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# Twenty-Four Year Response of Forests Disturbed by Hurricane Hugo in the Coastal Plains of South Carolina, USA

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TWENTY-FOUR YEAR RESPONSE OF FORESTS DISTURBED BY HURRICANE  
HUGO IN THE COASTAL PLAINS OF SOUTH CAROLINA, USA

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A Thesis  
Presented to  
the Graduate School of  
Clemson University

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In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science  
Forest Resources

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by  
Christian Reid Heaton  
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Accepted by:  
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## ABSTRACT

In 1989, Hurricane Hugo inflicted catastrophic damage on approximately 1.8 million hectares of forested land in South Carolina. This study's purpose was to monitor species compositional shifts and structural changes in several forest types following the disturbance from Hurricane Hugo. The immediate consequences of hurricane damage are well documented. However, there are few studies based on the long-term compositional and structural changes that may result from hurricane disturbance, especially in temperate forest ecosystems. Fifty plots were monitored within four study areas, receiving varying degrees of hurricane damage: Beidler Forest, Santee Experimental Forest, Hobcaw Barony, and Congaree National Park. Inventories included species, damage class, tree diameter, and small regeneration. The objectives of this study were 1) to discover whether the coastal forests damaged by Hurricane Hugo are regaining a structure and composition that resembles the pre-hurricane forest; 2) to compare the recovery speed of wetland forests, e.g. bottomland hardwood swamps and cypress tupelo swamps to that of upland pine and hardwood forests; and 3) to discover how the degree of hurricane wind damage can affect the timing and the pattern of forest recovery in the coastal plain. Over the 24-year period following the hurricane, successional pathways have been variable among plots of different forest types and intensity of initial disturbance. We have observed an expected increase in basal area following the disturbance. Sapling populations in many species increased dramatically and some of these populations have begun to thin in recent years. In several forest types, *Pinus taeda* (not a predominant

species at these sites prior to the hurricane) responded quickly and overtook some dominant species in basal area and tree/sapling abundance. Several other species that were not a major component of the tree strata (*Morella cerifera*, *Fraxinus pennsylvanica*, and the invasive *Triadica sebifera*) showed a large increase in sapling population, taking advantage of the increase in site resources before declining in density due to self-thinning. Overall, recovery speed and species resilience was specific to forest types and study sites.

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## CHAPTER I

### INTRODUCTION

A hurricane is a tropical cyclone that forms over the warm waters of the Atlantic and the Gulf of Mexico. The storm brings strong winds, heavy rain, and clouds that swirl in a counter-clockwise direction. Hurricane winds can have dramatic physical and biological effects on forest ecosystems. Topography is altered, biomass is displaced, and trees are defoliated, uprooted, and broken by strong winds. Salt carried by wind and by a storm surge can greatly impact forests located near the coast. The extent and nature of the damage is related to storm intensity, relation of the forest to the eyewall of the storm, forest structure, soil conditions, and frequency of disturbance, among other factors (Weaver, 1989; Busby *et al.*, 2008). The immediate effects of hurricanes have been documented extensively. An international review of short-term hurricane effects on forests was published by Everham and Brokaw (1996). However, little is known about the long-lasting effects that hurricanes can have on forest structure and composition. Alterations caused by initial hurricane damage can dictate forest structure and composition for many years (Turner *et al.*, 1998). Lugo (2008) refers to these long-term alterations as “invisible” hurricane effects and summarizes the findings on the subject. Much of the information available on these effects is based on tropical forest ecosystems, although some research has been done in the temperate forests of the United States.

Regrowth of forests that have experienced a large scale disturbance occurs at varying rates and can take on many alternative pathways (Oliver and Larson, 1996). The pre-disturbance composition and structure of the forest, the level of disturbance intensity in the area, and the past exposure of the forest to other disturbance events can all have a significant impact on the timing and nature of the response (White, 1979). However, some common successional patterns have been identified based on the limited number of long-term studies that have been performed. An increase in tree mortality rates and tree density is expected in the period of a few years following a major hurricane (Xi, 2008; Lugo, 2008). The period of regrowth results from an increase in canopy space and nutrient availability. During the regrowth period, basal area, biomass, and tree density will increase rapidly up to a threshold (Fu *et al.*, 1996; Scatena *et al.*, 1996; Frangi and Lugo, 1998). Tree density will begin to fall when the thinning phase begins, around 15 years following the storm (Lugo, 2008). The thinning is accompanied by an increase in basal area and biomass as surviving trees take advantage of increased canopy space. The degree of intensity of the initial hurricane disturbance is the most important variable in determining the length of the building and thinning stages (Vandermeer *et al.*, 1998; Zhao *et al.*, 2006; Song *et al.*, 2012). Forests with higher levels of initial damage are expected to have longer stages of succession. Species composition, forest structure, and topography may also determine forest response pathways and recovery speed (Wunderle *et al.*, 1992; Walkera *et al.*, 1996; Zhao *et al.*, 2006).

The Harvard Forest in central Massachusetts has been surveyed periodically following a 1938 hurricane, resulting in the most extensive study of the long-term effects

of hurricane damage on temperate forests to date (Foster, 1992; Motzkin *et al.*, 1999). From 1938 to 1987, a decrease in *Pinus* species across the region resulted from preferential hurricane damage as well as changes in land-use practices. This change coincided with an increase in hardwood stands, an increase in successional and sprouting species and a decrease in long-lived tolerant species (Foster, 1992). By 1992, 55 years after the hurricane, the average basal area of surveyed plots was found to exceed pre-hurricane levels. Tree species increased in basal area over the time period, excluding *Pinus strobus* (Motzkin *et al.*, 1999). Other variables outside of hurricane damage contributed to these results including historical land-use, an increase in logging following the hurricane, and a decline in forest management activities. Sixty-five years after the hurricane, subtle but significant differences in structure that were correlated with damage from the 1938 hurricane were found in the Harvard Forest using LiDAR data (Weishampel *et al.*, 2007).

Hurricane Hugo reached the coast of South Carolina, USA near midnight September 21-22, 1989. The storm was moving at a speed of 48 k/h (30mph) with winds up to 60 m/s (135 mph) (Brennen, 1991). The resulting damage amounted to 1.8 million hectares of damaged forested land across 23 counties. Coastal counties were the most affected, with 90 percent of timberland damaged across six counties (Purvis, 1996). Damage surveys of commercial timberland were performed (Sheffield and Thompson, 1992), as well as surveys of non-commercial forested land (Gresham *et al.*, 1991 – Hobcaw Forest; Hook *et al.*, 1991 – Santee Experimental Forest; Putz and Sharitz, 1991 – Congaree National Park; Duever and McCollum, 1992 – Beidler Forest). A study was

designed to combine the initial surveys of hurricane damage at these four areas with data collected from long-term monitoring plots in order to examine the resilience and recovery of southeastern coastal forests from a hurricane disturbance. At Congaree Forest, effects on community composition and structure over a 12-year period following the hurricane were found to be complex and to vary based on pre-hurricane composition and structure (Zhao *et al.*, 2006). Stands with high levels of initial damage had increased tree density but relatively low basal area. The basal area of less damaged stands was near pre-hurricane levels. No evidence was found to support the hypothesis that high species diversity can contribute to high resilience to hurricane disturbance (Zhao *et al.*, 2006).

An analysis of forest community and structural change that occurred over the 14 years following Hurricane Hugo was performed using permanent plots in Congaree National Park, Santee Experimental Forest, Beidler Forest, and Hobcaw Barony (Song *et al.*, 2012). Species composition and the level of initial hurricane damage were found to be important variables controlling forest resilience and recovery. Qualitative analysis of post-hurricane data allowed for species to be classified within a forest type in terms of resistance and resilience to disturbance based on the interpretations of Bellingham *et al.* (1995) and Batista and Pratt (2003). Species were classed as relatively resistant (bald cypress - *Taxodium distichum*, water tupelo - *Nyssa aquatica*, longleaf pine - *Pinus palustris*), relatively resilient (sweetgum - *Liquidambar styraciflua*, loblolly pine - *Pinus taeda*, laurel oak - *Quercus laurifolia*), susceptible (willow oak - *Quercus phellos*, water oak - *Quercus nigra*, and laurel oak), and usurpers (American hornbeam - *Carpinus caroliniana*, loblolly pine). Some species assumed different roles depending on the

surrounding forest type. For example, loblolly pine was found to be resilient in pine-hardwood stands but acted as a usurper in longleaf pine and cypress-tupelo stands. Bottomland hardwood and cypress-tupelo forest types were found to have changed little in density and basal area, except in areas that experienced heavy wind damage. The basal area and density of early-successional species increased over the monitoring period, especially on sites with high wind damage (Song *et al.*, 2012).

The purpose of this study was to continue to monitor the recovery of southeastern coastal forests that were disturbed by Hurricane Hugo. The data collected from permanent plots in South Carolina will add to our understanding of forest resilience and succession following a major disturbance by providing an analysis of the changes that have occurred over a 24-year period following the hurricane. Our primary objectives were to compare the recovery speed and resilience of several forest types following a hurricane and to discover how the degree of hurricane wind damage can affect the timing and the pattern of forest recovery in the coastal plain. This was achieved using data collected from permanent plots originally established by Dr. Charles Gresham in 1994. A total of 50 plots were established and classified into seven forest cover types. Eight plots and two forest cover types located on Hobcaw Barony were excluded from the analysis due to controlled burns that occurred during the monitoring period, resulting in a total of 42 plots and five forest types. Data collection methods are discussed further in Chapter 3.

## CHAPTER II

### LITERATURE REVIEW

#### Long-term Forest Response to Hurricane Disturbance

The immediate consequences of hurricane damage on forest ecosystems are well documented (Everham and Brokaw, 1996). However, there has been little research done on the long-term compositional and structural changes that may result from hurricane forces, especially in temperate forest ecosystems. Long-term dynamics in forest composition and structure following hurricanes have been analyzed to some extent in tropical ecosystems, but comparatively few studies exist on the recovery of other forest ecosystem types. The level of initial hurricane effects may dictate forest structure and composition for many years following the event (Turner *et al.*, 1998), but disturbance intensity may not be an accurate predictor of forest response and other meteorological, historical, or biotic factors should be considered (Busby *et al.*, 2009). Large-scale disturbances can result in many alternative responses in terms of forest structure and species composition (Lugo, 2008). Some general response patterns have been identified, but questions remain on how the long-term trajectories of these responses can alter structure, composition, and species interaction in forest stands. This review will highlight the trends and outcomes in regards to long-term forest response to hurricane disturbance that researchers have noted when working with long-term data from several different forest ecosystems.

## Forest Structure

The conclusion is made in Lugo (2008) that the type of change in forest structure following any hurricane disturbance depends largely on the strength of the storm and the resulting tree mortality. Some general patterns have been observed in tropical forests in the years following those hurricane disturbances that reduce the level of structural indices. Increased tree mortality and decreased tree density have been observed during the first few years following a major storm (Weiman Xi, 2008; Lugo, 2008). A period of regrowth is expected following a significant loss of trees and the resulting increase in canopy space and nutrient availability. During the regrowth period, basal area, biomass, and tree density will increase rapidly up to a threshold (Fu *et al.*, 1996; Scatena *et al.*, 1996; Frangi and Lugo, 1998). Tree density will begin to fall when the thinning phase begins, around 15 years following the storm. The thinning is accompanied by an increase in basal area and biomass as surviving trees take advantage of increased canopy space. Some temperate forest stands of coastal South Carolina were found to have a Normalized Difference Vegetation Index (NDVI) equal to the pre-hurricane NDVI, ten years after Hurricane Hugo (Cosentino, 2013). These patterns may be useful in predicting general response to disturbance in forest systems, but there are many alternative forest responses and successional timelines that may occur. The impact and alterations that follow the disturbance are dependent on a number of variables including the pre-disturbance composition and structure of the forest, the level of disturbance intensity in the area, and the past exposure of the forest to other disturbance events (Oliver and Larson, 1996; White, 1979).

Vandermeer *et al* (1998) interprets tropical forest response to hurricane effects as a two-step process. The first step after the disturbance is a rebuilding stage that includes resprouting of damaged trees, delayed mortality of damaged trees, and the growth and arrival of saplings and seedlings, all growing at a relatively high rate. The growth rate is relative to the level of disturbance at the site; trees in heavily damaged sites are expected to grow at a faster rate than those at less damaged sites. The result of the building phase is a low, dense canopy. The next step is a thinning stage brought on by competition which will eventually result in a mature forest. The length of the building and thinning stages is largely a function of the degree of intensity of the initial hurricane disturbance. Based on the growth rates of tree species, study areas with higher levels of damage were found to have longer stages of succession. Six years after the hurricane, less-damaged sites were beginning to enter the thinning stage while heavily damaged sites remained in the building stage.

Results from temperate forests in South Carolina, USA suggest that the initial level of damage and the spatial variability in species composition are important factors contributing to long-term hurricane impacts (Zhao *et al.*, 2006, Song *et al.*, 2012). Song *et al* (2012) found that basal area and density of overstory trees in bottomland hardwood and cypress-tupelo plots changed little during ten years of monitoring. These results suggested that southeastern tree species common to these forest types are resistant to moderate hurricane winds. Species-specific resistance to hurricane winds was not evident in plots of the same forest type located in sites where hurricane winds were strongest. Song *et al.* expected the difference in recovery rates of upland and lowland ecosystems to



be significant. However, species composition and extent of damage were found to be more important to both recovery rate and recovery species composition than any topographic gradients found on study sites. Slow canopy recovery rates following a hurricane have been observed in Jamaican montane forests when compared to lowland forests (Wunderle *et al.*, 1992), and a similar difference has been observed in montane and lowland forests of Puerto Rico (Walker *et al.*, 1996; Weaver, 1986a).

### Species Composition and Dominance

Species that were dominant prior to a strong wind disturbance are expected to increase in importance as time passes following the disturbance (Glitzenstein and Harcombe, 1988; Frangi and Lugo, 1998), while importance of secondary species will eventually decrease (Fu *et al.*, 1996). However, this pattern is not always observed. Species that assume a dominant role soon after a disturbance may represent the future dominants of the stand (O'Hara, 1995; Oliver and Larson, 1996). Alternatively, species that initially inhabit the lower canopy can eventually become dominant (Oliver, 1980). Tree species with abundant residuals, or surviving individuals, are likely to control the regrowth of other species following a hurricane disturbance. The frequency and intensity of a disturbance determines the presence and composition of residuals, and the impacts that residuals have on forest structure and composition may be visible for centuries after the disturbance (Turner *et al.*, 1998). Late-successional species may be less likely to be found near the center of a disturbance event due to lower dispersal ability relative to

widely dispersed species (McClanahan, 1986). Dispersal rate can vary locally depending on weather, landscape, and competing vegetation present (Turner *et al.*, 1998).

Processes may speed up following a hurricane as primary productivity increases as a result of an increase in nutrient availability at the forest floor (Scatena *et al.*, 1996). These conditions may lead to species compositional changes and provide opportunities for invasive plant species (Conner *et al.*, 2014). Non-native plants can capitalize on canopy gaps created by hurricane disturbance, but populations may decrease as a result of the canopy closing in the following years (China, 1999; Thompson *et al.*, 2007). Invasive populations can persist and continue to grow in density and basal area more than twenty years past the disturbance (Bellingham *et al.*, 2005). Species with a historically minor role in a forest stand may become dominant following a large disturbance. Song *et al.* (2012) found that, for some forest types, non-predominant species such as *Pinus taeda* increased in sapling density and basal area and continued to assume a dominant role on several sites in which it was not a pre-dominant species up to fourteen years after Hurricane Hugo.

In Vandermeer *et al.* (2001), researchers interpreted post-hurricane tropical forest building and thinning stages by an equilibrium or non-equilibrium model. In equilibrium models, post-hurricane forest dynamics are related to niche segregation based on individual species traits, whereas chance and history are the driving factors of canopy development in non-equilibrium models. They found that in the low, dense canopy competitive thinning had begun ten years after the disturbance. Tree mortality in the thinning canopy was not random. Certain species had begun to occupy the upper canopy,

becoming competitive dominants, and others were pushed to the lower canopy. In this case, an equilibrium (niche) model was appropriate for the thinning canopy. However, a non-equilibrium (chance/history) model was a better fit for the building canopy, where species occupation was based more on life history and random chance.

Response to hurricane disturbance is variable among species. In Busby *et al.* (2008), shade-tolerant beech species benefitted from large canopy gaps created by hurricane winds, while shade-intolerant oak species did not benefit. Response may vary among species with the same rating of shade-tolerance. Zhao *et al.* (2006) compared the response of two shade-intolerant species in a South Carolina bottomland hardwood forest (*Pinus taeda* and *Liquidambar styraciflua*). *P. taeda* had high mortality and low recruitment levels, resulting in a decline in abundance following the hurricane, while *L. styraciflua* had high recruitment levels and increased abundance post-hurricane. Song *et al.* (2012) reported on species composition changes in the coastal plain forests of South Carolina fourteen years after Hurricane Hugo. Qualitative analysis of post-hurricane data allowed for species to be classified in terms of resistance and resilience to disturbance based on the classifications of Bellingham *et al.* (1995) and Batista and Pratt (2003). Species were classed as relatively resistant (*Taxodium distichum*, *Nyssa aquatica*, *Pinus palustris*), relatively resilient (*L. styraciflua*, *P. taeda*, *Quercus laurifolia*), susceptible (*Quercus phellos*, *Quercus nigra*, and *Q. laurifolia*), and usurper (*Carpinus caroliniana*, *P. taeda*). Some species assumed different roles depending on the surrounding forest type. For example, *P. taeda* was found to be resilient in pine-hardwood stands but acted as a usurper in longleaf and cypress-tupelo stands. Putz and Sharitz (1991) found that *P.*

*taeda* is often resilient to hurricane effects but can become susceptible when other factors limit regeneration. In Congaree National Park, *P. taeda* abundance decreased while *L. styraciflua* recruitment increased following Hurricane Hugo (Battaglia *et al.*, 1999).

### Species Diversity and Richness

Tree species diversity may increase for a period following hurricane alteration of forest structure. Initially, a high number of species will be competing for newly available resources, but this competition will eventually result in a decrease in species diversity (Lugo, 2008). Historical exposure of Caribbean forests to frequent hurricanes results in a forest dominated by a few species (Lugo and Scatena, 1995). Some studies suggest that pioneer species are favored by a regime of hurricane disturbances and can be expected to be found at higher densities in stands that are subject to a disturbance regime (Burslem and Whitmore, 1999; Thompson *et al.*, 2002). Experimental scale may skew results on species diversity and richness following hurricanes. Results from tropical forest studies have shown large scale experiments finding little to no change in diversity (Scatena and Lugo, 1995) and small scale (e.g., 1 ha) experiments finding significant patterns of change in diversity (Frangi and Lugo, 1998; Fu *et al.*, 1996). However, significant change in diversity following a hurricane event has been found on a whole-forest scale (Weaver, 1986). Motzkin *et al.* (1999) used logistic regression to correlate species dynamics on the Prospect Hill tract of Harvard Forest with historical and environmental variables. The presence of a few species was positively correlated with damage from a 1938 hurricane based on a survey taken 54 years after the disturbance. Species richness was not at all

correlated with hurricane damage. Overall dissimilarity in species composition, based on Bray-Curtis distance, was found to increase with higher levels of hurricane damage. These trends, however, were admitted to be relatively weak and may have been subject to other untested factors or variables.

Zhao *et al.* (2006) examined the twelve year response of bottomland hardwood forests in Congaree National Park to disturbance from Hurricane Hugo. Their results add to the debate over the role that diversity plays in forest resistance and response to hurricanes. The results suggested that pre-hurricane species composition and structure were key factors in forest response and resistance. However, forests with higher species diversity were not found to be more resistant to hurricane disturbance. These results are contrary to some studies performed in tropical forest ecosystems (Lugo *et al.*, 1983) that suggest that high species diversity can improve resistance to hurricane effects. Zhao *et al.* found changes in species richness and Shannon diversity to be insignificant in the tree layer over the twelve years following the hurricane. However, diversity and richness within the sapling layer were found to have increased in plots with high disturbance and showed either a slight increase or decrease in plots with low disturbance. Based on these results, they concluded that hurricane disturbance can restructure species composition in a bottomland hardwood forest, but the evidence for increased species diversity as a result of hurricane disturbance in these forests is not strong (Zhao *et al.*, 2006).

## Conclusion

The speed and character of succession of a post-hurricane forest has been shown to be strongly linked to the pre-hurricane structure and composition of the forest. Long-term data collection is essential in understanding how unique forest types respond in the decades following a major storm. Questions remain concerning the role that hurricane disturbance plays in long-term forest structure, species composition, and diversity. Results from species-rich tropical forests indicate that a more diverse forest will be more resilient to strong winds (Burslem and Whitmore, 1999). This correlation is not clear in the bottomland hardwood forest of the Southeastern United States (averaging around 20 species per hectare). Change in forest structure and composition and the speed at which these changes take place following a disturbance is closely related to the intensity of the initial disturbance. The roles that individual species (some native and unique to the Southeastern United States) assume throughout the successional stages following the storm is also important in understanding forest ecosystem response and how to best prepare and manage for large storm events in the future.

CHAPTER III  
TWENTY-FOUR YEAR RESPONSE OF FORESTS DISTURBED BY HURRICANE HUGO  
IN THE COASTAL PLAINS OF SOUTH CAROLINA, USA

Introduction

Coastal forests endure frequent hurricanes and suffer effects from high winds, heavy rain, flooding, and saltwater intrusion. These forces can drastically alter the composition of a forest in a matter of hours. Trees are broken, uprooted, and defoliated by wind and rain. Trees can also be damaged by salt brought ashore by the wind and storm surge. The remaining trees are left especially vulnerable to fire and to insect infestation (Hook *et al.*, 1991). The immediate consequences of hurricane damage are well documented (Everham and Brokaw, 1996). However, there has been little research on the long-term compositional and structural changes that may result from the catastrophic damage, especially in temperate forest ecosystems. Long-term alterations in forest species composition and structure have been analyzed in tropical ecosystems (Lugo, 2008), but little information exists on the recovery of other forest ecosystem types. One of the few studies focusing on long-term dynamics of temperate forests following a hurricane took place on selected sections of the Harvard Forest after a 1938 hurricane (Foster, 1992; Motzkin *et al.*, 1999). After four growing seasons, a high stem density and low basal area persisted relative to pre-storm levels. After 46 growing seasons, the basal area, density, and dominant species of the forest were beginning to

resemble pre-storm conditions. Stanturf *et al.* (2007) examined individual southeastern US tree species resistance to hurricane wind damage and management in the context of economic loss. Questions on long-term forest growth and dynamics, however, have remained unexamined. Many ecologists have adapted a Gleasonian view of succession in which, rather than a single stable equilibrium state existing for a given ecosystem, multiple equilibrium states may be reached based on varying environmental and historical factors (Uriarte *et al.*, 2009). Answering these questions is essential to understanding forest dynamics and assessing forest health, as the ability to recover from a massive disturbance is an indicator of a healthy forest ecosystem (Kolb *et al.*, 1994).

In 1989, Hurricane Hugo inflicted water and wind damage on approximately 1.8 million hectares of forested land in South Carolina (Hook *et al.*, 1991). A wind damage assessment for commercial timberland in the path of Hugo can be found in Sheffield and Thompson (1992). Wind damage done to selected non-commercial forests was assessed by Gresham *et al.* (1991)- Hobcaw Forest, Putz and Sharitz (1991)- Congaree National Park, Hook *et al.* (1991)- Santee Experimental Forest, and Duever and McCollum (1992)- Beidler Forest. These damage assessments provide us with information on the short-term effects that hurricane forces had on the forests of the coastal plain. The study plots that have been used for long-term monitoring were established within these four areas in order to test the resilience of coastal forests that have experienced high levels of hurricane disturbance. The sites are in various states of protection and were not subject to salvage logging following the hurricane. The plots have not been managed and have been allowed to recover with minimal anthropogenic influence.



The long-term monitoring of coastal plain forest recovery from Hurricane Hugo has the following principal objectives: (1) to discover how the degree of hurricane damage can affect the timing and the pattern of forest response in the coastal plain; (2) to compare the recovery speed of wetland forests, e.g. bottomland hardwood swamps and cypress tupelo swamps, to that of upland pine and hardwood forests; and (3) to compare individual species response patterns across different forest types and at different levels of initial damage.

## Materials and Methods

### Study Area

Study plots established in 1993 and have been continually monitored for this project (Song *et al.*, 2012). Four major study areas were chosen; Beidler Forest, Santee Experimental Forest, Hobcaw Barony, and Congaree National Park. These forests all received varying degrees and types of damage from Hurricane Hugo, are protected from industry, and have been allowed to regenerate naturally. Forest types are not evenly distributed throughout the measurement plots. The cypress-tupelo cover type is the only type that is present at all study sites.

(1) The Beidler Forest (Lat. 33° 9' N Long. 80° 19' W) is an approximately 6,500 ha forest preserve and instructional forest under the administration of the Nature Conservancy. Three major wetland forest types are represented by 12 plots; cypress-tupelo stands at the lowest elevations, bottomland hardwood (BLH) stands in the floodplain areas, and ridge bottom stands that are rarely flooded and are at higher

elevations than the bottomland hardwood stands. The ridge bottom forest type is unique to Beidler Forest (**Table 3.1**). These plots are 69 km from the coast and were 21 km west of the center of Hugo.

(2) Congaree National Park (Lat. 33° 49' N Long. 80° 50' W) contains the largest contiguous tract (approx. 9,000 ha) of old-growth bottomland hardwood forest in the United States. The Congaree River floodplain is dominated by bottomland hardwood stands. Cypress-tupelo stands are located in creeks and sloughs. Ten 1-ha plots established by Putz and Sharitz (1991) were divided into subsections (1/5 ha) for use in this study. One plot is uniquely classified as tupelo swamp. These plots are 143 km from the coast and were 24 km west of the center of Hugo.

(3) Hobcaw Barony (Lat. 33° 20' N Long. 79° 12' W) is a 7,100 ha forested area on the southern tip of the Waccamaw peninsula north of Georgetown, SC. The plots at the Barony were established for this study following Hurricane Hugo. The cypress-tupelo plots are located within 100 m of drainage from the salt marsh of North Inlet. Salt water intrusion in this inlet from Hurricane Hugo reached a depth of approximately 2 m. The Hobcaw Barony plots are 5.5 km from the coast and were 72 km east of the center of Hugo.

(4) The Santee Experimental Forest (Lat. 33° 7' N Long. 79° 47' W) is a section of the Francis Marion National Forest, located north of Charleston, SC. The floodplain of a small creek supports cypress-tupelo and bottomland hardwood forest types. These forest types are separated by an earthen dike built to control water for rice cultivation during the 18 and 19<sup>th</sup> centuries. The pine-hardwood plots are in a watershed that has not been

disturbed since 1969. The Santee Experimental Forest plots are 28 km from the coast and were 14 km east of the center of Hugo.

**Table 3.1** A breakdown of the number of study plots present among four major sites and seven forest cover types.

<b>Cover type</b>	Beidler Forest	Congaree Park	Santee Forest	Hobcaw	<b>Total</b>
Cypress Swamp	4	3	4	4	15
Bottomland Hardwood	4	5	4		13
Upland Pine-Hardwood		1	4	4	9
Ridge Bottom	4				4
Tupelo Swamp		1			1
<b>Total</b>	12	10	12	8	<b>42</b>

#### Data Collection

Plots were measured in 1994, 1997, 2000, 2003, 2007, 2010, and 2013. Four plots were established in 1993 for each type of forest cover at Beidler, Santee, and Hobcaw Barony. At Congaree, plots were located based on the spatial distribution of forest cover types. A total of 42 study plots of dimensions 20 m X 100 m based on five forest cover types were periodically surveyed (**Table 3.1**). Each plot was divided into five 20m X 20 m subplots and marked by aluminum poles. Consistent techniques of tree measurement, based on the work of Dr. Charles Gresham, have been used throughout the

study (Song *et al.*, 2012). Tree stems with a DBH (diameter at breast height) of at least 2.5 cm were marked with a permanent ID tag to ensure that data remained consistent throughout the study. Marked trees were identified by species and given a damage class. Data collected during each field season consisted of DBH, current damage class of trees, and small (< 2.5 cm DBH) regeneration. Stems with a DBH of 10 cm or greater were labeled as trees, while stems with a DBH of 2.5 to 9.9 cm were labeled as saplings.

Basal area was calculated from the DBH measurement of each tree and was converted to m<sup>2</sup>/ha using  $BA = \left( \pi \left( \frac{d}{2} \right)^2 \times \frac{5}{10000} \right)$  where BA is basal area in m<sup>2</sup>/ha and *d* is diameter at breast height in centimeters. Dominant species for each plot and forest cover type were identified by calculating Importance Values and by ranking species based on basal area and density (stems per ha). Importance Values were calculated for each tree species by combining the percentages of basal area (dominance) and number of stems within each plot ( $IV = [ ((Relative\ Density) + (Relative\ Dominance))/2] * 100$ ). These values allowed us to assess changes in species dominance and forest composition over the monitoring period.

## Results

Although data collected from 1994 to 2003 have been presented in Song *et al.* (2012), data trends from the entire study period to date (1994-2013) are presented here in order to display long-term changes (**Figs. 3.1-3.4**). Please note that although the format of the figures is uniform, the scale changes greatly due to varying overstory types.

## Beidler Forest

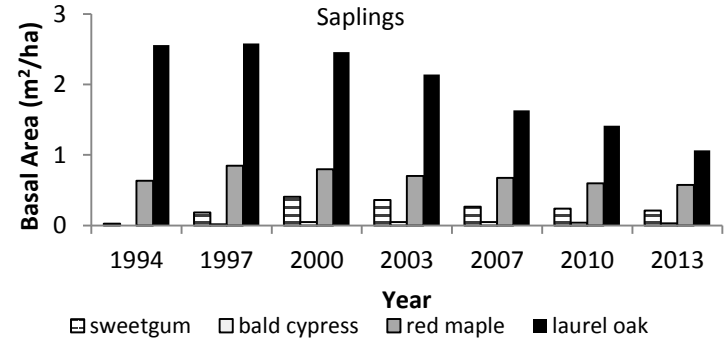
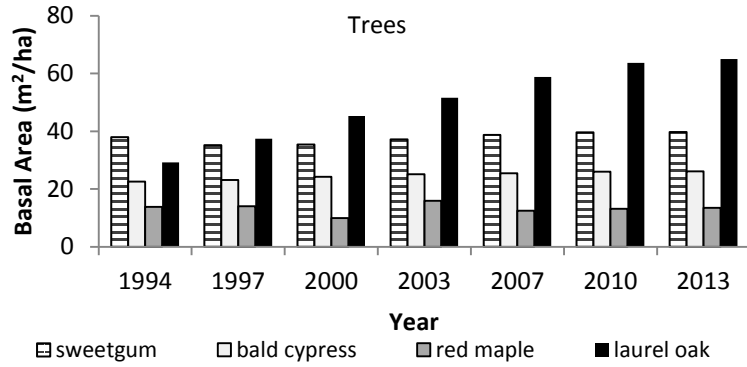
The bottomland hardwoods were dominated in 1994 (the first year of sampling) by sweetgum (*Liquidambar styraciflua*, 36 m<sup>2</sup>/ha, 50 stems/ha), laurel oak (*Quercus laurifolia*, 31.8 m<sup>2</sup>/ha, 211.3 stems/ha), and bald cypress (*Taxodium distichum*, 22.5 m<sup>2</sup>/ha, 53.8 stems/ha). The sapling layer consisted of laurel oak (215 stems/ha), hornbeam (*Carpinus caroliniana*, 143.8 stems/ha), green ash (*Fraxinus pennsylvanica*, 85 stems/ha), and red maple (*Acer rubrum*, 83.8 stems/ha). Tree-size bald cypress and sweetgum basal area increased slightly (**Fig. 3.1A**). Laurel oak trees increased in basal area throughout the study and have assumed a dominant position in the overstory. Tree-size laurel oak were the most abundant throughout the study period. In the sapling layer, the dominant laurel oak, hornbeam, and red maple numbers were steady until 2000 but have declined since then (**Fig. 3.1A**).

Cypress-tupelo plots were dominated in 1994 by bald cypress (117.1 m<sup>2</sup>/ha, 105 stems/ha) and water tupelo (*Nyssa aquatica*, 143.7 m<sup>2</sup>/ha, 286 stems/ha) trees with a smaller blackgum (*Nyssa sylvatica*) component. The sapling layer was almost exclusively made up of green ash throughout the study period. Sapling-size green ash stems decreased 26% from 1994 to 2013 (1249 to 924 stems/ha) but remained relatively high. The density of green ash tree-size stems increased steadily by 36% from 1994 to 2013. Bald cypress, tupelo, and blackgum basal area and density changed little in both trees and saplings.

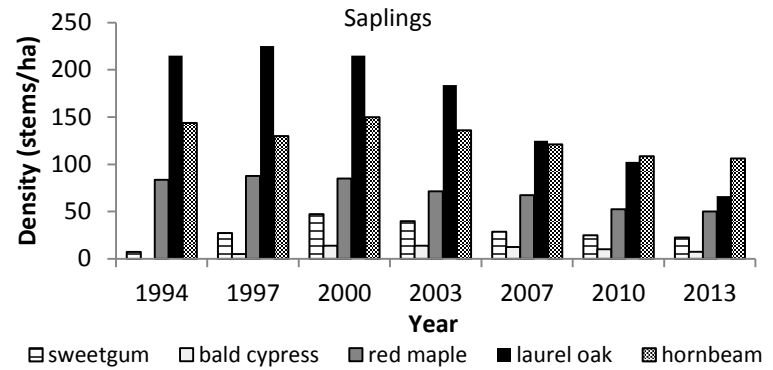
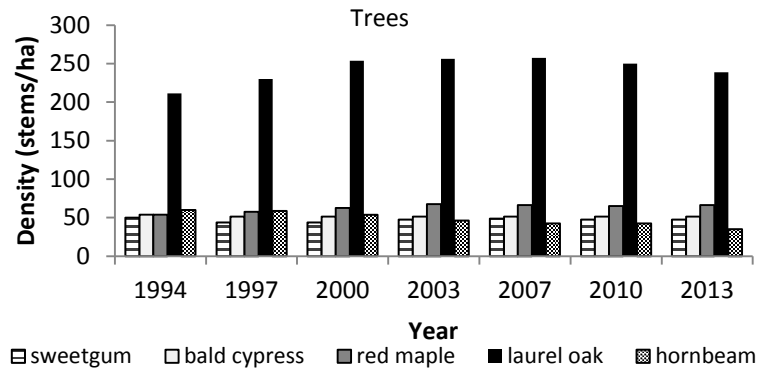
In 1994, the ridge-bottom plots contained a diverse overstory of sweetgum (9.4 m<sup>2</sup>/ha), water oak (*Quercus nigra*, 6.8 m<sup>2</sup>/ha), hornbeam (5.3 m<sup>2</sup>/ha), pignut hickory

(*Carya glabra*, 3.0 m<sup>2</sup>/ha), swamp chestnut oak (*Quercus michauxii*, 2.9 m<sup>2</sup>/ha), and laurel oak (1.7 m<sup>2</sup>/ha). Sweetgum, water oak, hornbeam, and laurel oak trees increased in basal area and density up to 2013. The most dominant tree was hornbeam (247.5 stems/ha, 14.6 m<sup>2</sup>/ha) whose density doubled between 1994 and 2000. In 2013 hornbeam remained the most abundant while the less-dense sweetgum had the highest basal area (82.5 stems/ha, 17.2 m<sup>2</sup>/ha). The sapling layer was mostly hornbeam in 1994 but included sweetgum, water oak, and laurel oak. Hornbeam remained dominant in the sapling layer throughout the study.

A. Bottomland hardwood



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**Fig. 3.1** Basal area and density changes for important species in the (A) bottomland hardwood, (B) cypress-tupelo, and (C) ridge bottom forest types at Beidler Forest.

B. Cypress-tupelo

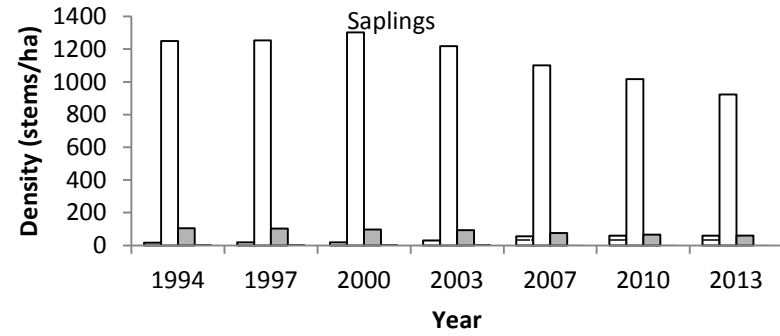
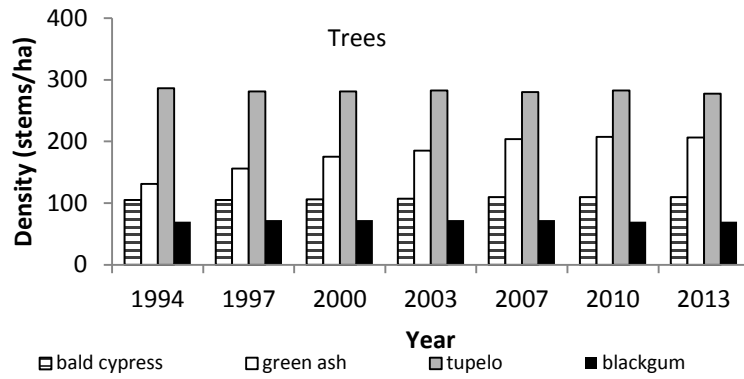
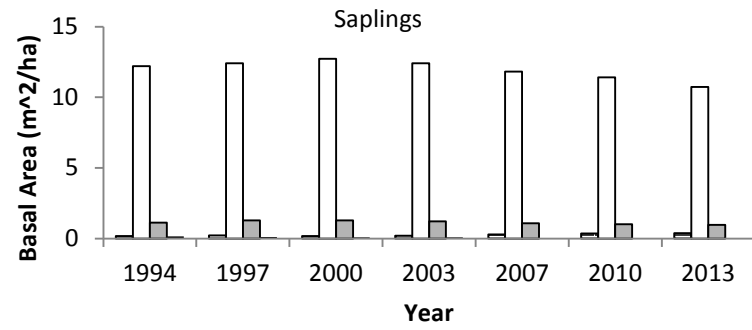
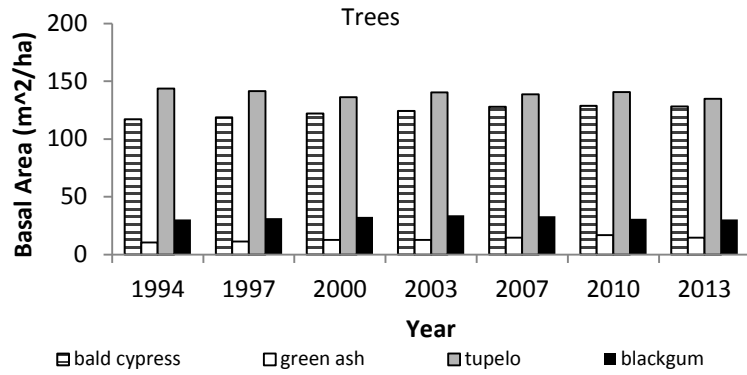


Fig. 3.1 Continued...



C. Ridge bottom

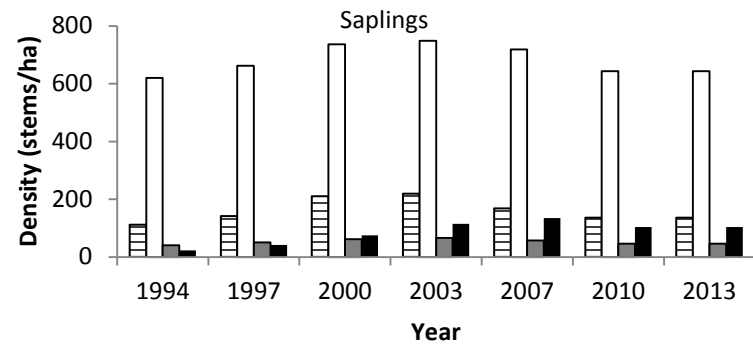
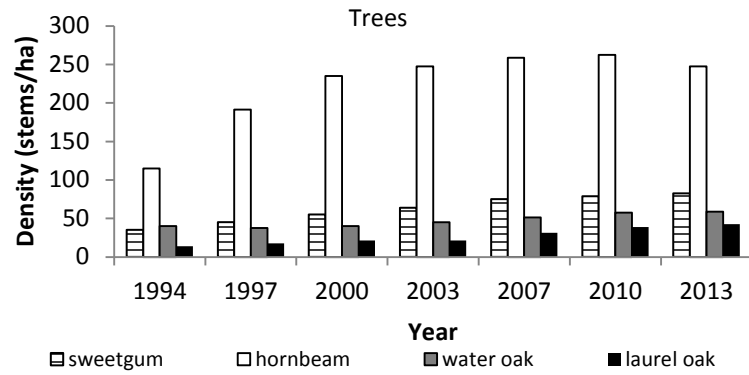
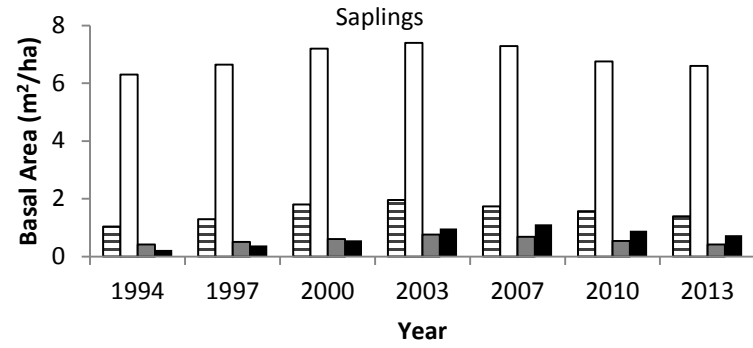
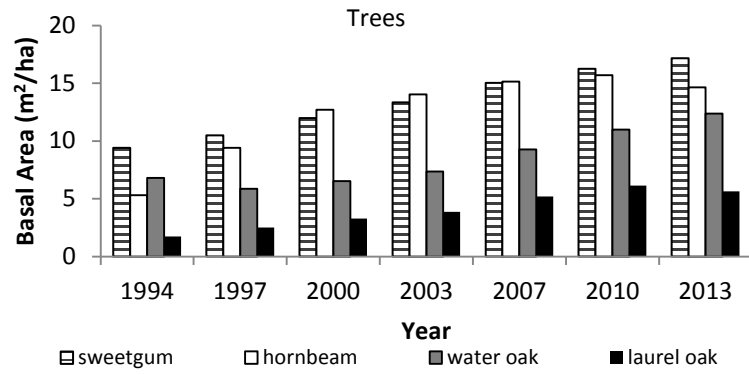


Fig. 3.1 Continued.

## Congaree National Park

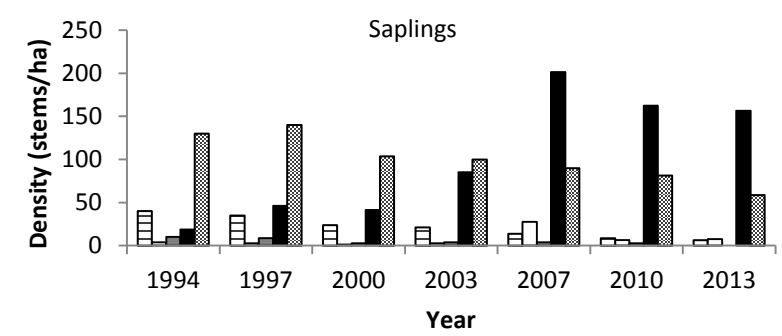
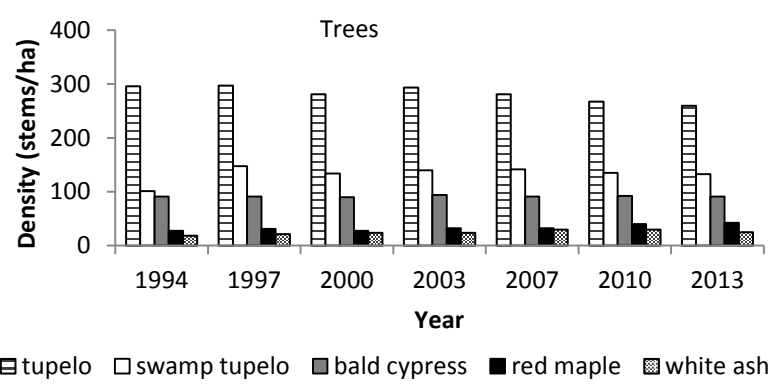
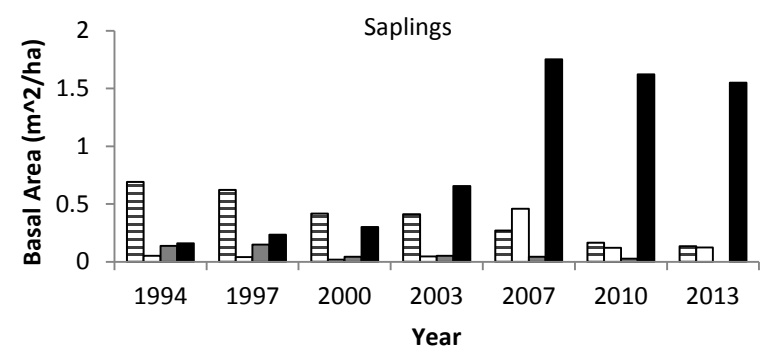
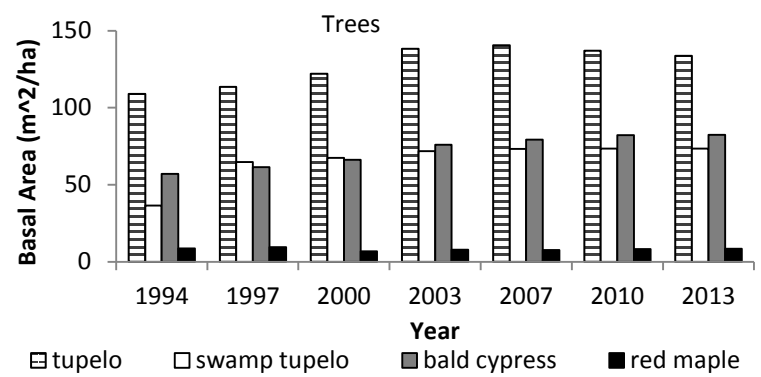
The cypress-tupelo forest type plots were dominated in 1994 in the tree size class by water tupelo (108.9 m<sup>2</sup>/ha, 296.25 stems/ha), bald cypress (57.1 m<sup>2</sup>/ha, 91.25 stems/ha) and swamp tupelo (*Nyssa biflora*, 36.5 m<sup>2</sup>/ha, 101.25 stems/ha). Most of the 1994 sapling strata consisted of white ash (*Fraxinus americana*, 130 stems/ha) and water tupelo (40 stems/ha). Water tupelo, bald cypress, and swamp tupelo trees increased in basal area during the study period (**Fig. 3.2A**), while other species changed little in basal area. Red maple sapling density increased nearly five-fold by 2007, then decreased by about 20% by 2013. The density of white ash saplings decreased throughout the study period, resulting in a 2013 population of less than half of the 1994 population (**Fig. 3.2B**).

In 1994, the bottomland hardwood plots were dominated by sweetgum (101.8 m<sup>2</sup>/ha) and to a lesser extent American holly (*Ilex opaca*, 14.1 m<sup>2</sup>/ha). The sapling layer was initially dominated by deciduous holly (*Ilex decidua*, 0.9 m<sup>2</sup>/ha, 109 stems/ha) and paw paw (*Asimina triloba*, 0.5 m<sup>2</sup>/ha, 99 stems/ha). Deciduous holly, American holly, and paw paw sapling density increased dramatically between the 2003 and 2007 censuses. The basal area of sweetgum and American holly trees changed little throughout the study.

The pine-hardwood plot of Congaree was dominated in 1994 in the tree strata by loblolly pine (28.3 m<sup>2</sup>/ha, 14 stems/ha) and hornbeam (4.2 m<sup>2</sup>/ha, 60 stems/ha). The sapling layer was established in 2007 and was mostly hornbeam (1.5 m<sup>2</sup>/ha, 134 stems/ha), American holly (0.5 m<sup>2</sup>/ha, 46 stems/ha), and red maple (0.3 m<sup>2</sup>/ha, 30 stems/ha). Tree-size loblolly pine basal area increased slightly by 2013 and the density of

tree-size loblolly pine remained consistent. Hornbeam was the most abundant in the tree layer and in the sapling layer throughout the study.

A. Cypress-tupelo



**Fig. 3.2** Basal area and density changes for important species in the (A) cypress-tupelo, (B) bottomland hardwood, and (C) pine hardwood forest types at Congaree National Park.

B. Bottomland hardwood

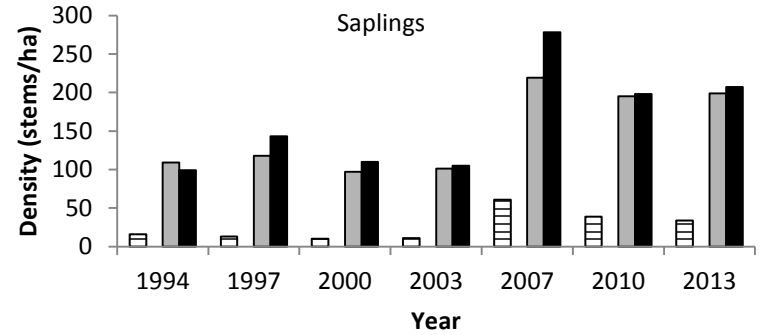
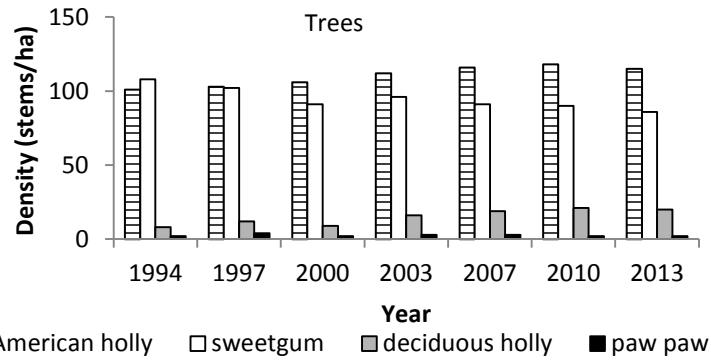
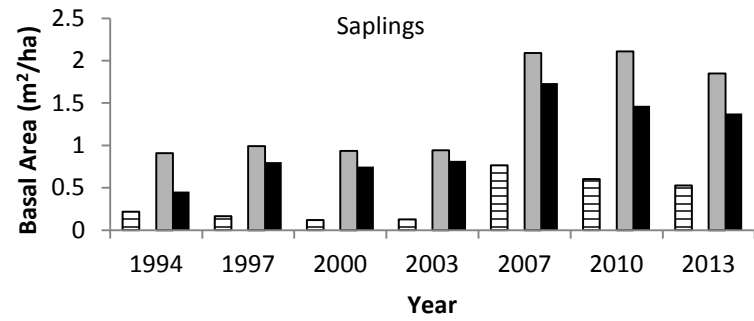
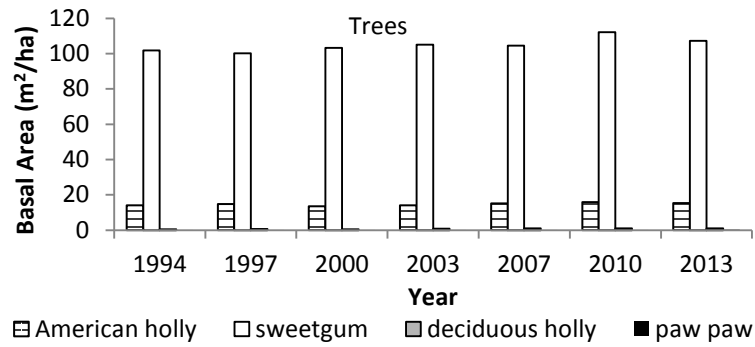
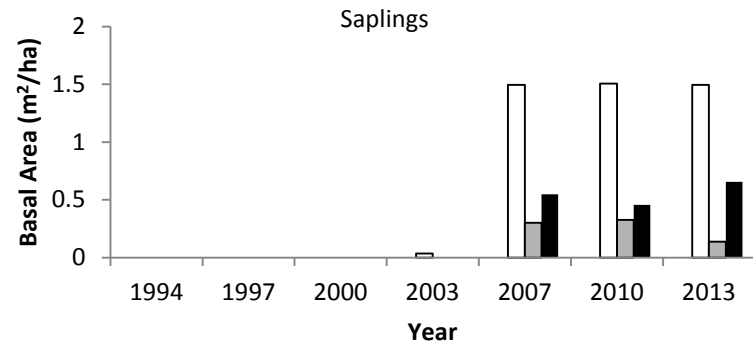
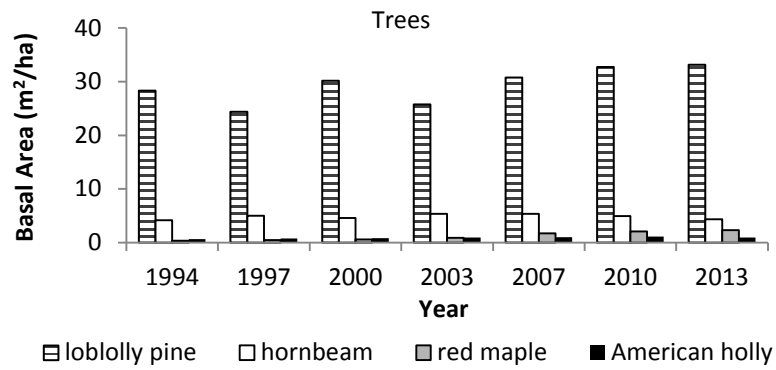


Fig. 3.2 Continued...

C. Pine-hardwood



30

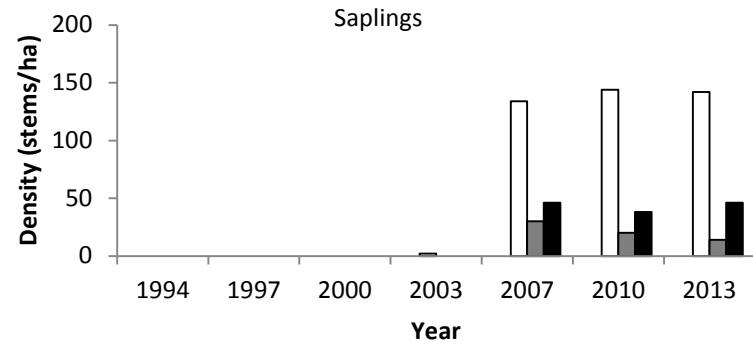
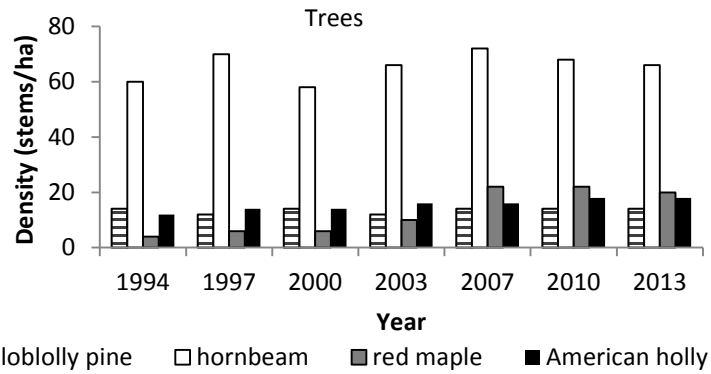


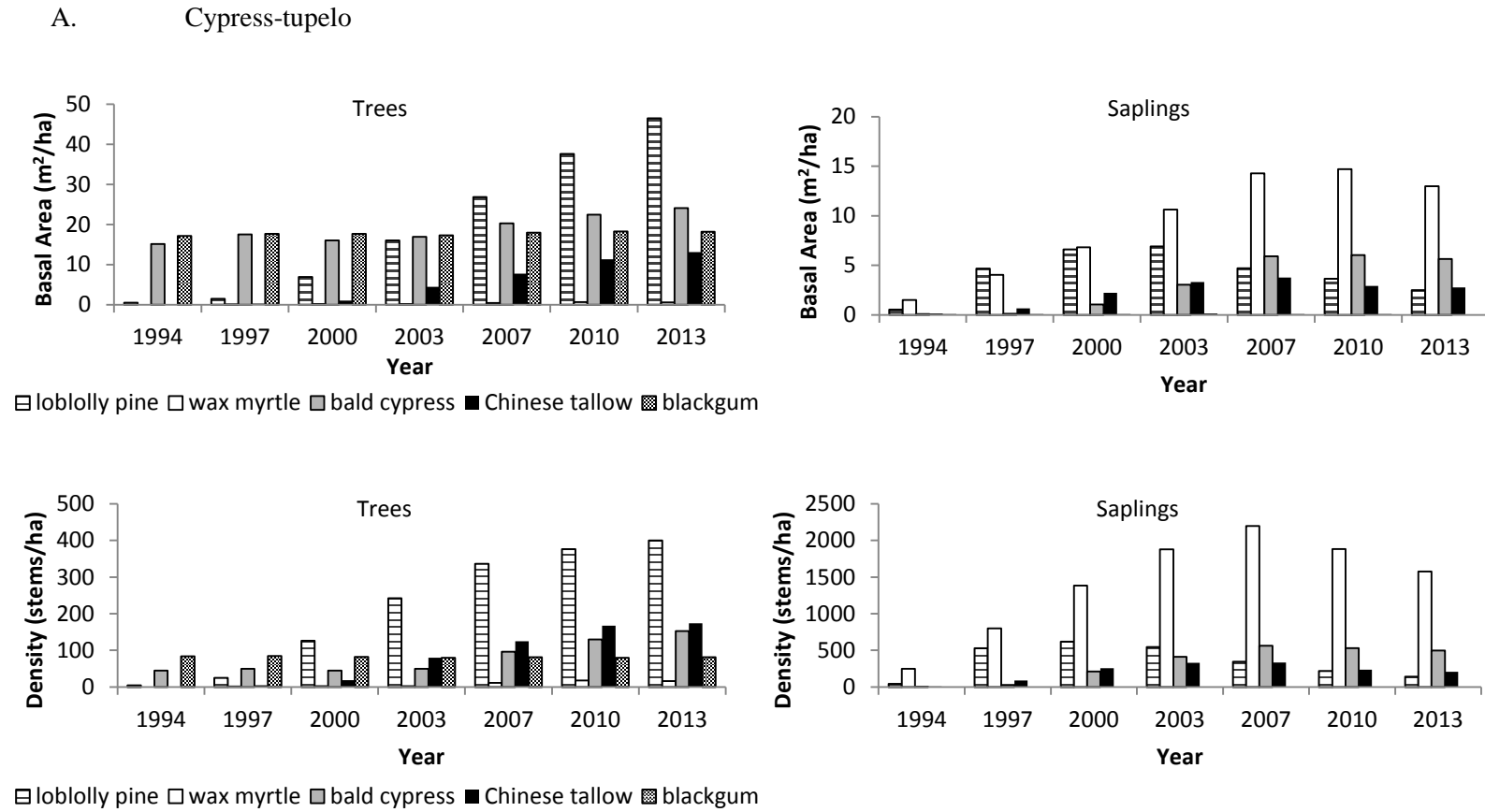
Fig. 3.2 Continued.

## Hobcaw Barony

In 1994, the tree strata of the cypress-tupelo plots consisted of blackgum (*Nyssa sylvatica*, 17.2 m<sup>2</sup>/ha, 83.8 stems/ha), bald cypress (15.2 m<sup>2</sup>/ha, 45 stems/ha), and laurel oak (4.4 m<sup>2</sup>/ha, 7.5 stems/ha). Most sapling-sized stems were wax myrtle (*Morella cerifera*, 250 stems/ha), loblolly pine (45 stems/ha), and redbay (33.8 stems/ha).

Blackgum tree basal area and density remained consistent throughout the study period. Loblolly pine basal area increased to nearly fifty times the initial amount by 2013 and loblolly density increased as well (**Fig. 3.3A**), surpassing blackgum in both tree basal area and density. Cypress tree density tripled over the 20-year period, while other tree densities were relatively unchanged (**Fig. 3.3B**). The number of wax myrtle stems entering the tree layer was low throughout the study and by 2013 wax myrtle tree density reached 11.25 stems/ha. In the sapling strata, wax myrtle density rose substantially from 250 stems/ha in 1994 to 2,196.3 stems/ha in 2007, then decreased to 1,575 stems/ha by 2013 (**Fig. 3.3B**). Cypress, loblolly, and red bay sapling densities also increased, resulting in a dense sapling layer by the end of the study period.

Both the tree and the sapling layer in upland pine-hardwood plots were dominated by loblolly pine throughout the study. Live oak tree-size stems increased by 52% in basal area and 45% in density over the study period. Wax myrtle and red bay represented a smaller component of the sapling layer and had slight growth in density and basal area from 1994 to 2013.



**Fig. 3.3** Basal area and density changes for important species in the (A) cypress-tupelo and (B) upland pine-hardwood forest types at Hobcaw Barony.



B. Upland pine-hardwood

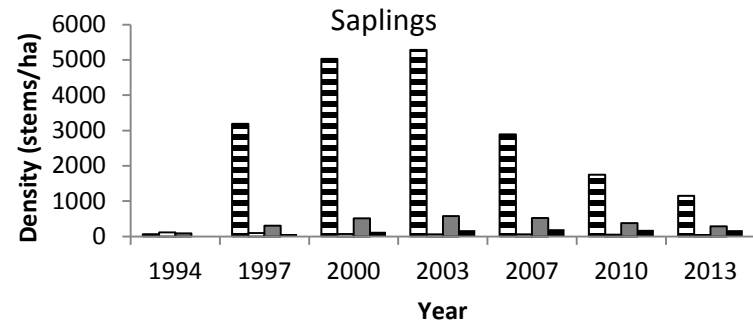
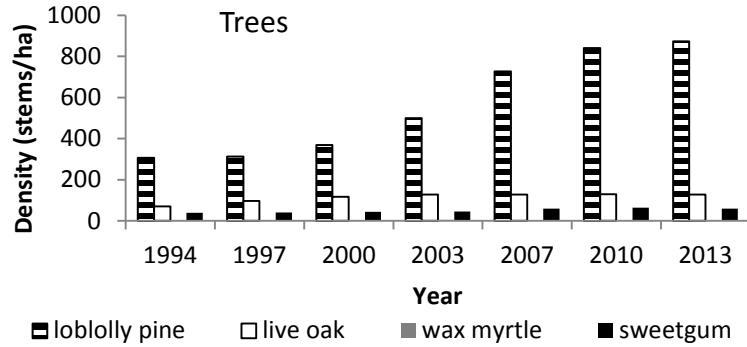
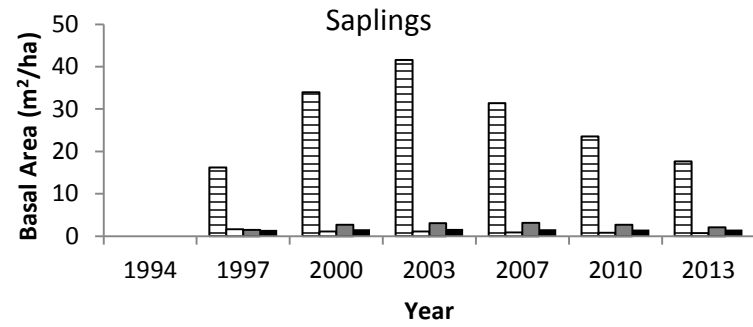
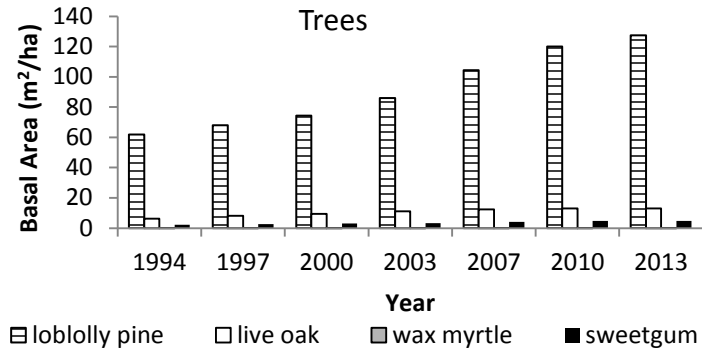


Fig. 3.3 Continued.

## Santee Experimental Forest

The cypress-tupelo type plots in Santee were adjacent to the BLH plots and were divided by Nicholson Creek. In 1994, bald cypress contributed 41.3 m<sup>2</sup>/ha (30 stems/ha) to the cypress-tupelo forest type (total of 91.2 m<sup>2</sup>/ha in basal area). Other less-dominant overstory species included sweetgum (11 m<sup>2</sup>/ha, 11.3 stems/ha), loblolly pine (2.3 m<sup>2</sup>/ha, 5 stems/ha), and overcup oak (*Quercus lyrata*, 4.8 m<sup>2</sup>/ha, 5 stems/ha). Sapling strata consisted of laurel oak (218 stems/ha), green ash (187 stems/ha), hornbeam (170 stems/ha), and American holly (98 stems/ha). The basal area and density of laurel oak trees increased substantially over the course of the study, while other species changed little in basal area and density (**Fig. 3.4A**). In the sapling strata, green ash and hornbeam increased greatly. Green ash density almost tripled and hornbeam density more than doubled by 2003, but had begun to decline by 2013. American holly sapling density nearly doubled by 2013, but tree basal area of the species saw a slight decline throughout the study. Other species in the sapling strata did not increase greatly in density.

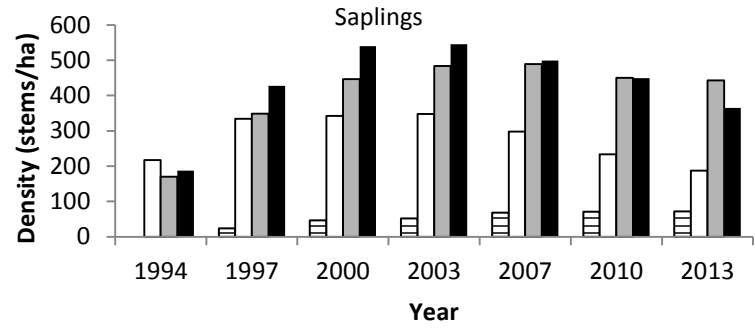
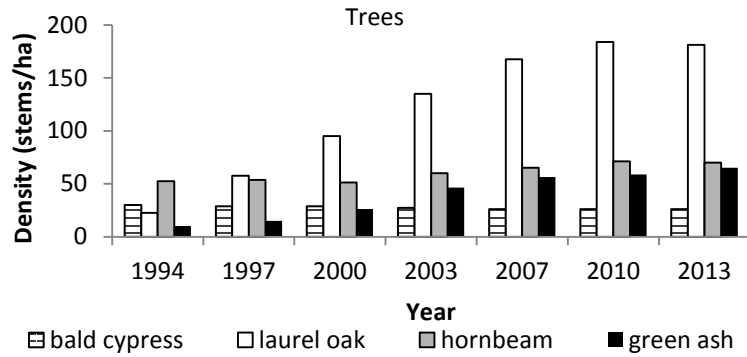
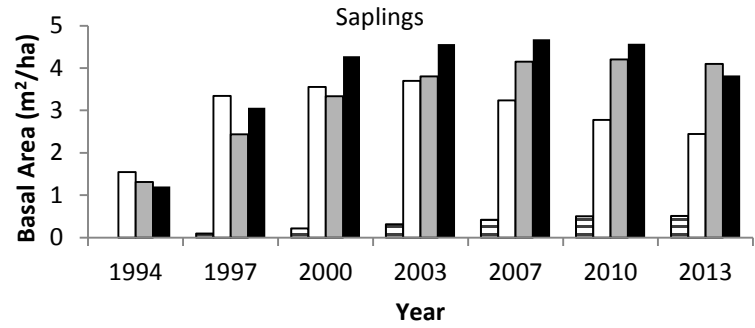
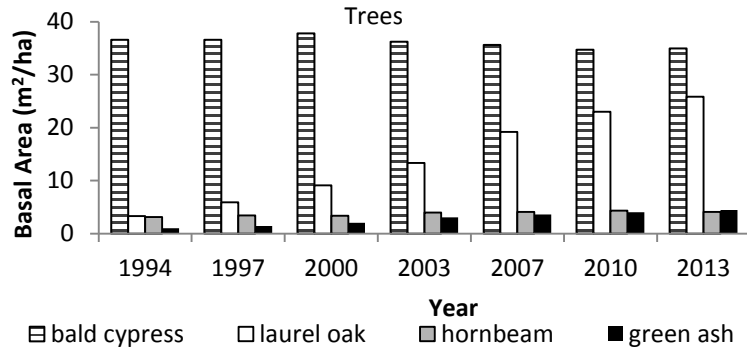
The bottomland hardwood plots were dominated in 1994 by red maple (14.7 m<sup>2</sup>/ha, 160 stems/ha), laurel oak (5.9 m<sup>2</sup>/ha, 21.3 stems/ha), and sweetgum (11.6 m<sup>2</sup>/ha, 75 stems/ha) tree-size stems. The basal area of red maple, laurel oak, and sweetgum increased with each census (**Fig. 3.4B**). Red maple and sweetgum basal area doubled and laurel oak basal area was over five times the initial basal area in 2013. Red maple saplings reached a peak density (880 stems/ha) at the 2000 census and laurel oak saplings were at peak density (598.75 stems/ha) in 2003. By 2013 red maple and laurel oak sapling density had decreased by 35% and 25%, respectively. Between 2000 and 2013,

red maple and laurel oak tree densities increased by 31% and 34%, respectively.

Hornbeam sapling basal area and density increased throughout the study, and hornbeam remained a minor component of the tree layer.

The tree layer of the upland pine-hardwood plots mostly consisted of loblolly pine (19.5 m<sup>2</sup>/ha, 70 stems/ha), blackgum (5.9 m<sup>2</sup>/ha, 105 stems/ha), and water oak (4.4 m<sup>2</sup>/ha, 66.3 stems/ha) in 1994. Tree-size loblolly pine basal area and density increased substantially throughout the study. Blackgum and water oak had less dramatic increases in size and abundance and were a much smaller component of the tree layer compared to loblolly pine by 2013. Sapling-size loblolly pine basal area and density rose rapidly, reached a peak in 2003, and subsequently decreased by 34% by 2013. Loblolly pine tree density increased by 54% between 2003 and 2013. Water oak saplings followed a similar trend to loblolly saplings but with less dramatic changes in basal area and density. Red maple saplings reached a peak density in 2000 (335 stems/ha) and decreased slightly in the following years, while the density of tree-size red maple increased.

A. Cypress-tupelo



**Fig. 3.4** Basal area and density changes for important species in the (A) cypress-tupelo, (B) bottomland hardwood, and (C) upland pine-hardwood forest types at Santee Experimental Forest.

B. Bottomland Hardwood

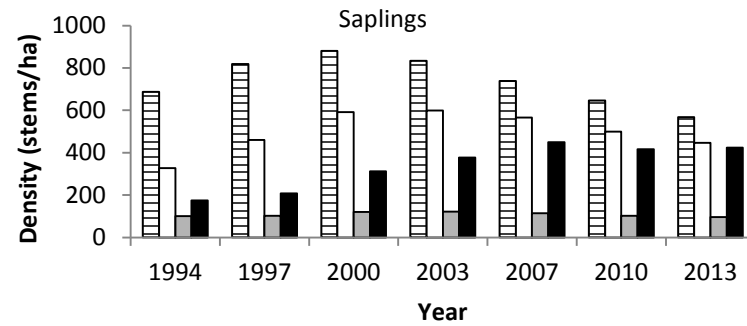
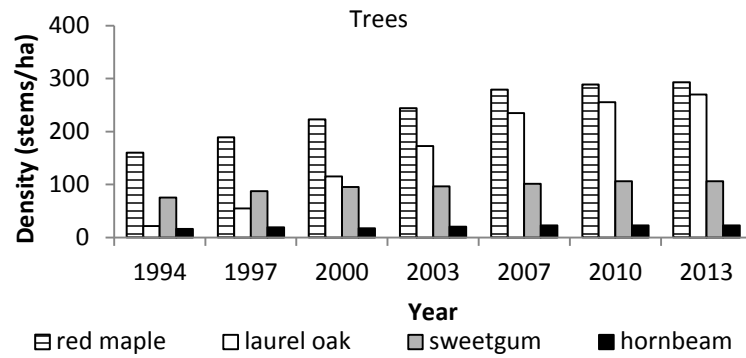
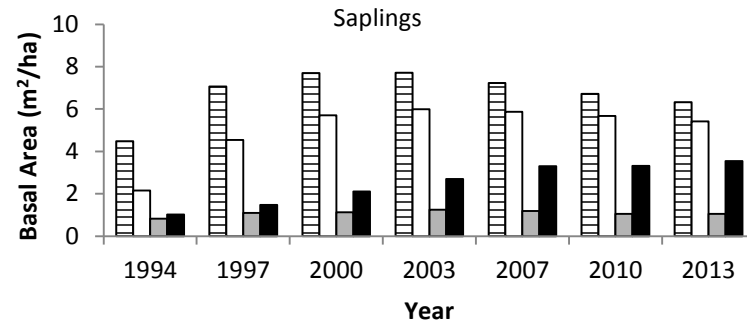
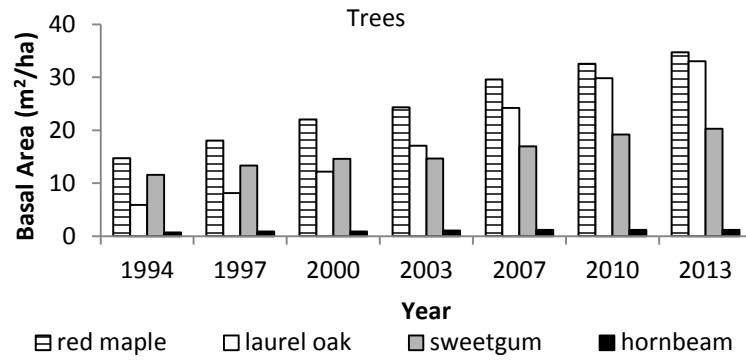
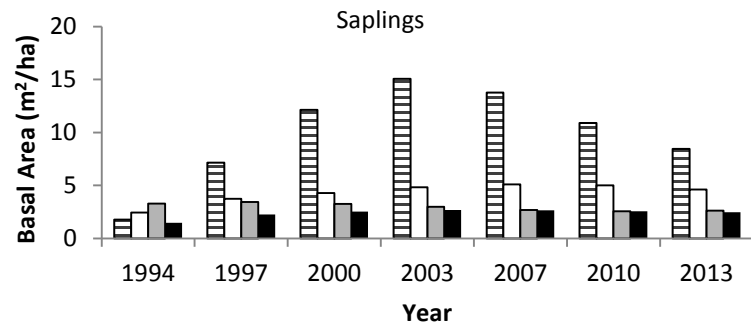
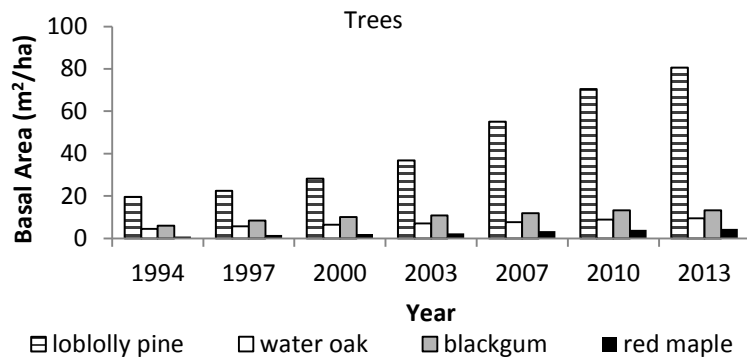


Fig. 3.4 Continued...

C. Upland pine-hardwood



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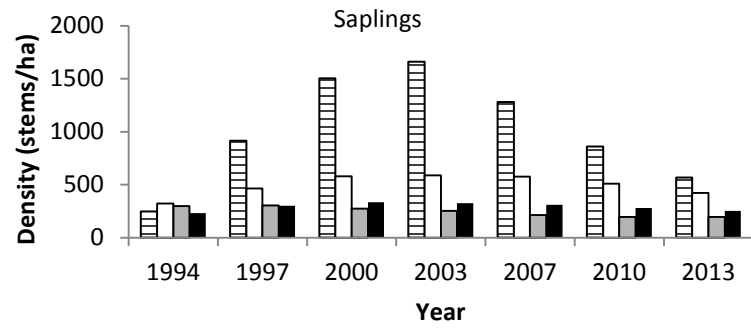
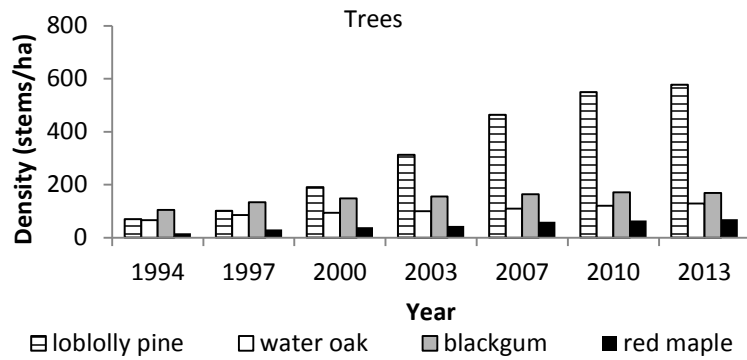


Fig. 3.4 Continued.

**Table 3.2A** Overview of species Importance Values (IV) within two forest cover types at Hobcaw Barony throughout the study period.

Cover type	Species 1994	Importance Value 1994	Species 2003	Importance Value 2003	Species 2013	Importance Value 2013
Cypress	<i>Nyssa sylvatica</i>	33.32	<i>Morella cerifera</i>	28.94	<i>Morella cerifera</i>	27.76
	<i>Taxodium distichum</i>	20.86	<i>Pinus taeda</i>	23.09	<i>Pinus taeda</i>	24.68
	<i>Morella cerifera</i>	17.52	<i>Taxodium distichum</i>	16.58	<i>Taxodium distichum</i>	18.00
	<i>Pinus taeda</i>	10.36	<i>Triadica sebifera</i>	10.94	<i>Triadica sebifera</i>	11.59
	<i>Persea borbonia</i>	9.68	<i>Nyssa sylvatica</i>	10.62	<i>Nyssa sylvatica</i>	7.23
	<i>Quercus laurifolia</i>	5.73				
Loblolly	<i>Pinus taeda</i>	55.38	<i>Pinus taeda</i>	78.83	<i>Pinus taeda</i>	71.11
	<i>Pinus serotina</i>	16.82	<i>Pinus serotina</i>	9.03	<i>Pinus serotina</i>	7.63
	<i>Quercus virginiana</i>	15.43	<i>Morella cerifera</i>	5.62	<i>Quercus virginiana</i>	6.12
	<i>Morella cerifera</i>	11.72	<i>Quercus virginiana</i>	4.94	<i>Morella cerifera</i>	5.56
	<i>Liquidambar styraciflua</i>	8.43	<i>Liquidambar styraciflua</i>	3.04	<i>Liquidambar styraciflua</i>	4.68
	<i>Triadica sebifera</i>	4.47				

**Table 3.2B** Overview of species Importance Values (IV) within four forest cover types at Congaree National Park throughout the study period.

Cover type	Species 1994	Importance Value 1994	Species 2003	Importance Value 2003	Species 2013	Importance Value 2013
Bottomland						
Hardwood	<i>Liquidambar styraciflua</i>	39.04	<i>Liquidambar styraciflua</i>	37.85	<i>Liquidambar styraciflua</i>	32.12
	<i>Ilex opaca</i>	16.02	<i>Ilex opaca</i>	15.98	<i>Ilex opaca</i>	15.13
	<i>Ilex decidua</i>	10.72	<i>Ilex decidua</i>	10.02	<i>Ilex decidua</i>	15.00
	<i>Fraxinus sp.</i>	7.22	<i>Fraxinus sp.</i>	8.26	<i>Asimina triloba</i>	13.96
	<i>Asimina triloba</i>	6.92	<i>Asimina triloba</i>	7.63	<i>Fraxinus sp.</i>	6.51
			<i>Ulmus americana</i>	5.04	<i>Celtis laevigata</i>	4.94
Pine Hardwood						
	<i>Pinus taeda</i>	32.68	<i>Pinus taeda</i>	28.49	<i>Carpinus caroliniana</i>	26.06
	<i>Carpinus caroliniana</i>	27.10	<i>Carpinus caroliniana</i>	27.44	<i>Pinus taeda</i>	25.83
	<i>Liquidambar styraciflua</i>	18.29	<i>Liquidambar styraciflua</i>	15.40	<i>Liquidambar styraciflua</i>	10.76
	<i>Quercus phellos</i>	6.02	<i>Quercus phellos</i>	6.40	<i>Acer rubrum</i>	7.89
	<i>Ilex opaca</i>	5.20	<i>Ilex opaca</i>	5.97	<i>Ilex opaca</i>	7.69
	<i>Acer rubrum</i>	1.86	<i>Ulmus alata</i>	5.42	<i>Quercus phellos</i>	5.28
			<i>Acer rubrum</i>	4.01		
Cypress						
	<i>Nyssa aquatica</i>	48.28	<i>Nyssa aquatica</i>	46.30	<i>Nyssa aquatica</i>	45.14
	<i>Taxodium distichum</i>	23.21	<i>Taxodium distichum</i>	24.27	<i>Taxodium distichum</i>	26.44
	<i>Fraxinus americana</i>	13.40	<i>Fraxinus americana</i>	11.59	<i>Acer rubrum</i>	10.47
	<i>Nyssa biflora</i>	11.89	<i>Nyssa biflora</i>	10.92	<i>Nyssa biflora</i>	10.15
	<i>Acer rubrum</i>	5.56	<i>Acer rubrum</i>	9.06	<i>Fraxinus americana</i>	9.88
Tupelo						
	<i>Nyssa biflora</i>	66.62	<i>Nyssa biflora</i>	71.52	<i>Nyssa biflora</i>	51.25
	<i>Acer rubrum</i>	9.98	<i>Ilex opaca</i>	7.40	<i>Ilex opaca</i>	14.16
	<i>Quercus laurifolia</i>	9.06	<i>Liquidambar styraciflua</i>	6.98	<i>Acer rubrum</i>	12.84
	<i>Liquidambar styraciflua</i>	8.03	<i>Quercus laurifolia</i>	6.53	<i>Quercus laurifolia</i>	8.26
	<i>Ilex opaca</i>	4.02	<i>Acer rubrum</i>	5.46	<i>Liquidambar styraciflua</i>	5.75



**Table 3.2C** Overview of species Importance Values (IV) within three forest cover types at the Santee Experimental Forest throughout the study period.

Cover type	Species 1994	Importance Value 1994	Species 2003	Importance Value 2003	Species 2013	Importance Value 2013
Bottomland						
Hardwood	<i>Acer rubrum</i>	32.88	<i>Acer rubrum</i>	29.28	<i>Acer rubrum</i>	26.89
	<i>Quercus laurifolia</i>	13.90	<i>Quercus laurifolia</i>	21.31	<i>Quercus laurifolia</i>	24.49
	<i>Liquidambar styraciflua</i>	13.52	<i>Liquidambar styraciflua</i>	10.34	<i>Liquidambar styraciflua</i>	10.47
	<i>Ulmus sp.</i>	8.86	<i>Ulmus sp.</i>	7.32	<i>Carpinus caroliniana</i>	8.31
	<i>Fraxinus pennsylvanica</i>	7.72	<i>Carpinus caroliniana</i>	7.10	<i>Ulmus sp.</i>	6.65
	<i>Carpinus caroliniana</i>	5.38				
Upland Pine						
Hardwood	<i>Pinus taeda</i>	29.71	<i>Pinus taeda</i>	49.25	<i>Pinus taeda</i>	48.86
	<i>Nyssa sylvatica</i>	19.74	<i>Quercus nigra</i>	14.65	<i>Quercus nigra</i>	13.60
	<i>Quercus nigra</i>	17.22	<i>Nyssa sylvatica</i>	12.08	<i>Nyssa sylvatica</i>	11.21
	<i>Liquidambar styraciflua</i>	13.91	<i>Liquidambar styraciflua</i>	7.87	<i>Acer rubrum</i>	7.54
	<i>Acer rubrum</i>	8.63	<i>Acer rubrum</i>	6.92	<i>Liquidambar styraciflua</i>	7.38
Cypress	<i>Taxodium distichum</i>	22.66	<i>Taxodium distichum</i>	15.68	<i>Quercus laurifolia</i>	18.61
	<i>Quercus laurifolia</i>	12.42	<i>Quercus laurifolia</i>	15.62	<i>Taxodium distichum</i>	14.40
	<i>Carpinus caroliniana</i>	11.00	<i>Carpinus caroliniana</i>	12.80	<i>Carpinus caroliniana</i>	13.78
	<i>Fraxinus pennsylvanica</i>	8.59	<i>Fraxinus pennsylvanica</i>	12.45	<i>Fraxinus pennsylvanica</i>	11.56
	<i>Liquidambar styraciflua</i>	7.77	<i>Liquidambar styraciflua</i>	7.66	<i>Liquidambar styraciflua</i>	7.25
	<i>Acer rubrum</i>	6.92	<i>Acer rubrum</i>	5.39	<i>Acer rubrum</i>	5.46
	<i>Ilex opaca</i>	6.82	<i>Pinus taeda</i>	5.26		
	<i>Pinus taeda</i>	5.91				

**Table 3.2D** Overview of species Importance Values (IV) within three forest cover types at Beidler Forest throughout the study period.

Cover type	Species 1994	Importance Value 1994	Species 2003	Importance Value 2003	Species 2013	Importance Value 2013
Bottomland						
Hardwood	<i>Quercus laurifolia</i>	27.33	<i>Quercus laurifolia</i>	31.73	<i>Quercus laurifolia</i>	33.35
	<i>Liquidambar styraciflua</i>	14.43	<i>Liquidambar styraciflua</i>	13.85	<i>Liquidambar styraciflua</i>	14.25
	<i>Acer rubrum</i>	12.07	<i>Acer rubrum</i>	11.35	<i>Acer rubrum</i>	10.66
	<i>Carpinus caroliniana</i>	9.41	<i>Taxodium distichum</i>	9.45	<i>Taxodium distichum</i>	9.73
	<i>Taxodium distichum</i>	9.29	<i>Fraxinus pennsylvanica</i>	8.32	<i>Fraxinus pennsylvanica</i>	7.82
	<i>Fraxinus pennsylvanica</i>	7.51	<i>Carpinus caroliniana</i>	7.58	<i>Carpinus caroliniana</i>	6.73
	<i>Nyssa aquatica</i>	6.57	<i>Nyssa aquatica</i>	5.18	<i>Ilex opaca</i>	5.21
Cypress	<i>Fraxinus pennsylvanica</i>	32.69	<i>Fraxinus pennsylvanica</i>	35.08	<i>Fraxinus pennsylvanica</i>	33.89
	<i>Nyssa aquatica</i>	32.40	<i>Nyssa aquatica</i>	29.46	<i>Nyssa aquatica</i>	29.42
	<i>Taxodium distichum</i>	21.26	<i>Taxodium distichum</i>	21.16	<i>Taxodium distichum</i>	23.14
	<i>Nyssa sylvatica</i>	6.81	<i>Nyssa sylvatica</i>	7.15	<i>Nyssa sylvatica</i>	6.82
	<i>Quercus laurifolia</i>	2.59	<i>Quercus laurifolia</i>	3.20	<i>Quercus laurifolia</i>	2.86
Ridge Bottom	<i>Carpinus caroliniana</i>	32.23	<i>Carpinus caroliniana</i>	31.20	<i>Carpinus caroliniana</i>	29.57
	<i>Liquidambar styraciflua</i>	12.30	<i>Liquidambar styraciflua</i>	13.64	<i>Liquidambar styraciflua</i>	12.64
	<i>Persea borbonia</i>	10.72	<i>Persea borbonia</i>	11.33	<i>Quercus nigra</i>	11.49
	<i>Quercus nigra</i>	8.70	<i>Quercus nigra</i>	7.05	<i>Persea borbonia</i>	8.86
	<i>Ilex opaca</i>	7.27	<i>Ilex opaca</i>	6.64	<i>Ilex opaca</i>	8.67
	<i>Fraxinus sp.</i>	6.50	<i>Quercus laurifolia</i>	5.56	<i>Quercus laurifolia</i>	6.27
			<i>Fraxinus sp.</i>	5.05	<i>Carya ovata</i>	5.07

## Discussion

The pre-disturbance composition and structure of the forest, the level of hurricane intensity in the area, and the past exposure of the forest to other disturbance events are important factors in determining the long-term effects of hurricane disturbance (Oliver and Larson, 1996; White, 1979). The four sites sampled for this study were all subjected to varying degrees of hurricane intensity. The presence of certain species within a site is also relevant, as individual species of the southeastern forest differ in their resistance to hurricane damage (Stanturf *et al.*, 2007). The Santee Experimental Forest was the nearest site to the northeast eyewall (the portion of the Northern Hemisphere hurricanes with the highest peak wind speed, Busby *et al.*, 2008) of Hurricane Hugo and received the greatest wind damage of all four sites. The average volume of wood per ha in the post-hurricane forest was estimated to be 13.4% of pre-hurricane levels (Hook *et al.*, 1991). Mature stands of loblolly pine, longleaf pine, and bottomland hardwood were found to have approximately 75%, 91%, and 87% damaged stems, respectively (Hook *et al.*, 1991). Hobcaw Barony, located 72 km east of the hurricane eyewall, received less wind damage and had a lower rate of tree mortality from wind (Gresham *et al.*, 1991). However, the site's close proximity to the ocean (5 km) resulted in a saltwater surge of up to 2 meters that reached roughly 1 km into the forest (Gardner *et al.*, 1991). Delayed mortality from saltwater intrusion persisted for at least 18 months following the hurricane (Williams, 1996). Congaree National Park and Beidler Forest were southwest of the eye of the storm. Beidler Forest received hurricane winds estimated at mean 116 kmh with gusts up to 185 kmh (Purvis *et al.*, 1990). A survey of Beidler Forest performed two years after

the storm reported an overall tree mortality of 21% (Duever and McCollum, 1992). Congaree National Park is over 100 km inland and much of the tree damage received at this site consisted of crown breakage and defoliation. A post-hurricane survey classified 33% of trees at Congaree National Park as seriously damaged and 18% uprooted or snapped off (Putz and Sharitz, 1991).

Bald cypress and tupelo trees are resistant to mortality from wind damage (Stanturf *et al.*, 2007). Many mature bald cypress and tupelo trees survived Hugo and continue to dominate the overstory of the cypress-tupelo plots of Congaree and Beidler Forest (**Fig. 3.1B, 3.2A**). A high percentage of non-dominant trees within the cypress-tupelo forests of Congaree were uprooted by hurricane winds (Putz and Sharitz, 1991). The dramatic increase in sapling abundance of shade-tolerant species (e.g., red maple, laurel oak, paw paw) may be a result of unoccupied space becoming available in the cypress-tupelo canopy. Several studies have shown that the formation of canopy gaps will likely benefit both seedlings and saplings of shade-tolerant species more than gap-demanding species (Uhl *et al.*, 1988; Brown and Whitmore, 1992; Webb, 1989). The storm surge at Hobcaw Barony carried salt water to the cypress-tupelo plots resulting in the eventual salt-induced mortality of bald cypress, water tupelo, and blackgum trees, among other species (Conner and Inabinette, 2003). The decline in the density of these dominant species allowed for loblolly pine, wax myrtle, and red bay to become established in the understory, along with the invasive Chinese tallow. Loblolly pine stems have been successful in capitalizing on canopy gaps and are present with a basal area exceeding that of bald cypress and tupelo stems (**Fig. 3.3A**). Strong winds at Santee

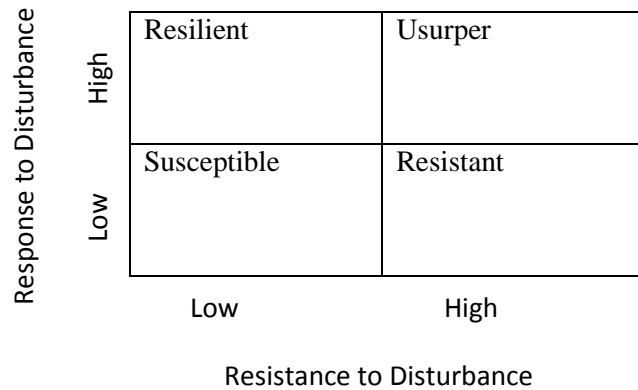
Experimental Forest lowered density in the cypress-tupelo overstory and allowed for the growth of high numbers of laurel oak stems. Laurel oak had become a major component of the tree layer by 2013. Green ash and hornbeam produced large numbers of sapling-size stems, likely due to canopy gaps created following the wind-induced mortality of larger trees.

The upland pine hardwood stand type contains many species that have an intermediate resistance or are susceptible to wind damage (loblolly pine, water oak, willow, laurel oak) (Gresham *et al.*, 1991; Stanturf *et al.*, 2007). Loblolly pine increased in dominance at Santee and Hobcaw pine-hardwood stands and maintained dominance at Congaree stands. At Hobcaw and Santee, loblolly pine sapling density rose to high levels, reaching a peak density level around 14 years after the disturbance. Loblolly sapling density at Hobcaw and Santee decreased in the 10 years following 2003, indicating that the seedling establishment period had ended. Loblolly pine is known as a pioneer species on disturbed land and seedlings were able to exploit the increase in light availability that resulted from the initial mortality of mature trees in this stand type.

The bottomland hardwood cover type also contains many species that are susceptible or have intermediate resistance to hurricane wind damage. Sites of this type at Congaree and Beidler Forest were heavily damaged despite being exposed to comparatively low wind speeds. Sweetgum had a dominant role at these sites, similar to that of loblolly pine in the upland pine hardwood stands. Red maple and laurel oak (two species with low resistance to wind damage, Stanturf *et al.*, 2007) population densities increased following the disturbance while sweetgum had a low number of saplings

recruited throughout the study. Laurel oak and red maple sapling populations eventually declined at these sites while tree density remained relatively high (**Fig. 3.1A, 3.2B**). At Congaree, pawpaw, American holly, and deciduous holly took advantage of newly available resources and established large numbers of saplings.

Our results are consistent with the Gleasonian view of succession that regards ecosystems as self-organized systems of individual plant species that may have multiple successional pathways and equilibriums (Uriarte *et al.*, 2009). Along with other hurricane studies in tropical and temperate forest ecosystems, species trends in this study imply that differences in recovery pathways may be largely influenced by pre-hurricane composition, location in relation to the path of the storm and by local hurricane intensity (Lugo, 2008; Turner *et al.*, 1998; White, 1979; Zhao *et al.*, 2006; Song *et al.*, 2012; Uriarte *et al.*, 2009). Individual species may be classified within a forest type in terms of resistance and resilience to disturbance based on the interpretations of Bellingham *et al.* (1995) and Batista and Pratt (2003). The possible roles that a species may assume following a disturbance are summarized in (**Fig. 3.5**).



**Fig. 3.5** A diagram of categorizations of individual species roles within a forest type after a hurricane disturbance (adapted from Bellingham *et al.*, 1995).

A species that is resistant (e.g., bald cypress, tupelo, live oak, longleaf) to hurricane effects responds with little to no change in survival or growth of adult trees and little to no change in recruitment or growth of saplings. A resilient species (e.g., sweetgum, loblolly pine, laurel oak) experiences a decrease in survival and growth of adults, but an increase in recruitment and growth of saplings. A susceptible species (e.g., willow and water oaks) shows a decrease in growth and survival of adults and no change or a decrease in recruitment and growth of saplings. A usurper species (e.g., hornbeam, loblolly pine) shows little to no change in the adult population and an increase in recruitment or growth of saplings (Batista and Pratt, 2003). Similar classifications have been applied to tropical forest species (Boucher *et al.*, 1990, 1994; Tanner *et al.*, 1991; Lugo and Scatena, 1996; Bellingham *et al.*, 1995). These classifications are broad generalizations and are often specific to a stand or a population. Species may be assigned more than one role based on where they lie on the spectrum of damage and response.

Loblolly pine was a usurper in longleaf and cypress-tupelo stands, but was resilient in pine-hardwood stands. Bald cypress is relatively resistant but was resilient in Hobcaw cypress stands that were inundated with salt water. It is likely that the degree of damage to dominant bald cypress and water tupelo trees from saltwater intrusion and wind was the factor that resulted in resilient loblolly pine assuming the role of usurper. Loblolly pine remains abundant in the tree layer of Hobcaw cypress-tupelo stands, and further monitoring will be necessary to discover whether the “primary” forest species will replace the pioneer loblolly pine in the future. Laurel oak was relatively resilient in bottomland hardwood stands, but acted as a usurper at the cypress-tupelo stands at Santee where laurel oak tree density was far greater than all other species present in 2013.

### Conclusion

This examination of 4 to 24 years of recovery trends of seven forest types from four sites after Hurricane Hugo has added to our understanding of the long-term impacts that hurricanes may have on temperate forest ecosystems. The pre-hurricane composition of a disturbed forest is a determinant of the impacts that the disturbance may have on forest structure and composition (Duever and Mccollum, 1992; Putz and Sharitz, 1991; Gresham *et al.*, 1991). Although our study lacks quantitative data on pre-hurricane composition and structure, we have observed trends in post-hurricane succession and structural changes and related them to hurricane intensity, level of damage, and forest type. Plots in Beidler Forest and Congaree National Park showed relatively little change



in composition and structure over the twenty year study period. However, some forest types displayed varying recovery pathways within these sites. Cypress-tupelo stands at Beidler Forest were found to have lost around 1% of water tupelo and bald cypress stems in a survey performed two years after Hurricane Hugo. Maintaining these large overstory stems resulted in very little compositional or structural change in these stands.

Stand structure and composition was more dynamic throughout the study period at the cypress-tupelo stands of Hobcaw Barony and Santee Experimental Forest, where the initial basal area and density of primary forest species was relatively low due to high mortality from winds and (in the case of Hobcaw Barony) salt from the tidal surge. These conditions may provide opportunities for the establishment of invasive plant species (Lugo, 2000). This was the case with non-native Chinese tallow in cypress-tupelo stands at Hobcaw Barony as well as bottomland hardwood forests of south-central Louisiana (Conner *et al.*, 2014). Non-native plants can capitalize on canopy gaps created by hurricane disturbance, but populations may decrease as a result of the canopy closing in the following years (Chinea, 1999; Thompson *et al.*, 2007). Trends in composition and structure at most stand types indicate that forests are trending towards a canopy dominated by “primary” forest species, with pioneer or usurper populations beginning to thin as the canopy closes. However, there are ongoing changes in stand composition occurring at all four major sites, with these changes being generally more apparent at forests that were altered most dramatically by the hurricane disturbance. Further monitoring will reveal whether these forests will eventually resemble a pre-hurricane forest in structure and composition.

CHAPTER IV  
TRENDS IN MORTALITY, REGENERATION, AND SPECIES DIVERSITY IN COASTAL  
PLAIN FORESTS OF SOUTH CAROLINA FOLLOWING HURRICANE HUGO

Introduction

The immediate effects that a hurricane may have on forest ecosystems have been documented (e.g., Everham and Brokaw, 1996). In addition to visible forest alteration, hurricanes also cause long-term or “invisible” changes in forest structure and composition. Lugo *et al.* (1999) describe forest response as a feedback loop with many alternative pathways. The two main hurricane forces, wind and rain, interact with the canopy and soil and cause short-term and long-term changes in forest structure, mortality, and rates of processes. However, long-term trajectories of forest response to hurricanes may vary based on many factors, including the pre-disturbance composition and structure of the forest, the level of disturbance intensity in the area, and the past exposure of the forest to other disturbance events (Oliver and Larson, 1996; White, 1979).

Lugo (2008) defines several periods of change that take place in a disturbed forest following a hurricane. The first 20 years is characterized by rapid change in forest structure and composition. During this period of regrowth, stands will reach a peak in tree density. A thinning phase will follow that includes increased mortality and decreased tree density, allowing for surviving trees to grow and increase basal area and biomass of the stands. Researchers have noted changes in species composition during the regrowth period as existing species and pioneer species compete for available resources. In the years following a hurricane, the dominance of

primary forest species is expected to increase as the population of secondary or pioneer species decreases (Fu *et al.*, 1996). The level of change in species diversity may be highly dependent on the scale of sampling. High levels of compositional change that are found on a 1-ha experimental scale may not be apparent on a watershed scale (Scatena and Lugo, 1995; Fu *et al.*, 1996).

The state of South Carolina is affected by at least one hurricane on average every three years, and its coastal forests are vulnerable to extreme winds and hurricane storm surge (Purvis, 1996). Hurricane Hugo was one of the most impactful storms in recorded history to reach the Eastern United States. Around 1.8 million ha of forested land in South Carolina was disturbed by the storm (Sheffield and Thompson, 1992). A long-term study was devised in 1993 in order to identify the resilience of coastal forests to the effects of high-intensity hurricanes. This paper uses data from these long-term plots that was collected at 3 to 4 year intervals from 1994 to 2013, resulting in a 19-year dataset that extends to 24 years after the storm. Long-term patterns of tree mortality, regeneration, diversity, and growth following Hurricane Hugo are examined within several forest community types of South Carolina, USA in order to better understand patterns of temperate forest response to hurricane damage and to compare these response patterns with those of other forest ecosystems.

## Materials and Methods

### Study Area

Study plots established in 1993 by Dr. Charles Gresham have been continually monitored for this project (Song *et al.*, 2012). Four major study areas were chosen; Beidler Forest, Santee Experimental Forest, Hobcaw Barony, and Congaree National Park. These forests all received varying degrees and types of damage from Hurricane Hugo. Initial damage assessments of these sites can be found in Gresham *et al.* (1991)- Hobcaw Forest, Putz and Sharitz (1991)- Congaree

National Park, Hook *et al.* (1991)- Santee Experimental Forest, and Duever and McCollum (1992)- Beidler Forest. Forest cover types are not evenly distributed throughout the measurement plots. The cypress-tupelo cover type is the only type that is present at all study sites (**Table 3.1**).

Beidler Forest and Congaree National Park are located farther inland than Hobcaw Barony and Santee Experimental Forest and were positioned west of the hurricane eyewall, resulting in lower damage from winds at these sites. A survey of Beidler Forest performed two years after the storm reported an overall tree mortality of 21% (Duever and McCollum 1992). A post-hurricane survey of Congaree National Park classified 33% of trees as seriously damaged and 18% uprooted or snapped off (Putz and Sharitz 1991). Hobcaw Barony was subjected to high winds as well as a tidal surge with a depth of approximately 2 m that reached around 1 km inland and resulted in delayed tree mortality for up to 18 months (Williams, 1996). Santee Experimental Forest was located nearest to the northeast eyewall and received the highest winds of all four sites. Damage from these winds resulted in approximately 90% overall mortality for trees (Hook *et al.*, 1991). More information on the location and character of these sites can be found in the Materials and Methods section of Chapter 3.

#### Data Collection

Plots were measured in 1994, 1997, 2000, 2003, 2007, 2010, and 2013. Four plots of each of the dominant forest cover types were established in 1993 at Beidler, Santee, and Hobcaw Barony. At Congaree, plots were located based on the spatial distribution of forest cover types. A total of 42 study plots of dimensions 20 m X 100 m based on five forest cover types were established (**Table 3.1**). Each plot was divided into five 20 m X 20 m subplots and marked by aluminum poles. Consistent techniques of tree measurement, based on the work of Dr. Charles Gresham, have been used throughout the study. Tree stems with a DBH (diameter at breast height) of at least 2.5 cm were marked with a permanent ID tag to ensure that data remained

consistent throughout the study. Marked trees were identified by species and given a damage class. Data collected during each field season included DBH, current damage class of trees, and small (< 2.5 cm DBH) recruitment. Seedling recruitment was measured within ten 3.25 m radius subplots located in each main plot. Woody seedlings were tallied and identified by species and height class.

### Analysis

Annual mortality and recruitment rates of tree species were calculated for each study plot. Crude annual mortality rates were calculated using  $M = 100 [(N_d/N_0) 1/t]$ , where M is the percentage annual mortality rate,  $N_0$  is the number of living stems at the previous measurement,  $N_d$  is the number of dead stems observed at the time of the current measurement, and t is the number of years between field measurements. Annual recruitment rates were calculated using  $R = 100 [(N_r/N_0) 1/t]$ , where R is the percentage annual recruitment rate,  $N_0$  is the number of living stems at the previous measurement,  $N_r$  is the number of new individuals added to the tree size class (>2.5 cm DBH) in the current measurement, and t is the number of years between field measurements. Relative basal area increment (RBAI) was calculated for all stems at each inventory using

$$\frac{RBAI = \ln BA_{t1} - \ln BA_{t0}}{t_1 - t_0}$$

where BA is basal area in square meters (derived from DBH) and t is the time in years (Bellingham *et al.* 1995). RBAI was not calculated for Congaree National Forest plots due to individual tree ID tags being disallowed. One-way ANOVAs were used to test correlations between response variables (recruitment, mortality, growth rate, diversity, and species richness) and categories (measurement period, forest cover type, site, and species). Species diversity was calculated for each cover type using Shannon's diversity index. Diversity and richness indices were calculated using the vegan package (Oksanen *et al.* 2015) in R version 3.2.

## Results

### Mortality and Recruitment

Annual mortality rates across all species were, on average, greatest between the years 2000 and 2007, or 11-18 years post-hurricane (hereafter referred to as PH) (**Table 4.1A**). Mortality rates across all species remained relatively high during the period of 18-24 years PH, but were lower on average from the 11-18 year PH period across all species. Mortality rates from all monitoring periods combined varied among study sites [ $F(3, 4674) = 7.64, p < 0.0001$ ]. A post-hoc Tukey test ( $p < 0.05$ ) revealed that mortality rates were significantly lower throughout the study at Congaree National Forest when compared to the other three major sites. An ANOVA test revealed differences in recruitment rates across all species between monitoring periods [ $F(5, 1835) = 41.04, p < 0.0001$ ] and between sites [ $F(3, 1835) = 11.44, p < 0.0001$ ]. Annual recruitment rates were greatest from 5 to 8 years PH and rates from 8 to 11 years PH were significantly greater than rates in all of the later monitoring periods (Tukey test,  $p = 0.05$ ). Recruitment rates in Hobcaw and Santee plots were significantly greater than those at Congaree and Beidler plots (Tukey test,  $p = 0.05$ ).

**Table 4.1A** Annual mortality rates, annual recruitment rates, and mean annual RBAI by species at Hobcaw Barony and Congaree National Park. Time periods between measurements are referred to as: period 1 (1994 – 1997), period 2 (1997 – 2000), period 3 (2000 – 2003), period 4 (2003 – 2007), period 5 (2007 – 2010), and period 6 (2010 – 2013).

Site	Cover type	Species	Mortality (%stems/yr)						Recruitment (%stems/yr)						Mean RBAI					
			1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Hobcaw	Cypress	All species combined	2.1	1.93	2.89	2.98	2.5	2.47	8.4	5.83	2.95	3.74	0.54	1.31	0.011	0.026	0.045	0.042	0.034	0.007
		<i>Morella cerifera</i>	12.2	3.1	2.2	3.5	4.2	5.5	27.2	19.7	11.9	6.9	1.5	2.3	0.033	0.028	0.019	0.025	0.016	0.002
		<i>Nyssa sylvatica</i>	2.3	2.6	0.5	0.4	0.9	0.3	2.9	0.9	0.0	0.0	0.0	0.0	0.022	0.052	0.052	0.049	0.033	0.020
		<i>Persea borbonia</i>	1.4	1.2	0.6	1.7	2.8	0.9	18.4	12.7	13.2	1.6	0.0	2.3	0.016	0.159	0.142	0.067	0.058	0.030
		<i>Pinus taeda</i>	0.9	0.4	0.8	3.3	4.3	3.0	30.7	9.3	3.7	1.5	0.0	0.4	0.003	0.016	0.083	0.124	0.053	0.017
		<i>Taxodium distichum</i>	0.6	1.3	0.0	0.1	0.2	0.9	13.3	21.3	14.6	9.4	1.3	0.7	0.004	0.064	0.131	0.085	0.057	0.028
		<i>Triadica sebifera</i>	0.0	4.2	1.3	0.7	2.3	1.5	30.5	19.3	15.8	4.1	1.4	2.7	0.030	0.047	0.035	0.040	0.028	0.013
	Loblolly	<i>Liquidambar styraciflua</i>	3.0	1.7	1.9	2.4	0.8	2.2	11.7	7.1	2.2	2.2	0.5	0.7	0.019	0.040	0.031	0.024	0.018	0.003
		<i>Morella cerifera</i>	1.6	1.5	3.2	5.8	9.0	9.3	23.3	13.0	4.3	4.3	0.2	1.9	0.010	0.071	0.062	0.075	0.043	0.028
		<i>Persea borbonia</i>	0.0	0.0	1.4	1.4	1.1	1.8	31.2	15.9	8.2	4.8	0.2	0.5	0.004	0.097	0.063	0.026	0.015	0.005
		<i>Pinus taeda</i>	0.8	0.5	1.2	9.5	8.9	7.0	29.6	12.1	3.6	0.8	0.0	0.1	0.087	0.044	0.036	0.024	0.018	0.001
		<i>Quercus virginiana</i>	1.9	1.7	1.3	1.2	1.3	2.7	4.1	2.0	0.0	0.2	0.0	0.0						
Congaree	BLH	<i>Asimina triloba</i>	2.6	4.4	4.2	14.5	1.0	0.6	13.7	0.1	6.0	21.4	1.1	1.4						
		<i>Ilex decidua</i>	1.8	1.3	0.8	4.8	0.2	0.1	5.3	0.0	2.6	15.9	1.3	1.1						
		<i>Ilex opaca</i>	2.3	2.8	0.6	0.3	3.0	0.3	0.7	1.0	0.6	6.0	0.2	2.8						
		<i>Liquidambar styraciflua</i>	1.7	1.6	1.0	2.1	0.2	1.2	0.0	0.9	0.5	0.2	0.0	0.0						
	Pine-hardwood	<i>Acer rubrum</i>	0.0	0.0	0.0	0.0	1.3	0.0	11.1	0.0	13.3	20.2	5.6	0.0						
		<i>Carpinus caroliniana</i>	4.4	2.9	1.0	4.3	0.6	1.2	8.6	2.0	1.9	18.0	3.0	0.0						
		<i>Ilex decidua</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.0	0.0	0.0						
		<i>Ilex opaca</i>	0.0	0.0	0.0	3.1	0.0	1.0	4.8	0.0	4.2	19.4	1.0	1.0						
		<i>Pinus taeda</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0						
	Cypress	<i>Acer rubrum</i>	1.7	0.8	3.7	1.3	1.3	1.0	9.8	3.7	8.7	4.3	0.2	0.0						
		<i>Fraxinus americana</i>	0.0	1.5	5.4	3.4	2.7	3.7	3.3	0.8	0.7	1.5	1.3	0.0						
		<i>Nyssa aquatica</i>	0.5	0.3	1.4	1.9	1.9	0.9	0.1	0.1	0.1	0.0	0.0	0.0						
		<i>Nyssa biflora</i>	1.7	0.9	2.5	1.4	2.1	1.2	1.6	0.0	0.0	0.0	0.0	0.0						
		<i>Taxodium distichum</i>	1.7	0.8	0.7	1.4	0.3	2.3	0.2	1.5	1.4	0.0	0.0	0.0						

**Table 4.1B** Annual mortality rates, annual recruitment rates, and mean annual RBAI by species at Santee Experimental Forest and Beidler Forest. Time periods between measurements are referred to as: period 1 (1994 – 1997), period 2 (1997 – 2000), period 3 (2000 – 2003), period 4 (2003 – 2007), period 5 (2007 – 2010), and period 6 (2010 – 2013).

Site	Cover type	Species	Mortality (%stems/yr)						Recruitment (%stems/yr)						Mean RBAI					
			1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Santee	BLH	<i>Acer rubrum</i>	0.9	2.7	1.8	2.1	2.9	3.1	6.7	5.3	0.9	0.9	0.0	0.2	0.104	0.055	0.030	0.033	0.015	0.013
		<i>Carpinus caroliniana</i>	2.2	2.9	1.8	1.8	1.7	0.9	7.5	12.5	7.3	5.3	0.3	0.6	0.041	0.030	0.035	0.039	0.027	0.023
		<i>Liquidambar styraciflua</i>	2.4	2.0	0.8	1.5	1.0	1.0	5.5	5.9	1.1	1.5	0.0	0.0	0.088	0.054	0.036	0.043	0.025	0.012
		<i>Quercus laurifolia</i>	0.4	1.6	0.8	1.1	1.4	1.8	10.7	10.7	3.2	1.8	0.0	0.3	0.108	0.085	0.086	0.067	0.040	0.024
		<i>Ulmus rubra</i>	1.5	1.1	0.4	0.5	1.4	1.2	1.9	3.1	0.9	0.9	0.0	0.0	0.120	0.046	0.027	0.024	0.010	0.011
	Upland PH	<i>Acer rubrum</i>	1.9	1.4	1.4	1.8	2.1	1.8	9.2	5.0	1.0	2.6	0.3	0.1	0.090	0.052	0.031	0.036	0.023	0.012
		<i>Liquidambar styraciflua</i>	4.3	4.9	2.7	3.9	2.8	1.1	7.2	4.8	1.5	3.2	0.1	0.4	0.069	0.030	0.021	0.027	0.013	0.005
		<i>Nyssa sylvatica</i>	1.5	2.1	2.2	1.8	1.9	0.3	3.9	1.2	1.3	0.8	0.3	0.0	0.063	0.038	0.018	0.020	0.014	0.000
		<i>Pinus taeda</i>	1.6	0.6	0.9	4.2	5.7	5.8	22.1	13.5	5.8	2.3	0.1	0.0	0.043	0.088	0.104	0.064	0.043	0.016
		<i>Quercus nigra</i>	2.3	2.7	1.7	2.4	3.1	4.0	11.5	8.5	2.4	3.3	0.2	0.5	0.071	0.042	0.046	0.037	0.028	0.013
	Cypress	<i>Carpinus caroliniana</i>	5.2	1.2	1.3	2.6	1.2	1.8	18.6	7.4	4.9	2.9	0.7	2.2	0.048	0.042	0.052	0.036	0.025	0.008
		<i>Fraxinus pennsylvanica</i>	0.8	1.0	1.2	2.5	1.7	5.2	20.6	7.6	3.1	1.8	0.6	1.1	0.058	0.057	0.056	0.037	0.017	0.002
		<i>Liquidambar styraciflua</i>	0.0	0.0	3.6	1.7	2.0	1.1	21.7	8.2	0.7	3.2	0.7	1.3	0.051	0.085	0.090	0.058	0.037	0.016
		<i>Quercus laurifolia</i>	3.7	1.1	0.8	2.3	2.1	2.7	15.4	5.3	3.8	1.7	0.1	0.0	0.106	0.084	0.081	0.051	0.030	0.014
		<i>Taxodium distichum</i>	0.8	0.3	1.3	2.1	0.6	2.4	9.1	11.2	5.2	6.7	0.0	3.9	0.004	0.029	0.036	0.024	0.022	0.000
		<i>Triadica sebifera</i>	0.0	2.0	1.9	0.4	0.6	0.6	4.8	0.0	12.2	8.3	0.0	0.0	0.144	0.117	0.053	0.045	0.022	0.015
Beidler	BLH	<i>Acer rubrum</i>	1.0	1.1	3.0	1.9	4.8	0.6	3.3	3.4	0.3	1.3	0.0	0.0	0.126	0.058	0.044	0.035	0.022	0.010
		<i>Carpinus caroliniana</i>	3.5	3.2	3.9	5.0	4.6	2.1	2.0	5.8	0.6	1.7	0.6	1.1	0.076	0.033	0.029	0.026	0.020	0.015
		<i>Liquidambar styraciflua</i>	4.8	0.5	1.6	2.3	3.4	1.2	11.2	8.2	0.0	0.0	0.5	1.7	0.057	0.090	0.040	0.022	0.013	0.004
		<i>Quercus laurifolia</i>	0.9	1.6	2.3	3.5	2.0	4.1	4.1	2.5	0.6	0.1	0.1	0.0	0.123	0.074	0.042	0.034	0.025	0.011
		<i>Taxodium distichum</i>	1.2	0.0	1.5	0.6	1.7	4.2	6.7	5.1	1.5	0.0	0.0	2.2	0.032	0.030	0.016	0.015	0.001	0.006
	RB	<i>Carpinus caroliniana</i>	0.5	1.6	1.7	2.5	2.4	1.6	5.1	5.7	2.5	2.5	0.5	5.7	0.083	0.048	0.030	0.023	0.015	0.006
		<i>Carya ovata</i>	0.6	0.0	0.5	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.094	0.061	0.089	0.059	0.040	0.022
		<i>Ilex opaca</i>	1.9	1.5	1.7	0.8	1.3	1.5	6.6	5.6	3.3	4.0	0.7	5.6	0.040	0.023	0.025	0.037	0.029	0.018
		<i>Liquidambar styraciflua</i>	2.9	1.1	0.4	4.0	3.5	1.1	11.5	12.3	3.8	1.0	0.3	12.3	0.070	0.068	0.044	0.030	0.009	0.002
		<i>Persea borbonia</i>	4.4	2.9	1.0	2.9	2.3	2.9	7.9	10.9	1.3	2.7	0.0	10.9	0.095	0.079	0.064	0.046	0.021	0.006
		<i>Quercus laurifolia</i>	0.0	2.2	0.2	2.7	4.2	2.2	12.0	11.4	3.7	4.7	1.0	11.4	0.031	0.039	0.048	0.060	0.031	0.010
		<i>Quercus nigra</i>	11.4	1.8	0.7	2.6	1.8	1.8	5.4	5.2	2.8	2.4	0.2	5.2	0.065	0.064	0.059	0.055	0.039	0.024
	Cypress	<i>Fraxinus pennsylvanica</i>	1.8	2.2	2.6	3.1	2.4	2.2	4.0	3.9	1.3	1.5	0.5	0.8	0.034	0.026	0.022	0.024	0.015	0.004
		<i>Nyssa aquatica</i>	0.8	1.3	0.5	1.5	0.6	0.9	0.4	0.4	0.3	0.1	0.0	0.4	0.032	0.023	0.012	0.013	0.014	0.005
		<i>Nyssa sylvatica</i>	1.1	0.8	0.0	1.0	0.5	0.6	0.9	0.8	0.0	0.0	0.0	0.0	0.018	0.016	0.014	0.000	0.004	0.001
<i>Quercus laurifolia</i>		3.0	0.7	0.2	2.9	2.0	4.6	5.8	4.3	2.2	1.5	0.0	0.7	0.041	0.052	0.041	0.038	0.028	0.014	
<i>Taxodium distichum</i>		0.9	0.0	0.0	0.6	0.0	0.2	0.7	1.7	4.4	3.5	0.6	0.2	0.018	0.015	0.012	0.023	0.024	0.007	



## Hobcaw Barony

Recruitment rates of *Pinus taeda* were initially high in the cypress plots at Hobcaw Barony. *P. taeda* recruitment rate began with 30.7% stems/yr and decreased throughout the study, falling to 0.4% stems/yr by 2013. *P. taeda* seedling counts dropped dramatically 18 to 24 years PH (6 to 15 seedlings/ha). *P. taeda* mean mortality rate rose from 2003 to 2013, coinciding with decreased recruitment rates. *Morella cerifera* recruitment rates were greatest during the first monitoring period (27.2% stems/yr) and decreased throughout the study, reaching 2.3% stems/yr recruitment during the final monitoring period (**Table 4.1A**). Total seedling counts of *M. cerifera* fell from high levels 14 to 18 years PH after being relatively high in previous measurements. *M. cerifera* mortality rates were relatively high throughout the study, and were greatest 5 to 8 years PH (12.2 % stems/yr). *Nyssa sylvatica* recruitment rates and seedling counts were also greatest during the first monitoring period (2.9% stems/yr, 501 seedlings/ha), but were lower than those of other important species in the cypress plots. *N. sylvatica* mortality rates were relatively high from 1994 to 2000 and decreased in the following years. *Taxodium distichum* recruitment rates were relatively high (9.4 – 21.3% stems/yr) 5 to 18 years PH and fell to low levels (0.7 – 1.3% stems/yr) 18 to 24 years PH. Recruitment rates of the invasive *Triadica sebifera* were high (15.8 – 30.5% stems/yr) in the period 5 to 14 years PH and relatively low in the following years. A large number (1,409 seedlings/ha) of *T. sebifera* seedlings were observed 18 years PH.

Recruitment rate trends in the upland (loblolly, upland hardwood, and longleaf) plots of Hobcaw Barony are generally similar to trends in the cypress plots. The highest levels of recruitment occurred in the period of 5 to 11 years PH. Some upland species such as *Quercus virginiana*, *Quercus falcata*, and *Pinus palustris* had relatively low rates or no recruited stems during this period. Mortality rates of *P. taeda* and *M. cerifera* in loblolly plots were relatively high (5.8% to 9.5% stems/yr) 18 to 24 years PH. Mortality rates of *Persea borbonia* in upland

hardwood plots rose to relatively high levels 14 to 24 years PH and remained high throughout the study period.

### Congaree

Mean recruitment rates across all species in bottomland hardwood and pine hardwood plots in the period 14 to 18 years PH were  $8.78\% \pm 1.0$  and  $15.6\% \pm 2.38$ , respectively. In cypress plots, the period of greatest mean recruitment rates took place 11 to 14 years PH ( $6.84\% \pm 1.9$  stems/yr). Mortality rates of all species combined on Congaree plots did not increase or decrease linearly with time. Overall, mortality rates were highest during period 4, 14 to 18 years PH ( $1.9\% \pm 0.6$  stems/yr). Congaree plots had the lowest overall mean mortality rate ( $1.99\% \pm 0.22$  stems/yr) compared to the other three major sites.

In bottomland hardwood plots, *Asimina triloba* and *Ilex decidua* had increased mortality and recruitment rates 14 to 18 years PH. *A. triloba* seedlings accounted for the most seedlings in bottomland hardwood plots with counts greater than 600 seedlings/ha during all measuring periods except for 8 to 11 years PH. *Ilex opaca* also had increased recruitment ( $6.0\%$  stems/yr) in the 14 to 18 year PH period. Three hundred and thirty-eight *I. opaca* seedlings/ha were observed in the 5 to 8 years PH period and seedling counts were low for the remaining measurements. Other important species in this cover type had relatively low mortality rates through all monitoring periods. Recruitment rates in the single pine-hardwood plot were greatest in the 14 to 18 year PH period (**Table 4.1A**). *P. taeda* recruitment remained at 0 % throughout the study in this plot, and seedling counts reached a maximum 90 seedlings/ha. There was little to no mortality recorded in this plot for species other than *C. caroliniana*. In cypress plots, *A. rubrum* recruitment was highest in the 5 to 8 ( $9.8\%$  stems/yr) and 11 to 14 ( $8.7\%$  stems/yr) year PH periods, with little to no recruitment recorded after 21 years PH. Recruitment of *Fraxinus americana* was greatest 5 to 8 years PH, while mortality rates of this species were highest ( $5.4\%$

stems/yr) 11 to 14 years PH, with mortality occurring through all of the following monitoring periods. Little to no recruitment was recorded in important species on cypress plots 18 to 24 years PH.

#### Santee Experimental Forest

At Santee, mean recruitment rates of all species combined were highest 5 to 11 years PH, in all cover types. Recruitment rates decreased and were generally low throughout the following monitoring periods. Timing of peak mortality rates across all species varied by cover type. In cypress plots, recruitment rates of *C. caroliniana*, *Fraxinus pennsylvanica*, *L. styraciflua*, and *Quercus laurifolia* were highest in the first monitoring period. *T. distichum* recruitment was also high, but peaked 8 to 11 years PH (11.2 % stems/yr). Recruitment of the invasive *T. sebifera* was greatest 11 to 18 years PH (12.2 and 8.3 % stems/yr) and seedling counts of *T. sebifera* rose to 186 seedlings/ha 14 to 18 years PH before falling to 17 seedlings/ha 18 to 21 years PH. Mortality rates of *C. caroliniana* were highest during the first monitoring period and were lower during the later periods. *F. pennsylvanica* mortality rates were relatively low but increased 21 to 24 years PH (5.2 % stems/yr). *L. styraciflua* mortality increased to 3.6 % stems/yr in 11 to 14 years PH after having no recorded dead stems in previous monitoring periods.

In upland pine-hardwood plots, high recruitment rates and seedling counts of *A. rubrum*, *L. styraciflua*, *P. taeda*, and *Quercus nigra* were observed in the first monitoring period. Recruitment rates of all important species were low after 18 years PH (0.0 to 0.5% stems/yr). Mortality rates of *A. rubrum* in these plots were relatively consistent throughout the study (1.4 to 2.1 % stems/yr). *L. styraciflua* had higher rates of mortality in 5 to 11 years PH (4.2 and 4.9 % stems/yr) and mortality dropped to 1.1 % stems/yr 21 to 24 years PH. *P. taeda* mortality rates increased after 14 years PH and remained relatively high throughout the remaining periods (5.7 to 5.8 % stems/yr). Recruitment rates across all species in bottomland hardwood plots were greater 5

to 11 years PH when compared to other monitoring periods. Mortality rates across all species were relatively low (1.63 % stems/yr) 5 years PH, then increased between 8 to 18 years PH. *C. caroliniana* recruitment rates remained relatively high through the first 4 monitoring periods and dropped significantly after 18 years PH.

#### Beidler

Tree mortality rates on Beidler Forest plots were relatively consistent until 21 years PH when rates decreased. Recruitment rates were relatively high in earlier measurement periods (5 to 11 years PH) and dropped to lower levels in later periods. Recruitment rates of important species in bottomland hardwood plots were high between 5 to 11 years PH, and then decreased and remained low for the remaining periods. *L. styraciflua* recruitment rates were the highest recorded (11.2%, 8.2% stems/yr from 5 to 11 years PH), but counts were low relative to other important species. Mortality of *C. caroliniana* was relatively high throughout the study and peaked at 5.0 % stems/yr 14 to 18 years PH. In ridge bottom plots, recruitment rates of *I. opaca*, *L. styraciflua*, *P. borbonia*, and *Q. laurifolia* were high 5 to 11 years PH before falling to relatively low rates in the remaining periods. *Q. nigra* mortality rate was highest 5 to 8 years PH at 11.4% stems/ha before dropping to low rates ( $\leq 2.6\%$  stems/yr) for the remainder of the study.

#### Growth Rates

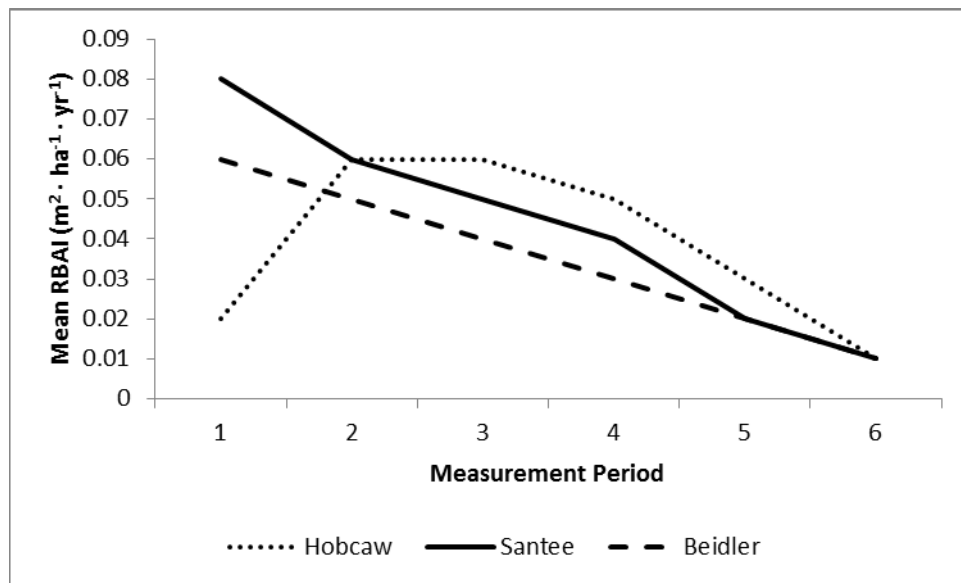
A one-way ANOVA was conducted to test the effect of time on relative basal area increment (RBAI) of all species combined over our measurement periods. RBAI changed significantly over the 6 measurement periods [F(5, 236) 27.38,  $p < 0.0001$ ]. A post hoc Tukey test ( $p = 0.05$ ) revealed that while RBAI was not significantly different between 5 to 14 years PH, each successive measurement period had significantly lower RBAIs than the last, across all species. The general decline in growth rates across all species over time is illustrated in **Figure 4.1**. RBAI was not significantly different among forest cover types. There were

significant differences in RBAI means among species [F(16, 236) 5.43,  $p < 0.0001$ ]. When comparing RBAI from all measurement periods, *P. palustris*, *Q. falcata*, and *N. aquatic* had generally low levels of growth ( $0.1$  to  $0.2 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) while *P. taeda*, *Carya ovata*, and *T. sebifera* had the highest levels of growth ( $0.6$  to  $0.7 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ). A significant difference in RBAI between cover types was not found when combining plots of the same cover type from all four sites.

An ANOVA test comparing the effect of forest cover type on RBAI for all species at Beidler Forest over all measurement periods revealed a significant difference in RBAI between cover types [F(2, 83) = 20.09,  $p < 0.0001$ ]. Growth rates of trees located in cypress plots were significantly lower than those in bottomland hardwood and ridge bottom plots at Beidler Forest (Tukey test,  $p = 0.05$ ). RBAI varied significantly between species at Beidler Forest throughout the study [F(11, 83) = 4.24,  $p = 0.0001$ ]. Growth rates of all species combined on Beidler plots were highest 5 to 11 years PH, intermediate 11 to 18 years PH, and lowest 18 to 24 years PH. On Beidler plots, the tree species with the lowest mean growth rate was *N. sylvatica*, and the species with the highest mean growth rate was *C. ovata*.

RBAI differed significantly between measurement periods on Hobcaw Barony plots [ANOVA, F(5, 52) = 6.24,  $p < 0.0001$ ]. Mean growth rates of all species combined on Hobcaw plots were lowest 5 to 8 years PH and 21 to 24 years PH, highest 8 to 18 years PH, and intermediate 18 to 21 years PH. There was no significant difference in growth rate among Hobcaw forest cover types. *P. palustris* and *Q. falcata* had the lowest mean growth rates in Hobcaw plots ( $0.01 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ). *T. distichum*, *P. taeda*, and *T. sebifera* had higher mean growth rates than those of other species. An ANOVA test revealed that RBAI varied significantly between measurement periods on Santee plots [F(5, 78) = 25.37,  $p < 0.0001$ ]. Mean growth rates across all species on Santee plots were lowest 18 to 24 years PH, highest 5 to 11 years PH, and

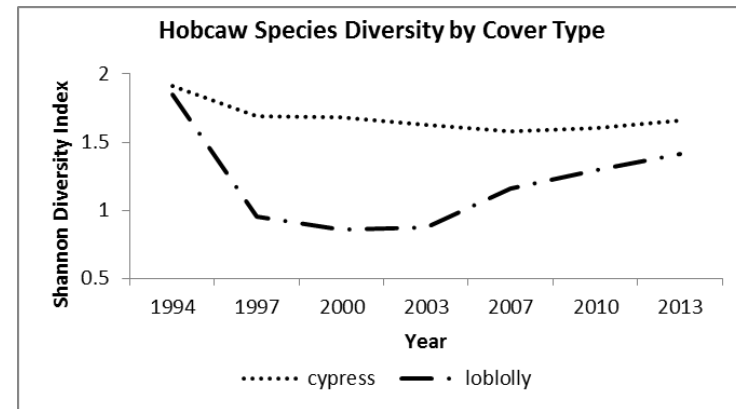
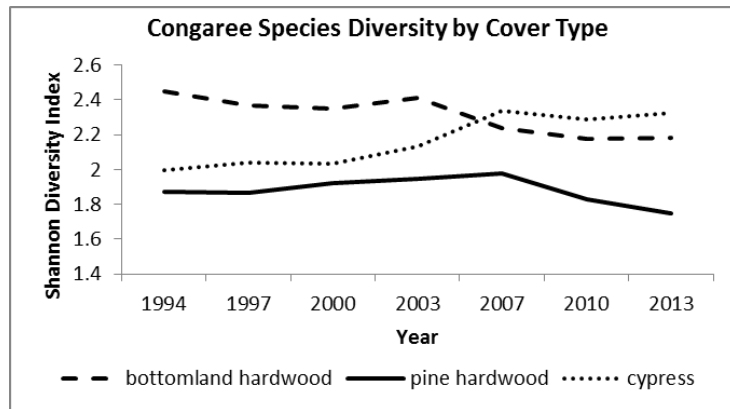
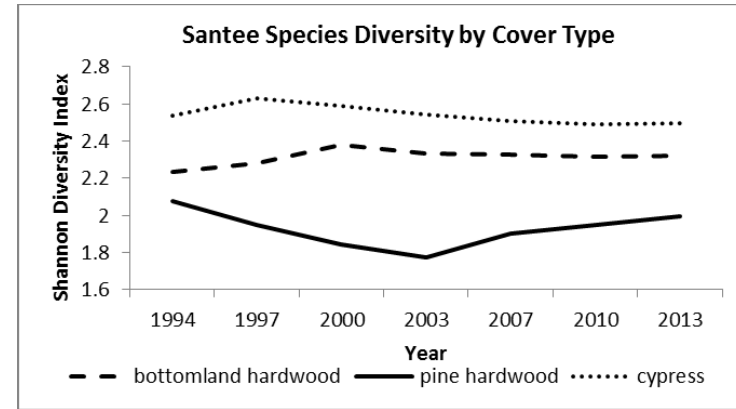
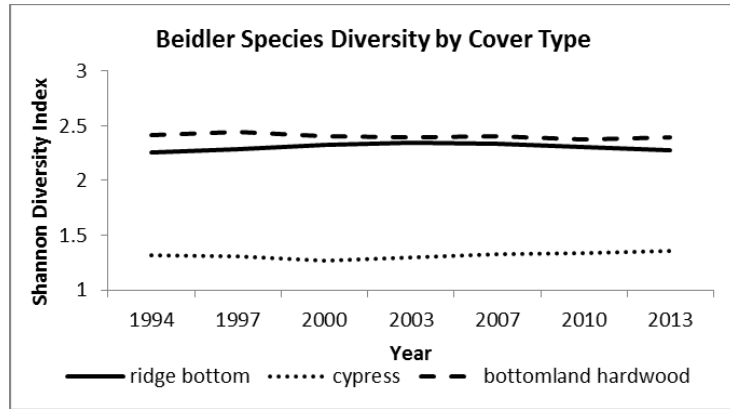
intermediate 11 to 18 years PH. There was no difference in mean growth rates among Santee cover types. *T. distichum* and *N. sylvatica* had the lowest mean growth rate and *T. sebifera* had the highest mean growth rate on Santee plots.



**Figure 4.1** Mean RBAI (relative basal area increment) trends for all species combined at Hobcaw Barony, Santee Experimental Forest, and Beidler Forest.

#### Species Diversity and Richness

An ANOVA test combining Shannon Diversity Indices of all sites and cover types revealed that species diversity did not change significantly with time overall [ $F(6, 75) = 0.42, p = 0.86$ ] (**Figure 4.2**). A test of change in species diversity within sites of Beidler Forest, Santee, and Congaree plots of all cover types also did not change significantly with time. A subtle change in diversity over time was found in Hobcaw plots using an ANOVA test [ $F(6, 18) = 2.7, p = 0.04$ ]. Mean species diversity of Hobcaw plots of all cover types was greatest in 1994. Overall diversity of Hobcaw plots showed little change after 1994 (mean SDI range of 0.1).



**Figure 4.2** Trends in Shannon Diversity Index across all monitoring periods for all study plots of different forest types at all four study sites.

There are not any obvious common trends in species richness change for cover types. Most cover types had a net loss of species between 2007 and 2010, with a total net change of -13 species across all sites. Beidler Forest had a net loss of 6 species when combining all cover types over the entire study. Bottomland hardwood plots at Beidler Forest lost species for most of the study periods, with a net change of -5 species overall. The single pine-hardwood plot at Congaree had a net gain of 8 species between 2003 and 2007 (**Table 4.2**). Species richness of all sites and cover types combined varied significantly between study sites [ $F(3, 81) = 14.85, p < 0.001$ ] but did not change significantly with time according to an ANOVA test. Richness of Beidler and Hobcaw plots did not change significantly with time. Congaree plots had higher species richness in 2007 (18 years PH). Species richness of Santee plots was highest in 2003 (14 years PH), and lowest in 1994 (5 years PH) (**Table 4.2**).

**Table 4.2** Net change in naïve species richness over all monitoring periods for different forest types and study sites.

Site	Cover	Net species richness change						Total
		1994 - 1997	1997 - 2000	2000 - 2003	2003 - 2007	2007 - 2010	2010 - 2013	
<b>Beidler</b>	<b>All</b>	<b>0</b>	<b>-3</b>	<b>0</b>	<b>0</b>	<b>-4</b>	<b>1</b>	<b>-6</b>
	Ridge bottom	1	-1	1	0	-1	0	0
	Cypress	1	-1	-1	1	-1	0	-1
	Bottomland hardwood	-2	-1	0	-1	-2	1	-5
<b>Congaree</b>	<b>All</b>	<b>-1</b>	<b>-3</b>	<b>9</b>	<b>9</b>	<b>-5</b>	<b>-1</b>	<b>8</b>
	Bottomland hardwood	-1	-2	3	1	-3	2	0
	Pine-hardwood	0	0	1	8	-1	-4	4
	Cypress	0	-1	5	0	-1	1	4
<b>Santee</b>	<b>All</b>	<b>7</b>	<b>4</b>	<b>1</b>	<b>-4</b>	<b>-3</b>	<b>2</b>	<b>7</b>
	Bottomland hardwood	2	2	0	-1	-2	2	3
	Pine-hardwood	2	0	0	-3	0	0	-1
	Cypress	3	2	1	0	-1	0	5
<b>Hobcaw</b>	<b>All</b>	<b>2</b>	<b>3</b>	<b>-1</b>	<b>2</b>	<b>-1</b>	<b>-1</b>	<b>4</b>
	Cypress	1	2	-2	0	0	-2	-1
	Loblolly	1	1	1	2	-1	1	5
	<b>Total</b>	<b>8</b>	<b>1</b>	<b>9</b>	<b>7</b>	<b>-13</b>	<b>1</b>	



## Discussion and Conclusions

Mean annual mortality rates across all species were found to be greatest between 11 and 18 years following the hurricane. Mortality rates in this period were often high for species that exhibit rapid post-disturbance establishment such as *P. taeda*, *M. cerifera*, and *L. styraciflua*. These results are consistent with those of Vandermeer *et al.* (1998) that suggest that post-hurricane forest regeneration can be broadly described in two phases; a building phase followed by a thinning phase. The thinning process begins as the establishment of pioneer species, as well as the regrowth of primary forest species, results in high tree density and intense competition for resources. Ostertag *et al.* (2005) found that, in a subtropical moist forest, tree species with slow tree growth were correlated with lower rates of hurricane induced mortality, and species with higher annual growth were correlated with high mortality rates following a hurricane.

As expected, mean annual recruitment rates across all plots were much higher in the earlier years of the study and fell 7.1 % from the first to the last measurement period. A period of regrowth is expected following a significant loss of trees and the resulting increase in canopy space and nutrient availability. During the regrowth period, basal area, biomass, and tree density will increase rapidly up to a threshold (Fu *et al.*, 1996; Scatena *et al.*, 1996; Frangi and Lugo, 1998). These results, along with those of Weaver (1986a, b; 1989) are consistent with the significant decline in relative basal area increment and annual recruitment percentage that was observed throughout the course of this study. Individual species recruitment rates varied significantly. Tree species response to wind damage can vary significantly based on a number of factors including their resistance to

wind damage of a given intensity, the type of damage sustained, and their ability to recover through various methods of reproduction and repair (Uriarte *et al.*, 2009; Glitzenstein and Harcombe 1988; Boucher *et al.*, 1990; Ostertag *et al.*, 2005).

Tree species diversity is often high following a major disturbance and decreases as species compete for available resources (Lugo, 2008). An analysis on the Luquillo Experimental Forest of Puerto Rico on forest characteristics 50 years after a major hurricane revealed a decline in species richness for the whole forest (Weaver, 1986a). This pattern was not evident in the coastal plain forests of South Carolina following Hurricane Hugo. Our results are consistent with those of Zhao *et al.* (2006) who found that, in the 12 years following Hurricane Hugo, bottomland hardwood plots of South Carolina showed little change in Shannon diversity index. Experimental scale may skew results on species diversity and richness following hurricanes. Results from tropical forest studies have shown large scale experiments finding little to no change in diversity (Scatena and Lugo, 1995) and small scale (e.g., 1 ha) experiments finding significant patterns of change in diversity (Frangi and Lugo, 1998; Fu *et al.*, 1996). However, significant change in diversity following a hurricane event has been found on a whole-forest scale (Weaver, 1986a). The number of plots per forest cover type in this study was not consistent, and this may have skewed diversity index values computed for all plots of the same forest type. The pine-hardwood cover type at Congaree was represented by a single plot, potentially influencing species richness and diversity index for this cover type at this location.

Growth increments were relatively high during the initial measurements and generally decreased with time throughout the study. Higher growth rates are expected during the regrowth period following a disturbance, due to newly available resources for surviving trees as well as the recruitment of small stems with rapid growth (Bellingham *et al.*, 1995; Merrens and Peart, 1992). Decreasing growth rates may indicate that the amount of available ecological space created by the disturbance has begun to decrease to near pre-hurricane levels. Comparatively low growth rates measured on Hobcaw Barony plots during the 5 to 8 year post-hurricane period may have been related to the tidal surge of 3-4 m that impacted the area for at least 18 months after the hurricane (Williams, 1996), but this is speculative. The buildup of salt in tree leaves hastens leaf mortality, potentially limiting the supply of assimilates or hormones and slowing tree growth (Munns, 1993).

This study represents a 19-year dataset and provides us with understanding of how these forests have changed up to 24 years following Hurricane Hugo. A major hurricane disturbance can dictate forest structure and composition for many years following the event, and legacy effects may be apparent >100 years after the storm (Lugo *et al.*, 2000; Lugo, 2008; Scatena and Lugo, 1995; Foster, 1992). We have observed several trends in forest progression throughout the period of measurement. Annual tree mortality was generally higher 11 to 18 years after the storm, and then decreased. Annual tree recruitment was significantly higher 5 to 8 years after the storm, and then decreased throughout the study. Annual basal area increments were generally high in early measurement periods and decreased steadily through the following periods. Differences

in species diversity between measurement periods were not found to be significant throughout the study. Tree species entered and exited the forests between measurement periods, but a common trend in species richness change was not apparent. Further monitoring will reveal how these forests will continue to reorganize and to grow in the coming years.

## CHAPTER V

### SUMMARY AND CONCLUSIONS

The results of this study add to our understanding of the long-term effects of a hurricane disturbance on southeastern coastal forests and are consistent with others (Zhao *et al.*, 2006; Song *et al.*, 2012) that have suggested that the pre-hurricane composition and structure of the forest and the level of hurricane intensity are important factors in determining the long-term changes that take place in the years following a hurricane disturbance. Although this study lacks quantitative data on pre-hurricane composition and structure, we have observed trends in post-hurricane succession and structural changes and related them to the initial level of damage and to forest type. Stands in Beidler Forest and Congaree National Park showed relatively little change in composition and structure over the twenty year study period. The composition and structure of stands with high levels of initial damage from wind and storm surge continues to change as the populations of some pioneer and usurper species (*P. taeda*, *M. cerifera*, *C. caroliniana*) decline due to self-thinning. Mortality rates for these species were found to be greatest between 11 and 18 years following the hurricane.

Some studies have found that tree species diversity is often high following a major disturbance and decreases as species compete for available resources (Lugo, 2008). This trend was not evident in the 24 year period following Hurricane Hugo. This result may have been skewed by the scale and location of our study plots. Results from large

scale (whole watershed) experiments have found little to no change in diversity (Scatena and Lugo, 1995) and small scale (e.g. 1 ha) experiments finding significant patterns of change in diversity (Frangi and Lugo, 1998; Fu *et al.*, 1996). Tree growth rates were greatest in early monitoring periods and declined as the study continued. Higher growth rates are expected during the regrowth period following a disturbance due to newly available resources for surviving trees as well as the recruitment of small stems with rapid growth (Bellingham *et al.*, 1995; Merrens and Peart, 1992).

The structure and composition of coastal forests that were disturbed by Hurricane Hugo continues to change as a result of the damage sustained in 1989. Stands that sustained heavy damage due to their location relative to the coast and hurricane eyewall (Hobcaw Barony, Santee Experimental Forest) exhibited the most change as some pioneer and invasive species rapidly increased in density before populations began to thin around 11 years after the hurricane. The overstory of stands with relatively low levels of wind damage (Congaree National Park, Beidler Forest) did not change much in structure or composition. However, the density of some species (*F. americana*, *C. caroliniana*, *A. rubrum*) increased following the storm, then eventually decreased towards the end of the study. The overstory of cypress-tupelo forests changed little in structure and composition throughout the study. Bald cypress and tupelo trees are resistant to wind damage (Stanturf *et al.*, 2007), and many of the large trees in these stands survived the disturbance. One exception was the cypress-tupelo plots of Hobcaw Barony, where salt from the storm surge resulted in the death of some large bald cypress and the subsequent growth of loblolly pine and wax myrtle populations.

Continued monitoring will reveal whether these heavily altered forests will eventually resemble the pre-hurricane forests in structure and composition. The intensity of hurricanes may increase in the future as sea surface temperatures rise with climate change (Emanuel, 1987; Emanuel, 2005; Goldenberg *et al.*, 2001). However, the results of Donnelly and Woodruff (2007) suggest that hurricane intensity is controlled by the El Niño Southern Oscillation Index rather than by sea surface temperatures. Knowing how coastal forests respond to major hurricanes in the long-term and short-term will aid us in preparing for future hurricanes and for potential changes in disturbance regimes.

## LITERATURE CITED

- Batista, W.B. and Pratt, W.J. (2003). Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology*, 91, 197-212.
- Battaglia, L. L., Sharitz, R. R., & Minchin, P. R. (1999). Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. *Canadian Journal of Forest Research*, 29(1), 144-156.
- Bellingham, P.J., Tanner, E.V.J., Healey, J.R. (1995). Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, 7, 2562-2580.
- Boucher, D. H., Vandermeer, J. H., Yih, K., & Zamora, N. (1990). Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology*, 71(5), 2022-2024.
- Brennen, J.W. (1991). Meteorological summary of Hurricane Hugo. *Journal of Coastal Research*, 8, 1-12.
- Brown, N.D. and Whitmore, T.C. (1992). Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society of London*, 335, 269-378.
- Burslem, D. F. and Whitmore, T. C. (1999). Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science*, 10(6), 767-776.
- Busby, P. E., Motzkin, G., and Boose, E. R. (2008). Landscape-level variation in forest response to hurricane disturbance across a storm track. *Canadian Journal of Forest Research*, 38(12), 2942-2950.
- Busby, P. E., Canham, C. D., Motzkin, G., and Foster, D. R. (2009). Forest response to chronic hurricane disturbance in coastal New England. *Journal of Vegetation Science*, 20(3), 487-497.



China, J.D. (1999). Changes in the herbaceous and vine communities at the Bisley Experimental Watersheds, Puerto Rico, following Hurricane Hugo. *Can. J. For. Res.*, 29, 1433-7.

Conner, W. H., Duberstein, J. A., Day Jr, J. W., and Hutchinson, S. (2014). Impacts of changing hydrology and hurricanes on forest structure and growth along a flooding/elevation gradient in a south Louisiana forested wetland from 1986 to 2009. *Wetlands*, 34(4), 803-814.

Cosentino, G. R. (2013). Comparing vegetation cover in the Santee Experimental Forest, South Carolina (USA), before and after hurricane Hugo: 1989-2011. Retrieved from Georgia State University Digital Archive.

Donnelly, J. P. and Woodruff, J. D. (2007). Intense hurricane activity over the past 5,000 years controlled by El Niño and the West African monsoon. *Nature*, 447(7143), 465-468.

Duever, M. and McCollom, J. (1992). Hurricane Hugo effects on old-growth floodplain forest communities at Four Hole Swamp, South Carolina. P197-202 In Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. *USDA Forest Service, SFES Gen. Tech. Rept. SO-93*.

Emanuel, K. A. (1987). The dependence of hurricane intensity on climate. *Nature*, 326(6112), 483-485.

Emanuel, K. A. (2005). Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, 436(7051), 686-688.

Everham, E. M. III and Brokaw, N.V. L. (1996). Forest damage and recovery from catastrophic wind. *Botanical Review*, 62, 113-85.

Foster, D.R. (1992). Land-use history (1730-1990) and vegetation dynamics in central New England, USA. *Journal of Ecology*, 80, 753-772.

Frangi, J. L. and Lugo, A. E. (1998). A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. *Biotropica*, 30, 339-48.

Fu, S., Rodríguez Pedraza, C. and Lugo, A. E. (1996). A twelve-year comparison of stand changes in a mahogany plantation and a paired natural forest of similar age. *Biotropica*, 28, 515-24.

Gardner, L. R., Michener, W. K., Blood, E. R., Williams, T. M., Lipscomb, D. J., & Jefferson, W. H. (1991). Ecological impact of Hurricane Hugo—salinization of a coastal forest. *Journal of Coastal Research*, 301-317.

Glitzenstein, J. S. and Harcombe, P. (1988). Effects of December 1983 tornado on forest vegetation of the Big Thicket, Southeast Texas, USA. *Forest Ecology and Management*, 25, 269-90.

Goldenberg, S. B., Landsea, C. W., Mestas-Nuñez, A. M., and Gray, W. M. (2001). The recent increase in Atlantic hurricane activity: Causes and implications. *Science*, 293(5529), 474-479.

Gresham, C.A., Williams, T.M., and Lipscomb, D.J. (1991). Hurricane Hugo wind damage to southeastern U.S. coastal forest tree species. *Biotropica*, 23, 420-426.

Hook, D. D., Buford, M.A., and Williams, T.M. (1991). Impact of Hurricane Hugo on the South Carolina coastal plain forest. *Journal of Coastal Research*, SI #8, 1-356.

Jubinsky, G. and Anderson, L.C. (1996). The invasive potential of Chinese tallow-tree (*Sapium sebiferum* Roxb.) in the Southeast. *Castanea*, 226-231.

Kolb, T. E., Wagner, M.R., and Covington, W.W. (1994). Concepts of forest health: utilitarian and ecosystem perspectives. *Society of American Foresters*, July, 1994.

Lugo, A.E., Applefield, M., Pool, D.J., and McDonald, R.B. (1983). The impact of Hurricane David on the forests of Dominica. *Canadian Journal of Forest Research*, 13, 201-211.

Lugo, A. E. (2000). Effects and outcomes of Caribbean hurricanes in a climate change scenario. *Science of the Total Environment*, 262, 243–51.

Lugo, A.E. (2008). Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Australian Ecology*, 33, 368-398.

Lugo, A.E. and Scatena, F.N. (1996). Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica*, 28, 585-599.

Lugo, A. E., Baron, J. S., Frost, T. P., Cundy, T. W., & Dittberner, P. (1999). Ecosystem processes and functioning. *Ecological stewardship: a common reference for ecosystem management*, 1, 219.

- Lutz, J. A. and Halpern, C.B. (2006). Tree mortality during early forest development: a long-term study of rates, causes, and consequences. *Ecological Monographs*, 76(2), 257-275.
- McClanahan, T. R. (1986). The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio*, 65(3), 175-178.
- Merrens, E. J. and Peart, D. R. (1992). Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *Journal of Ecology*, 787-795.
- Motzkin, G.M., Wilson, P., Foster, D.R. and Allen, A. (1999). Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *Journal of Vegetation Science*, 10, 903-920.
- Munns, R. (1993). Physiological processes limiting plant growth in saline soils: some dogmas and hypotheses. *Plant, Cell and Environment*, 16(1), 15-24.
- O'Hara, K. L. (1995). Early height development and species stratification across five climax series in the eastern Washington Cascade range. *New forests*, 9(1), 53-60.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. and Wagner, H. (2015). vegan: Community Ecology Package. R package version 2.3-2. <http://CRAN.R-project.org/package=vegan>
- Oliver, C. D. (1980). Forest development in North America following major disturbances. *Forest ecology and management*, 3, 153-168.
- Oliver, C. D. and Larson, B.C. (1996). *Forest stand dynamics*. John Wiley and Sons.
- Ostertag, R., Silver, W. L., & Lugo, A. E. (2005). Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica*, 37(1), 16-24.
- Purvis, J.C., Sidlow, S.F., Smith, D.J., Tyler, W. and Turner, I. (1990). Hurricane Hugo. *Climate Report G-37*. Columbia, SC: South Carolina Water Resources Commission. 82 p.

- Purvis, J. C. (1996). History of damaging storms affecting South Carolina forests including a review of Hurricane Hugo's impact on South Carolina forests. *Hurricane Hugo: South Carolina Forest Land Research and Management Related to the Storm*. Gen. Tech. Rep. SRS-5. US Dept Agric. Forest Service Southern Research Station, Asheville, NC, 2-5.
- Putz, F. E., & Sharitz, R. R. (1991). Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. *Canadian Journal of Forest Research*, 21(12), 1765-1770.
- Scatena, F. N. and Lugo, A. E. (1995). Geomorphology, disturbance, and the soil and vegetation of two subtropical wet stepland watersheds of Puerto Rico. *Geomorphology*, 13, 199-213.
- Scatena, F. N., Moya, S., Estrada, C. and China, J. D. (1996). The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28, 424-440.
- Sheffield, R.M. and Thompson, M.T. (1992). Hurricane effects on South Carolina's forest resource. USDA Forest Service, 51pp.
- Song, B., Gresham, C.A., Trettin, C.C., and Williams, T.M. (2012). Monitoring the recovery of coastal plain forests from Hurricane Hugo. *Tree and Forestry Science and Biotechnology*, 6 (SI 1), 60-68.
- Stanturf, J.A., Goodwick, S.L., Outcalt, K.W. (2007). Disturbance and coastal forests: A strategic approach to forest management in hurricane impacted zones. *Forest Ecology and Management*, 250, 119-135.
- Tanner, E. V. J., Kapos, V., & Healey, J. R. (1991). Hurricane effects on forest ecosystems in the Caribbean. *Biotropica*, 513-521.
- Thompson, J., Lugo, A.E., Thomlinson, J. (2007). Land use history, hurricane disturbance, and introduced species survival in a subtropical wet forest in Puerto Rico. *Plant Ecology*, 192, 289-301.
- Turner, M. G., Baker, W.L., Peterson, C.J., and Peet, R.K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, 1(6), 511-523.

- Uhl, C., Clark, K., Dezzio, N. and Maquirino, P. (1988). Vegetation dynamics in Amazonian treefall gaps. *Ecology*, *69*, 751-763.
- Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M. and Haines, B.L. (2009). Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecological Monographs*, *79*(3), 423-443.
- Vandermeer, J., Brenner, A. and Granzow de la Cerda, I. (1998). Growth rates of tree height six years after hurricane damage at four localities in eastern Nicaragua. *Biotropica*, *30*, 502-9.
- Vandermeer, J., Boucher, D. H., Granzow de la Cerda, I. and Perfecto, I. (2001). Growth and development of the thinning canopy in a post-hurricane tropical rain forest in Nicaragua. *Forest Ecology and Management*, *148*, 221-42.
- Walker, L. R., Zimmerman, J. K., Lodge, D.J. and Guzmàn Grajales, S. (1996). An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal of Ecology*, *84*, 877-89.
- Weaver, P. L. (1986a). Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*, *22*(1-2), 53-70.
- Weaver, P.L. (1986b). Growth and age of *Cyrilla racemiflora* L. in montane forests of Puerto Rico. *Interciencia*, *11*, 221-8.
- Weaver, P.L. (1989). Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia*, *14*, 181-92.
- Webb, S.L. (1989). Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. *Ecology*, *70*, 1167-1180.
- Weishampel, J. F., Drake, J. B., Cooper, A., Blair, J. B., and Hofton, M. (2007). Forest canopy recovery from the 1938 hurricane and subsequent salvage damage measured with airborne LiDAR. *Remote Sensing of Environment*, *109*(2), 142-153.
- White, P.S. (1979). Pattern, process, and natural disturbance in vegetation. *Botanical Review*, *45*, 229-299.

Williams, T. M. (1996). Verification of contaminant flow with GIS and aerial photography. In *Environmental problem solving with geographic information systems. USEPA Conf. Proc. EPA/625/R-95/004, Center for Environ. Res. Inf., Cincinnati, OH* (pp. 74-81).

Xi, W., Peet, R. K., and Urban, D. L. (2008). Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. *Journal of Plant Ecology*, 1(1), 43-57.

Zhao, D., Allen, B. and Sharitz, R.R. (2006). Twelve year response of old-growth southeastern bottomland hardwood forests to disturbance from Hurricane Hugo. *Canadian Journal of Forest Research*, 36(12), 3136-3147.