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Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality, and coarse woody detritus

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Abstract Patch dynamics, tree injury and mortality, and coarse woody detritus were quantified to examine the ecological impacts of Hurricane Fran on an oak-hickory-pine forest near Chapel Hill, NC. Data from long-term vegetation plots (1990–1997) and aerial photographs (1998) indicated that this 1996 storm caused patchy disturbance of intermediate severity (10–50% tree mortality; Woods, J Ecol 92:464–476, 2004). The area in large disturbance patches (>0.1 ha) increased from <1% to approximately 4% of the forested landscape. Of the forty-two 0.1-ha plots that were studied, 23 were damaged by the storm and lost 1–66% of their original live basal area. Although the remaining 19 plots gained basal area (1–15% increase), across all 42 stands basal area decreased by 17% because of storm impacts. Overall mortality of trees >10 cm dbh was 18%. The basal area of standing dead trees after the storm was 0.9 m^2/ha, which was not substantially different from the original value of 0.7 m^2/ha. In contrast, the volume and mass of fallen dead trees after the storm (129 m^3/ha; 55 Mg/ha) were 6.1 and 7.9 times greater than the original levels (21 m^3/ha; 7 Mg/ha), respectively. Uprooting was the most frequent type of damage, and it increased with tree size. However, two other forms of injury, severe canopy breakage and toppling by other trees, decreased with increasing tree size. Two dominant oak species of intermediate shade-tolerance suffered the largest losses in basal area (30–41% lost). Before the storm they comprised almost half of the total basal area in a forest of 13% shade-tolerant, 69% intermediate, and 18% shade-intolerant trees. Recovery is expected to differ with respect to vegetation (e.g., species composition and diversity) and ecosystem properties (e.g., biomass, detritus mass, and carbon balance). Vegetation may not revert to its former composition; however, reversion of biomass, detritus mass, and carbon balance to pre-storm conditions is projected to occur within a few decades. For example, the net change in ecosystem carbon balance may initially be negative from losses to decomposition, but it is expected to be positive within a decade after the storm. Repeated intermediate-disturbance events of this nature would likely have cumulative effects, particularly on vegetation properties.

Keywords Canopy gap dynamics · Coarse woody debris · Forest ecosystem · Intermediate disturbance · Net ecosystem carbon balance · North Carolina Piedmont · Snag dynamics · Wind disturbance

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Introduction

Wind is a leading agent of disturbance in the temperate deciduous forests of eastern North America (White 1979; Lorimer 1980; Runkle 1985). Within the eastern deciduous forest (sensu Barbour et al. 1980) small patches (or canopy gaps) created by the death of one or a few trees are the most frequent form of disturbance (Runkle 1982, 1985; Lorimer 1989). Yet, hurricanes and other violent windstorms can create larger patch disturbances having strong ecological impacts that differ quantitatively and qualitatively from those of small-patch disturbances (Dunn et al. 1983; Canham and Loucks 1984; Foster 1988; Peart et al. 1992; Boose et al. 1994; Peterson and Pickett 1995; Greenberg and McNab 1997; Frelich 2002; Woods 2004). Hurricane disturbance in the eastern deciduous forest is not fully characterized with respect to immediate impacts and long-term impacts on vegetation and ecosystems. What types of forest damage occur over the landscape and within stands, and the implications for dynamics of vegetation and ecosystems require attention. Consideration of vegetation and ecosystem recovery processes and rates following hurricane disturbance contributes toward understanding of long-term dynamics of these forests.

In this article, we examine the impacts of Hurricane Fran, which passed through the North Carolina Piedmont in September 1996, on community and ecosystem attributes of an eastern deciduous forest. Windstorm impact is usually assessed through basal area loss, but one can include other measures such as estimates of the size, abundance and dynamics of disturbance patches (e.g., Platt et al. 2000) as well as the changes in canopy cover (e.g., Peart et al. 1992), coarse woody detritus (CWD) (e.g., Whigham et al. 1991), and ecosystem carbon dynamics to better quantify disturbance severity and impacts on the forest community and ecosystem (Everham and Brokaw 1996).

Relying primarily on a set of permanent vegetation plots established prior to Hurricane Fran in oak-hickory-pine forest, we consider changes in forest structure, composition, and ecosystem properties following the storm. Our general hypothesis is that the hurricane disturbance differs from small-gap disturbances in its impacts on vegetation and ecosystems. We ask the following questions: (1) How different is the size of disturbance patches created by the storm compared to other disturbances in this system? (2) Do the type and degree of damage differ by tree size, by tree species, and by ecological guild (e.g., shade-tolerance class)? (3) How are the forest composition and succession affected? (4) To what degree are detritus levels and forest ecosystem processes related to carbon dynamics altered? In addressing these objectives and questions, we assess both live and dead trees, allowing evaluation of vegetation and ecosystem impacts. Long-term impacts and the role of cumulative disturbance effects due to successive hurricanes are projected and discussed.

Study area

The North Carolina Botanical Garden is a 242-ha tract of oak-hickory-pine forest (Braun 1950; Greller 1988) in Chapel Hill, North Carolina (35°53′ N, 79°2′ W). The development, dynamics, and environment of the Piedmont hardwood forest of North Carolina are well studied (Oosting 1942; Peet and Christensen 1980). It is an area defined by undulating topography, soils of poor to good quality, and a temperate climate. Soils of the study area include Wedowee sandy loam and Goldston slaty silt loam (Dunn 1977). The climatic regime of the area fits Thornthwaite's (1948) humid mesothermal class, with a mean annual temperature of 16°C and a mean annual precipitation of 116 cm (NOAA 1974).

Human history of the study area is incompletely known. Some productive sites (e.g., floodplains and lower slopes) of the study area were farmed starting from the mid- to late 1700s and ending between the late 1800s and 1920. It is likely that some of the upland forests studied here survived as woodlots in the farm landscape, with occasional cutting of trees for firewood or lumber and with understory grazing; oaks were considered a valuable source of forage for livestock. Fire was used by Native Americans prior to 1700 and by farmers thereafter. Some lower slope forest patches are about 80 years old, whereas most forests are probably 120 years old, and the older woodlots have been continuously in the forest for hundreds of years and support occasional trees that are 200–250 years old.

Hurricane Fran, a category three storm, passed through the region on the morning of 6 September 1996. The eye passed about 7 km east of the study area. Wind data from the closest meteorological station at Raleigh-Durham International Airport

40 km east of Chapel Hill indicated sustained winds of 72 km/h and gusts of up to 128 km/h during the storm (NOAA, unpublished data).

Methods

Sampling prior to the hurricane

Forty two 0.1-ha (20 × 50 m) plots were established in upland forests of the North Carolina Botanical Garden from March 1990 to May 1991. A 100 × 100 m grid was surveyed across garden lands prior to the establishment of the plots. The grid of 1-ha cells covered a landscape ca. 50 ha in area. Plots were dispersed so that no more than one plot occurred in each 1-ha grid cell. Design of the permanently marked plots followed that of the North Carolina Vegetation Survey (Peet et al. 1998), featuring nested subplots for multiscale sampling of composition, structure, and diversity.

During the initial sampling, we laid out each 0.1-ha plot with ten contiguous10 × 10 m subplots. Within each subplot, all trees larger than 1 cm dbh (diameter at breast height) were identified according to species and measured for diameter. In addition, all live and dead trees over 10 cm dbh were mapped to allow subsequent data collectors to track individual stems. Each fallen dead stem of this size was mapped and assigned to a 10-cm diameter class. Vegetation type (pine, mixed, or hardwood), canopy height, elevation, aspect, slope, and soil characteristics such as nutrient content and density of soil were measured and documented for each plot during pre-hurricane sampling (White et al. 1991, 1992).

Sampling after the hurricane

In the summer of 1997, we re-sampled all of the 42 original upland plots. We re-measured every tree greater than 1 cm dbh and assigned one of the four damage-type codes to hurricane-damaged individuals: uproot (H1, if uprooted by wind), breakage (H2, if canopy was damaged by the wind), leaner angle (H3, if the tree was leaning), and leaner support (H4, if the tree was supporting another tree). A damage severity level (1–3 or 1–4) was assigned as well, depending on the damage-type code (e.g., H1 = 3 for a tree completely uprooted by wind) yielding a total of 15 classes of damage type and severity (H1 = 1–3, H2 = 1–4, H3 = 1–4, and H4 = 1–4). All trees greater than 10 cm dbh in the previous survey were incorporated into a dataset summarizing the fates of individual large stems (White 1999).

To quantify differences in damage among plots, the amount of basal area severely damaged by the hurricane was determined within each plot (Everham and Brokaw 1996). We considered severely damaged stems to be those that had been completely tipped up (H1 = 3), had lost >35% of canopy from breakage (H2 = 3 or 4), or had fallen with their bole lying on the ground (trees fallen, H3 = 4; or toppled and pinned by other trees, H4 = 4). If any of these categories applied to the individual tree in question, it was effectively eliminated from the canopy of the forest because it was no longer fully present as a live tree in the canopy. We excluded any tree considered severely damaged from our canopy live basal area estimates after the hurricane.

Fallen CWD (diameter >10 cm) and canopy disturbance were measured after the hurricane. In 1997, all fallen boles and branches were sampled using the planar transect method (Brown 1974; Harmon and Sexton 1996). Pieces intercepted by the 50-m centerline of each plot were measured for diameter at point of intercept. In addition, each piece was classified as input before or after the hurricane. The amount of decay was noted for each piece using the two-stage classification of Brown (1974). Total volume was calculated following VanWagner (1968):

$$V = \pi^2 \left(\Sigma D^2\right) / 8L$$

where V is the volume in m^3/m^2, L is the transect length (50 m), and D is the diameter of individual pieces (m). Mass was calculated using the approximate density of fresh wood (0.46 Mg/m^3—averaged across all species) and decomposed wood (0.29 Mg/m^3—averaged across all species and decay classes). Density was determined by sawing out sections from recently fallen trees as well as those in various states of decomposition. Volume of the sections was calculated from surface measurements and mass was determined by weighing the entire section and then subsampling it to determine moisture content. Density was calculated as the dry mass (oven dried at 55°C) divided by the undried volume.

Changes in net ecosystem carbon balance (NECB, Chapin et al. 2006) after the 1996 hurricane were projected using net primary production (NPP) and mass decay of CWD:

$$\mathrm{NECB} = \mathrm{NPP_b} - D_{\mathrm{CWD}},$$

where $\mathrm{NPP_b}$ is bole NPP of the relatively undisturbed forest plots and D_{CWD} are the losses due to the decay of CWD. $\mathrm{NPP_b}$ was estimated using measurements of stem diameter growth and allometric equations for stem biomass of trees grouped by genus or species (Ter-Mikaelian and Korzukhin 1997). The losses from decomposition were calculated as:

$$D_{\mathrm{CWD}} = M_{\mathrm{CWD}t} - M_{\mathrm{CWD}t-1},$$

where $M_{\mathrm{CWD}t}$ is the mass of CWD at time t calculated with a negative exponential model (Olson 1963):

$$M_{\mathrm{CWD}t} = M_{\mathrm{CWD0}}\, \mathrm{e}^{-kt},$$

where k is the decomposition rate constant, assumed to range between 0.1 and 0.2/year (Onega and Eickmeier 1991).

Canopy disturbance after the hurricane was assessed at the plot level and at the landscape level. The amount of canopy loss in each plot was quantified with a canopy densitometer, taking measurements at 10-m intervals along the plot centerline. For landscape-level estimates, stereoscopic aerial photographs taken in April 1998 were examined for large canopy gaps (≥0.1 ha) across a 45-ha area covering undeveloped garden lands. We only included openings with an unobstructed view of the ground surface. The length and width of all canopy gaps approximately 0.1 ha or larger were measured. Area of individual gaps was estimated using the formula for the area of an ellipse (Runkle 1982):

$$A = \pi L \times W/4,$$

where A is gap area (m^2), L is gap length (m), and W is gap width (m). Upper and lower estimates of the size of each gap were obtained using a tolerance of 6 m for gap length and width. The tolerance level represented the precision of gap length and width measurements from the photographs. Using these methods, upper, intermediate, and lower estimates of total land area in gaps ≥0.1 ha were generated.

Several plot-level variables such as basal area, dead tree density, CWD volume, and CWD mass, were compared before and after the hurricane. Statistical differences before and after were assessed with paired t-tests (SAS Institute Inc 1985) using plot-level values from before and after. Two-tailed probabilities were used to assess the significance of changes.

Results

Landscape disturbance

The initial, pre-hurricane survey of forested lands in the study area indicated that large, naturally created gaps (≥0.1 ha) were either rare or absent. Circa 1990, prior to the hurricane, large gaps occupied less than 1% of the undeveloped land area. Two years after the hurricane, the estimated total land area in large gaps (≥0.1 ha) was 4%. The lower and upper bounds for this estimate based on the measurement tolerances were 1 and 7%, respectively (see Methods).

Physical structure of stands

Basal area

Over the entire study area, live basal area declined significantly by 17% (Table 1). The coefficient of variation, indicating the variability among plots, increased from 19 to 33%. Of the 42 plots visited after the hurricane, 23 lost 1–66% of their original live basal area (Fig. 1). The mean amount of basal area lost in these damaged stands was 25%. In the 19 plots that were relatively undamaged by the hurricane, basal area increased on average by 8% over the sampling interval (ca. 1990–1997). Basal area gains ranged from 1 to 15% in these plots over this interval.

Canopy cover

Although canopy cover was not measured prior to the hurricane, comparison of cover between damaged and undamaged stands provided an indication of the amount of cover lost in the storm. Mean canopy cover was 92% in the 19 undamaged plots and 81% in the 23 damaged plots (see Appendix Table A1), respectively. Canopy cover ranged from 89 to 95% in the undamaged plots, and from 60 to 93% in the damaged plots.

Table 1 Live trees, standing dead trees, and fallen trees before and after the 1996 hurricane (ca. 1990 vs. 1997)

	Mean	Std. Dev.	Min.	Max.	Coeff. Var.	*N*
Basal area of live trees (m^2/ha)						
Before storm	27	5	19	43	19	42
After storm	22**	7	6	43	33	42
Basal area of standing dead trees (m^2/ha)						
Before storm	0.7	1	0	3.1	108	42
After storm	0.9	1	0	4.9	112	42
Added by storm	0.9	1	0	4.6	110	42
Density of standing dead trees >10 cm DBH (stems/ha)						
Before storm	22	18	0	70	83	42
After storm	30**	20	0	80	66	42
Added by storm	29	38	0	80	67	42
Density of standing dead trees >30 cm DBH (stems/ha)						
Before storm	2	4	0	10	226	42
After storm	4	9	0	40	225	42
Added by storm	4	8	0	30	213	42
Density of standing dead trees >50 cm DBH (stems/ha)						
Before storm	0.5	2	0	10	453	42
After storm	0.5	2	0	10	453	42
Added by storm	0.2	2	0	10	648	42
Volume of fallen trees >10 cm diameter (m^3/ha)						
Before storm	24	26	3	110	107	40
After storm	129**	126	6	532	97	40
Added by storm	105	126	0	522	120	40
Mass of fallen trees >10 cm diameter (Mg/ha)						
Before storm	7	7	1	32	106	40
After storm	55**	58	2	244	105	40
Added by storm	48	58	0	240	120	40

For several variables the amount added by the storm was measured directly; this amount did not necessarily equal the difference between 1990 and 1997 values. Significant differences between before and after values are noted (** significance at the $p < 0.01$ level)

Standing dead trees

Pre-hurricane basal area of standing dead trees (or snags) across the study area was low (0.7 m^2/ha) (Table 1). Density of standing dead trees (>10 cm dbh) averaged 24 stems/ha. Few of the dead trees exceeded 30 cm dbh (2 stems/ha). As a result of hurricane damage, across the study area an average of 0.9 m^2/ha of new dead basal area was added. An average of 29 stems/ha of new standing dead trees >10 cm dbh was added, and a significantly higher mean value of 30 m^2/ha was attained. The associated coefficient of variation declined from 80 to 66% indicating decreased variability among plots.

Fallen trees

Prior to the hurricane the volume and mass of downed CWD in the study forest averaged 24 m^3/ha and 7 Mg/ha, respectively (Table 1). Although the range of values was quite large, for example, volume ranged from 3 to 110 m^3/ha, the average value is quite typical for a warm temperate deciduous forest (Muller and Liu 1991). The hurricane increased CWD volume approximately sixfold to an average of 129 m^3/ha (Table 1). Mass increased to a greater degree, approximately eightfold to 55 Mg/ha, because of the higher density of fresh wood added by the disturbance.

The volume of CWD after the storm was much greater in the stands that lost live basal area (see Appendix Table A1). Nonetheless, the hurricane did not substantially alter the relative variability of downed CWD among plots as the coefficients of variation for pre- versus post-hurricane volume were 107 and 97, respectively (Table 1).

Tree damage

Of all stems greater than 10 cm dbh, 18% were severely damaged by the hurricane event (Table 2). Certain types of injury were dependent on tree size. For example, the occurrence of full uprooting increased with tree size (Fig. 2a). By contrast, the occurrence of severe canopy breakage (Fig. 2b) and of toppling by other trees (Fig. 2c) decreased with tree size. When all of these forms of damage were considered, the tendency was for small-sized trees to suffer the least damage (Fig. 2d).

Two moderately shade-tolerant species, red oak (*Quercus rubra*) and black oak (*Quercus velutina*), suffered the largest average basal area losses per plot (41% and 30%, respectively), as shown in Table 3. Conversely, shade-intolerant pine species lost only 7% of their basal area on average over all plots

Fig. 1 Basal area change in the set of study plots before and after the 1996 hurricane (ca. 1990 to 1997)

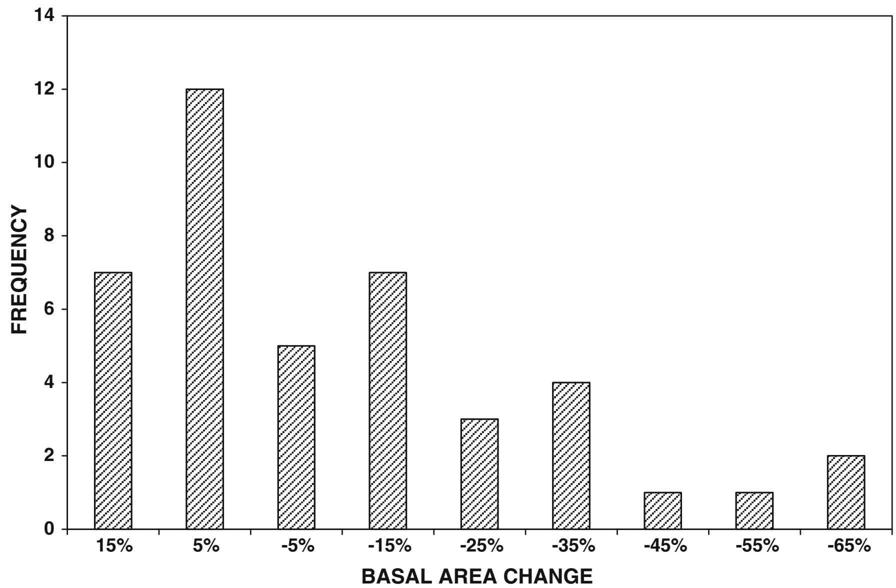

Table 2 Comparison of all stems and larger-sized stems with respect to frequency snapped (H2 = 3 or 4), frequency uprooted (H1 = 3), and frequency severely damaged (H1 = 3, H2 = 3 or 4, H3 = 4, or H4 = 4)

Damage parameter	All stems >1 cm dbh (*n* = 10,547)	All stems >10 cm dbh (*n* = 1,899)
Frequency snapped	297 stems	117 stems
Percent snapped	2.8%	6.2%
Frequency uprooted	325 stems	210 stems
Percent uprooted	3.1%	11.2%
Frequency severely damaged	1014 stems	332 stems
Percent severely damaged	9.6%	17.7%

Values are for the entire 4.2-ha area sampled in summer 1997 after the September 1996 hurricane

(Table 3). Deciduous canopy species such as tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), beech (*Fagus grandifolia*), white oak (*Quercus alba*), and ash (*Fraxinus* sp.) suffered light to moderate damage (7–19%). Consequently, they showed large gains in importance (relative basal area) after the hurricane. Their shade-tolerance classifications range from intolerant to tolerant.

Despite the differences in damage among species, damage was not restricted to a particular shade-tolerance class (Table 4). However, in undamaged stands all but the shade-intolerant class increased in relative basal area. For shade-tolerant species the loss of basal area in damaged plots was partially offset by gains in undamaged plots. Overall, damage caused little change in the relative basal area of various shade-tolerance classes.

Projected changes in NECB

The NPP of boles in undamaged stands was 2.5 Mg/ha/year. Assuming that level of NPP is maintained despite hurricane damage, the losses of mass due to decomposition were projected to exceed forest inputs during 5–10 years (Fig. 3). After that point the forest should have a positive NECB.

Discussion

Disturbance patterns, patch dynamics, and succession

Hurricane disturbance on the upland landscape was patchy. About half of the study stands suffered basal area loss. Even in those stands, canopy disturbance was incomplete at the scale of 0.1 ha. Stands that were damaged lost, on average, one-quarter of their original live basal area and about one-tenth of their canopy cover. The lowest canopy cover estimate after the disturbance was 60% across a 0.1-ha area. Nonetheless, inputs of CWD in damaged stands were

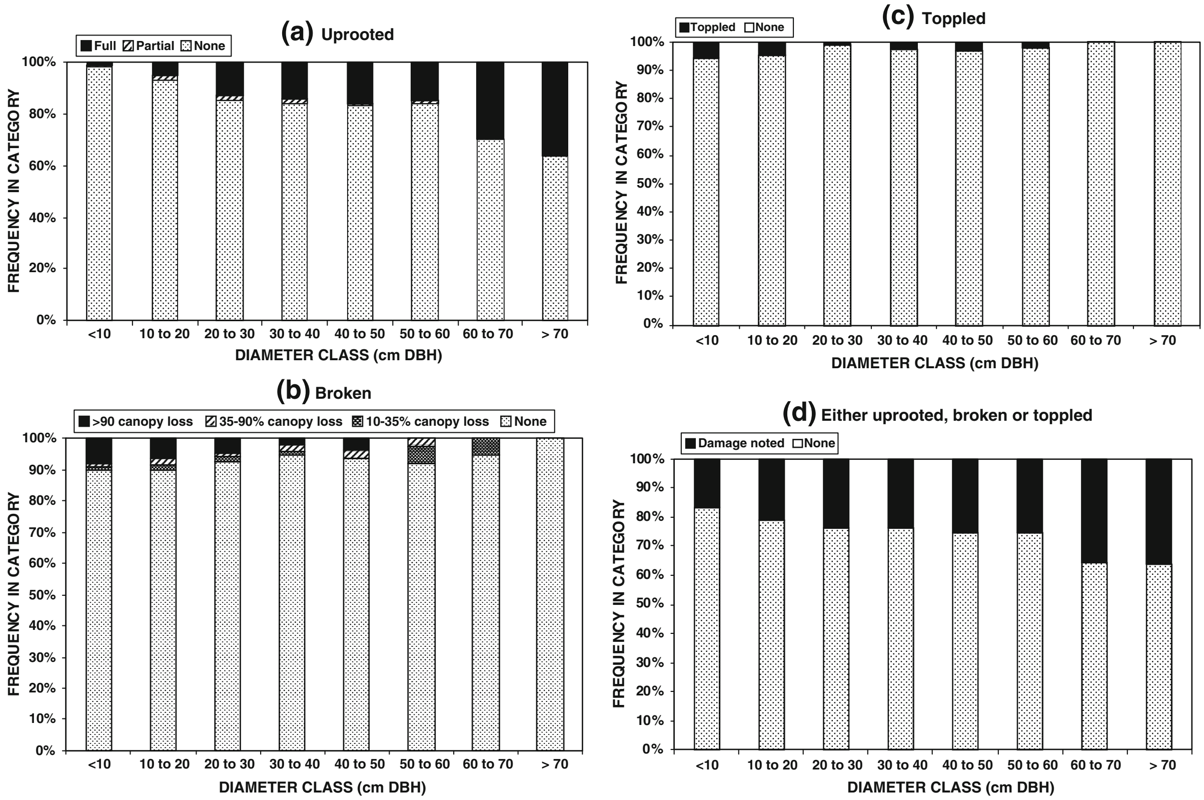

Fig. 2 Hurricane damage by type and tree size for **a** uprooted trees, **b** broken trees, **c** toppled trees, and **d** all damaged trees. Sample sizes vary by class (*left* to *right*, n = 8648, 938, 371, 250, 203, 89, 37 & 11)

substantial. Forest-wide, including both damaged and undamaged stands, live basal area and canopy cover declined only moderately, but necromass levels increased markedly.

Whereas long-term studies of tree mortality in the eastern deciduous forest give a mean rate of nearly 1% of the population dying per year (Parker et al. 1985; Runkle 2000; Busing 2005), the storm produced much higher levels of mortality. For stems >10 cm dbh, 18% were classified as severely damaged; most were uprooted (11%) or had broken boles (6%) (Table 2). Given that the mean return interval of hurricanes of category three or higher is at least 40 year in the Chapel Hill area (NOAA, unpublished data) and assuming a mean annual mortality rate of nearly 1%, hurricanes probably account for less than half of the total long-term mortality of forest trees.

Overall, larger trees suffered the greatest damage (cf. DeCoster 1996). The pattern of increasing injury and mortality with tree size did not fully conform to Everham and Brokaw's (1996) two generalized conceptual models of hurricane disturbance effects on forests. Neither the unimodal response model, wherein intermediate-sized trees suffer the most damage, nor the bimodal response model, wherein intermediate-sized trees suffer the least amount of damage, was followed. However, the commonly observed tendency of minimal damage to small stems (Everham and Brokaw 1996) was exhibited in this case. The observed pattern contrasted sharply with that of tree mortality between storm events, where mortality of small trees is relatively high (Peet and Christensen 1987).

Damage also varied by species and by patch composition prior to the storm. The broad-leaved deciduous species tended to suffer higher losses of basal area than the needle-leaved coniferous species. The fact that these deciduous species were in leaf at the time of the storm was important. Their relatively broad leaves and crowns made them susceptible to wind damage. By contrast, early successional patches of needle-leaved coniferous species (e.g., *Pinus*) were

Table 3 Frequency of trees in plots, basal area before and after the 1996 hurricane, basal area change, and percent of total basal area lost or gained between the two sampling periods (ca. 1990 vs. 1997)

	Frequency	Basal area before storm (m^2)	Basal area after storm (m^2)	Change in basal area (%)	Shade tolerance
Canopy species					
Acer barbatum	18	0.38	0.29	−24	Tolerant
Acer rubrum	42	8.50	7.39**	−13	Tolerant
Carya species	39	16.42	13.06**	−21	Intermediate
Fagus grandifolia	29	4.53	3.83	−16	Tolerant
Fraxinus species	30	1.29	1.20	−7	Intermediate
Liriodendron	34	8.79	7.12*	−19	Intolerant
Pinus species	23	18.43	17.11**	−7	Intolerant
Quercus alba	42	39.87	36.37*	−9	Intermediate
Quercus rubra	36	9.19	5.39**	−41	Intermediate
Quercus velutina	22	3.46	2.43	−30	Intermediate
Sub-canopy species					
Carpinus caroliniana	19	0.09	0.09	0	Tolerant
Cercis canadensis	16	0.06	0.06	0	Tolerant
Cornus florida	42	2.16	1.63**	−25	Tolerant
Crataegus species	11	0.01	0.02	50	Unknown
Ilex decidua	13	0.04	0.05*	25	Tolerant
Juniperus	36	0.72	0.82	14	Intolerant
Liquidambar	23	1.31	1.19	−9	Intolerant
Morus rubra	17	0.05	0.06	20	Tolerant
Nyssa sylvatica	40	1.69	1.41*	−17	Tolerant
Ostrya virginiana	30	0.68	0.62	−9	Tolerant
Oxydendron	39	4.98	4.86	−2	Tolerant
Ulmus species	17	0.11	0.13	18	Intermediate

Basal area is the total over the 4.2 ha area sampled. Significant differences are noted (** significance at the $p < 0.05$ level, * significance at the $p < 0.10$ level). Shade tolerance classifications (1 is the highest tolerance class) are according to Baker (1949) or Burns and Honkala (1990) (*Liriodendron* = *Liriodendron tulipifera*, *Liquidambar* = *Liquidambar styraciflua, Juniperus* = *Juniperus virginiana, Oxydendron* = *Oxydendron arboreum*)

less affected. The variation in susceptibility among species has implications for community dynamics. First, the initial impacts of the storm altered forest composition directly by reducing the abundance of certain dominant deciduous species. Second, resources (e.g., light and nutrients) made available by disturbance appear to have enhanced the growth of some species.

Overall, the forest continued to be dominated by intermediate and shade-tolerant species after the storm despite the newly created disturbance patches. Taken as a group, shade-tolerant species have increased in basal area in undamaged stands, whereas shade-intolerant species have not increased in these same stands. Thus, the trends in undamaged stands are consistent with patterns in mid-successional forests, as shade-intolerant species are giving way to shade-tolerant species. In damaged stands, the loss in basal area included species from all shade-tolerance classes. Yet, some intolerant species were unaffected by the storm, potentially stalling or setting succession back to an earlier stage, at least in the disturbance patches.

Ecosystem dynamics

The loss of tree basal area (and biomass) resulting from the storm is a disruption to ecosystem development in this otherwise aggrading forest. Large amounts of organic debris were transferred to the

Table 4 Basal area of major species before and after the 1996 hurricane by tolerance grouping and stand damage (ca. 1990 vs. 1997)

Shade tolerance class	Basal area before storm (m^2 ha^{-1})	Basal after storm (m^2 ha^{-1})	Change in basal area (%)
Damaged stands ($n = 23$)			
Tolerant	4.0	2.9**	−27
Intermediate	20.2	13.5**	−33
Intolerant	3.9	2.6**	−34
Undamaged stands ($n = 19$)			
Tolerant	3.0	3.2**	8
Intermediate	16.8	17.3**	3
Intolerant	6.4	6.3	−0.1
All stands ($n = 42$)			
Tolerant	3.5	3	−14
Intermediate	18.6	15.1**	−19
Intolerant	5.0	4.3**	−15

Damaged stands are defined as those with lower live basal area after the storm. Mean basal area values and percent change are provided. Significant differences are noted (** significance at the $p < .01$ level)

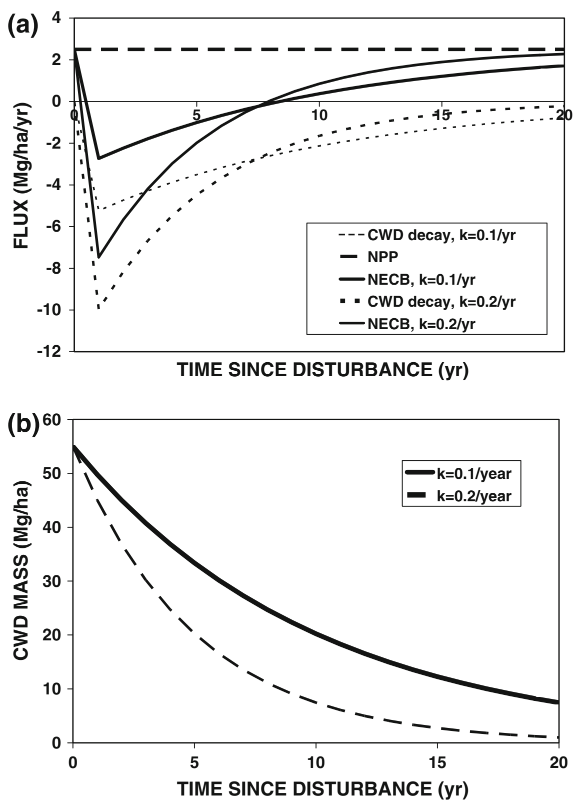

Fig. 3 Projected net ecosystem carbon balance (NECB) and major components after the 1996 hurricane showing **a** fluxes and **b** detritus mass decay

forest floor during the storm, particularly in heavily damaged stands with new CWD. The rate of decomposition of detritus can have important consequences for ecosystem energetics and nutrient dynamics (Harmon et al. 1986). Much of the detritus is wood, which decomposes slowly in temperate forests (<15% mass lost per year).

NECB, the overall change in organic matter, was likely negative immediately following the hurricane. Negative NECB would have been caused by the large input of newly decomposing wood with losses exceeding forest gains by net primary production (NPP) (Fig. 3). The duration of the period of negative NECB through losses to the atmosphere depends on the decomposition rate and the time required for NPP to recover to pre-hurricane levels. It is possible that NPP of boles was temporarily reduced by the hurricane and this may delay the switch from negative to positive NECB. However, alternative calculations with delays in NPP recovery did not alter our conclusions regarding the time required to go from negative to positive NECB as long as NPP reached pre-hurricane levels within a decade. In contrast, delaying the recovery of NPP promoted a negative NECB because the lower NPP failed to offset decomposition losses.

Long-term consequences

The changes in forest patch structure, composition, and coarse detritus brought about by this disturbance event are expected to last for decades. Reversion toward the pre-hurricane state is expected for at least some parameters, however. For ecosystem parameters such as live biomass and necromass, a direct but potentially slow, recovery toward pre-hurricane levels is anticipated. With the recovery of leaf area and the additional resources made available by disturbance, NPP will be maintained or increased during the recovery period (Beard et al. 2005). Based on published rates of CWD decomposition in similar ecosystems (Onega and Eickmeier 1991; Busing 2005), CWD added by the hurricane should be largely gone within 20–30 years (Fig. 3).

In contrast to biomass, forest composition and diversity may initially diverge further from pre-disturbance levels as a result of new colonization and recruitment. The direction and duration of community-level dynamics are potentially complex given that much of the pre-hurricane forest was in mid-succession. A simple projection, based on community resilience through positive feedback mechanisms, is that after initial divergence, composition and diversity will revert to their pre-hurricane states. For example, seeds, seedling banks, and sapling banks generated by existing adult trees would be expected to maintain recruitment of existing canopy species. If post-hurricane recruitment of shade-tolerant seedlings, presumably established before the storm, is relatively successful then succession may be accelerated (Abrams and Scott 1989); however, elevated recruitment of shade-tolerant tree seedlings was not detected shortly after the storm (White 1999). An increase in exotic plants was evident within the first 2 years after the storm (White 1999). If the hurricane disturbance facilitates invasion (Crawley 1987), novel composition and dynamics may result. For these reasons, full recovery of pre-hurricane composition and dynamics is unlikely.

Although hurricane disturbance is rarely catastrophic in Piedmont forests, episodic events of this nature may have important, lasting impacts on forests (Foster et al. 1998). Yet, the long-term effects of hurricane disturbances in the Piedmont are not well studied. It is increasingly clear that partial damage to stands, as observed in this study, is typical of the regional disturbance regime. The long-term response of ecological parameters to intermediate-disturbance events similar to the one described here is less clear. Responses are likely to vary among community and ecosystem parameters. It would be particularly useful to know which parameters exhibit delayed recovery or no recovery at all. If recovery times approach or exceed the return interval for disturbances of this severity, then the possibility of cumulative effects of multiple intermediate-disturbance events on forest dynamics must be considered.

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Appendix

Table A1 Forest stand parameters by 0.1 ha study plot in the North Carolina Botanical Garden before and after the 1996 hurricane

Plot number	Basal area before storm (m^2/ha)	Basal area after storm (m^2/ha)	Basal area change (%)	Densitometer reading after storm (Cover, %)	CWD before storm (m^3/ha)	CWD after storm (m^3/ha)
50	22.1	7.6	−65.6	ND	74.6	170.7
25	28.0	10.9	−61.1	60.3	20.5	363.6
72	28.2	12.9	−54.2	63.8	8.49	412.2
8	22.6	13.2	−41.5	82.3	40.8	105.3
51	33.2	20.2	−39.1	86.0	38.9	413.6
24	35.5	21.9	−38.2	87.0	75.4	207.6
36	32.5	22.2	−31.8	63.8	20.9	287.9
33	25.7	18.0	−30.1	81.0	6.3	101.6
47	26.7	20.1	−24.8	83.2	17.8	183.1
28	33.3	25.1	−24.5	80.5	15.3	209.5
65	30.0	23.1	−22.9	89.0	ND	ND
42	25.2	20.3	−19.6	71.0	11.9	211.2
67	34.9	28.3	−19.0	90.3	36.5	36.9

Table A1 continued

Plot number	Basal area before storm (m^2/ha)	Basal area after storm (m^2/ha)	Basal area change (%)	Densitometer reading after storm (Cover, %)	CWD before storm (m^3/ha)	CWD after storm (m^3/ha)
54	35.3	28.7	−18.6	81.7	4.8	160.4
40	28.1	22.9	−18.4	70.0	25.1	190.8
71	38.2	31.4	−17.8	88.3	6.5	21.8
34	27.0	23.1	−14.3	90.2	ND	ND
41	28.9	24.9	−13.7	92.8	11.9	84.3
4	32.1	28.9	−9.9	ND	18.1	233.3
32	29.2	27.2	−6.9	83.7	8.9	90.5
44	33.1	31.1	−6.0	86.2	12.0	90.4
70	22.5	21.4	−5.0	80.8	10.3	532.0
35	30.2	29.9	−1.1	ND	108.6	132.1
37	27.2	27.5	1.0	89.8	4.2	9.4
39	25.7	26.1	1.6	90.0	10.5	47.7
55	44.6	46.2	3.6	91.7	7.2	18.3
14	28.8	29.9	3.7	90.2	16.7	63.2
48	30.6	31.8	4.0	90.5	11.3	100.5
16	26.8	28.0	4.6	89.8	17.5	61.2
3	28.4	29.9	5.4	93.0	5.9	20.8
22	30.3	32.1	5.8	93.2	2.9	59.4
43	20.8	22.0	6.0	89.2	20.6	75.4
31	20.4	21.8	7.1	92.3	39.0	39.3
30	26.1	28.0	7.2	ND	6.3	8.3
46	21.6	23.7	9.7	88.7	22.7	26.3
2	27.1	29.9	10.2	93.7	26.7	99.5
49	28.9	31.9	10.3	94.8	4.4	5.7
52	37.7	41.7	10.6	90.7	20.5	83.0
1	29.9	33.2	11.0	90.5	11.4	13.1
68	21.2	23.9	12.7	92.3	33.8	51.4
9	26.0	29.7	14.4	95.3	17.8	17.8
17	28.8	33.1	14.9	92.2	109.8	124.1

Plots are ranked by change in basal area. Basal area change represents basal area losses from severe damage and gains due to growth between sampling periods (ca. 1990 and 1997). Densitometer readings consist of the average of six measurements along the centerline to determine cover of the canopy in each plot (ND = no data). Coarse woody detritus (CWD) is the amount of fallen wood bisecting the 50 m centerline plane (ND = no data)

References

Abrams MD, Scott ML (1989) Disturbance-mediated accelerated succession in two Michigan forest types. For Sci 35:42–49

Baker FS (1949) A revised tolerance table. J For 47:179–181

Barbour MG, Burk JH, Pitts WD (1980) Terrestrial plant ecology. Benjamin Cummings, New York

Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardottir R, Siccama TG, Crowl TA (2005) Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecol Monogr 75:345–361. doi:10.1890/04-1114

Boose ER, Foster DR, Fluet M (1994) Hurricane impacts to tropical and temperate forest landscapes. Ecol Monogr 64:369–400. doi:10.2307/2937142

Braun EL (1950) Deciduous forests of eastern North America. Blakiston, Philadelphia

Brown JK (1974) Handbook for inventorying downed woody material. USDA Forest Service GTR INT-16, Ogden, Utah

Burns RM, Honkala BH (1990) Silvics of North America. USDA Forest Service, Washington

Busing RT (2005) Tree mortality, canopy turnover and woody detritus in old cove forests of the southern Appalachians. Ecology 86:73–84. doi:10.1890/04-0410

Canham CD, Loucks OL (1984) Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65:803–809. doi:10.2307/1938053

Chapin FS et al (2006) Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9:1041–1050. doi:10.1007/s10021-005-0105-7

Crawley MJ (1987) What makes a community invasible? In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonization, succession and stability. Blackwell Scientific, Oxford, pp 429–453

DeCoster J (1996) Impacts of tornados and hurricanes on the community structure and dynamics of North and South Carolina forests. Ph.D. Dissertation, University of North Carolina, Chapel Hill, North Carolina, USA

Dunn J (1977) Soil survey of Orange County, North Carolina. Department of Agriculture, Soil Conservation Service, in cooperation with the North Carolina Agricultural Experiment Station and the Orange County Board of Commissioners

Dunn CP, Gutenspergen GR, Dorney JR (1983) Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. Can J Bot 61:211–217. doi:10.1139/b83-023

Everham EM, Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. Bot Rev 62:113–185. doi:10.1007/BF02857920

Foster DR (1988) Species and stand response to catastrophic wind in central New England, U.S.A. J Ecol 76:135–151

Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510. doi:10.1007/s100219900046

Frelich LE (2002) Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge

Greenberg CH, McNab WH (1997) Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For Ecol Manage 104:179–191. doi:10.1016/S0378-1127(97)00246-6

Greller AM (1988) Deciduous forest. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, New York, pp 287–316

Harmon ME, Sexton J (1996) Guidelines for measurements of woody detritus in forest ecosystems. Publication no. 20. U.S. LTER Network Office. University of Washington, Seattle, Washington

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133–302. doi:10.1016/S0065-2504(08)60121-X

Lorimer CG (1980) Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169–1184. doi:10.2307/1936836

Lorimer CG (1989) Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology 70:565–567. doi:10.2307/1940207

Muller RN, Liu Y (1991) Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can J For Res 21:1567–1572. doi:10.1139/x91-218

NOAA (1974) Climates of the states: eastern states. Water Information Center, Port Washington

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331. doi:10.2307/1932179

Onega TL, Eickmeier WG (1991) Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull Torrey Bot Club 118:52–57. doi:10.2307/2996975

Oosting HJ (1942) An ecological analysis of the plant communities of the Piedmont, North Carolina. Am Midl Nat 28:1–126. doi:10.2307/2420696

Parker GR, Leopold DJ, Eichenberger JK (1985) Tree dynamics in an old-growth deciduous forest. For Ecol Manage 11:31–57. doi:10.1016/0378-1127(85)90057-X

Peart DR, Cogbill CV, Palmiotto PA (1992) Effects of logging history and hurricane damage on canopy structure in a northern hardwoods forest. Bull Torrey Bot Club 119:29–38. doi:10.2307/2996917

Peet RK, Christensen NL (1980) Hardwood vegetation of the North Carolina Piedmont. In: Leith H, Landolt E (eds) Contributions to the knowledge of flora and vegetation in the Carolinas. Veroff. Geobot. ETH, Zurich, pp 14–38

Peet RK, Christensen NL (1987) Competition and tree death. Bioscience 37:586–595. doi:10.2307/1310669

Peet RK, Wentworth TR, White PS (1998) A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63:262–274

Peterson CJ, Pickett STA (1995) Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76:763–774. doi:10.2307/1939342

Platt WJ, Doren RF, Armentano TV (2000) Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). Plant Ecol 146:43–60. doi:10.1023/A:1009829319862

Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests in eastern North America. Ecology 63:1533–1546. doi:10.2307/1938878

Runkle JR (1985) Disturbance regimes in temperate forests. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp 17–33

Runkle JR (2000) Canopy tree turnover in old-growth mesic forests of eastern North America. Ecology 81:554–567

SAS Institute Inc. (1985) SAS/STAT guide for personal computers. SAS Institute Inc., Cary

Ter-Mikaelian MT, Korzukhin MD (1997) Biomass equations for sixty-five North American tree species. For Ecol Manage 97:1–24. doi:10.1016/S0378-1127(97)00019-4

Thornthwaite CW (1948) An approach towards a rational classification of climate. Geogr Rev 38:55–94. doi:10.2307/210739

VanWagner CE (1968) The line intersect method in forest fuel sampling. For Sci 14:20–26

Whigham DF, Olmstead I, Harmon ME (1991) The impact of hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. Biotropica 23:434–441. doi:10.2307/2388263

White PS (1979) Pattern, process, and natural disturbance in vegetation. Bot Rev 45:229–299. doi:10.1007/BF02860857

White RD (1999) The impacts of Hurricane Fran on a North Carolina Piedmont woodland. M.A. Thesis, University of North Carolina, Chapel Hill

White PS, Busing RT, Larke JO (1991) Conservation project: the William Lanier Hunt Arboretum and Gray Bluff Garden. Technical Report, University of North Carolina, Chapel Hill

White PS, Busing RT, Larke JO (1992) Conservation project: Mason farm biological reserve. Technical Report, University of North Carolina, Chapel Hill

Woods KD (2004) Intermediate disturbance in a late-successional hemlock-northern hardwood forest. J Ecol 92:464–476. doi:10.1111/j.0022-0477.2004.00881.x