $p < 0.05$).

The effect of carbon addition on total biomass of tillers varied among soil types. The soil x carbon interaction approached statistical significance ($F_{2,173} = 1.95$, $p = 0.06$). Carbon addition had opposite effects on total biomass of tillers grown in live rosemary soil and torpedograss

sward soil (planned contrasts, $F_{1,173} = 7.26$, $p < 0.01$). Carbon addition significantly decreased growth in torpedograss sward soil ($F_{1,173} = 4.42$, $p = 0.04$) while having a significant positive effect on overall biomass in live rosemary soil ($F_{1,173} = 4.42$, $p = 0.05$). Based on the results of separate above- and belowground biomass analysis, the decrease in overall biomass in torpedograss sward soil is due to a reduction in root production, while the increase in overall biomass in live rosemary soil is due to an enhancement in aboveground growth (Figure 3-5).
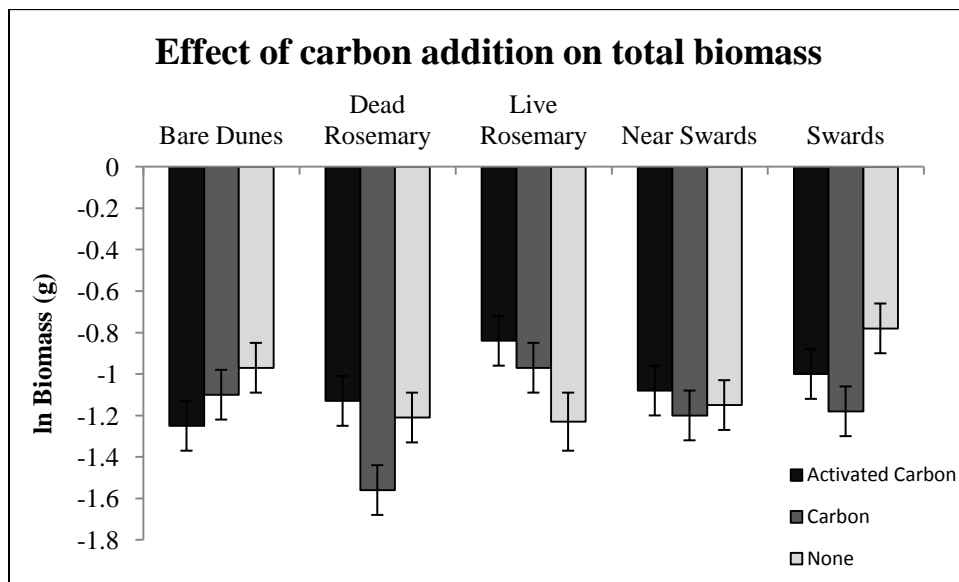
Figure 3-5: Effect of carbon addition on total torpedograss biomass. Error bars are ±1 standard error.

Total biomass was not affected by litter addition, but carbon addition had a significant main effect ($F_{2,67} = 5.03$, $p = 0.01$). Activated and non-activated carbon addition significantly increased overall biomass in live rosemary soil (planned contrasts, $F_{1,67} = 8.83$, $p < 0.01$), a difference due to increased aboveground growth based on the separate above- and belowground biomass analyses.

Table 3-1: Summary of effects of soil type and litter addition on torpedograss biomass.

	Soil Type	Litter Addition to Live Rosemary Soil
Aboveground biomass	Increases in live rosemary soil with carbon addition	Increases with carbon addition regardless of litter
Belowground biomass	Highest in torpedograss sward and live rosemary soils Decreases in torpedograss sward soil with carbon addition	Decreases with litter addition
Total biomass	Highest in torpedograss sward and live rosemary soils Increases in live rosemary soil with carbon addition Decreases in torpedograss sward soil with carbon addition	Increases with carbon addition, regardless of litter addition

Aboveground performance over time

Differences in tiller number were primarily observed in the second half of the experiment (Figure 3-6). Repeated-measures analysis of variance conducted on tiller counts from weeks 6-12 indicated an effect of soil type ($F_{24,587} = 2.42$, $p < 0.01$) and a soil x source population interaction ($F_{48,831} = 1.48$, $p = 0.02$). Planned contrasts on soil type showed that tiller production was significantly higher in soil from torpedograss swards ($F_{6,168} = 2.85$, $p = 0.01$), and tiller production in live rosemary soil was intermediate between that within torpedograss soil and the other three treatments ($F_{6,168} = 3.00$, $p = 0.01$). In the soil x population interaction, tiller production was greater in torpedograss from ABS than from the barrier islands when grown in soil from beneath dead rosemary shrubs, bare dunes, or near torpedograss swards. However, in torpedograss sward soil or soil from beneath live rosemary shrubs there was no population-based difference in performance. The litter addition experiment provides a little more resolution. In live rosemary soil (the only soil type used in this experiment, providing more replication and higher power), there was no effect of litter addition or carbon addition on tiller production, but there was a main effect of source population ($F_{22,112} = 1.92$, $p = 0.01$). There was a significant

trend in tiller growth, with ABS tillers performing best and Petit Bois Island tillers exhibiting the least growth (planned contrasts, $F_{11,56} = 2.38$, $p = 0.02$).
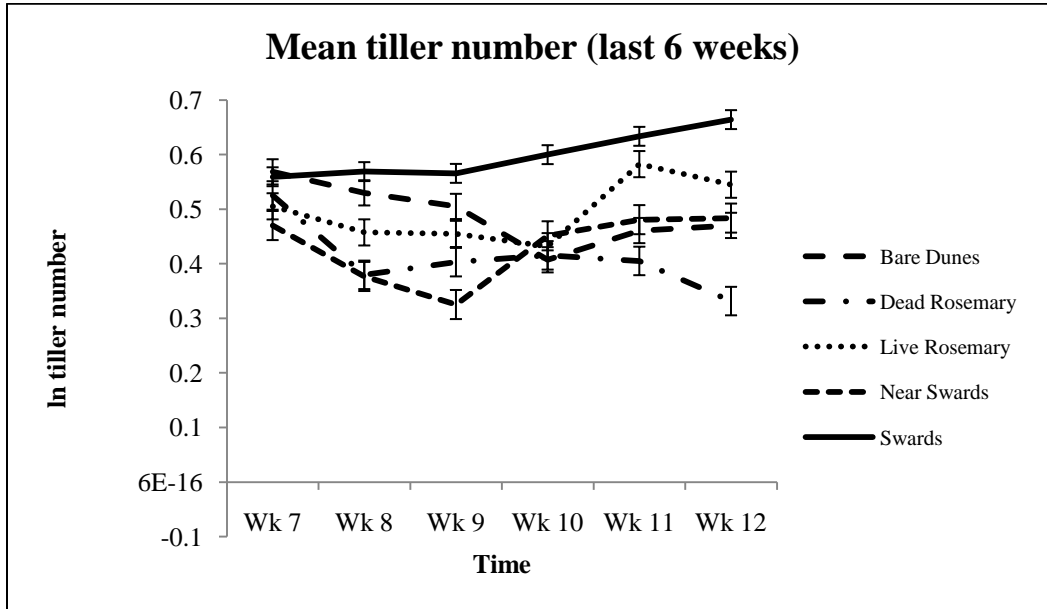
Figure 3-6: Changes in torpedograss tiller abundance over time. Error bars are ±1 standard error.

Soil type had a significant effect on changes in tiller height ($F_{44,614} = 1.72$, $p < 0.01$), showing a trend of green tissue production that was lowest in soil from bare dunes, near torpedograss swards, and dead rosemary shrubs; intermediate in soil from beneath live rosemary shrubs; and highest in soil from within torpedograss swards (planned contrasts, $F_{11,160} = 3.80$, $p < 0.01$). A significant soil x source population interaction ($F_{88,1059} = 1.33$, $p = 0.02$) was due to increased performance in tillers from the barrier islands within soil from torpedograss swards and live rosemary, while tillers from ABS performed well in all soil types (planned contrasts, $F_{11,160} = 2.42$, $p < 0.01$).

Neither litter addition, carbon addition, nor source population had a significant effect on the height of tillers grown in live rosemary soil.

73

Hydrocinnamic acid addition:

Slightly fewer than one-half of the rhizome nodes sprouted and produced aboveground tillers during the three-month experiment, although when they were uprooted at the end of the third month some unsprouted tillers were still alive and had begun to produce shoots. There was no significant effect of hydrocinnamic acid addition on survival (here defined as aboveground tiller production), relative growth rate, belowground growth, or aboveground growth; only initial rhizome node biomass affected survival (Wald $\chi^2 = 5.12$, $p = 0.02$). There was a strong positive correlation between log-transformed values for final total dry weight and initial rhizome biomass ($t_{111} = 14.00$, $p < 0.01$), so initial rhizome node size was included as a covariate in factorial analysis of above- and belowground biomass.

HCA addition negatively impacted growth rate relative to controls for torpedograss tillers from one source population, but not the other. In 2-way analysis of covariance on aboveground relative growth rate, the effect of tiller treatment with HCA approached significance ($F_{3,111} = 2.14$, $p = 0.10$), and tillers from ABS exhibited a higher RGR than those from Horn Island ($F_{1,111} = 4.77$, $p = 0.03$). Planned contrasts showed that HCA application significantly lowered aboveground growth relative to the control treatment, regardless of application concentration ($F_{1,111} = 5.20$, $p = 0.02$). When pots that did not sprout were excluded from analysis, ABS tillers still showed a higher growth rate ($F_{1,41} = 4.70$, $p = 0.04$), but there was also a significant source x HCA interaction ($F_{3,41} = 4.34$, $p = 0.01$). ABS tillers showed a negative response to HCA addition at all concentrations ($F_{1,41} = 15.96$, $p < 0.01$), including the low (25ppm) treatment ($F_{1,41} = 7.10$, $p = 0.01$), but Horn Island RGR showed no response relative to the control treatment (Figure 3-7). HCA tillers in the Horn Island control treatment performed unusually poorly, exhibiting a significantly lower RGR than that of ABS tillers in the same treatment (planned

contrasts, $F_{1,41} = 12.03$, $p < 0.01$), and this treatment may have been an anomaly. Aboveground biomass of tillers from Horn Island was significantly lower for medium and high concentrations of HCA than for low concentrations ($F_{1,41} = 8.69$, $p < 0.01$).
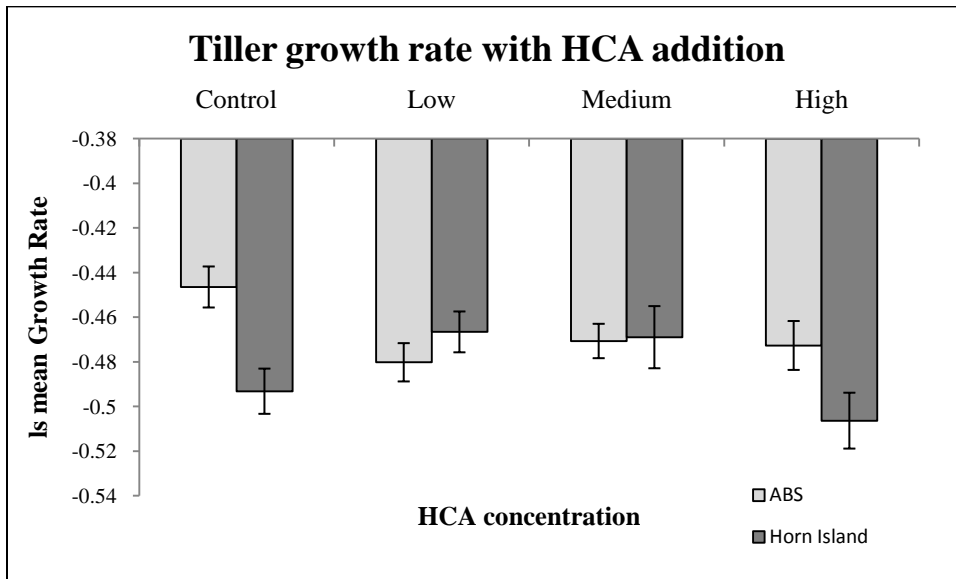
Figure 3-7: Response of surviving tillers to direct hydrocinnamic acid addition at low (25ppm), medium (200 ppm), and high (400 ppm) concentrations. Error bars are ±1 standard error.

Two-way analysis of covariance of final belowground dry weight indicated no significant impact of source population or treatment; only the initial rhizome biomass covariate was significant ($F_{1,111} = 11.26$, $p < 0.01$). When pots that did not sprout were excluded from analysis, source population became a significant factor ($F_{1,41} = 7.87$, $p < 0.01$), but ABS belowground biomass was consistently lower than Horn Island biomass, a reversal of the trend in aboveground growth.

Litter addition field study:

There was no effect of rosemary litter addition upon any measure of torpedograss performance in the field. In repeated-measures analyses of variance, there was a significant effect of site upon maximum torpedograss height ($F_{45,160} = 3.84$, $p < 0.01$), tiller number ($F_{63,192} = 3.41$, $p < 0.01$), and panicle number ($F_{63,192} = 5.08$, $p < 0.01$).

There was a significant effect of site on mean tiller persistence (Wald $\chi^2 = 34.07$, $p < 0.01$), but no effect of litter addition.

Discussion

This study provides partial support for the hypothesis that a native ecosystem engineer, *Ceratiola ericoides*, reduces the performance of an invasive, non-native grass, *Panicum repens*. In both the soil and the litter analyses, pots of torpedograss grown in live rosemary soil with non-activated carbon showed aboveground performance intermediate between pots treated with activated carbon and those without carbon addition. The significant increase in aboveground biomass in the presence of activated carbon compared to non-activated carbon is evidence for an allelopathic effect rather than inadvertent fertilization or nutrient sequestration. By contrast, carbon addition (with or without activation) decreased belowground and total biomass in torpedograss sward soil, the soil type otherwise associated with highest root biomass. The decrease in total biomass suggests this was not merely an allocation shift, and is unlikely to be a fertilization effect, but it is possible that the addition of carbon to this soil type, the most organic and probably the most nutrient-rich of the five types, facilitated the growth of microorganisms that reduced nutrient availability to torpedograss. That the reduction of biomass due to nutrient

immobilization would result from a reduction in root biomass instead of aboveground biomass is counterintuitive, however, and not consistent with an optimal allocation shift.

The negative effect of HCA addition upon torpedograss growth from ABS rhizomes also suggests that Florida rosemary may be capable of inhibiting torpedograss via allelopathy, at least in some populations of torpedograss. Although HCA addition did not reduce aboveground growth rate relative to Horn Island controls, pots receiving medium and high applications of HCA produced less aboveground biomass than pots receiving low applications of HCA in this treatment. The control treatment may have performed poorly due to chance, or there may be differences in sensitivity to HCA among torpedograss populations. In this study, rhizome node size impacted tillers' ability to produce aboveground biomass and gain access to photosynthetic energy sources, but once green tissue sprouted, rhizome node size ceased to be a statistically significant factor in tiller performance. These thickened nodes appeared to contribute greatly to its ability to survive, concurring with prior observations that "ginger-like" rhizomes represent a way for torpedograss to store resources (Hossain et al. 1999).

I did not observe any evidence that Florida rosemary inhibits belowground growth of torpedograss. Two experiments tested for a belowground effect of live rosemary soil, litter addition, or HCA addition on torpedograss. Litter addition reduced root biomass, but this effect could not be definitively linked to allelopathy because carbon addition did not improve root biomass. During the course of the experiment, litter added to the soil surface formed a dense mat. There was no reduction in tiller production associated with litter addition, suggesting that this litter mat does not mechanically inhibit the emergence of new torpedograss stems, but it may have reduced water loss through evaporation, allowing torpedograss to allocate more resources to aboveground growth rather than its root network and producing the observed reduction in root

biomass relative to controls. (While plastic chips were added to the other treatments in an attempt to compensate for the addition of material to the soil surface, these chips had a tendency to splash out during rainfall events and may not have effectively mimicked the addition of organic litter.) Direct HCA addition also had no effect on belowground biomass, reinforcing the conclusion that Florida rosemary cannot inhibit torpedograss root growth. This is a distinct difference from the effect of Florida rosemary on root growth in recently germinated native bunch grasses (Richardson and Williamson 1988).

Assuming the rosemary litter added to the pots indeed yielded hydrocinnamic acid (as the sour scent under moist, sunny conditions during the study period suggested), the results of the HCA addition study would suggest that litter addition should have had a negative effect on aboveground biomass. My failure to observe such an effect may be due to other inadvertently positive effects of litter addition (such as increasing soil moisture retention) or the effect may have been masked within the negative impact of live rosemary soil, which was the only soil type to which litter was added.

Litter also failed to elicit a negative response from torpedograss in the fourteen-month field study, despite the observed effects of rosemary soil and hydrocinnamic acid in an experimental setting. This suggests that the allelopathy associated with Florida rosemary litter might not be powerful enough to significantly inhibit the spread of torpedograss within field conditions over longer periods of time. However, because I was unable to locate torpedograss growing in the rosemary scrub in Florida, my study sites were located along roadsides, where the impact of scrub soil chemistry and competition with Florida rosemary and other scrub species could not be tested. These synergistic effects may be of great importance (see Chapter 2).

Soil taken from beneath dead rosemary shrubs included dead stem tissue to account for the possibility that skeletons of rosemary shrubs might provide allelochemicals, a hypothesis with some indirect support that has not yet been tested (Quintana-Ascencio and Menges 2000, Hunter and Menges 2002). I found no evidence of inhibition by dead rosemary tissue in this experiment, as soil from beneath dead rosemary shrubs did not differ consistently from soil from bare dunes or areas near torpedograss swards, and carbon addition did not improve torpedograss growth in soil from beneath dead rosemary shrubs. However, this question bears closer examination as I did not test direct inhibition by tissue washes, a more frequent method for examining allelopathic effects.

Torpedograss from Archbold Biological Station consistently performed better compared to torpedograss collected from populations on the barrier islands in all but two cases. First, ABS tiller belowground biomass was generally lower than Horn Island tiller belowground biomass in the HCA addition experiment. Second, in repeated-measures analysis of aboveground biomass in the shadehouse experiment, the differences in performance based on source population disappeared when tillers were grown in soil from torpedograss swards or live rosemary shrubs. Otherwise, the overall trend from greatest performance in ABS tillers to poorest performance in Petit Bois Island tillers was overwhelming. Transplant effects probably account for some of these differences, since barrier island tillers were moved several times and endured a longer out-of-soil holding time before the shadehouse experiment. When ABS tillers were held out-of-soil longer than Horn Island tillers (prior to the HCA addition experiment), ABS belowground biomass was reduced relative to Horn Island belowground biomass. Another possibility is that available reserves differed among source populations. In the shadehouse study when Horn and Petit Bois Island tillers were grown in live rosemary soil or soil from beneath torpedograss

swards, they produced as much aboveground biomass as ABS tillers. These two soil types may have differed from the others because they possessed a greater amount of soil organic matter (see Chapter 2), and therefore were likely to have a higher nutrient content. Tiller production in all but these two soil treatments also dropped off drastically in the last half of the study. This suggests that a depletion of soil nutrients, compounded by exhaustion of nutrient stores that varied among populations based on holding time, is a better explanation for variation in tiller performance than genetic differences among populations. The especially poor performance of torpedograss from Petit Bois Island may also be partially attributable to the condition of available tillers, since fewer suitable tillers were collected from the sparse population there. As a result, tillers selected for the shadehouse experiment were less likely to be in optimal condition than tillers from Horn Island or ABS.

The use of activated carbon is frequently cited (Mahall & Callaway 1992, Nilsson 1994, Callaway & Ashehoug 2000, Ridenour & Callaway 2001, Prati and Bossdorf 2004, Abhilasha et al. 2008) as an important demonstration of allelopathy in plant ecology: If the presence of a plant or plant extract reduces the growth of a competitor species, but addition of activated carbon eliminates the adverse effect, allelopathy is supported as a mechanism for inhibition. Incontrovertible evidence for allelopathy can be difficult to collect, and the use of activated carbon can be a powerful tool in that regard; but its use has recently come under question, as the addition of carbon to the soil may cause unintended changes in plant growth unrelated to allelopathy, including inadvertent fertilization, pH alteration, and capture of allelopathic chemicals universally present in the potting media (Lau et al. 2008). It is likewise possible that activated carbon, like sources of non-activated carbon (e.g., sawdust), may decrease plant biomass by creating a substrate for the growth of bacteria, which then sequester nutrients and

reduce their availability to roots (Blumenthal et al. 2003). My results support the caution that Lau et al. (2008) advise in the interpretation of results of activated carbon addition.

I suggest the use of non-activated carbon as a potential method for separating chemical adsorption from unintentional alteration of growth rates, a method I used here with some success. Since the process of activation removes tars and increases porosity, and thus the surface area available for binding allelochemicals (Cheremisinoff & Ellerbusch 1978), non-activated carbon could reveal any unintentional consequences of carbon addition but be less efficient at removing any allelochemicals. If carbon is altering performance by reducing allelopathy, activated and non-activated carbon ought to have effects of the same direction, but different magnitudes. If the addition of carbon is having an unintentional effect on plant growth, then the magnitude of the change is more likely to be similar.

Each of the three tests described here explored a different aspect of Florida rosemary's ability to inhibit torpedograss growth, and each design had its own strengths. The shadehouse experiment separated the effects of rosemary litter addition from soil-based differences in performance, but was complicated by the addition of activated carbon and the inability to quantify the effective concentration of HCA being added to treated pots. The hydrocinnamic acid addition experiment was less biologically realistic, but offered a direct test of inhibitory response to HCA at known concentrations, chosen to be similar to concentrations expected in the rosemary scrub, and eliminated the uncertainty of variation in initial aboveground photosynthetic material. Finally, the field study examined the effects of rosemary litter addition upon torpedograss over fourteen months of exposure to regional environmental conditions, although neither the effective concentration of allelochemical nor belowground response to litter addition could be tested.

The results of this study (summarized in Table 3-2) suggest that Florida rosemary may be capable of inhibiting aboveground, but not belowground, growth of torpedograss tillers. This inhibition does not necessarily result directly from litter addition to the soil surface, but is apparently caused by some lasting characteristic of soil associated with living Florida rosemary shrubs. The negative effect of HCA and the ability of carbon addition to improve growth in live rosemary soil are complementary evidence that allelopathy may be at work. Although HCA and its similarly inhibitory product acetophenone are microbially decomposed and do not persist for more than 5 or 6 days (Jordan 1990), it is possible that rosemary litter mixed into the soil can continue to release inhibitory compounds over long periods of time as it decays. Alternately, microbial communities associated with living rosemary shrubs may play a role in inhibiting torpedograss growth. Exotic plant cover has been negatively correlated with the cover of cryptobiotic soil crusts (Stohlgren et al. 2001), but several components of microbial soil crusts in the scrub decrease rather than increase with proximity to rosemary shrubs, perhaps due to allelopathy (Hawkes and Fletcher 2002). This suggests that any negative effect of soil crusts on torpedograss growth should be weaker, rather than stronger, in soil taken from beneath living rosemary shrubs.

Table 3-2: Summary of results related to the allelopathic effects of Florida rosemary on torpedograss tillers.

Experiment	Aboveground performance	Belowground performance
Shadehouse study **(Soil, litter, and carbon treatments)**	Carbon addition increases growth in live rosemary soil	Highest in live rosemary & sward soil Litter addition decreases growth in live rosemary soil Carbon addition decreases growth in sward soil
HCA addition	All concentrations reduced aboveground biomass relative to ABS control (but possible reduced sensitivity in Horn Island tillers)	none
In situ litter addition	none	N/A

To the best of my knowledge, all previous studies of Florida rosemary's allelopathic effects have been conducted on seeds and their germinants. It is possible that Florida rosemary's best window of opportunity for inhibition occurs early in the life of grasses, and that torpedograss, which spreads primarily (perhaps exclusively in North America) via rhizomes, is less responsive than native bunch grasses to the effects of hydrocinnamic acid. Wilcut et al. (1988) report that torpedograss produces no viable seed in North America, and Smith (in Sutton 1996) found no more than one seed in one thousand to be viable in Florida. In a germination test I attempted to conduct in 2009 using seeds collected from Archbold Biological Station, controls completely failed to germinate. Torpedograss can re-sprout from a single rhizome node, so mild inhibition of aboveground biomass may be insufficient to have an overall impact on the growth of this invasive species in the field, as suggested by the roadside litter addition study. This suggests a corollary to the Novel Weapons Hypothesis: A species may become invasive in part because it possesses morphological or life-history characteristics that make it less vulnerable to defense mechanisms of species that coevolved with one another, but not the invader, in its introduced range.

However, little is known about the importance of allelopathic effects under field conditions in the scrub (Menges & Hawkes 1998), and some authors have suggested that even moderate allelopathic inhibition can impact community composition (Prati and Bossdorf 2004). Others have called attention to the importance of designing bioassays with ecological relevance (Romeo & Weidenhamer 1998) and observed that allelochemicals and their actions are influenced by soil chemical ecology, sometimes resulting in indirect effects that may be more important than direct inhibition (Inderjit & Weiner 2001). The mild reduction in aboveground torpedograss growth observed in the shadehouse and HCA addition experiments, when coupled

83

with resource competition or soil chemistry, may be far more potent than the effect of litter addition alone under conditions where torpedograss has been long-established in monoculture or in association only with other grasses and sedges. Rosemary scrub in general, and the Mississippi barrier islands in particular, also contain other species with suspected allelopathic effects, including the abundant woody goldenrod, *Chrysoma pauciflosculosa* Michx. (Eleuterius 1979). The results from this study cannot address the synergistic effects of an intact scrub community upon torpedograss growth. Torpedograss spreads rapidly and is resistant to eradication, and adult rosemary shrubs can take a decade to reach reproductive age and are large and difficult to transplant intact; these characteristics make the testing of competitive interactions through transplant experiments a serious challenge to future study.

Rosemary scrub is by nature a transient ecosystem, sometimes described as the rosemary phase of sand pine scrub (Abrahamson 1984), and requires infrequent fires in order to avoid being overgrown. Florida rosemary may reduce the frequency of proximate fires by inhibiting seed germination and radicle growth of native grasses (Fischer et al. 1988, Richardson and Williamson 1988, Williamson et al. 1992). Conner et al. (1989) liken disturbance from hurricanes to fire events in terms of their impact upon the maintenance of disturbance-dependent ecosystems, and point out that coastal plant communities have had ample time to adapt to periodic disturbance by tropical storms. However, when an invasive species such as torpedograss enters the picture, the rules change. Because unlike native scrub grasses, torpedograss spreads primarily through clonal growth, torpedograss may be less susceptible to allelopathy from Florida rosemary. Although as a facultative wetland plant it may not grow as well on the dune ridges preferred by Florida rosemary, torpedograss can survive and spread amply under dry conditions (Holm 1977, Wilcut et al. 1988b, Akamine et al. 2007). Florida

rosemary seedlings at lower elevations therefore may be particularly vulnerable to invasion by this pervasive grass following frequent large-scale disturbances. If local flammability and fire frequency increase, extant rosemary balds may shrink or gradually be replaced by a system with a different community assemblage and fire regime and fewer bare patches to serve as refugia for gap-dependent, obligate seeders between fires. Florida rosemary has shown some ability to inhibit aboveground torpedograss growth, but it is uncertain whether or not this form of ecosystem engineering, combined with competition and other emergent properties of the scrub community, is sufficient to prevent invasion of the rosemary scrub by torpedograss in a real-world setting. In the century since visitors to Horn and Petit Bois Island first observed torpedograss on the barrier islands, this invader has not yet permanently invaded the rosemary scrub. However, if the frequency or severity of hurricanes increases over the next few decades as current models predict (Goldenberg et al. 2001, Trenberth 2005, Webster et al. 2005, Hoyos et al. 2006, Knight et al. 2006, Black et al. 2007, Saunders & Lea 2008; but see Emanuel 2005), then the balance between native community and exotic invader on these two barrier islands could shift in unexpected ways. A greater understanding of the defenses that native species can bring to bear, as individuals and as a community, may allow us to better predict the impact of torpedograss invasion upon these and other examples of the rosemary scrub association.

IV: ROADSIDE POPULATIONS OF INVASIVE PANICUM REPENS: SOURCES OF

INVASION INTO UNDISTURBED COMMUNITIES OR INVASION SINKS FROM

DISTURBED HABITATS?

Abstract

Panicum repens L. (torpedograss), a perennial, rhizomatous C_4 grass, is an aggressive invader in many parts of the world. This species frequently occurs in roadsides and in other, larger disturbed habitats. Roads have the potential to serve as dispersal corridors for this species and possibly as sources of invasion into pristine scrub habitat in south Florida. In order to determine whether ramet population growth rates differed between roadside populations adjacent to different habitats, I quantified torpedograss density, growth, and panicle production at ten roadside sites at Archbold Biological Station every other month for 14 months. Four populations were adjacent to disturbed pasture containing established populations of torpedograss, while six populations were adjacent to undisturbed scrub lacking torpedograss. Growth rate from 2009 – 2010 was negative in five of the six sites bounded by scrub, and positive in three of the four sites bounded by old pastureland containing torpedograss, and I observed no evidence of invasion of undisturbed scrub, results consistent with the hypothesis that roadside populations of this species were sinks rather than sources of invasion. I observed no evidence of recruitment from seed and the majority of vegetative recruitment occurred between February and June, during which adjacent scrub sites, if disturbed, might be unusually vulnerable to invasion. Results suggest that

land managers should give higher priority to restoring disturbed pasture to scrub than to eradicating roadside populations of this species.

<u>Introduction</u>

Exotic invaders are frequently ranked as a threat to rare and endangered species in the United States second only to habitat destruction (Wilcove et al. 1998). Because roadsides represent frequently disturbed habitats that are unusually interconnected and free of normal ecological barriers to dispersal, it has been suggested that they may act as corridors facilitating the movement of invasive species across great distances, or serve as points of establishment for invasive plant propagules, after which encroachment into previously uninvaded adjacent habitat may occur (Pauchard and Alaback 2003, Hansen and Clevenger 2005, Christen and Matlack 2009). Alternately, roadsides may represent an exploitable habitat for non-native species without contributing to the invasion of nearby communities (Christen and Matlack 2006, Kalwij et al. 2008), effectively functioning as sinks rather than sources for invasive plants.

Whether roadsides are sources of invasive propagules or sinks where non-native species persist, but from which they do not spread, is a distinction with great implications for invasive species management plans. If roadsides act as corridors, then careful monitoring and investment in early eradication of invasive colonists is an important strategy, particularly if corridors are in place to facilitate interconnectivity among fragmented populations of declining native species. However, if non-native species flourish along roads but cannot use them as a staging ground for invasion, then they may be of lesser concern unless the adjacent habitat is rendered vulnerable through disturbance. The function of roadside populations is likely to vary depending on factors including the nature of the adjacent community, its disturbance regime and hence resource

87

fluctuation (Davis et al. 2000), road substrate and its similarity to the surrounding habitat (Greenberg et al. 1999), and individual life-history characteristics of potential invaders (Christen and Matlack 2009).

I monitored populations of *Panicum repens* L., an invasive rhizomatous grass, for fourteen months in order to determine whether sandy roadsides in the Lake Wales Ridge, Florida act as a propagule sink from neighboring pasture and disturbed scrub or as a source of invasion into adjacent undisturbed scrub habitat. In addition, I examined patterns of tiller persistence, density, and panicle production in association with local seasonal variation that might impact the spread of torpedograss in this region. Determining whether roadsides facilitate invasion of native scrub habitat by torpedograss and characterizing its seasonal growth patterns may provide valuable insight into ways in which this species, and perhaps other invaders with similar characteristics, may be effectively controlled while exploring an important question in invasive species biology.

Materials and Methods

Study species and location

Torpedograss (*Panicum repens* L.) has long been recognized as a troublesome invader in the United States (Tabor 1952) and as a weed of numerous crops elsewhere in the world. A perennial, rhizomatous C_4 grass, torpedograss is cold-intolerant and grows within the tropics and subtropics from approximately 35° S to 43° N latitude (Holm et al. 1977). Although its origins are uncertain as it is now found worldwide, it is believed to have been introduced to North America either as cattle forage or in the ballast of lumber ships (Tabor 1952), and now thrives in the southeast, Hawaii, and California; the first recorded collection of torpedograss in the United

States occurred in 1876. The grass is extremely difficult to eradicate once established (Holm et al. 1977, USDA NRCS 2007) and is currently listed as a noxious weed in four states (USDA NRCS 2007). When introduced into an area, torpedograss spreads rapidly, primarily (perhaps entirely) through rhizomatous clonal growth, although it also produces wind-dispersed seeds. Although it is a facultative wetland plant and can establish itself and flourish under flooded conditions (Sutton 1996, Hanlon and Brady 2005), torpedograss is also highly drought-resistant (Holm et al. 1977, Wilcut et al. 1988b). Torpedograss is listed as a Category I invasive species in the state of Florida (FLEPPC 2009), where it is present in many public lakes and rivers, some of which have been heavily impacted (Bodle and Hanlon 2001, Hanlon and Brady 2005).

Archbold Biological Station ("Archbold"), located in Highlands County, Florida, occupies over 5,000 acres on the southern end of the Lake Wales Ridge and adjoins the 3500+ acre Archbold Reserve ("the Reserve"). It is among the largest intact representations of natural southern ridge habitat remaining, composed chiefly of xeric plant communities within sandhills, flatwoods, and scrub assemblages (Abrahamson 1984). Torpedograss is seldom seen growing within the scrub community at Archbold, but occurs frequently in firelanes (sandy roadsides), along the edges of Lake Annie, and on the adjoining Reserve, where the removal of invasive exotics and pasture grasses, including torpedograss, and the restoration of native habitats is a long-term goal (ABS 2011). The pasture and disturbed scrub of the Reserve (sometimes generalized hereafter as pasture) adjoin Archbold along the west boundary firelane, a sandy road approximately 10m wide.

Methods

In June 2009, I chose ten sites at Archbold Biological Station where torpedograss was abundant along the edges of the west boundary firelane and two perpendicular roads cutting across the interior of the Archbold scrub. Four of the sites were on the Reserve side of the west boundary firelane, adjacent to well-established populations of torpedograss (designated P1 – P4). The other six sites were on roadsides adjacent to undisturbed scrub: Three on the scrub-side of the boundary firelane bordering the Reserve (RS1 – RS3) and three on interior roads within Archbold (IS1 – IS3; Figure 4-1). At each site, six 25cm radius plots were randomly established along a 20 or 30 meter transect with at least 1 meter between plot edges for a total of sixty plots. Tillers were defined as individual upright stems not visibly connected to another stem above the soil surface. Tiller number, maximum tiller height, and panicle production (i.e., the flowering raceme, which was not included in measurements of maximum tiller height) were assessed at the beginning of the study and every other month through August 2010. (Maximum tiller height data collection began in August 2009 rather than June 2009.) Tiller persistence was estimated by marking five tillers per plot with colored plastic ties, then recording survival of these tillers over time. When a tiller died, another tiller was chosen randomly. Half of the plots were treated with litter from *Ceratiola ericoides* Michx. (Florida rosemary) to evaluate torpedograss response to potential allelopathic effects from this native shrub (see Chapter 3), but statistical analysis indicated no difference in any of the measured parameters between treated and untreated plots, so they are all included in analysis here.
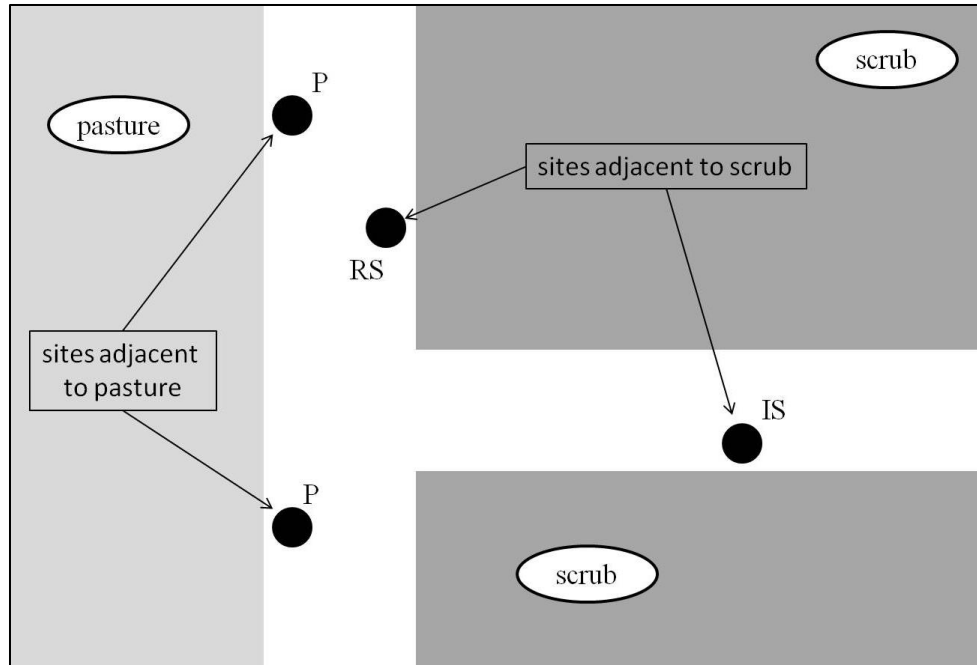
Figure 4-1: Illustration of torpedograss plot location types relative to undisturbed scrub or grass-dominated pasture. IS = plot adjacent to interior scrub; RS = plot adjacent to undisturbed west boundary scrub; P = plot adjacent to pasture and disturbed scrub.

One plot was lost during the study due to disturbance by feral hogs, resulting in a final sample size of 59. To determine if torpedograss abundance was increasing or decreasing at each site, I calculated an exponential growth rate constant (*r*) for each plot using the formula

$$r = \frac{ln(N_t) - ln(N_0)}{t}$$

for the time period of August 2009 – August 2010 ($t = 1$ year; N represents tiller density). I used ANOVA to determine the effect of site and site nested within adjacent habitat type (boundary scrub, interior scrub, or pasture) upon growth rate. Tiller density data were log-transformed before analysis by repeated-measures ANOVA.

A Survival/Reliability test (JMP 5.0.1a, SAS Institute Inc.) was used to analyze the persistence of marked tillers. Persistence was defined as the number of months between the time a tiller was randomly selected and marked until the month it was found dead. Tillers that could

not be relocated were excluded from analysis. Tillers that were alive at the end of the study were

identified as censored individuals for the Survival/Reliability test, which accounts for the

unknown fate of individuals that were still surviving when data collection ended. Tillers that

were not obviously new recruits when they were selected and marked (very newly emerged

blades were paler green and had not completely unfurled) were assumed to be at least one month

old at the time of selection, so an additional month was added to their persistence score. I tested

for the effect of site, adjacent habitat type, and the month in which tillers were marked upon their

persistence.

Results of the bimonthly tiller counts were used to establish general seasonal patterns of

tiller abundance, height, and panicle production. I used repeated-measures ANOVA to

determine the effect of site upon these parameters. Monthly mean tiller densities across all sites

were compared via multiple linear regression with monthly mean temperature, relative humidity,

drought index, and rainfall, all factors not significantly correlated with one another with the

potential to impact growth of this moisture-loving, warm-climate grass. Climate data were

collected by Archbold Biological Station's Automated Main Weather Station and accessed with

permission.

Results

Mean per capita instantaneous growth rate was positive for torpedograss plots adjacent to

pasture and negative for torpedograss plots adjacent to scrub (Figure 4-2). Growth rate (r) was

significantly higher in sites adjacent to pasture than in sites adjacent to scrub in a nested

ANOVA ($F_{1,49} = 19.17$, $p < 0.01$). Growth rate also varied by site within habitat type ($F_{8,49} =$
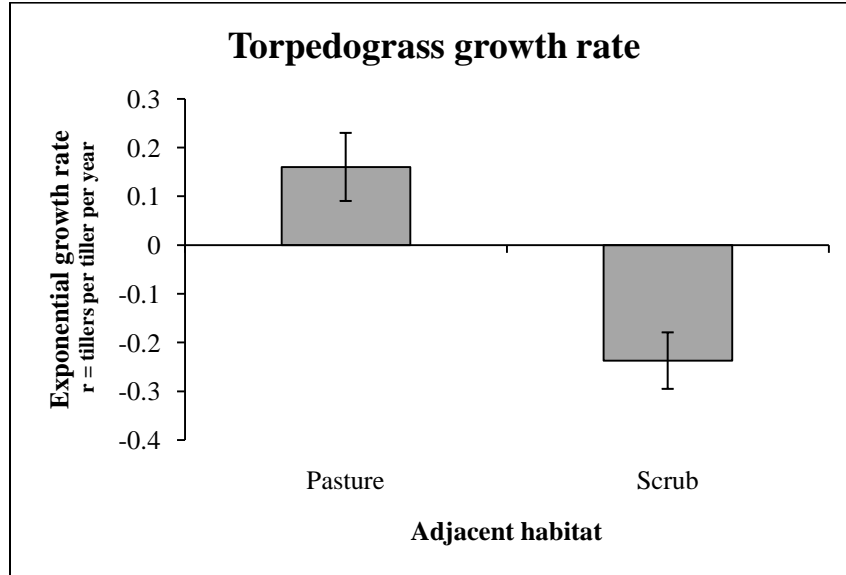
2.49, $p = 0.02$).

Figure 4-2: Per capita instantaneous growth rate means for torpedograss sites adjacent to pasture and scrub. Error bars are ±1 standard error.

Sites adjacent to pasture had higher growth rates than sites adjacent to boundary scrub, which in turn exhibited higher growth rate than sites adjacent to interior scrub (Figure 4-3). Site nested within habitat type was not significant in a nested ANOVA when adjacent scrub was specified as interior (IS) or boundary (RS), but plot type remained significant ($F_{2,49} = 13.10$, $p < 0.01$). In planned contrasts, both IS and RS had a lower mean growth rate than sites adjacent to pasture ($F_{1,49} = 19.17$, $p < 0.01$), and IS sites had a significantly lower mean growth rate than RS sites ($F_{1,49} = 7.52$, $p < 0.01$).
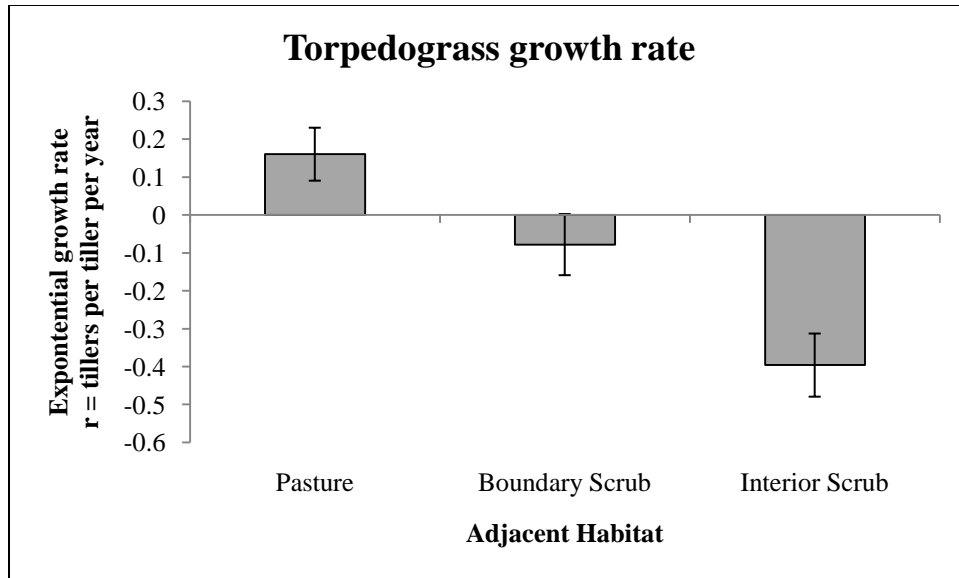
Figure 4-3: Mean growth rate of torpedograss adjacent to pasture, Reserve boundary scrub, or interior scrub. Error bars are ±1 standard error.

Adjacent habitat did not affect tiller longevity, although tiller persistence varied among sites (Figure 4-4). Tillers initiated in February tended to be the longest lived, with persistence decreasing steadily throughout the rest of the calendar year except for the month of June (Figure 4-5). A Survival/Reliability test indicated a significant effect of site (Wald $\chi^2 = 20.15$, $p = 0.02$) and month tagged (Wald $\chi^2 = 353.52$, $p < 0.01$) on persistence, but not adjacent habitat (Wald $\chi^2 = 0.50$, $n.s.$).
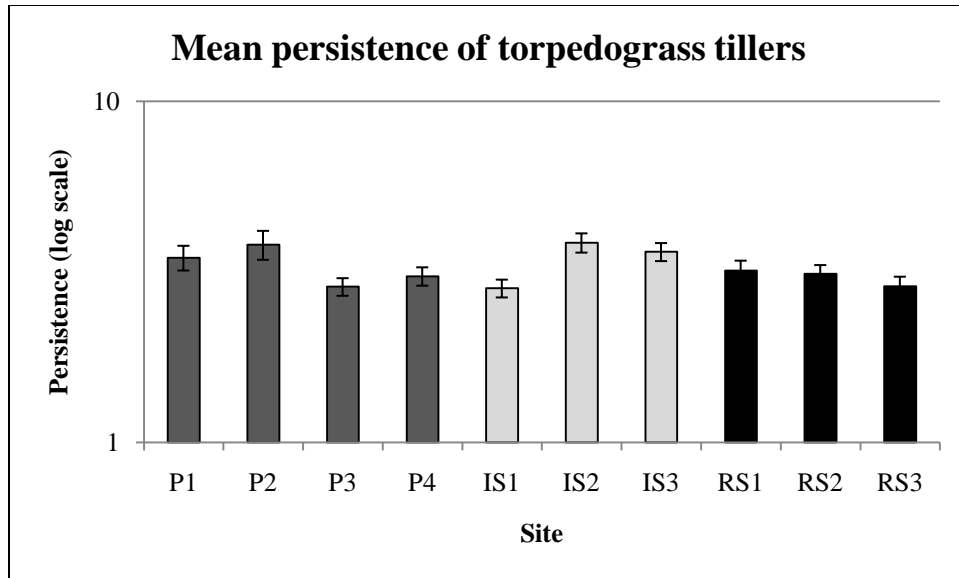
Figure 4-4: Differences in mean tiller persistence at ten sites. Labels indicate adjacent habitat: P = pasture; IS = interior scrub; RS = boundary scrub. Error bars are ±1 standard error.
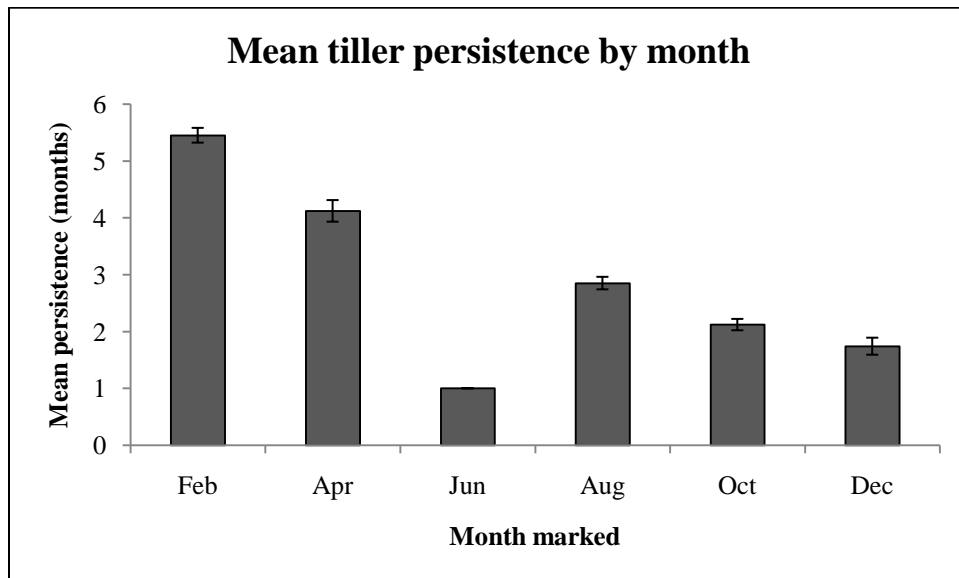
Figure 4-5: Mean tiller persistence based on the month tillers were marked for tracking. Error bars are ±1 standard error.

Seasonal variation:

Tiller density peaked between July and September and was lowest during the winter months, when temperatures at Archbold were coldest (Figure 4-6). In February, some plots

contained no living tillers. Density was consistently greatest at site P3 and lowest at sites IS2

and IS3 (Figure 4-7). In a repeated-measures ANOVA there was a significant effect of time

(main effect: $F_{7,43} = 151.91$, $p < 0.01$) and site (site x time interaction: $F_{63,248} = 3.63$, $p < 0.01$) on

tiller density.
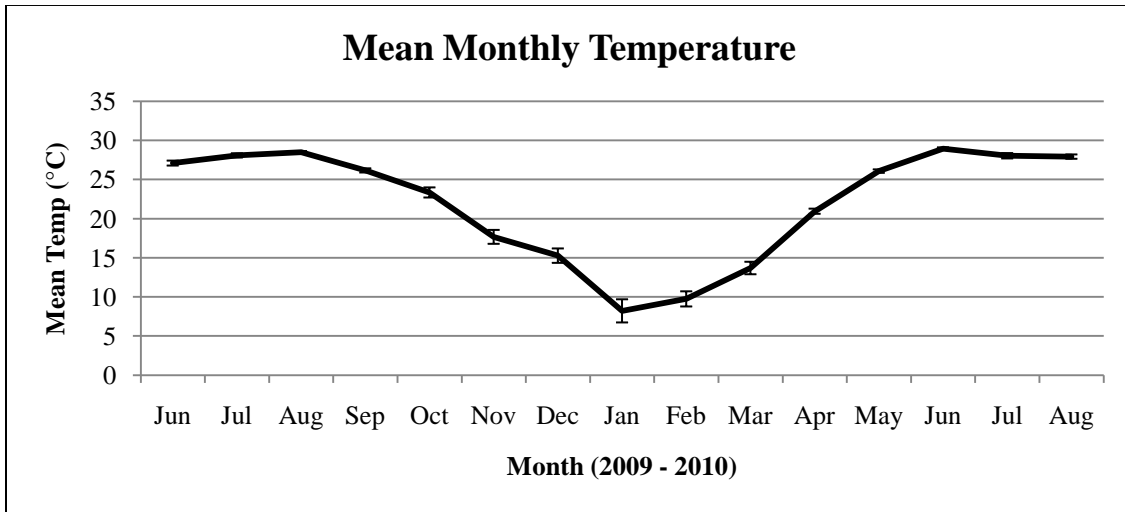
Figure 4-6: Average monthly temperatures at Archbold Biological Station, summer 2009 - 2010. (Data from ABS Automated Main Weather Station.) Error bars are ±1 standard error.
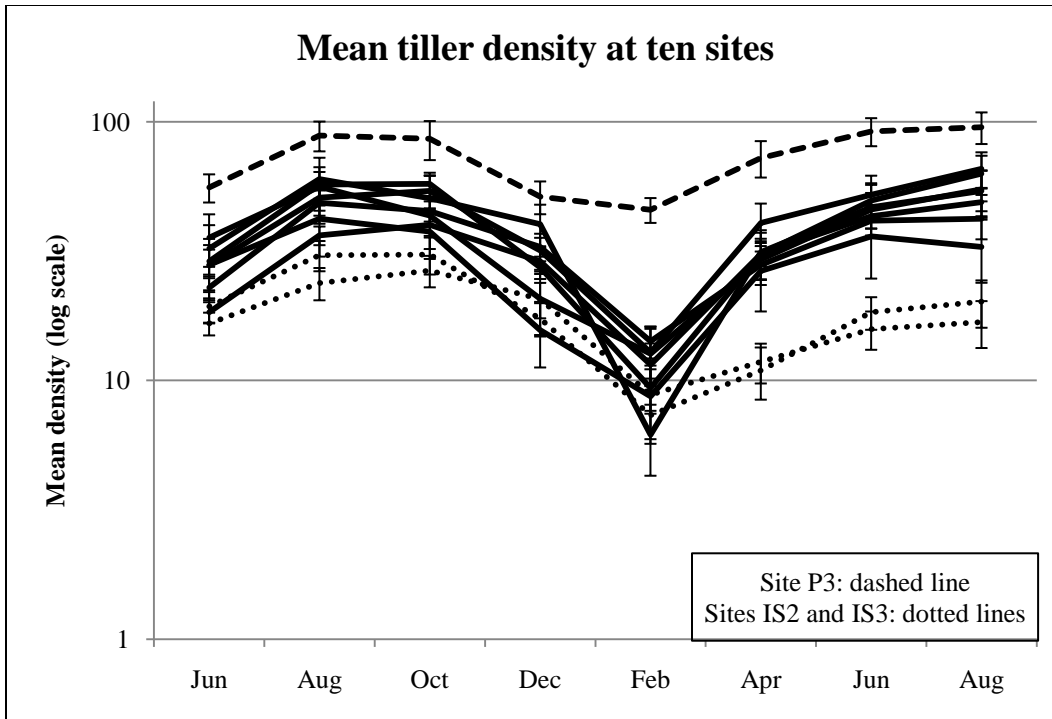
Figure 4-7: Differences in mean tiller density among sites over a 14-month period. Error bars are ±1 standard error.

The best model predicting variation in torpedograss density included monthly mean temperature and relative humidity, and predicted over 90% of mean density according to a backward stepwise multiple linear regression (Table 4-1). Other factors eliminated from the model included average monthly rainfall and drought index.

Table 4-1: Potential models predicting torpedograss density. All data are monthly means. DI = drought index, R = rainfall, RH = relative humidity, T = temperature. An asterisk indicates the best model.

Model	R^2_{adj}	AIC_a	Δi	w
T+RH*	0.91	25.74	0.00	0.59
T+DI+RH	0.92	26.60	0.86	0.38
T+R+DI+RH	0.89	32.14	6.40	0.02
T	0.62	35.37	9.63	0.00

Panicle production began between April and June, with the maximum rate of production occurring between June and August. All panicles were dead by December (and probably earlier), though some dead stems persisted into the next flowering season. Dead stems were no longer included in panicle counts once green stems began emerging. Repeated-measures ANOVA indicated that panicle production varied across sites ($F_{63,248} = 5.42$, $p < 0.01$). During August and October, peak flowering time for torpedograss in this study, Sites RS2 and P3 produced the most panicles. Sites IS2 and IS3 produced the fewest panicles.

Maximum tiller height exhibited a similar pattern across all sites since bolting precedes flowering, and reached a maximum from August to October, although mean height differed significantly among sites (Figure 4-8). Repeated-measures ANOVA indicated a significant effect of time ($F_{5,45} = 254.21$, $p < 0.01$) and site (time x site interaction: $F_{45,204} = 3.77$, $p < 0.01$) on tiller height.
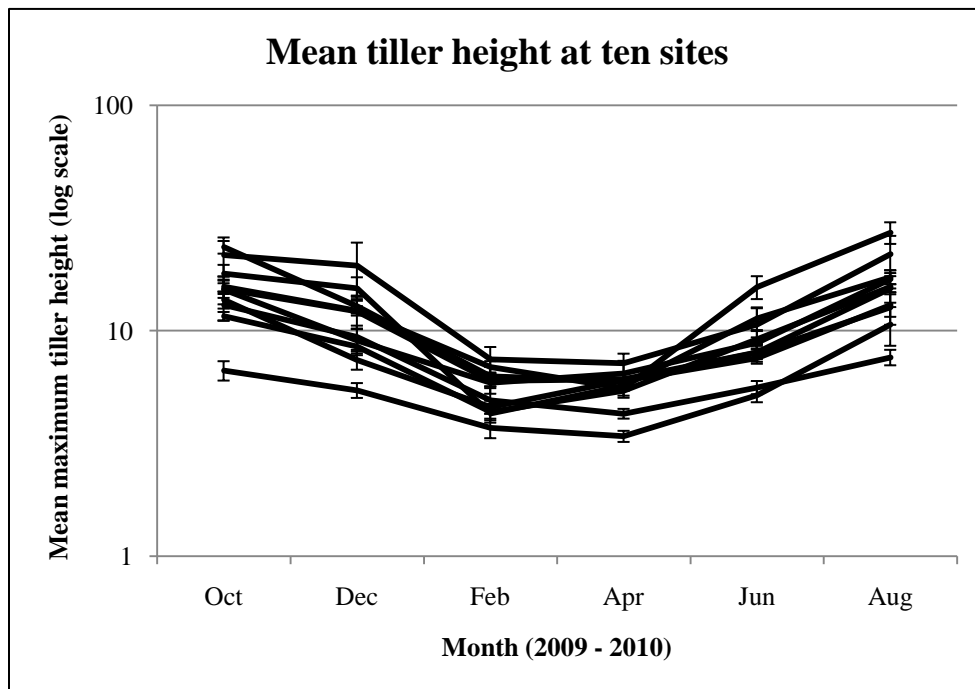

Figure 4-8: Differences in mean torpedograss tiller height from October 2009 to August 2010. Error bars are ±1 standard error.

Discussion

Propagule pressure has been suggested as an important component of invasibility (Levine 2000, Von Holle and Simberloff 2005). I found that growth rates of torpedograss along roadsides were greater in populations adjacent to pastures containing established populations of torpedograss than in populations along roadsides adjacent to undisturbed scrub. Differences in ramet population growth rates between pasture edge populations and scrub edge populations were attributable to differences in rates of tiller addition and not to differences in ramet survivorship. Although I was not able to trace the origin of newly initiated tillers, it seems likely that at least some tiller addition within roadside edges adjacent to pasture originated from within pasture population. Because most scrub edge populations were declining (and declining more rapidly in interior roads than in boundary roads) and most pasture edge populations were increasing, dispersal from disturbed pasture habitats could play an important role in rescuing roadside populations from local extinction. If this hypothesis is correct, then managers should give higher priority to restoring pasture to scrub than to treating roadside patches of torpedograss. Although the soil disturbance associated with roadsides may reduce competition from native vegetation and thus promote colonization by torpedograss, the smaller size of roadside populations could make them vulnerable to stochastic extinction. Cutting off the source of the propagules could play a vital role in limiting the spread of this species.

Exotic species seldom invade the Florida scrub without disturbance, and the xeric scrub ecosystem may be somewhat invasion-resistant even when disturbed (Greenberg et al. 1997), but it is possible that communities could be vulnerable in the wake of fires or following soil agitation (Menges 1999). I found no evidence of scrub invasion by torpedograss during this study, and while roadsides at Archbold represented a sink for torpedograss propagules, they did not appear

99

to provide a source of invasion into undisturbed habitat. Reducing or removing torpedograss abundance in roadside habitats adjacent to scrub by reducing propagule supply from the Reserve may be especially beneficial at Archbold, since these habitats sometimes function in a manner similar to gaps, and may provide refugia to endemic gap specialists in the absence of fire (Hawkes and Menges 1996, Petrů and Menges 2004, Quintana-Ascencio et al. 2007).

Seasonal torpedograss density was strongly tied to relative humidity and temperature, which together predicted 91% of its variation. This supports previous observations that torpedograss sprouting is temperature-limited; Hossain et al. (2001) did not observe sprouting below 5°C and reported increased and accelerated sprouting as temperatures increased from 10-20°C to 20-35°C. Relative humidity was a better predictor than rainfall, suggesting that water loss during transpiration was a greater challenge to torpedograss than was availability of soil water. Similarly, drought index was not a good predictor of torpedograss abundance; the species has previously been described as drought-resistant (Holm et al. 1977, Wilcut et al. 1988b). Akamine et al. (2007) provide evidence that the swollen "ginger-like" rhizome nodes characteristic of torpedograss promote drought resistance by storing moisture, as decreased sprouting was associated with lower moisture content in these structures.

Month-dependent differences in tiller persistence were also seasonal in nature. Except for the month of June, for which sample size was relatively small ($n = 39$) compared to other months ($50 \leq n \leq 329$), mean tiller persistence decreased with time since the beginning of the growing season (February-April). New recruits were observed during the months of December and February as well as in April, so some degree of torpedograss recruitment appears to occur throughout the year in south-central Florida's climate, but the bulk of recruitment occured from

February through June. Tillers that sprouted later in the year were likely to survive for shorter spans of time before succumbing to winter dieback.

The most aggressive period of torpedograss tillering at the study sites occurred between February and June, at which time adjacent sites, if disturbed, might be vulnerable to invasion. Panicle production is likely to be of little interest from a management perspective, as torpedograss seed appears to be inviable in North America (Wilcut et al. 1988b), or at best possesses extremely low viability (0.1%; Smith 1995 in Sutton 1996). I did not test viability directly, but an attempted germination study in 2009 was aborted when no torpedograss seedlings emerged in the control treatment. Spread via rhizomatous growth is the mechanism of greatest concern.

Panicum repens, a rhizomatous grass invasive in many parts of the southeastern United States, takes advantage of disturbed sandy roadsides and can establish dense colonies there, particularly when these roadsides adjoin large, well-established populations of torpedograss in disturbed habitat. However, torpedograss does not appear to use roads as a staging ground for invasion of undisturbed Florida scrub, and roadside populations adjacent to scrub may remain sparse or decline in the absence of a more abundant source of propagules. Since torpedograss spreads primarily or exclusively via rhizome, its dispersal is largely limited to immediately adjacent habitats unless rhizomes are uprooted and transported by vehicular or animal movement (e.g., rooting and distribution by feral hogs).

Some invasive species use roadsides as corridors for dispersal. Cogongrass (*Imperata cylindrica*), another rhizomatous invasive grass, is capable of invading undisturbed, nutrient-poor habitats from roadsides, forming dense monocultures and displacing native habitat specialists (Brewer 2008). Torpedograss shares many characteristics with cogongrass: It is an

invasive grass infamously capable of growing in monoculture, spreads rhizomatously and rapidly, and establishes along roadsides adjacent to another nutrient-poor habitat, Florida scrub. But while roadsides are a source of invasion by propagules of cogongrass, they appear to provide a propagule sink for torpedograss (at least at Archbold Biological Station). Kalwij et al. (2008) have also demonstrated the capacity of roadsides to retain invasive species without apparent contribution to their dispersal. This study supports the importance of determining the role of roadsides in the spread of invasive species (Christen and Matlack 2006) and suggests that doing so may assist land managers in assigning conservation priorities and control strategies.

CONCLUSIONS

Florida rosemary, a native ecosystem engineer, and torpedograss, a non-native ecosystem engineer, both showed community-wide responses to Hurricane Katrina. Rosemary exhibited signs of adapting to the current hurricane regime by reproducing at an earlier age in coastal populations than in inland populations and by resprouting when adults were damaged by storm surge. Torpedograss was capable of taking advantage of increased resource availability (either due to the removal of the native community or as a result of hurricane-associated nutrient and moisture enrichment) to expand its range; but at present it appears that torpedograss will continue retreating to low-lying swales as the native xerophytic community recovers.

Coastal communities on Horn and Petit Bois Islands exhibited decreased resistance to torpedograss invasion in the several years after Hurricane Katrina, perhaps in part due to a reduction of alleopathic inhibition by living Florida rosemary shrubs. I was unable to link rosemary litter to this inhibition, but production of photosynthetic tissue was reduced when torpedograss was grown in soil from beneath living rosemary shrubs or in the presence of rosemary's primary allelochemical, hydrocinnamic acid; and on Horn and Petit Bois Islands, torpedograss density was lower around large adult snags where there were many rosemary seedlings. Emerging rosemary seedlings appeared to enjoy protection from competition in the first few years of growth as a result of some lingering effect associated with soil beneath living rosemary shrubs.

Hurricanes represent an important source of disturbance for populations of coastal rosemary, and may also have other long-term effects upon coastal rosemary scrub, such as the removal of lichens. I found no evidence that individual rosemary shrubs at sufficiently high elevation were protected from the storm surge associated with Category 3 hurricanes such as Katrina and Ivan. The only factor contributing to greater density of living adults was the passage of time sufficient for recovery. Because the survival of Florida rosemary is heavily impacted by major hurricanes, an increase in hurricane return interval, as predicted by many climatologists, could alter patterns of disturbance and recovery within coastal rosemary scrub, either by preventing sufficient revitalization of the seed bank between storm events or by shifting the balance of community composition in favor of invasive torpedograss, which appeared to benefit from hurricane-induced disturbance.

Inland scrub communities at Archbold Biological Station (regardless of the presence of Florida rosemary) appeared resistant to invasion by torpedograss ramets populating roadside habitats. Torpedograss growing adjacent to pasture and disturbed scrub, a source of propagules, showed a positive growth rate over one year's time, while torpedograss adjacent to undisturbed scrub, exhibited a negative growth rate. This growth rate was further decreased in torpedograss populating interior roads further from the pasture. Tiller persistence did not vary between sites adjacent to pasture and sites adjacent to scrub, suggesting these different growth rates represent a difference in recruitment. I saw no evidence of recruitment from seed by torpedograss. It appeared that roadsides were a convenient sink for torpedograss ramets, but not a source of invasive propagules into undisturbed native communities. If this is so, then the best approach to managing torpedograss at Archbold Biological Station is to continue restoration of the disturbed Archbold Reserve, rather than focusing on eradicating roadside populations.

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110

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