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Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest

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Summary

1 We assessed the responses of tree populations in an old-growth Southern mixed-hardwood forest in northern Florida to hurricane disturbance. The most recent, Hurricane Kate (1985), damaged 41% and killed 7% of the overstorey trees, eliminated 8% of the basal area, and increased the area in canopy gaps from 31% to 62%.

2 We focused on changes in recruitment, growth and mortality of trees of the 10 most abundant tree species (> 93% of the basal area). We analysed data from 7149 trees ≥ 2 cm d.b.h., recorded in periodic censuses of a 4.5-ha plot over the period spanning 7 years before and 7 years after the disturbance.

3 After Hurricane Kate, recruitment into the ≥ 2 cm d.b.h. class increased sixfold, and rates of growth and survival increased for saplings and understorey trees, but decreased for overstorey trees.

4 We classified the tree populations into four previously defined syndromes of response to disturbance according to observed mortality, recruitment and growth patterns. *Pinus glabra* exhibited the Resilient syndrome, with high tree mortality but massive recruitment after the hurricane. Two subcanopy species (*Carpinus caroliniana* and *Ostrya virginiana*) and three canopy species (*Liquidambar styraciflua*, *Quercus michauxii* and *Q. nigra*), exhibited the Usurper syndrome, showing low tree damage, some release of understorey trees and saplings, and substantial recruitment. *Ilex opaca* (subcanopy), and *Fagus grandifolia* and *Nyssa sylvatica* (canopy), exhibited the Resistant syndrome, characterized by low tree damage and little increase in recruitment. The main canopy dominant, *Magnolia grandifolia*, exhibited the Susceptible syndrome; it had large reductions in growth and survival and no detectable release of understorey individuals.

5 Short-term persistence was not compromised by Hurricane Kate in any of the 10 tree populations because the majority of trees were resistant to hurricane damage. The long-term persistence of populations exhibiting the Resistant syndrome appeared to be independent of hurricane disturbance. Long-term persistence appeared to depend on periodic hurricanes (or equivalent large-scale disturbances) for Resilient and Usurper syndromes, but might become compromised by recurrent hurricanes for the Susceptible syndrome.

Key-words: forest, hurricane, Southern mixed hardwood forest, tree-population dynamics, Woodyard Hammock

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Introduction

In hurricane-prone forests, populations of trees persist over successive disturbances (e.g. Zimmerman *et al.* 1994; Bellingham *et al.* 1995; Everham & Brokaw 1996; Batista *et al.* 1998). Adult trees may be resistant to wind damage, with high likelihoods of survival and regrowth into the canopy (Boucher *et al.* 1990; Yih *et al.* 1991; Tanner *et al.* 1991; Basnet 1993; Slater *et al.* 1995). Alternatively, understorey individuals may respond with increased recruitment, growth and survival after the disturbance (Boucher *et al.* 1994; Lugo & Scatena

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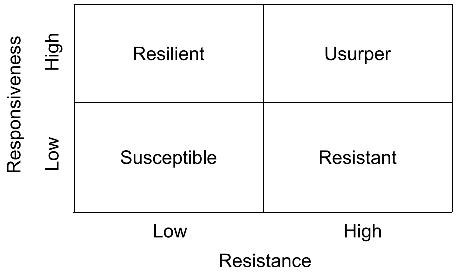

Fig. 1 Syndromes of tree-population response to hurricane disturbance proposed by Bellingham *et al.* (1995).

1996). Resistance and responsiveness to hurricane disturbance vary among tree species (e.g. Gresham *et al.* 1991; Walker 1991; Merrens & Peart 1992; Zimmerman *et al.* 1994; Everham & Brokaw 1996).

Bellingham *et al.* (1995) developed a conceptual model of demographic responses to hurricane disturbance based on the implicit notion that tree populations could exhibit independent combinations of resistance and responsiveness (cf. Walker 1991; Merrens & Peart 1992; Zimmerman *et al.* 1994). Different combinations of high and low resistance and responsiveness were proposed to produce four syndromes of population response to disturbance (Resilient, Usurper, Resistant and Susceptible, Fig. 1), with all four combinations occurring in a forest in Jamaica (Bellingham *et al.* 1995). However, syndromes were assigned to tree species on the basis of damage and responsiveness relative to other populations in the forest. Such relative assignment of syndromes does not provide a general procedure to compare responses among sites and hurricanes or to assess the relative importance of demographic mechanisms accounting for the persistence of tree populations.

We assessed the responses of tree populations to hurricane disturbance in a forest in northern Florida (USA) using a non-relative analysis based on demographic data collected in a mapped forest plot over a 14-year period that spanned the occurrence of a moderate-intensity hurricane. We compared pre- and post-hurricane population structure, as well as recruitment, growth and mortality of trees in the most abundant tree populations of the forest. Because trees in different strata might respond differently, we performed separate comparisons for trees grouped in different size categories, an approach adopted by Boucher *et al.* (1990, 1994), but uncommon among other studies of hurricane effects (e.g. Zimmerman *et al.* 1994; Bellingham *et al.* 1995).

First, we identified the response syndrome exhibited by different tree populations based on a suite of expected demographic responses. We recognize that syndromes might be influenced by both the structure of tree populations and the composition of the forest at the time of the hurricane, as well as by the characteristics of each hurricane. Nonetheless, the syndromes identified are likely to be characteristic of the populations studied because demographic responses also depend on traits intrinsic to each species, and because moderate-intensity hurricanes have frequently affected this forest.

Secondly, we assessed the relative importance of tree resistance to damage and responsiveness by understorey individuals for short-term persistence of the different tree populations. We anticipated that resistance would be the prevalent cause of short-term persistence because return time of hurricanes has been short compared with the life cycles of most tree species in the forest and because opportunities for regeneration and growth of small individuals are somewhat limited by the large numbers of canopy trees that survive most hurricanes (Bellingham *et al.* 1995; Everham & Brokaw 1996).

Thirdly, we projected the likely influence of repeated moderate-intensity hurricanes on long-term trends in tree populations. Regeneration is necessary for long-term persistence and is most likely to be associated with the post-hurricane environment. We thus anticipated that long-term persistence of many tree populations in the studied forest would be dependent on hurricane disturbance.

Methods

STUDY SITE

The Devil's Woodyard (hereafter Woodyard Hammock) is a 30-ha old-growth stand of the Southern mixed-hardwood forest type (Quarterman & Keever 1962). It is located in Leon County, Florida (30°35′ N, 84°20′ W), on the coastal plain of the northern Gulf of Mexico. The forest at Woodyard Hammock is diverse (Blaisdell *et al.* 1974; Platt & Schwartz 1990; Batista & Platt 1997). The canopy is dominated by *Magnolia grandiflora*, *Fagus grandifolia*, *Liquidambar styraciflua*, and *Pinus glabra*, with 11 less common canopy species. Like other warm temperate forests along the Gulf coast (Marks & Harcombe 1975; Quigley & Platt 1996, 2003; Batista & Platt 1997), the understorey contains small individuals of many canopy species and numerous subcanopy species such as *Ostrya virginiana*, *Carpinus caroliniana*, and *Ilex opaca*.

The Gulf coast region has a long history of exposure to hurricanes. Palaeological studies of sea-water ingression in coastal lakes indicate that periodic hurricanes have occurred over the past several thousand years (Liu & Fearn 2000). Stands of Southern mixed-hardwood forest located in this region have typically been affected by four to six hurricanes during the last century (Batista & Platt 1997). Woodyard Hammock has been within 100 km of the track of a hurricane with maximum sustained wind-speeds of 100–200 km h^{-1} on four occasions between 1886 and 1992 (in 1886, 1894, 1941 and 1985) (Jarvinen *et al.* 1984; Clark 1986). Recurrent hurricanes have been proposed to have a major effect on the dynamics of Southern

Table 1 Basal area (m^2 ha^{-1}) of tree species in the Woodyard Hammock plot between 1978 and 1992. Dominant species were defined as those that had average basal area > 0.5 m^2 ha^{-1}. Hurricane Kate affected the forest in 1985

	1978	1984	1986	1992
Dominant species				
Magnolia grandiflora	11.29	11.58	11.2	9.77
Fagus grandifolia	5.36	5.45	5.15	5.23
Liquidambar styraciflua	4.12	4.33	4.18	4.33
Pinus glabra	3.75	3.88	2.54	2.2
Nyssa sylvatica	2.16	2.24	2.24	2.3
Ilex opaca	1.57	1.54	1.5	1.45
Carpinus caroliniana	1.23	0.64	0.54	0.47
Ostrya virginiana	1.08	0.91	0.84	0.95
Quercus michauxii	1.03	1.13	1.15	1.34
Quercus nigra	0.7	0.67	0.61	0.66
*Non-dominant species (25)	2.36	2.48	2.2	2.12
Total	34.65	34.81	32.14	30.81

*Non-dominant species are: *Acer rubrum*, *Aralia spinosa*, *Callicarpa americana*, *Carya cordiformis*, *C. glabra*, *Cercis canadensis*, *Cornus florida*, *Cyrilla racemiflora*, *Fraxinus pennsylvanica*, *Ilex coriacea*, *Liriodendron tulipifera*, *Magnolia virginiana*, *Morus rubra*, *Osmanthus americanus*, *Oxydendron arboreum*, *Pinus taeda*, *Prunus serotina*, *Quercus alba*, *Q. hemisphaerica*, *Q. shumardii*, *Q. stellata*, *Q. virginiana*, *Sambucus canadensis*, *Symplocos tinctoria*, and *Ulmus alata*.

mixed-hardwood forests. Dominant tree populations are likely to persist after hurricane disturbance, and some might even depend on repeated canopy disruption for long-term persistence (Harcombe & Marks 1978; Glitzenstein *et al.* 1986; Platt & Schwartz 1990; Peters & Platt 1996; Batista *et al.* 1998).

The most recent hurricane to affect this area was Hurricane Kate, a well-organized, late-season hurricane of moderate intensity that originated off the coast of West Africa. The eye passed within 5–10 km of Woodyard Hammock on 21 November 1985, following heavy rainfalls that had saturated the soil. During this hurricane, tropical-storm-force winds lasted for about 8 hours in Leon County, with gusts of wind up to 160 km h^{-1} (Clark 1986). Tropical-storm records and sediments from coastal lakes suggest that hurricanes substantially more intense than Kate (e.g. Hurricane Camille, which crossed the Mississippi coast several hundred km to the west in 1969, Touilatos & Roth 1971), have been rare in the Gulf coast region (Jarvinen *et al.* 1984). Over the past several millennia, such extraordinary hurricanes have crossed the northern coast of the Gulf of Mexico at any point only once every few hundred years (Liu & Fearn 2000). Hurricane Kate may have been among the most intense storms to have occurred at Woodyard Hammock within the past several hundred years.

Hurricane Kate did not cause large changes in species composition, which remained relatively stable at this site over the 7-year periods preceding and following the hurricane (Tables 1 and 2). Data from the closest weather stations, at Quincy and Monticello, Florida, suggest that patterns of monthly rainfall and mean temperatures were also unchanged (NOAA 1982). However, the area in canopy gaps, as mapped by polygons connecting the bases of the bordering canopy trees (i.e. expanded gaps of Runkle 1982), was doubled from 31% to 62% (Batista & Platt 1997).

FIELD DATA

A 4.5-ha (225 × 200 m) permanent study plot was established in Woodyard Hammock in 1978 (Hirsh 1981; Platt & Hermann 1986). All trees with diameter at 1.5 m height (d.b.h) ≥ 2 cm were mapped and tagged, identified to species, measured for d.b.h., and recorded as understorey (≤ 15 m tall) or overstorey (> 15 m tall).

Table 2 Densities (individuals ha^{-1}) of overstorey trees (> 15 m tall), understorey trees (≤ 15 m tall; d.b.h. ≥ 4 cm) and saplings (2 cm ≤ d.b.h. < 4 cm), in the Woodyard Hammock plot between 1978 and 1992. Dominant species were defined as those that had average basal area > 0.5 m^2 ha^{-1}

	Overstorey trees				Understorey trees				Saplings			
	1978	1984	1984	1992	1978	1984	1986	1992	1978	1984	1986	1992
Dominant species												
Canopy												
Magnolia grandiflora	49.1	48.9	45.8	42.2	12.9	10.9	11.3	9.3	2.2	2.4	2.2	2.7
Fagus grandifolia	18.9	19.3	18	18.9	77.8	79.1	82.4	83.6	31.1	25.6	23.6	18.9
Liquidambar styraciflua	34.2	36	36.4	36.7	85.3	63.1	52.4	42	4.2	3.1	4.2	15.6
Pinus glabra	26.7	24.4	15.3	12.2	13.3	5.1	3.8	14.7	0	0	4.9	84.2
Nyssa sylvatica	14	14	14.2	14.2	11.6	9.6	8.7	7.3	0	0	0	0.2
Quercus michauxii	3.8	4.4	4.7	5.6	72.2	56.4	53.8	50	18.2	11.6	8.4	8.9
Quercus nigra	5.1	5.3	5.1	6	19.3	14.9	12.7	8.2	3.6	2.4	3.1	8.7
Subcanopy												
Ilex opaca	0.7	0.7	0.9	0.9	88.2	82.7	80.7	78.9	25.8	26.4	27.6	26.2
Carpinus caroliniana	0.2	0.2	0.2	0	98.9	62	56.7	58.7	36.7	31.1	34.7	66
Ostrya virginiana	0.4	0.2	0	0	76	61.8	61.3	79.8	14	24.2	50.2	219.6
Non-dominant species (25)	12.6	12.5	11.5	10.8	85.7	63.6	59.8	59.2	51.7	54.2	69.7	89.5
Total	165.8	166	152.2	147.6	641.3	509.1	483.6	491.6	187.6	181.1	228.7	540.4

Censuses of the entire plot were conducted biennially to record tree recruitment and growth in d.b.h. Stems that grew into the d.b.h. ≥ 2 cm size class were recorded as recruits, tagged and mapped. Mortality was recorded annually until 1985 and biennially starting in 1986. The 1985 mortality census was completed a few weeks before Hurricane Kate and damage to each mapped tree was assessed within 2 months of the storm. Trees were classified as 'without major damage' if they were not leaning and had no branches with diameter > 5 cm broken, and as 'with major damage' if they had any of these, or had more severe injuries (e.g. topped, snapped-off, bent-to-ground, tipped-up). Data obtained between 1978 and 1992 were organized in a database containing records for 7149 trees.

ANALYSIS

General approach

We focused our analysis on the 10 tree populations with the largest total basal area in the Woodyard Hammock plot (hereafter, the dominant species). These populations collectively accounted for > 93% of the basal area, and > 83% of all trees, throughout the 1978–92 period (Tables 1 and 2). We assessed the responses of these populations to Hurricane Kate through a battery of tests comparing the pre- and post-Kate rates of recruitment, growth and mortality of trees. These tests were performed for three mutually exclusive size classes: saplings (2 cm ≤ d.b.h. < 4 cm), understorey trees ≥ 4 cm d.b.h., and overstorey trees. Depending on the availability of data, five to nine tests were conducted on each population. We also compared the pre- and post-Kate size frequency distributions.

We identified the syndrome of response exhibited by each dominant tree population by comparing the results of our tests with the suite of changes in recruitment and in adult and juvenile-tree performance expected under each of four syndromes (see Table 3), names and general ideas as proposed by Bellingham *et al.* (1995). For the canopy species, we assumed that adults were the overstorey trees and juveniles were the understorey trees and saplings. For subcanopy species, we assumed that adults were the understorey trees and juveniles were the saplings.

We took into consideration two statistical problems associated with identification of the syndromes. First, several tests were involved in the classification of each tree species into a syndrome of response, and we therefore adjusted P-values to control the species-wise error rate. Adjustment was done by the Dunn-Sidak method (Sokal & Rohlf 1995) as $Padj = 1 - (1-P)^q$, where q is the number of tests performed for a species. Each P_{adj} represents an upper bound for the species-wise error rate, i.e. the probability of observing a P-value at least as extreme as the one obtained, had the null hypotheses held simultaneously for all tests performed for the corresponding species. Critical P_{adj} was set to 0.15, which corresponded to P-values (test-wise error rates) between 0.018 and 0.032, depending on the number of tests. However, most rejections of null hypotheses (32 out of 38) were based on $P_{adj} < 0.05$. Secondly, as some syndromes are identified by the absence of substantial

Table 3 Diagnostic characteristics of the four syndromes of response to hurricane disturbance. Syndrome names follow Bellingham *et al.* (1995). Adult trees include overstorey individuals of canopy species and understorey trees ≥ 4 cm d.b.h. of subcanopy species. Recruitment is the graduation into the d.b.h. ≥ 2 cm size class. Juvenile trees are understorey trees ≥ 4 cm d.b.h. of canopy species and saplings (trees 2–4 cm d.b.h.) of both canopy and subcanopy species

Syndrome	Growth and survival of adult trees	Recruitment into tree life-cycle stages	Growth and survival of juvenile trees	Expected post-hurricane characteristics
Resilient	Decreased	Increased	Increased	Adults are negatively affected by a hurricane, but recruitment and/or juvenile performance increase: population can increase or decrease after a hurricane, size frequency distribution is expected to have large changes
Usurper	Not decreased	Increased	Increased	Adult performance is not changed by a hurricane, and recruitment and/or juvenile performance is increased: population increases after a hurricane, size frequency distribution is expected to change
Resistant	Not decreased	Neither increased nor decreased	Neither increased nor decreased	No aspect of the demography is markedly affected by a hurricane: population does not increase or decrease after a hurricane, size frequency distribution is not expected to change substantially
Susceptible	Decreased	Decreased, or not increased	Decreased, or not increased	Adult performance is negatively affected by a hurricane. Neither recruitment nor juvenile performance increase: population declines after a hurricane, size frequency distribution may or may not change

hurricane effects on certain demographic rates (Table 3), we assessed the power of the non-significant tests, so that we could measure the confidence with which the results could be attributed to the absence of substantial effects rather than to lack of sufficient data (Bickel & Doksum 1977). We considered tests with power ≥ 0.75 as sufficient evidence to conclude that the rate in question changed less than proposed by an appropriate alternative hypothesis (see below).

We assessed the relative importance of resistance and responsiveness for short-term persistence of tree populations with the numbers of species not showing and showing the Resilient syndrome. We assumed that resistance of adult trees would be responsible for short-term persistence except with the Resilient syndrome (i.e. the population exhibited decreased adult performance and increased juvenile performance). The available data were not sufficient to build demographic models for all the dominant tree populations and we therefore used a qualitative assessment to project the likely influences of repeated moderate-intensity hurricanes on the long-term trends in these populations. We assumed that populations whose regeneration is associated with hurricanes would depend on these disturbances for long-term persistence, while others might be compromised over the long-term if tree survival were affected.

Mortality comparisons

Pre-Kate mortality was estimated as the proportion of trees found alive at the 1978 census that died prior to the 1985 census, and post-Kate mortality was estimated as the proportion of trees alive in the 1985 census (i.e. exposed to Hurricane Kate) that died before the 1992 census. Total post-Kate mortality was further subdivided into what we called direct Kate mortality and additional non-direct post-Kate mortality. Direct Kate mortality was the proportion of trees exposed to Kate that had major damage and died before the 1986 census, and non-direct post-Kate mortality was the proportion of trees exposed to Kate that did not qualify as direct mortality but died before the 1992 census. Non-direct post-Kate mortality included the delayed death of trees damaged by Kate, as well as mortality not necessarily related to the hurricane.

We tested two non-independent null hypotheses about mortality (Table 4). First, the no Kate-effect hypothesis stated that total post-Kate mortality was equal to the pre-Kate mortality. Secondly, the background-mortality hypothesis stated that non-direct post-Kate mortality was equal to pre-Kate mortality. To test these hypotheses we built single-degree-of-freedom chi-square tests (Agresti 1996) comparing the observed and expected distribution of trees in the categories pre-Kate, direct-Kate and non-direct post-Kate mortality, and surviving. Expected numbers of trees were calculated as the maximum-likelihood estimates based on the multinomial distribution (Bickel & Doksum 1977). For each of these tests, we calculated the critical value of our statistic as the corresponding percentile of its empirical distribution in 10 000 multinomial-data simulations performed under the null hypothesis. When the null hypothesis was not rejected, we calculated the power of our tests as the rejection rate in 1000 data sets simulated for alternative hypotheses that corresponded to what we subjectively considered small and large changes in mortality for each size class (see Table 4). In these simulations, total tree numbers were the same as in the corresponding original data, and the pre-Kate mortalities were set to the observed values. Simulations were generated with the SAS Language (SAS Institute 1990b) and rejection rates were computed with SAS Proc FREQ (SAS Institute 1990c).

Table 4 Hypotheses tested to identify tree-population syndromes of response to hurricane disturbance. Adult trees include overstorey individuals of canopy species and understorey trees ≥ 4 cm d.b.h. of subcanopy species. Recruitment is the graduation into the d.b.h. ≥ 2 cm size class. Juvenile trees are understorey trees ≥ 4 cm d.b.h. of canopy species and saplings (trees 2–4 cm d.b.h) of both canopy and subcanopy species

	Demographic processes	Null hypothesis	Alternative hypotheses (for power assessment)
Performance of adult trees	Mortality 1 No-Kate-effect hypothesis	Total Post-Kate = Pre-Kate	Post-Kate ≥ 2x Pre-Kate Post-Kate ≥ 4x Pre-Kate
	Mortality 2 Background-mortality hypothesis	Non-direct Post-Kate = Pre-Kate	Post-Kate ≥ 2x Pre-Kate Post-Kate ≥ 4x Pre-Kate
	Growth	Post-Kate = Pre-Kate	Post-Kate ≤ 0.5x Pre-Kate
Performance of juvenile trees	Recruitment into tree life cycle stages	Post-Kate = Pre-Kate	Post-Kate ≥ 3x Pre-Kate
	Mortality 1 No-Kate-effect hypothesis	Total Post-Kate = Pre-Kate	Post-Kate ≤ 0.5x Pre-Kate Post-Kate ≤ 0.25x Pre-Kate
	Mortality 2 (understorey trees ≥ 4 cm d.b.h. only) Background-mortality hypothesis	Non-direct Post-Kate = Pre-Kate	Post-Kate ≤ 0.5x Pre-Kate Post-Kate ≤ 0.25x Pre-Kate
	Growth	Post-Kate = Pre-Kate	Post-Kate ≥ 2x Pre-Kate

Recruitment comparisons

We tabulated the number of individuals of each species that reached 2 cm d.b.h. during, and survived to the end of, the periods 1978–84 (pre-Kate) and 1986–92 (post-Kate). Individuals reaching 2 cm d.b.h. between 1984 and 1986 were not considered because we could not unequivocally assign them to either pre- or post-hurricane recruitment. For each species, we tested for differences in expected recruit counts between periods using the Pearson chi-square statistic (Agresti 1996). When the null hypothesis of equal recruitment was not rejected, we calculated the power of our test assuming that recruit counts followed Poisson distributions and that the expected totals of pre- and post-Kate recruit counts were equal to the observed totals. The alternative hypothesis in these power calculations (Table 4) was chosen based on model results for *Fagus grandifolia* in Woodyard Hammock that suggested that 3x is the smallest increase that would significantly modify the asymptotic growth rate of this population (Batista *et al.* 1998).

Growth-rate comparisons

For each tree, we compiled the d.b.h. increments over the periods 1978–84 (pre-Kate) and/or 1986–92 (post-Kate). ANOVA models were used to compare pre- and post-Kate growth for saplings, understorey trees and overstorey trees of each species. In the models, we allowed for heteroscedasticity between pre- and post-Kate growth, as well as for non-null covariance between periods, because some of the measurements had been obtained from the same trees in both periods and thus were not independent. We used SAS Proc MIXED (SAS Institute 1996) to fit these models by restricted maximum likelihood (Wolfinger 1993). When the null hypothesis of equal mean growth between periods was not rejected, we assessed the power of our test as the rejection rate in 500 data sets simulated under an alternative hypothesis corresponding to what we subjectively considered as a large change in growth rate for each size class (Table 4). In the simulations, the number of trees measured in both periods and in either period only was the same as in the corresponding original data, pre-Kate expected growth rate was equal to the observed mean, and the errors followed a normal distribution with covariance structure equal to that estimated from the corresponding original data. These simulations were programmed and executed using SAS Proc MIXED, SAS Proc FREQ (SAS Institute 1996) and the SAS Macro Processing facility (SAS Institute 1990a).

Size frequency distributions

For each dominant species, we constructed the d.b.h. cumulative frequency distributions in 1978 and 1992. To compare these distributions, we calculated the Kolmogorov-Smirnov D statistic (Sokal & Rohlf 1995), which, in these cases, has only descriptive value because the distributions were not independent.

Results

MORTALITY OF CANOPY SPECIES

Overstorey trees

Hurricane Kate increased mortality of overstorey trees for some time after the storm crossed Woodyard Hammock. Overall mortality of overstorey trees increased from 6.8% over the pre-Kate period (1978–85) to 15.7% over the post-Kate period (1985–92). Direct Kate mortality was 6.9%, and non-direct mortality during the 7-year post-Kate period was 8.8%, a 30% increase over the pre-Kate mortality.

Patterns of overstorey-tree mortality differed among the dominant species (Table 5), with most of the increased mortality attributable to the two evergreen species, *Magnolia grandiflora* and *Pinus glabra*, which had significantly higher total post-Kate than pre-Kate mortality (Table 5). *Magnolia grandiflora* had low direct-Kate mortality, but non-direct post-Kate mortality was highly and significantly increased relative to pre-Kate mortality (Table 6). In contrast, *P. glabra* had very high direct Kate mortality, but non-direct post-Kate mortality was only moderately higher than pre-Kate mortality (Table 6). Three overstorey species, *Fagus grandifolia*, *Liquidambar styraciflua* and *Quercus nigra*, showed low direct-Kate mortality and no significant differences between pre-Kate mortality and either total or non-direct post-Kate mortality in tests whose power was sufficient to accept the hypothesis that there were no large mortality increases after Kate (Tables 5 and 6). In contrast, for the remaining overstorey species, *Nyssa sylvatica* and *Q. michauxii*, the power of the corresponding tests was not sufficient to conclude that the non-significant changes in mortality indicated that large increases did not occur (Tables 5 and 6).

Understorey trees (d.b.h. ≥ 4 cm)

Understorey trees of dominant canopy species had low direct mortality from Hurricane Kate, and their mortality over the following 7-year period was decreased with respect to pre-Kate mortality. Overall mortality decreased from 22.7% over the pre-Kate period to 15.8% (2.2% direct, and 13.6% non-direct) over the post-Kate period.

Patterns of understorey-tree mortality differed among canopy species. *Fagus grandifolia*, *Liquidambar styraciflua* and *Quercus nigra* in the understorey had low direct Kate mortality and no significant difference between pre-Kate mortality and either total or non-direct post-Kate mortality. As the power of the corresponding tests was sufficient to detect a large difference, mortality of understorey trees of these species did not appear to have had a large decrease after Kate

Table 5 Percentage mortality of trees of the 10 dominant species in Woodyard Hammock over the 7-year periods preceding and following Hurricane Kate. Post-Kate mortality includes both mortality directly caused and not directly caused by the hurricane. χ^2 statistics test the hypothesis that total mortality did not differ between periods. Each P-value was obtained from the observed null distribution of the statistic in 10 000 multinomial simulations. P_{adj} were adjusted by the Dunn-Sidak method to account for multiple testing within species. Alternative hypotheses used to assess test power are given in Table 4

	Pre-Kate 1978–85	Post-Kate 1985–92	χ^2	P	P_{adj}	Power	Power
						Small diff.	Large diff.
Canopy species							
Overstorey trees							
Magnolia grandiflora	2.3	15	23	< 0.001	**0.001**		
Fagus grandifolia	4.8	11.1	2.82	0.089	0.567	0.176	**0.867**
Liquidambar styraciflua	4.7	6.7	0.67	0.439	0.994	0.29	**0.971**
Pinus glabra	13	51.4	44.99	< 0.001	**0.001**		
Nyssa sylvatica	3.1	4.8	0.24	0.711	0.998	0.106	0.504
Quercus michauxii	4.5	4.8	0	1	1	0.077	0.328
Q. nigra	15.4	22.7	0.43	0.505	0.998	0.187	**0.889**
Understorey trees							
Magnolia grandiflora	13.3	13.2	0	0.974	1	0.061	0.263
Fagus grandifolia	6	8.5	1.48	0.226	0.9	0.318	**0.801**
Liquidambar styraciflua	30.8	26.6	1.29	0.251	0.926	**0.983**	**0.999**
Pinus glabra	56.9	36	2.78	0.098	0.513	0.426	**0.946**
Nyssa sylvatica	19.6	7.3	2.73	0.101	0.413	0.15	0.456
Quercus michauxii	25.9	11.2	18.25	< 0.001	**0.001**		
Q. nigra	26.2	29.7	0.22	0.65	1	0.296	**0.809**
Saplings							
Magnolia grandiflora	40	40	0.17	0.691	1	0.041	0.112
Fagus grandifolia	17.1	5.5	19.56	< 0.001	**0.001**		
Liquidambar styraciflua	52.6	33.3	1.89	0.162	0.797	0.091	0.313
Quercus michauxii	41.5	19.1	11.83	0.001	**0.01**		
Q. nigra	62.5	44.4	2.1	0.146	0.758	0.086	0.316
Subcanopy species							
Understorey trees							
Ilex opaca	11.5	10.7	0.11	0.743	1	**0.958**	**> 0.999**
Carpinus caroliniana	45.3	28.1	18.99	< 0.001	**0.001**		
Ostrya virginiana	23.9	14.1	8.73	0.002	**0.013**		
Saplings							
Ilex opaca	17.2	8.6	7.75	0.005	**0.048**		
Carpinus caroliniana	32.1	16.4	15.81	< 0.001	**0.001**		
Ostrya virginiana	17.5	16.6	0.94	0.32	0.901	0.291	0.738

(Tables 5 and 6). Although *Magnolia grandiflora* and *Nyssa sylvatica* showed similar responses, the power of the tests was not sufficient to reasonably reject alternative hypotheses of large mortality changes in these species (Tables 5 and 6). Only *Quercus michauxii* had low direct Kate mortality and both total and non-direct post-Kate mortality that was significantly lower than pre-Kate mortality (Tables 5 and 6). In contrast to all other canopy species, understorey *Pinus glabra* had high direct Kate mortality and, in addition, non-direct post-Kate mortality was significantly lower than pre-Kate mortality (Table 6). As a result, total post- and pre-Kate mortality was not significantly different for understorey *P. glabra*, and the power of our test allowed us to conclude that there was no large mortality reduction (Table 5).

Saplings (trees 2–4 cm d.b.h.)

Direct Kate mortality of saplings of canopy tree species was extremely low (1.1%). Overall sapling mortality decreased from 30.7% over the pre-Kate period to 14.4% over the post-Kate period. While observed mortality of saplings was lower over the post-Kate than over the pre-Kate period for all species, these differences were significant only for the moderate responses of *Fagus grandifolia* and *Quercus michauxii* (Table 5). The remaining species either were absent from the sapling component at least in the pre-Kate period or had no significant change in sapling mortality. In the latter case, the power of the tests was not sufficient to reject possible large differences (Table 5).

MORTALITY OF SUBCANOPY SPECIES

Understorey trees (d.b.h. ≥ 4 cm)

Trees (i.e. adult individuals) of subcanopy species had decreased mortality after Hurricane Kate. Overall mortality decreased from 27.9% over the pre-Kate

Table 6 Percentage mortality of trees of the 10 dominant species in Woodyard Hammock in the pre- and post-Kate 7-year periods. χ^2 statistics test the hypothesis that post-Kate mortality not directly caused by the hurricane was equal to pre-Kate mortality. Each *P*-value was obtained from the observed null distribution of the statistic in 10 000 multinomial simulations. Alternative hypotheses are given in Table 4

	Pre-Kate 1978–85	Post-Kate 1985–92		Statistical comparison *a* vs. *c*				
							Power	
	Total *a*	Kate Direct *b*	Non-direct *c*	χ^2	*P*	P_{adj}	Small diff.	Large diff.
Canopy species								
Overstorey trees								
Magnolia grandiflora	2.3	2.8	12.2	16.99	< 0.001	**0.001**		
Fagus grandifolia	4.8	4	7.1	0.58	0.46	0.996	0.165	**0.831**
Liquidambar styraciflua	4.7	1.8	4.9	0.02	0.885	1	0.233	**0.965**
Pinus glabra	13	33.6	17.8	5.92	0.015	**0.103**		
Nyssa sylvatica	3.1	0	4.8					
Quercus michauxii	4.5	0	4.8					
Q. nigra	15.4	4.5	18.2	0.11	0.803	1	0.204	**0.903**
Understorey trees								
Magnolia grandiflora	13.3	3.8	9.4	0.33	0.572	1	0.087	0.269
Fagus grandifolia	6	0.9	7.6	0.69	0.425	0.993	0.32	**0.798**
Liquidambar styraciflua	30.8	2.7	23.9	2.83	0.092	0.581	**0.98**	**0.999**
Pinus glabra	56.9	24	12	8.32	0.004	**0.024**		
Nyssa sylvatica	19.6	0	7.3					
Quercus michauxii	25.9	0.8	10.4	20.21	< 0.001	**0.001**		
Q. nigra	26.2	3.1	26.6	0.03	0.885	1	0.288	**0.8**
Subcanopy species								
Understorey trees								
Ilex opaca	11.5	0.6	10.2	0.3	0.584	1	**0.971**	**> 0.999**
Carpinus caroliniana	45.3	7.3	20.8	31.96	< 0.001	**0.001**		
Ostrya virginiana	23.9	2.3	11.8	12.84	< 0.001	**0.002**		

period to 16.9% (3.1% direct and 13.8% non-direct) over the post-Kate period.

For *Carpinus caroliniana* and *Ostrya virginiana*, both non-direct post-Kate and total post-Kate mortality were significantly lower than pre-Kate mortality (Tables 5 and 6). Direct Kate mortality was moderate for *C. caroliniana*, and low for *O. virginiana* (Table 6). For *Ilex opaca*, direct Kate mortality was low and pre-Kate mortality was not significantly different from either total post-Kate or non-direct post-Kate mortality. The power of the corresponding tests was sufficient to conclude that large mortality increases did not occur (Tables 5 and 6). In addition, because we actually observed a small decrease in the mortality of *I. opaca*, we also assessed the power of the tests under the alternative hypotheses of 0.25x changes in mortality. Again, the power was sufficient to conclude that such large change did not occur (0.986 for the test of the no-Kate effect hypothesis, and 0.991 for the test of the background mortality hypothesis).

Saplings (trees 2–4 cm d.b.h.)

Direct Kate mortality of saplings of subcanopy species was low (0.8%), and overall mortality of these saplings decreased from 24.4% over the pre-Kate period to 14.0% over the post-Kate period. Sapling mortality decreases were moderate and significant for *Ilex opaca* and *Carpinus caroliniana* (Table 5). For *Ostrya virginiana*, the difference in sapling mortality between periods was not significant, and the power of the test was not sufficient to reject possible large differences (Table 5).

RECRUITMENT

Overall recruitment increased from 12.4 to 75.4 recruits ha^{-1} year^{-1} from the pre-Kate to the post-Kate period. Patterns of recruitment differed among tree populations (Table 7). Among the canopy species, *Pinus glabra* and *Liquidambar styraciflua* had very low or null recruitment before, and substantial recruitment after, Hurricane Kate (Table 7). At the time of the hurricane, *P. glabra* recruits were already present in small gaps as suppressed individuals 0.5–1 m tall (advance recruits); a large fraction of *L. styraciflua* recruits, which were present as advance recruits at the time of the hurricane, originated from root sprouts (W. J. Platt, personal observation). *Quercus michauxii* and *Q. nigra* had very low recruitment before, and slightly increased recruitment after, Hurricane Kate (Table 7), mostly due to growth of advance recruits (W.J. Platt, personal observation). *Fagus grandifolia* had substantial recruitment both before and after Kate, and the power of the chi-square test was sufficient to conclude that recruitment rate did not show a large increase (Table 7). In contrast,

Table 7 Numbers of recruits in the Woodyard Hammock plot before (1978–84) and after (1986–92) Hurricane Kate. χ^2 statistics test the hypotheses that expected recruitment was equal between periods. Recruits were trees that reached 2 cm d.b.h. within, and were alive at the end of, the corresponding period. Alternative hypothesis for power calculations is given in Table 4

	Pre-Kate 1978–84	Post-Kate 1986–92	χ^2	P	P_{adj}	Power
Dominant species						
Canopy						
Magnolia grandiflora	5	10	1.66	0.197	0.861	0.052
Fagus grandifolia	25	25	0	1	1	**0.895**
Liquidambar styraciflua	6	71	54.86	< 0.001	**< 0.001**	
Pinus glabra	0	416	415.98	< 0.001	**< 0.001**	
Nyssa sylvatica	0	1	0.98	0.322	0.857	< 0.001
Quercus michauxii	4	16	7.19	0.007	**0.057**	
Quercus nigra	5	31	18.77	< 0.001	**< 0.001**	
Subcanopy						
Ilex opaca	35	31	0.24	0.623	1	**0.965**
Carpinus caroliniana	42	223	123.62	< 0.001	**< 0.001**	
Ostrya virginiana	65	899	721.52	< 0.001	**< 0.001**	
Non-dominant species (25)	148	316				
Total	335	2039				

Nyssa sylvatica and *Magnolia grandiflora* had low recruitment throughout the pre- and post-Kate periods, but the power of the corresponding tests was not sufficient to reject possible large increases in recruitment (Table 7).

Among the subcanopy species, *Carpinus caroliniana* and *Ostrya virginiana* had substantial recruitment before, but large and significantly increased recruitment after Hurricane Kate (Table 7), associated with canopy gaps in both periods (W. J. Platt, personal observation). In contrast, recruitment of *Ilex opaca* was substantial both before and after Kate but did not differ significantly between periods. The power of the chi-square test was sufficient to accept that recruitment rate of *I. opaca* did not have a large increase (Table 7). Among 25 non-dominant species, six had significant recruitment increases after Kate (data not shown), although the moderate responses mean that none of them is likely to become dominant in the forest.

TREE GROWTH OF CANOPY SPECIES

Overstorey trees

Hurricane Kate apparently damaged overstorey trees that survived the hurricane. Mean d.b.h. growth of overstorey trees of the dominant canopy species was lower in the post- than in the pre-Kate period, significantly so for the five species with largest basal area (Table 8). Reductions in growth were substantial for the two evergreen species, *Magnolia grandiflora* and *Pinus glabra*, but were small for the deciduous *Fagus grandifolia*, *Liquidambar styraciflua* and *Nyssa sylvatica* (Table 8). In contrast, growth rates of *Quercus michauxii* and *Q. nigra* did not change significantly after Kate and we could accept that a large decrease in mean growth did not occur in overstorey individuals of these two species.

Understorey trees (d.b.h. ≥ 4 cm)

Mean growth rate of understorey individuals increased for most of the dominant canopy species after Hurricane Kate. This increase was significant for *Liquidambar styraciflua* and *Quercus michauxii*, whose mean growth rate more than doubled, and for *Fagus grandifolia* and *Q. nigra*, which had smaller increases (Table 8). Mean d.b.h. growth of understorey trees decreased significantly for *Nyssa sylvatica* and did not change significantly for *Magnolia grandiflora* and *Pinus glabra* (Table 8). For *M. grandiflora*, but not for *P. glabra*, the power of our tests was sufficient to accept that the growth rate of understorey trees did not double after Kate (Table 8).

Saplings (trees 2–4 cm d.b.h.)

Mean d.b.h. growth of saplings of canopy species was higher in the post- than in the pre-Kate period, significantly so for *Fagus grandifolia* and *Quercus michauxii* (Table 8). *Pinus glabra* saplings recruited after the hurricane also had high growth rates. Differences between pre- and post-Kate mean growth of *Magnolia grandiflora*, *Liquidambar styraciflua* and *Q. nigra* saplings were not significant, but we could not conclude that substantial differences did not occur (Table 8).

TREE GROWTH OF SUBCANOPY SPECIES

Understorey trees (d.b.h. ≥ 4 cm)

Mean growth increased for the three dominant subcanopy species. This increase was significant for *Carpinus caroliniana*, whose mean growth rate more than doubled, and for *Ostrya virginiana*, which had a smaller increase (Table 8). Mean growth rate of *Ilex opaca* did not change significantly, and the power of the test was

Table 8 Mean d.b.h. growth (mm year^{-1}) of trees of the 10 dominant species in the Woodyard Hammock plot before and after Hurricane Kate. Statistical comparisons test the hypothesis that mean growth was equal between periods. Alternative hypotheses used for power calculations are given in Table 4

	Pre-Kate 1978–84	Post-Kate 1986–92	d.f.	*F*	*P*	P_{adj}	Power
Canopy species							
Overstorey trees							
Magnolia grandiflora	2.34	0.5	214	235.76	< 0.001	**0.001**	
Fagus grandifolia	3.65	3.11	98	7.09	0.009	**0.079**	
Liquidambar styraciflua	3.55	2.77	164	25.15	< 0.001	**0.001**	
Pinus glabra	6.06	3.29	107	72.21	< 0.001	**0.001**	
Nyssa sylvatica	2.57	2.01	62	7.35	0.009	**0.043**	
Quercus michauxii	4.75	4.15	20	0.67	0.422	0.987	**0.758**
Q. nigra	6.84	5.68	21	2.2	0.153	0.775	**0.96**
Understorey trees							
Magnolia grandiflora	0.68	0.87	25	0.95	0.34	0.976	**0.848**
Fagus grandifolia	1.23	2.05	344	84.37	< 0.001	**0.001**	
Liquidambar styraciflua	0.75	1.55	277	31.02	< 0.001	**0.001**	
Pinus glabra	1.66	2.45	23	1.84	0.188	0.767	0.688
Nyssa sylvatica	0.51	0.17	36	6.85	0.013	**0.063**	
Quercus michauxii	1.07	2.18	258	61.68	< 0.001	**0.001**	
Q. nigra	1.88	2.6	67	7.69	0.007	**0.063**	
Saplings							
Magnolia grandiflora	0.98	1	11	0	0.975	1	0.098
Fagus grandifolia	0.82	1.36	162	43.14	< 0.001	**0.001**	
Liquidambar styraciflua	0.55	2.87	22	4.14	0.054	0.393	0.016
Pinus glabra		2.84					
Quercus michauxii	0.39	0.8	55	5.82	0.019	**0.144**	
Q. nigra	0.67	2.12	16	4.49	0.05	0.37	0.024
Subcanopy species							
Understorey trees							
Ilex opaca	0.43	0.47	376	0.78	0.377	0.942	**0.972**
Carpinus caroliniana	0.55	1.42	292	92.66	< 0.001	**< 0.001**	
Ostrya virginiana	0.51	0.88	290	20.63	< 0.001	**< 0.001**	
Saplings							
Ilex opaca	0.54	0.86	140	21.23	< 0.001	**0.001**	
Carpinus caroliniana	0.6	1.48	191	66.71	< 0.001	**0.001**	
Ostrya virginiana	1.04	2.34	226	87.13	< 0.001	**0.001**	

sufficient to accept that a large decrease had not occurred (Table 8). Because the observed change was an increase, we also assessed the power of the test under the alternative hypothesis of a 2x increase in growth. Again, the power was sufficient to conclude that such large change did not occur (0.856).

Saplings (trees 2–4 cm d.b.h.)

Mean d.b.h. growth of saplings of the dominant subcanopy species was higher in the post- than in the pre-Kate period. This difference was significant for all three species (Table 8).

CHANGES IN POPULATION STRUCTURE

Patterns of change in size frequency distributions between 1978 and 1992 differed among the 10 dominant species. For the canopy species *Magnolia grandiflora*, *Fagus grandifolia* and *Nyssa sylvatica*, as well as the subcanopy *Ilex opaca*, differences between the 1978 and the 1992 d.b.h.-frequency distributions were small (Fig. 2), as measured by the Kolmogorov-Smirnov statistic ($D < 0.15$). The populations of *Liquidambar styraciflua*, *Quercus nigra* and *Quercus michauxii* and *Carpinus caroliniana* had moderate differences between the 1978 and the 1992 d.b.h.-frequency distributions ($0.15 \le D < 0.3$, Fig. 2). The proportions of smaller individuals increased for *L. styraciflua* and *Q. nigra*, but decreased for *Q. michauxii* (Fig. 2). Large changes occurred in the d.b.h.-frequency distributions of *Pinus glabra* and *Ostrya virginiana* between 1978 and 1992 ($0.3 \le D$, Fig. 2), as a result of large increases in the proportion of smaller individuals.

Discussion

INDIVIDUAL SPECIES SYNDROMES OF RESPONSE

Hurricane Kate differentially influenced the demography of populations of the 10 dominant tree species at Woodyard Hammock. The large majority (eight) showed resistance, as expected, but six populations also showed

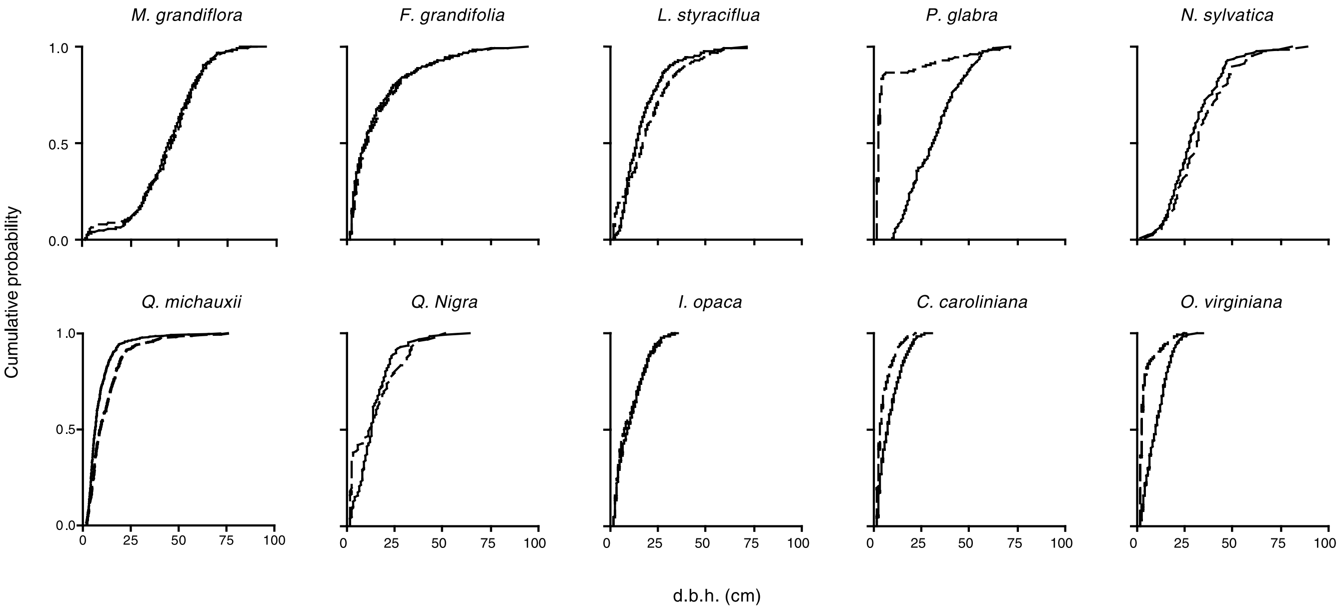

Fig. 2 Cumulative size-frequency distributions of the 10 dominant tree species in Woodyard Hammock in 1978 (full line) and 1992 (dashed line).

responsiveness following this moderate-intensity hurricane. In addition, all four combinations of low and high resistance and responsiveness to disturbance proposed in Fig. 1 were identified as occurring among the dominant tree populations (cf. Boucher *et al.* 1994; Bellingham *et al.* 1995).

One population, *Pinus glabra*, exhibited the Resilient syndrome. Overstorey and subcanopy trees of this species sustained more than a fourfold increase in mortality, but there was a large pulse of recruitment after the hurricane (Table 9). Recruitment of saplings, which was null in the pre-Kate period, was very abundant in the post-Kate period due to the release of numerous advance recruits present in small gaps (Platt & Hermann 1986; Platt & Schwartz 1990; Peters & Platt 1996). High mortality of overstorey trees and abundant recruitment essentially amounted to the replacement of one cohort by another and produced a large shift in the size frequency distribution (Table 9). Apparently, cohort replacement after hurricanes has been characteristic of this *P. glabra* population. Data from tree cores obtained by Hirsh & Platt (1981) indicated that most of the pre-Kate population consisted of trees recruited after the 1941 hurricane. Thus, the life history of *P. glabra* in Woodyard Hammock, and perhaps in other Southern mixed-hardwood forests, appears linked

Table 9 Summary of demographic changes of the dominant tree species in Woodyard Hammock after Hurricane Kate in 1985. Entries in the table are coded as: L, large; M, medium; S, small; NL, not large; NM, not medium. For recruitment, growth and mortality changes, L, M and S refer to the size of a significant difference between the pre- and the post-Kate periods, and NL and NM to the size of the smallest difference that could be ruled out based on the power of the corresponding test (see Table 4). For changes in the size frequency distribution (s.f.d.), L, M and S refer to the maximum vertical distance between the 1978 and the 1992 cumulative distributions (the Kolmogorov-Smirnov D statistic): L is 0.3 ≤ D; M, 0.15 ≤ D < 0.3; and S, D < 0.15. A syndrome is attributed to each species on the basis of the observed demographic patterns. Blank cells indicate that tests were not done due to lack of data and ? indicates that tests were not conclusive due to lack of power

	Saplings			Understorey trees			Overstorey trees		
	Recruitment increase	Growth increase	Mortality decrease	Growth increase	Mortality decrease	Growth decrease	Mortality increase	s.f.d. change	Syndrome
Pinus glabra	L			?	NL	S	L	L	Resilient
Ostrya virginiana	L	L	?	S	S			L	Usurper
Carpinus caroliniana	L	L	S	L	S			M	Usurper
Liquidambar styraciflua	L	?	?	L	NM	S	NL	M	Usurper
Quercus nigra	L	?	?	S	NL	NL	NL	M	Usurper
Q. michauxii	L	L	M	L	M	NL	?	M	Usurper
A. Fagus grandifolia	NL	S	M	S	NL	S	NL	S	Resistant
Ilex opaca	NL	S	M	NL	NL			S	Resistant
Nyssa sylvatica	?			S	?	S	?	S	Resistant
Magnolia grandiflora	?	?	?	NL	?	L	L	S	Susceptible

to successive hurricanes that remove many overstorey trees and initiate new cohorts. As survival of adult trees is likely to be related to hurricane intensity, differences in the intensity of successive hurricanes could increase or decrease the distinctiveness of these cohorts. In addition, because *P. glabra* trees are relatively short lived (Burns *et al.* 1990), and their regeneration is likely to depend on the presence of advance recruits in small gaps followed by large-scale canopy disruption before these gaps close (W. J. Platt, personal observation), long intervals between hurricanes could compromise the persistence of *P. glabra* in this forest.

Two subcanopy and three canopy species exhibited the Usurper syndrome. The subcanopy species *Carpinus caroliniana* and *Ostrya virginiana* exhibited little hurricane damage and substantial responsiveness to canopy disruption. These populations had low direct Kate mortality, most likely because individuals were sheltered from wind stress by canopy trees (cf. Battaglia *et al.* 1999; Fulton 1999). In the pre-Kate period, these populations had substantial recruitment associated with small canopy gaps, but high mortality resulted in declines in density, although these species are considered as shade-tolerant (cf. Burns & Honkala 1990; Platt & Schwartz 1990; Jones *et al.* 1994). After the hurricane, growth and survival of adults of these two species were increased, and massive recruitment and growth of saplings occurred in expanded gaps. As a result, these populations showed increased density as well as large changes in size frequency distributions (Table 9). These patterns suggest that periodic large-scale wind disturbance may enhance, or even be necessary for, long-term persistence of *C. caroliniana* and *O. virginiana* in this forest. Variation in the intensity of hurricanes, however, appears unlikely to compromise these populations in Woodyard Hammock, although it might influence their density as a result of differences in the amount and distribution of open space.

The canopy species *Liquidambar styraciflua*, *Quercus michauxii* and *Q. nigra* also sustained little hurricane damage and exhibited substantial response to canopy disruption. Overstorey *L. styraciflua* trees, which are very resistant to wind damage (Everham & Brokaw 1996), had low direct Kate mortality and no large reductions in growth or survival after the hurricane (Table 9). As wood of these trees is not very dense, elastic or resistant to breaking (Niklas 1992), wind-firmness is likely to result from underground connections, short and stout branches, and leaves with slender long petioles that readily detach from branches in wind (W. J. Platt, personal observations). *L. styraciflua* is shade-intolerant (Burns & Honkala 1990) and a decline in the population was reversed when the hurricane disrupted the canopy, resulting in large increases in recruitment and growth of understorey individuals (Table 9). Similar patterns were reported for *L. styraciflua* in a forest in South Carolina affected by Hurricane Hugo (Battaglia *et al.* 1999). According to tree-core data obtained before Hurricane Kate in Woodyard Hammock, the age distribution of *L. styraciflua* was discontinuous, with the oldest canopy trees over 200 years old, and the youngest recruited shortly after the 1941 hurricane (Platt 1984). *Quercus michauxii* and *Q. nigra* also had little direct Kate mortality and no large reduction in the growth of overstorey trees (Table 9). These species are also shade intolerant (Burns & Honkala 1990), and their density in the understorey was declining before hurricane Kate. After Kate, recruitment of these species increased, but was still sparse; *Q. michauxii* had largely increased growth and moderately increased survival of saplings and understorey trees, and *Q. nigra* only had small increases in growth of understorey trees (Table 9). Although long-term persistence of these three populations appears ultimately to depend on large-scale canopy disruption for successful regeneration, they are unlikely to be very sensitive to variations in hurricane frequency because of their longevity and the wind-firmness of their overstorey trees.

Three populations (one subcanopy species, *Ilex opaca*, and two canopy species, *Fagus grandifolia* and *Nyssa sylvatica*) sustained little hurricane damage and showed little responsiveness to canopy disruption and thus exhibited the Resistant syndrome. Wind resistance of individual trees is reportedly intermediate for *I. opaca*, and high for *F. grandifolia* and *N. sylvatica* (Everham & Brokaw 1996), and, in Woodyard Hammock, these species had low direct Kate mortality. In addition, adult *I. opaca* (understorey trees) and overstorey *F. grandifolia* had no large changes in growth and survival, and overstorey *N. sylvatica* had only small changes in growth (Table 9). Canopy disruption prompted no recruitment pulse and very limited release of understorey individuals (Table 9). Throughout the pre- and post-Kate periods, *Nyssa sylvatica*, a relatively shade-intolerant species (Burns & Honkala 1990), had low density of understorey trees and essentially null recruitment, whereas *I. opaca* and *F. grandifolia*, two species very tolerant to shading, maintained substantial recruitment and relatively high survival of saplings and understorey trees (Harcombe & Marks 1983; Platt & Hermann 1986; Burns & Honkala 1990). The density and size frequency distributions of these populations showed only minor changes throughout the pre- and post-Kate periods (Table 9). A demographic model of *F. grandifolia* showed that persistence of this species in Woodyard Hammock would not be affected by hurricane disturbance as damage and mortality would not be severe enough to move the population away from equilibrium (Batista *et al.* 1998). According to this model, increases in sapling growth and survival had little effect on the long-term population trend, and population persistence depended mainly on survival of medium-sized trees, a vital rate largely unaffected by Hurricane Kate (Batista *et al.* 1998). Although patterns of recruitment, growth and survival differed among *F. grandifolia*, *N. sylvatica* and *I. opaca*, all three populations were essentially unaffected by Hurricane

Kate. Persistence of these populations might be largely independent of hurricane frequency, and possibly over substantial variation in intensity.

The main canopy dominant, *Magnolia grandiflora*, exhibited the Susceptible syndrome. Increased mortality, coupled with decreased growth of overstorey trees damaged in the hurricane, produced 15% declines in density and basal area of this population. Our evidence about responsiveness of smaller *M. grandiflora* was mostly inconclusive because few individuals were recruited or present in the understorey (Table 9). Recruitment was infrequent, saplings were scarce and had low survival, and understorey trees had slow growth and high survival both before and after Kate. Although juvenile *M. grandiflora* are reportedly shade tolerant, they have been noted as abundant under deciduous overstorey trees but only rarely present where the overstorey is dominated by evergreen *M. grandiflora* (Kurz 1944; Blaisdell *et al*. 1974; Harcombe & Marks 1983; Glitzenstein *et al*. 1986). Moreover, in the early 1970s, few *M. grandiflora* in Woodyard Hammock were less than 65 years old and the oldest individuals were over 200 years old (Blaisdell *et al*. 1974; Peters & Platt 1996). Although recent hurricanes have not produced pulses of successful recruitment, and appear to have inflicted substantial damage of overstorey trees, they have not compromised short-term persistence or even the dominance of *M. grandiflora* in Woodyard Hammock. Persistence of this population should ultimately depend on regeneration, which might require release from intraspecific competition. This release could result from an extraordinarily intense storm felling many overstorey trees. Alternatively, slow thinning of overstorey *M. grandiflora* throughout the forest, as well as successive damage by moderate-intensity disturbances like Hurricane Kate, could result in slow shifts towards dominance by deciduous species, and eventually result in conditions suitable for recruitment of *M. grandiflora.*

HURRICANE DISTURBANCE: POPULATION RISK AND DEPENDENCE

Hurricane Kate did not directly compromise the short-term persistence of any of the 10 dominant tree populations in Woodyard Hammock. While persistence of *Pinus glabra* as a dominant species appeared to depend on replacement of trees killed by the storm, short-term persistence of all other dominant populations resulted primarily from resistance of the larger trees to wind damage (also see Boucher *et al*. 1994; Bond & Midgley 2001). Even the population of *Magnolia grandiflora*, though reduced, persisted and retained dominance in the forest because a substantial proportion of the trees survived. The prevalence of resistance to wind, which has emerged from most studies of hurricane damage (e.g. Boucher *et al*. 1990; Gresham *et al*. 1991; Foster & Boose 1992; Zimmerman *et al*. 1994; Armentano *et al*. 1995; Bellingham *et al*. 1995; Slater *et al*. 1995; Everham & Brokaw 1996) has given rise to the concept of 'direct regeneration' (Yih *et al*. 1991). In addition, the prevalence of resistance is consistent with evidence that short-term survival of individuals of high reproductive value, not short-term reproduction, is often the most critical vital rate for populations of trees (Silvertown *et al*. 1993; Batista *et al*. 1998; Lusk & Smith 1998; Bellingham & Sparrow 2000; Bond & Midgley 2001; Crone 2001). Nonetheless six of the 10 dominant tree populations showed responsiveness, indicating that advance recruits, present in most populations (Platt & Hermann 1986; Platt & Schwartz 1990), might contribute to regeneration of some forests after hurricanes.

We project that long-term population trends of the dominant species in Woodyard Hammock will be differentially affected by recurrent hurricane disturbance. Based on the observed effects of Hurricane Kate, dynamics of the populations with the Resistant syndrome appeared to be essentially independent of moderate intensity hurricanes; survival, growth and regeneration were not substantially affected. Nonetheless, the demography over the 14-year period studied suggests differences in long-term trends of these populations. The shade-tolerant *Fagus grandifolia* and *Ilex opaca* would likely remain close to equilibrium, as they had low mortality, continuous recruitment and slow but continual growth of trees (cf. Batista *et al*. 1998). In contrast, the shade-intolerant *Nyssa sylvatica* would likely decline at least for as long as it fails to regenerate in Woodyard Hammock.

We project that long-term persistence of populations that exhibited the Resilient and Usurper syndromes will depend on periodic large-scale canopy disturbance (i.e. release from shading). Regeneration in these populations was associated with the post-Kate environment. Time-scale of dependence from disturbance would vary among species. The longer-lived, canopy-tree populations, *Liquidambar styraciflua*, *Quercus michauxii* and *Q. nigra*, would be largely independent from regeneration after any single hurricane, whereas the shorter-lived, canopy and subcanopy populations, *Pinus glabra*, *Ostrya virginiana* and *Carpinus caroliniana*, are projected to depend on frequent large-scale canopy disruption. As the geographical distributions of some of these species extend outside the hurricane-frequented south-eastern USA (Burns & Honkala 1990), the dependence on periodic large-scale canopy disruption suggested by our data applies to the particular populations we studied in Woodyard Hammock, and probably to those in other hurricane-frequented forests (e.g. Gresham *et al*. 1991; Battaglia *et al*. 1999), but not necessarily to populations of these species elsewhere (cf. Veblen 1989).

Magnolia grandiflora, the population that exhibited the Susceptible syndrome, was the only one whose risk of local extinction in the long term might be increased by recurrent hurricanes like Kate. This population would decline unless substantial regeneration occurred, possibly after the density of adults decreased to some point. In such a case the syndrome of response of *M. grandiflora* might change from Susceptible to Resilient.

Based on tree-population responses to Hurricane Kate, Woodyard Hammock might appear as a paradox: a hurricane-frequented forest dominated by a Susceptible tree population and not by Usurpers, the tree populations that would appear most likely to be favoured by hurricanes. Clearly, syndromes of response to a single hurricane do not necessarily account for the relative success of the populations. First, the syndromes might vary with hurricane intensity. As intensity increases, the Susceptible or Resilient syndromes should become more common, although resistance has been shown to characterize many tree populations exposed to high-intensity hurricanes (e.g. Tanner *et al.* 1991; Yih *et al.* 1991; Basnet 1993; Boucher *et al.* 1994; Slater *et al.* 1995). Secondly, syndromes of response might vary with the structure of the population at the time of the hurricane (cf. Harcombe *et al.* 2002). In Woodyard Hammock, for example, the two dominant evergreen species, *Pinus glabra* and *Magnolia grandiflora*, sustained large damage of overstorey trees by Hurricane Kate. However, only *P. glabra*, which had abundant advance recruits (Platt & Hermann 1986), exhibited the Resilient syndrome. Thirdly, effects of hurricanes on tree-population dynamics are likely to interact with other disturbances that could affect the forest (e.g. Platt *et al.* 2002), as well as with ecological interactions that occur during disturbance-free periods (Sousa 1984). For example, if a ground fire had killed advance recruits shortly before Hurricane Kate, *Pinus glabra* might have exhibited the Susceptible instead of the Resilient syndrome. In addition, high mortality during the closed canopy periods, most likely as a result of shading, might be the actual limiting vital rate for populations of shade-intolerant species.

Assigning syndromes of response provides a useful conceptual framework to assess the role of hurricanes in driving the dynamics of forest-tree populations (Bellingham *et al.* 1995). Our study demonstrated that all four combinations of high and low resistance and responsiveness may occur in a hurricane-frequented forest. Short-term persistence after a hurricane was mainly a result of tree resistance to wind damage. Responsiveness of a number of species resulted from release of suppressed small individuals present at the time of the hurricane. Effects of successive hurricanes on long-term population trends vary among dominant tree species; populations likely to depend on hurricanes for long-term persistence coexist with others that are unaffected or might even become compromised by hurricanes. In Woodyard Hammock, hurricane disturbance acts as a major, but not the sole, driver of tree population dynamics.

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