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Recovery of Coastal Plain Forests from Hurricane Hugo in South Carolina, USA, Fourteen Years after the Storm

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ABSTRACT

Overstory species composition dynamics following a major disturbance integrates both the characteristics of individual species and competitive interactions. The purpose of this study was to monitor species composition shifts in several wetland and upland ecosystems receiving varying levels of damage from Hurricane Hugo that took place in 1989. Fifty permanent plots were established among four study sites in the Coastal Plain of South Carolina in 1994 and the trees and saplings re-inventoried in 1997, 2000, and 2003. Over the 10-year study period, the species composition and dominance of most of the species did not change greatly; there was just the expected slow growth of basal area. On several of the sites, especially those more heavily damaged, there was a large increase in the density of species in the sapling size class that were not in the tree size class. Loblolly pine, hornbeam, redbay, deciduous holly, and wax myrtle are examples of such species.

Keywords: succession, resiliency, composition, structure, dynamics

INTRODUCTION

Understanding resiliency in forests to impacts of catastrophic disturbances, such as hurricanes, may form a basis for restoration of ecosystem goods and services. An important aspect of hurricane impact concerns the long-term effect of this widespread wind damage. Lugo (2008) discusses hurricane impact as "visible", the immediate impact of wind and rain, or "invisible" the long term alteration of ecosystem structure and function due to differences in plants ability to recover after hurricane stress. While the immediate impact of wind and rain has been reported for several recent major hurricanes (e.g. Browkaw and Walker 1991; Everham and Browkay 1996; Haymond *et al.* 1996; Stanturf *et al.* 2007; Kupfer 2008), the "invisible effects are best understood only in tropical ecosystems (Lugo 2008). Our best understanding of temperate forests comes from a long-term recovery monitoring study of a hurricane damage on sections of the Harvard forest that were damaged in 1938 by periodic re-sampling of permanent plots (Foster 1992; Motzkin *et al*. 1999). In their studies, four growing seasons after the storm, the basal area was relatively low and the stem density was quite high compared to pre-storm levels. After 46 growing seasons the pre- storm species were regaining dominance, and the basal area and density were returning to pre-storm levels.

For southeastern US forests, understanding is limited to individual tree species resistance to hurricane wind damage and management to minimize economic losses (Stanturf *et al.* 2007). Several ecosystem level questions remain. Will the damaged forests return to a pre-hurricane floristic composition via growth and regeneration of existing species, or will secondary succession be initiated with pioneer species invading? Will wetland forests, such as bottomland hardwood swamps and cypress-tupelo swamps, recover faster or slower than upland pine or hardwood forests? Finally, does the degree of wind damage the forest received affect the pattern and timing of forest recovery? Answers to these questions not only contribute to an understanding of forest dynamics, but also measure forest health since resistance to catastrophic change and the ability to recover from catastrophic change are characteristics of a healthy forest ecosystem (Kolb *et al*. 1994).

Hurricane Hugo's movement through South Carolina in 1989 damaged 1.8 million hectares of timberland in 23 counties (Sheffield and Thompson 1992). Wind damage to commercial timberland was documented by Sheffield and Thompson (1992) and wind damage on selected non-commercial forests was reported by Gresham *et al.* (1991)- Hobcaw Forest; Hook *et al.* (1991)- Santee Experimental Forest, Putz and Sharitz (1991)- Congaree National Park, and Duever and McCollum (1992)- Beidler Forest. These studies described the immediate short-term impact of the hurricane on forest structure. A long-term monitoring study was set up on the areas studied by these four papers to identify the resilience of coastal forests after Hurricane Hugo (**Fig. 1**), These four sites were not subject to harvest of merchantable sections of dead or damaged trees (salvage logging) nor other management activities since the storm. Since this was not a planned experiment of the seven forest types examined, measurement plots were not evenly distributed among the seven timber types nor were all types present at all study sites (**Table 1**). The distribution of plots does allow examination of: remaining vs. invading species, upland vs. wetland types, and variation among severity levels of initial damage.

MATERIALS AND METHODS

The study that involved four study areas, seven forest types, and a total of 50 plots, distributed as in **Table 1**. Plots were inventoried in the summers of 1994, 1997, 2000, and 2003 by the following methods. The use of permanent aluminum tree tags assured that the data was accurately associated with each tree throughout the entire study.

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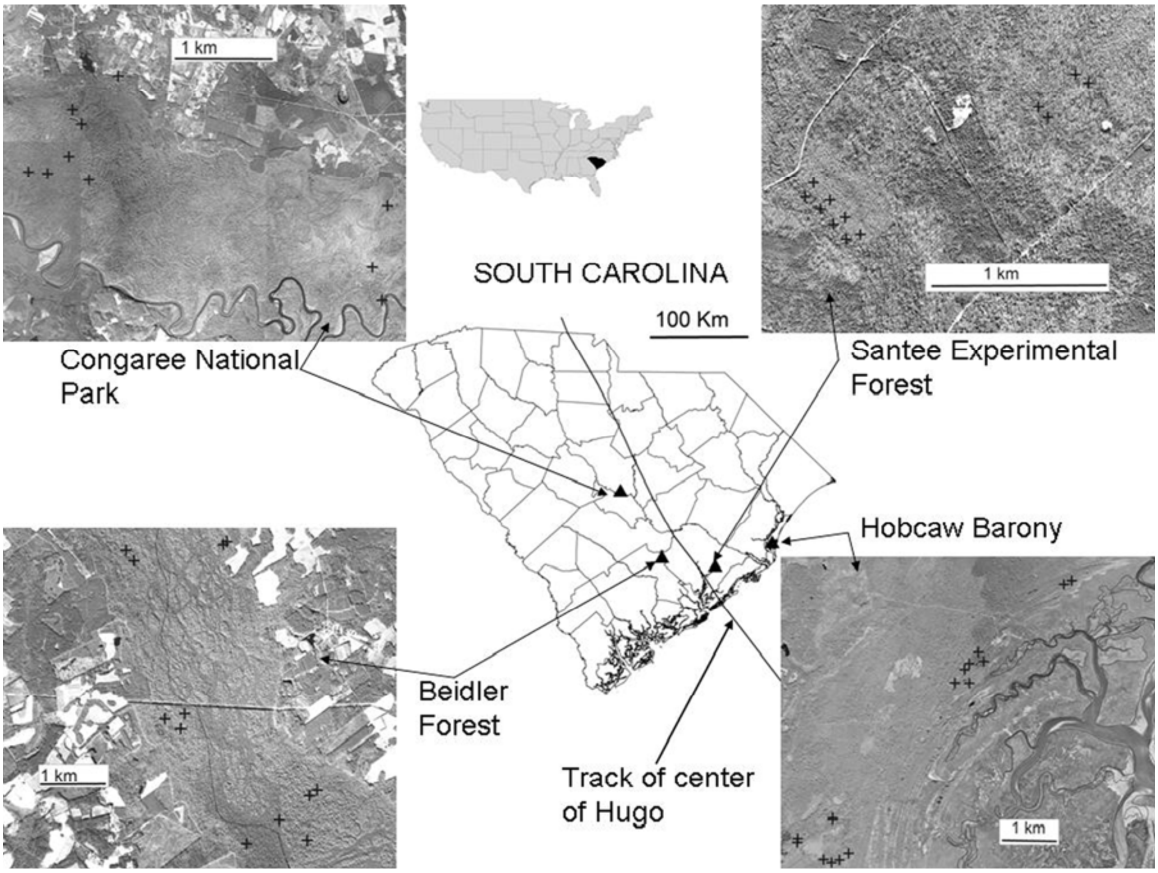

Fig. 1 Map of the study areas and plots. Location of each area, in relation to the path of the center of Hurricane Hugo, is designated by triangle on larger map of South Carolina. Plot locations in each area are designated by black cross in the individual photo-maps in each corner of the figure.

Study areas

(1) Beidler Forest (Lat. 33° 9′ N Long. 80° 19′ W): The Beidler Forest is administered as a forest preserve and instructional forest by the Nature Conservancy. It has a long history of research on many aspects of the swamp ecosystem. There, 12 plots included four plots representative of each of the three major wetland forest types; cypress-tupelo stands at the lowest elevations, bottomland hardwood (BLH) stands in the floodplain areas, and ridge-bottom areas that are rarely flooded, a type unique to this wetland (**Table 1**). The plots at the Beidler Forest 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): This National Park Service Park was established in the floodplain of the Congaree River south of Columbia S.C. in the late 1970s and is the largest expanse of old-growth floodplain forest in America, with approximately 9,000 ha. Most of the floodplain supports a bottomland hardwood forest type with creeks and sloughs supporting a cypress-tupelo swamp. Subsections (1/5 ha) of ten one hectare plots established by Putz and Sharitz (1991) were used in this study (**Table 1**). One plot of tupelo swamp from the nearby upland and was sampled as a unique forest type. The plots at the Congaree National Park 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): Hobcaw Barony, a 7,100 ha forested area on the southern tip of the Waccamaw peninsula north of Georgetown, S.C., is owned and managed by the Belle W. Baruch Foundation. The Barony is managed for research and forestry objectives and the plots located on the Barony have been designated for this study since Hurricane Hugo. The forest types at this site include longleaf pine (*Pinus palustris*), a type unique to this site (**Table 1**). The plots Hobcaw Barony are 5.5 km from the coast and were 72 km east of the center of Hugo.

(4) Santee Experimental Forest (Lat. 33° 7′ N Long. 79° 47′ W): The Santee Experimental Forest is a portion of the Francis Marion National Forest (established as a National Forest in 1936) just north of Charleston, SC. The pine-hardwood plots are in a control watershed that has not been disturbed since 1969. The other plots (**Table 1**) are in the floodplain of a small creek in the center of the forest with earthen dikes that were used to control water for rice cultivation during the 18 and 19th centuries. One of these dikes separates the cypress tupelo and BLH types. The Santee Experimental Forest Plots are 28 km from the coast and were 14 km east of the center of Hugo.

Table 1 Number of plots among sites and forest types.

Cover type	Study area				Total
	Beidler Forest	Congaree NP	Santee Forest	Hobcaw	
Cypress Swamp	4	3	4	4	15
Bottomland Hardwood	4	5	4		13
Upland Pine- Hardwood		1	4	4	9
Upland Hardwood				4	4
Longleaf Pine				4	4
Ridge Bottom	4				4
Tupelo Swamp		1			1
Total	12	10	12	16	50

Table 2 1994 mean site type basal area (B.A., m^2/ha) and density (stems/ha) for the tree and sapling size classes.

Study area	Cover type	Tree B.A.	Sapling B.A.	Tree density	Sapling density
Beidler	BLH	42.8	2.2	631	997
	Ridge Bottom	15.5	3.6	445	1642
	Cypress Tupelo	109.2	3.9	703	1580
Congaree	BLH	58.4	0.6	571	347
	Cypress Tupelo	69.7	1.3	744	484
	Pine Hardwood	32.4		325	
	Tupelo Swamp	23.2		395	
Hobcaw	Cypress Tupelo	11.8	0.8	192	425
	Upland Hardwood	22.1	1.5	321	778
	Longleaf	7.3	2.1	205	980
	Pine Hardwood	23.6	1.2	533	450
Santee	BLH	13.1	3.4	458	1961
	Cypress Tupelo	23.4	2.1	259	1118
	Upland Hardwood	9.2	3.4	351	1680

Data collection

Each plot is marked with a pipe in the corner (also located by GPS coordinates) at the end of the access trail. The plots are 20 m wide by 100 m long and divided into five 20 m × 20 m subplots. All woody stems, greater than 2.5 cm in Diameter at Breast Height (DBH) were marked with an aluminum tree tags. . Each tagged tree was measured in each plot, including its DBH, species, a damage class, and permanently tagged with unique number. Trees smaller than 2.5 cm in DBH were inventoried in ten 3.25 m radius subplots in each main plot by tallying woody stems by species and height class. Measurements were made by these methods in 1994, 1997, 2000, and 2003.

Basal area was computed for each tree from DBH measurement and converted to m^2/ha ($\pi(d/2)^2 \times 5/10000$). Total basal area and number of stems were determined by species for each plot. Importance Values were calculated by tree species combining both the percentages of basal area and number of stems within a plot (Helms 1998). With these parameters we looked at changes in both the basal area and tree densities at different size classes to quantify forest dynamics during the 10-year measurement period. The basal area and density for the major species in the tree and sapling size categories were plotted by study area and forest type over the time period of the study. Stems with a DBH of 10 cm and above were considered trees; stems with a DBH of 2.5 to 9.9 cm were considered saplings.

RESULTS

Initial average plot basal area and stem density (all stems) are given in **Table 2**. Changes during study are presented in **Figs. 2-12**. Please note that although all figures are uniform in presentation the scale changes greatly for some overstory types. Also some bars are not apparent at the scale chosen to represent all species.

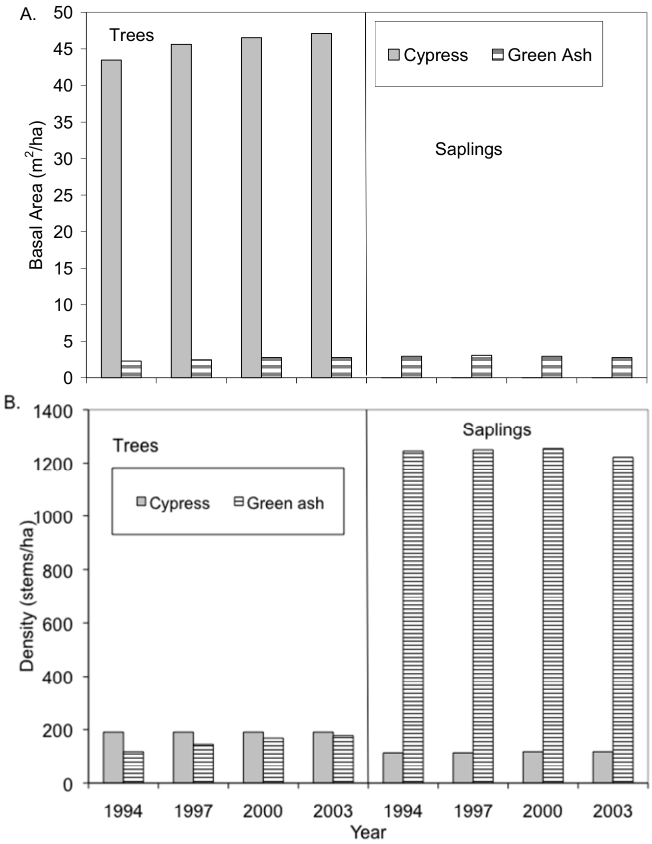

Fig. 2 Basal area (**A**) and density (**B**) changes for cypress and green ash in the cypress swamp forest type at Beidler Forest.

Beidler forest

In 1994 the cypress-tupelo overstory was mostly bald cypress (*Taxodium distichum*, 43.9 m^2/ha, 105 stems/ha) and swamp tupelo (*Nyssa biflora*, 50.7 m^2/ha, 286 stems/ha) and the sapling size class was dominated by green ash (*Fraxinus pennsylvanica*, 1,249 stems/ha) with a minor swamp tupelo component (110 stems/ha).

The basal area of cypress increased slightly during the study period (**Fig. 2A**) and there was a slight increase in the density of tree-sized green ash stems (**Fig. 2B**). None of the other species with tree-sized stems showed a noticeable change. In the sapling size class, the high density of green ash stems did not change much, and only laurel oak (*Quercus laurifolia*, showed a noticeable increase during the study period.

In 1994 the bottomland hardwoods were dominated by sweetgum (*Liquidambar styraciflua*, 9.5 m^2/ha, 50 stems/ha), laurel oak (7.3 m^2/ha, 211 stems/ha), and bald cypress (5.6 m^2/ha, 54 stems/ha), with the sapling layer consisting of laurel oak (219 stems/ha), hornbeam (*Carpinus caroliniana*, 142 stems/ha) green ash (113 stems/ha) and red maple (*Acer rubrum*, 112 stems/ha). Tree-sized cypress increased slightly in basal area (**Fig. 3A**). For the sapling size class, sweetgum and green ash showed noticeable increases in density (**Fig. 3B**) and slight increases in basal area. The higher ridge-bottom plots had the lowest initial total basal area, but were the most diverse, with the overstory consisting of sweetgum (2.4 m^2/ha, 35 stems/ha), green ash (2.0 m^2/ha, 5 stems/ha), water oak (*Quercus nigra*, 1.7 m^2/ha, 40 stems/ha), and hornbeam (1.3 m^2/ha, 115 stems/ha), with pignut hickory (*Carya glabra*) and American elm (*Ulmus americana*) in lesser amounts. The sapling size class was dominated by hornbeam (619 stems/ha), redbay (*Persea borbonia*, 212 stems/ha), and lesser amounts of American holly (*Ilex opaca*) and sweetgum. Sweetgum and hornbeam tree basal area (**Fig. 4A**) and density increased noticeably during the study period, with red maple and red hickory (*Carya ovalis*) increasing much less. The other species did not show a change in the basal area and density of the tree-

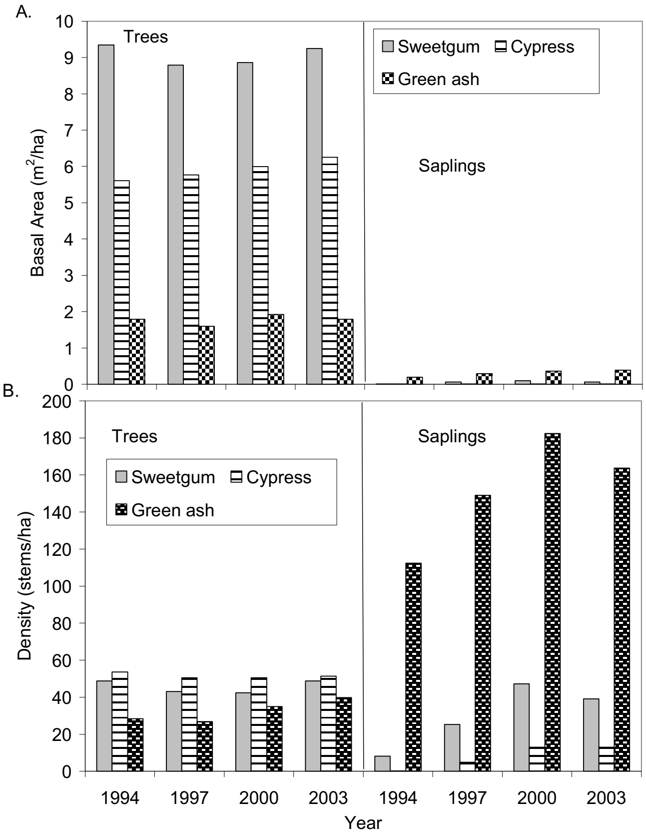

Fig. 3 Basal area (**A**) and density (**B**) changes for sweetgum, cypress, and green ash in bottomland hardwood forest type at Beidler Forest.

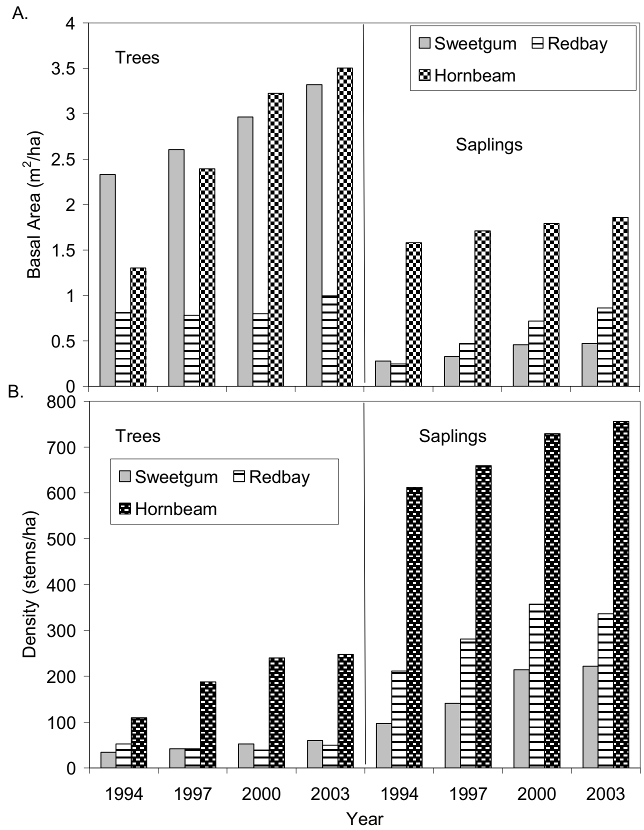

Fig. 4 Basal area (**A**) and density (**B**) changes for sweetgum, redbay, and hornbeam in the ridge bottomland hardwood forest type at Beidler Forest.

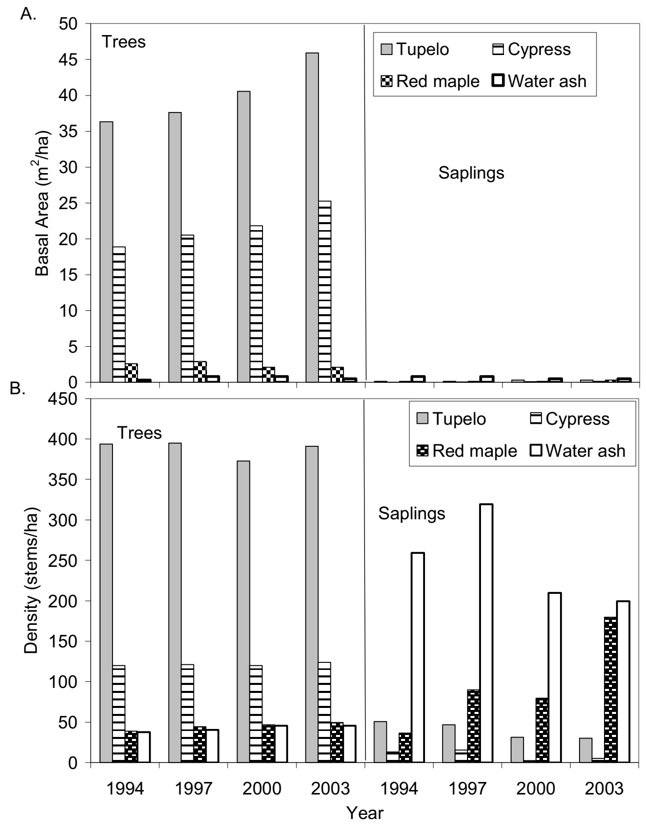

Fig. 5 Basal area (**A**) and density (**B**) changes for tupelo, cypress, red maple and water ash in the cypress-tupelo forest type at Congaree National Park.

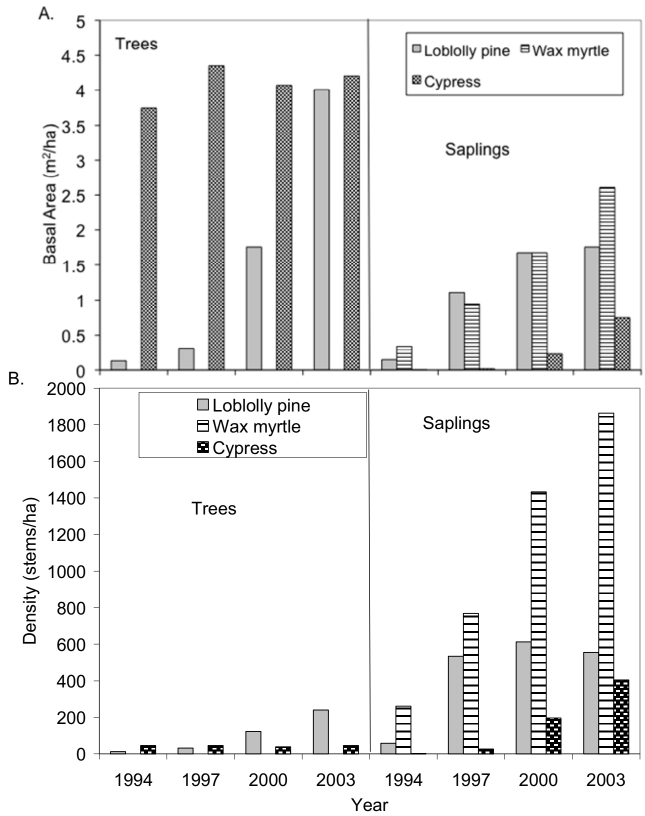

Fig. 6 Basal area (**A**) and density (**B**) changes for loblolly pine, wax myrtle, and cypress in the cypress-tupelo forest type at Hobcaw Barony.

sized stems. Hornbeam, redbay, and sweetgum sapling density increased greatly during the study period (**Fig. 4B**) with American holly density increasing slightly. The basal area of redbay only increased noticeably (**Fig. 4A**).

Congaree swamp national park

The cypress-tupelo forest type was dominated by water tupelo (*Nyssa aquatica*, 46.0 m^2/ha), bald cypress (25.3

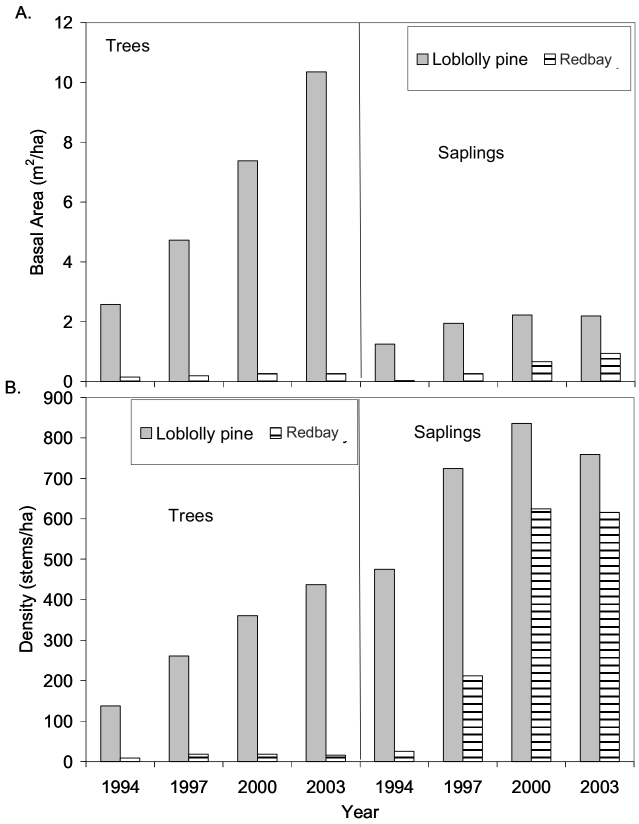

Fig. 7 Basal area (**A**) and density (**B**) changes for loblolly pine and redbay in the longleaf pine forest type at Hobcaw Barony.

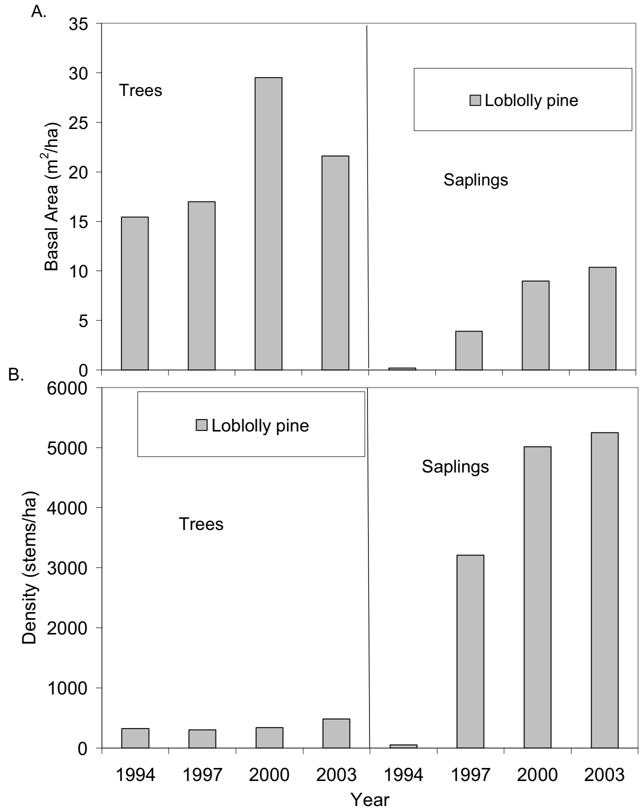

Fig. 8 Basal area (**A**) and density (**B**) changes for loblolly pine in the pine-hardwood forest type at Hobcaw Barony.

m^2/ha) and swamp tupelo (11.0 m^2/ha) in the tree size class and water ash (*Fraxinus caroliniana*, 200 stems/ha) and red maple (170 stems/ha) in the sapling size class in 1994. Both water tupelo and bald cypress trees grew noticeably during the 10-year study period (**Fig. 5A**), with the other tree species not showing much growth. In the sapling stem size class the density of red maple stems increased (**Fig. 5B**) four-fold and the density of water ash decreased about 20%.

In 1994 the bottomland hardwood forest type was dominated by sweetgum with a total basal area of 58.4 m^2/ha, and a sweetgum tree density of 95 stems/ha. Also contributing to tree basal area were green ash, American holly, and swamp chestnut oak (*Quercus michauxii*). The sapling layer was dominated by deciduous holly (*Ilex decidua*) and pawpaw (*Asimina triloba*). This forest type showed little change during the study period. Sweetgum tree density decreased slightly and American holly tree density increased slightly. For saplings, deciduous holly density decreased slightly.

The single pine-hardwood upland plot was dominated by loblolly pine (*Pinus taeda*, 17.7 m^2/ha, 35 stems/ha), sweetgum (6.9 m^2/ha, 50 stems/ha), willow oak (*Quercus phellos*, 2.9 m^2/ha, 10 stems/ha), and hornbeam (2.6 m^2/ha, 150 stems/ha) in 1994. Sapling data was not available. This forest type did not change during the measurement period, with the exception of a slight decrease in the density of American holly trees and a slight increase in hornbeam tree density.

The single tupelo swamp plot was dominated by swamp tupelo (18.1 m^2/ha, 220 stems/ha), red maple (2.9 m^2/ha, 30 stems/ha), sweetgum (1.1 m^2/ha, 45 stems/ha), and laurel oak (0.7 m^2/ha, 60 stems/ha) in 1994. Sapling data was not available. There was an increase in the basal area of water tupelo and density of American holly and sweetgum. Otherwise this plot changed little during the study.

Hobcaw barony

The cypress-tupelo plots are within drainage 100 m from the salt marsh of North Inlet. This drainage was filled with salt water during the Hurricane to a depth of approximately 2 m. The 1994 tree strata consisted of blackgum (*Nyssa sylvatica*, 4.3 m^2, 82.5 stems/ha), bald cypress (3.8 m^2/ha), laurel oak (1.4 m^2/ha, 10 stems/ha), and red maple (0.8 m^2/ha, 5 stems/ha). Most of the sapling-sized stems were wax myrtle (*Morella cerifera*, 251 stems/ha), loblolly pine (46.3 stems/ha), and redbay (32.5 stems/ha). During the study period, the major species, blackgum showed no change in the tree strata, but loblolly pine increased from a minor part of the tree strata (**Fig. 6A**), to slightly less basal area and density than blackgum. Cypress tree density increased slightly, but the other tree species remained unchanged during the 10-year period. In the sapling layer, wax myrtle increased 10-fold from 251 stems/ha to 1,873 stems/ha (**Fig. 6B**). Cypress and loblolly saplings also increased, producing a much denser sapling layer at the end of the study, while redbay also showed the similar trend.

The longleaf plots were on mesic sites. In 1994 the tree strata was dominated by longleaf pine (4.5 m^2/ha, 46.3 stems/ha) and loblolly pine (2.6 m^2/ha, 14 stems/ha). The sapling size class was mostly loblolly pine (475 stems/ha), sweetgum (252 stems/ha) and blueberry (*Vaccinium corymbosum*, 137 stems/ha). During the study period, loblolly pine became more predominant in the tree strata (**Fig. 7A**), and longleaf did not change. In the sapling strata, redbay increased dramatically from 24 to 626 stems/ha and loblolly pine density almost doubled (**Fig. 7B**).

The pine-hardwood plots were adjacent to the salt marsh and were also inundated with at least 2 m of saltwater during Hugo. The 1994 tree stratum was composed of loblolly pine (15.6 m^2/ha, 307 stems/ha), pond pine (*Pinus serotina*, 5.0 m^2/ha, 60 stems/ha), and live oak (*Quercus virginiana*, 1.6 m^2/ha, 79 stems/ha). The 1994 sapling strata was live oak (130 stems/ha), wax myrtle (90 stems/ha), sweetgum (88 stems/ha), and loblolly pine (56 stems/ha). During the study period, loblolly pine basal area and density increased noticeably (**Fig. 8A**), and live oak changed little. The loblolly pine tree basal area decreased between the 2000 and 2003 sampling, but the tree density remained

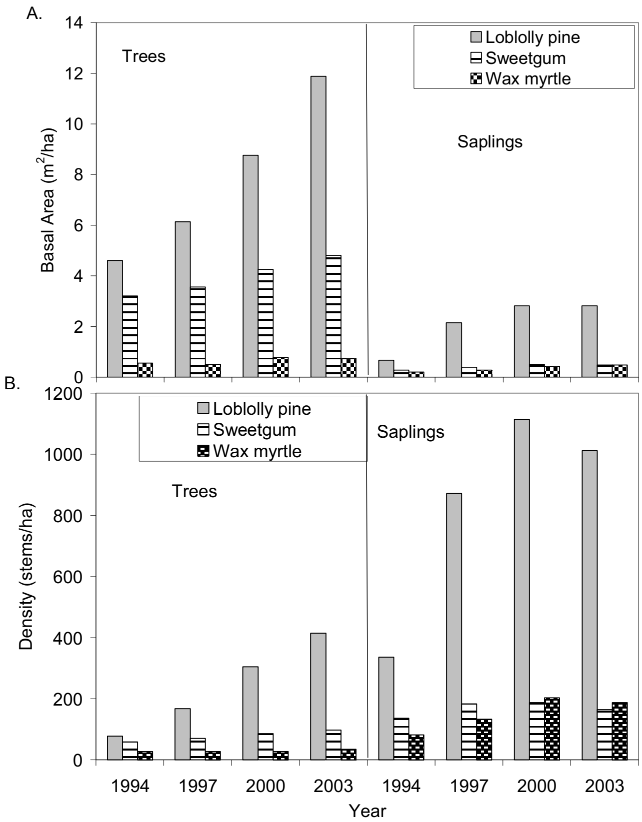

Fig. 9 Basal area (**A**) and density (**B**) changes for loblolly pine, sweetgum, and wax myrtle in the upland hardwood forest type at Hobcaw Barony.

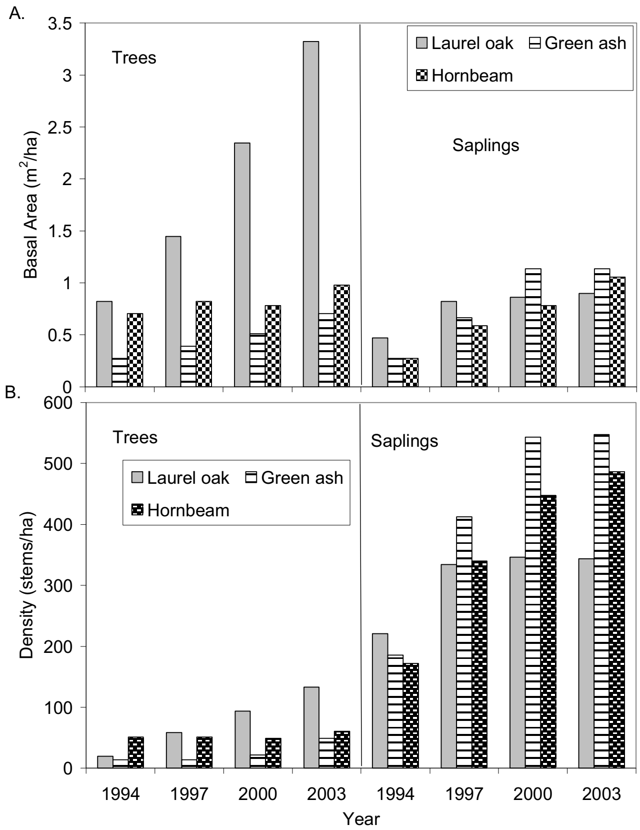

Fig. 10 Basal area (**A**) and density (**B**) changes for laurel oak, green ash, and hornbeam in the cypress-tupelo forest type at Santee Experimental Forest.

the same, possibly indicating mortality of some large pines. In the sapling strata, loblolly pine density increased 100 fold from 56 stems/ha to over 5500 stems/ha in 2003 (**Fig. 8B**). The other sapling species remained unchanged.

The upland hardwood plots were on excessively well-drained sands on ancient beach ridges and had a tree stratum of loblolly pine (4.6 m^2/ha, 81 stems/ha), sweetgum (3.2 m^2/ha, 58 stems/ha), longleaf pine (2.5 m^2/ha, 13 stems/ha), and southern red oak (*Quercus falcata*, 2.4 m^2/ha, 15 stems/ha) in 1994. Loblolly pine dominated the sapling strata (332 stems/ha), while sweetgum (140 stems/ha), wax myrtle (135 stems/ha), and redbay (84 stems/ha) comprised the sapling strata also. Loblolly pine tree basal area tripled (**Fig. 9A**) and its density increased much less during the study period. The other tree species changed little except sweetgum basal area, which increased slightly. In the sapling strata, loblolly pine sapling density more than doubled (**Fig. 9B**) and wax myrtle density doubled.

Santee experimental forest

The cypress-tupelo plots were adjacent to the BLH plots and were divided by Nicholson creek. Initially, bald cypress contributed 10.3 m^2/ha (30 stems/ha) of this forest type (total of 23.4 m^2/ha in basal area). Less dominant tree strata species included sweetgum (2.7 m^2/ha, 11.3 stems/ha), loblolly pine (2.3 m^2/ha, 5 stems/ha), and overcup oak (*Quercus lyrata*, 1.2 m^2/ha, 5 stems/ha). Laurel oak (224 stems/ha), green ash (187 stems/ha), hornbeam (170 stems/ha), and American holly (99 stems/ha) constituted the sapling strata. The basal area and density of laurel oak trees almost tripled during the study period (**Fig. 10A, 10B**) while the basal area and density of the other tree species changed little. In the sapling strata, green ash and hornbeam increased greatly. Green ash density almost tripled and hornbeam density more than doubled (**Fig. 10B**). Other species in the sapling strata did not increase noticeably in density.

The bottomland hardwood plots had a tree stratum of red maple (3.7 m^2/ha, 160 stems/ha), sweetgum (2.9 m^2/ha, 75 stems/ha), green ash (1.6 m^2/ha, 41 stems/ha), and laurel oak (1.5 m^2/ha, 21 stems/ha). Red maple constituted about a third of the sapling strata (686 stems/ha), with laurel oak (327 stems/ha), hornbeam (173 stems, ha), and slippery bark elm (*Ulmus rubra*, 132 stems/ha) being the other common sapling species in 1994.

During the study period, red maple and laurel oak tree basal area increased greatly, with a much smaller increase in density, indicate tree diameter growth (**Fig. 11A**). The other tree-strata species changed little during the 10-year period. The density of the sapling strata increased greatly, primarily due noticeable increases in hornbeam, laurel oak, and red maple sapling density (**Fig. 11B**).

The pine-hardwood plots were in an upland forest that had a canopy of large loblolly pines that were mostly destroyed by the hurricane. By 1994 total tree strata basal area was 9.2 m^2/ha with loblolly pine contributing 4.9 m^2/ha (70 stems/ha). Less predominant tree species included blackgum (1.5 m^2/ha, 105 stems/ha), water oak (1.1 m^2/ha, 66 stems/ha), and sweetgum (0.9 m^2/ha, 59 stems/ha). The dense sapling strata consisted of water oak (323 stems/ha), blackgum (295 stems/ha), sweetgum (266 stems/ha), and loblolly pine (247 stems/ha). Loblolly pine tree stem basal area increased from 4.9 m^2/ha to over 9.0 m^2/ha in 2003 with a much less increase in tree density (**Fig. 12A**). Blackgum and water oak tree basal area increase much less than loblolly pine. Loblolly pine sapling density increased almost 8-fold from 245 stems/ha to 1,660 stems/ha (**Fig. 12B**). Water oak showed a slight increase in sapling density (and the other sapling species changed little.

DISCUSSION

The findings highlight the variability of hurricane recovery. Brokaw and Walker (1991) found great variability of hurricane impact in tropical and temperate forests. They compared 15 hurricane damage studies and found branch

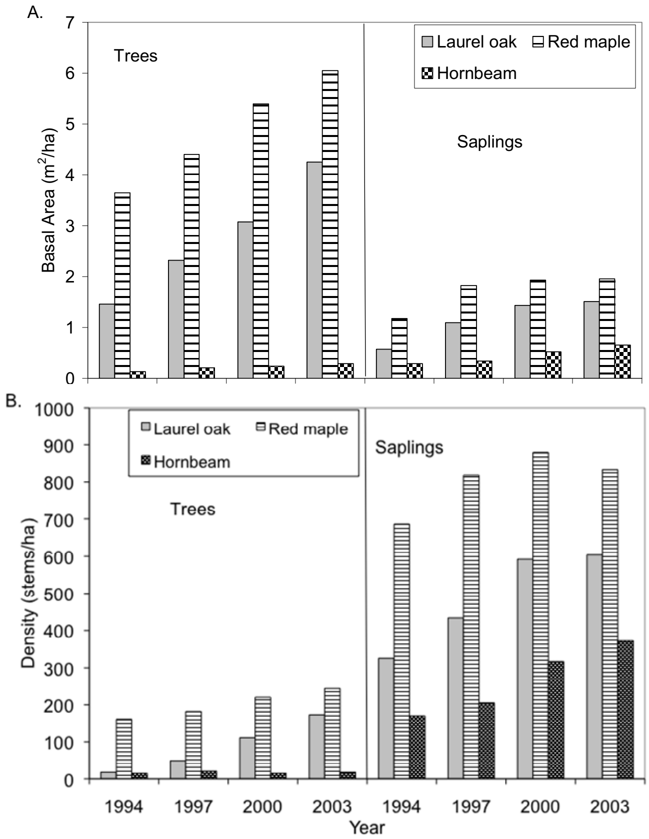

Fig. 11 Basal area (**A**) and density (**B**) changes for laurel oak, red maple, and hornbeam in the bottomland hardwood forest type at Santee Experimental Forest.

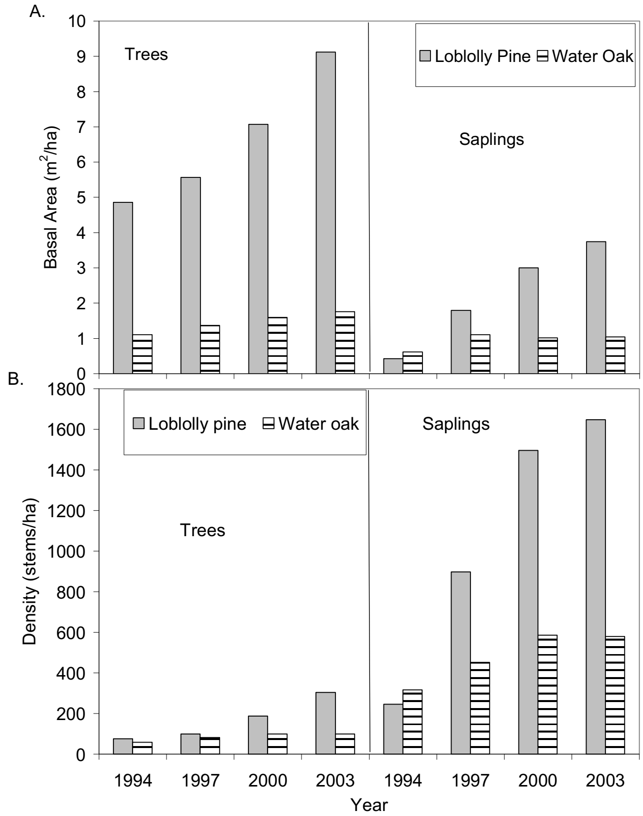

Fig. 12 Basal area (**A**) and density (**B**) changes for loblolly pine and water oak in the pine-hardwood forest type at Santee Experimental Forest.

damage varied from 13-72% of all stems, snapped trunks on 8-44% of all stems, uprooting of 4-91% of all stems, and death of 1-95% of all stems. Much of the variability in damage, on a regional scale, can be explained by wind distribution within the hurricane, while topographic modification of the predicted wind field best predicts distribution of damage to individual trees or stands in mountainous terrain (Boose *et al.* 1994; Busby *et al.* 2008). Finally, individual species of the southeastern forest differ in their resistance to hurricane damage (Touliatos and Roth 1971; Barry *et al.* 1993; Stanturf *et al.* 2007).

These study results must be viewed in light of the differences in original damage in each of the four study sites and differences in the resistance of the species of the stand types. Among the four sites, the Santee Experimental Forest was nearest to the northeast eyewall of Hurricane Hugo (**Fig. 1**, the area of peak winds in Northern Hemisphere hurricanes and typhoons, Busby *et al.* 2008) and received the greatest wind damage, with up to 90% mortality (Hook *et al.* 1991). While Hobcaw was 72 km east of the eyewall and had lower rates of mortality from wind (Gresham *et al.* 1991), it is also within 5 km of the ocean and received a surge of up to 2 meters of seawater roughly 1 km into the forest (Gardner *et al.* 1991). Salt water remained in the soil and caused delayed mortality at least 18 months after the storm (Williams 1996). Both Congaree Swamp and the Beidler Forest were to the southwest of the center of the storm (**Fig. 1**, Sheffield and Thompson 1992). Beidler Forest is nearer to the coast and had overall mortality of 21% two years after the storm (Duever and McCollum 1992). Congaree swamp is over 100 km inland and only 33% of the surveyed trees were considered seriously damaged and only 18% uprooted or snapped off (Putz and Sharitz 1991).

Cypress and tupelo are both resistant to wind mortality (Stanturf *et al.* 2007) and cypress-tupelo swamps are the only forest type that exists in all four forest sites (**Table 1**). At both Congaree and Beidler, the cypress-tupelo plots were dominated by mature trees that survived the storm. The only changes were a slight increase in growth and increase in the number of red maple saplings, both probably due to greater understory sunlight. The cypress-tupelo plots at Hobcaw were subject to salt water mortality for which cypress is more tolerant (Stanturf *et al.* 2007). There, the decline of swamp tupelo increased the dominance by cypress and also allowed loblolly pine seedlings to become established and dominate the sapling understory, along with redbay and wax myrtle shrubs. At Santee the cypress-tupelo overstory was greatly reduced by the stronger wind and a combination of laurel oak, green ash, and hornbeam are increasing in number and basal area. Laurel oak appears to have been in advanced reproduction as much of the increase has been in the tree size class. Green ash and hornbeam are more likely seedlings or sprouts as they are primarily saplings, which one would expect for trees 14 years or younger.

Upland pine hardwoods, which exist in every site but Beidler, have many species that are intermediate resistance or susceptible to wind damage (loblolly pine, water oak, willow, laurel oak) (Gresham *et al.* 1991; Stanturf *et al.* 2007). Loblolly pines remained or increased in dominance at all three sites. Note that in both the Hobcaw and Santee sites, the small loblolly pine stems dramatically increases during the 10-year period from 4-14 years after the hurricane, indicating continued seedling establishment for an extended period after the storm. The shade intolerant loblolly pines have been able to exploit the increase in sunlight due to higher mortality in this stand type. The unique longleaf pine type at Hobcaw had a similar increase in loblolly pine, as both growth of survivors and establishment in the sapling size class.

Like upland pine hardwoods, the bottomland hardwood types also have many intermediate resistance and susceptible species. Although this stand type only existed at the two sites with lower wind speeds the type had more damage at both sites. Sweetgum is playing the same role on these sites as loblolly pine in the pine hardwood types. The unique ridge bottomland hardwood type at Beidler also shows rel-

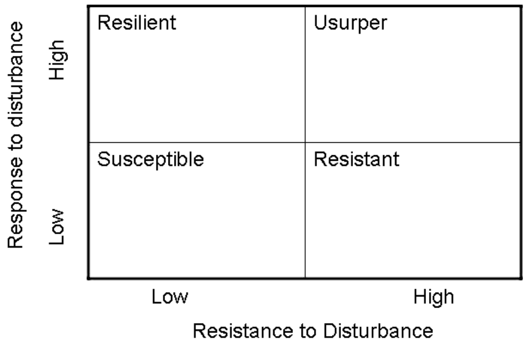

Fig. 13 A diagram of possible responses of individual species within a forest type after hurricanes adapted from Batista and Pratt (2003).

ease of understory hornbeam and redbay in addition to increases in sweetgum.

While this study has shown differences in recovery to be influenced by location in relation to the storm track and the extent of hurricane damage, it has not produced much insight into resilience of ecosystems or an inherent difference between upland and wetland forests. Better insight may come from a different view of ecosystem dynamics. Ecosystem resistance and resilience often are expressed in a Clementsian view of ecosystems that return to fixed equilibrium by succession after a disturbance. However, if we adapt a more Gleasonian view of ecosystems being self-organized systems of individual plant species that may have multiple successional pathways and equilibria (Uriarte *et al.* 2009), then our results are consistent with other studies of hurricanes in tropical and temperate areas. Bellingham *et al.* (1995) and Batista and Pratt (2003) present a useful new interpretation to resistance and resilience in regard to recovery of individual species within a forest type as a simple diagram of possible responses (**Fig. 13**). A species can be resistant to hurricane effects: no effect on survival or growth of adult trees, no change in recruitment or growth of young. Or it can be resilient: decrease in survival and growth of adults, but increased recruitment and growth of young. They (Batista and Pratt 2003) also add two classes, susceptible: decrease of growth and survival of adults and no change or decrease in recruitment and growth of young, and usurper: little or no effect on adults and increase in recruitment or growth of young (**Fig. 13**).

Although our study lacks data on pre-hurricane mortality and does not allow the quantitative analysis used by Batista and Pratt (2003), we can make qualitative judgments as Bellingham *et al.* (1995). We can see relatively resistant (cypress, tupelo, longleaf) species, relatively resilient (sweetgum, loblolly pine, laurel oak), susceptible (willow, water, laurel oaks), and usurpers (hornbeam, and loblolly). Some have proposed similar distinctions of resistant (Boucher *et al.* 1990; Tanner *et al.* 1991) and resilient species (Boucher *et al.* 1994; Lugo and Scatena 1996) within tropical systems exposed to hurricanes. The concept of susceptible and usurper are only meaningful in a stand or population context and have been primarily used by Bellingham *et al.* (1995). The results of qualitative comparisons may show a particular species in more than one role. Loblolly pine was a resilient species in the pine-hardwood type but a usurper in longleaf and cypress-tupelo stands. Large laurel oak are highly susceptible to hurricane winds (Gresham *et al.* 1991) but saplings and sprouts were able to play a usurper role in the cypress tupelo stands at Santee. The role of a resilient species may also vary based on the degree of damage. In Santee and Hobcaw the large cypress and tupelo were removed by high winds and salt water, respectively. Resilient loblolly pine became a usurper at Hobcaw, where salt killed advanced reproduction and seedling for several years, by prolific seed production. Without salt poisoning, laurel oak sprouts and advanced regeneration filled that role at Santee. Although limited data in this study show longleaf pine to be a resistant species at Hobcaw (wind speed app. 130-170 km/ph), data from the Francis Marion Forest showed it is susceptible to higher wind speeds (wind speed app. 210 km/h) (Hook *et al.* 1991).

CONCLUSION

This paper reports the changes in seven forest types from four locations that differed in initial damage due to their location in relation to the path of the hurricane for years 4 to 14 after the storm.

1) Little to no change was observed in the basal area and density of many tree and sapling species in all study areas. The tree strata in the Beidler cypress-tupelo plots and to a lesser extent the BLH plots, the BLH plots in the Congaree Park and the cypress-tupelo plots of Hobcaw Barony, changed little during the 10-year study period. This suggests that many common southeastern species are resistant to damage by moderate hurricane winds. However this was not true in the most heavily damaged plots in the Santee Experimental Forest, suggesting that resistance is a function of wind speed as well as forest species.

2) For several forest types, the species with the greatest increase in sapling density and to a lesser extent, basal area, were not the predominant species in the tree strata. In the Beidler Forest BLH plots ash was not a significant canopy component, but ash saplings increased greatly. Other sapling species showing great density increases are hornbeam, redbay, deciduous holly, and wax myrtle; and none of these were a major component of the tree strata. Batista and Pratt (2003) also concluded the hornbeam was a usurper species and they thought it required frequent hurricane damage to remain in the forest. Thus it appears that these species responded the fastest to the increase in site resources.

3) Loblolly pine, a recognized pioneer species, responded greatly to the increase in site resources by greatly increasing tree basal area and sapling density in several forest types at several study areas. In the pine-hardwood type it was a resilient species, while on Hobcaw Barony, loblolly pines became much more predominant in the cypress-tupelo and longleaf pine forest types, where it was a minor component at the beginning of the study. This was more evident on the pine-hardwood plots of Hobcaw and the Santee Experimental Forest, on both of which Hurricane Hugo damages were apparent, loblolly pine trees grew rapidly and loblolly saplings became much more abundant.

This study only represents a 10-year period, from 4 to 14 years after the hurricane, and cannot predict the long-term impacts of the hurricane. For example, loblolly pine and laurel oak are only moderately tolerant of flooding (Hook 1984) and survival of these species on sites formerly occupied by cypress and tupelo (highly flood tolerant) may be in jeopardy during a "wet" period. However, even this short period shows that initial hurricane wind speed interacts with species resistance to result in a variety of responses.

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