

Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina

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Abstract

We characterized five 0.2–1.1 ha gaps created by downbursts during Hurricane Opal in xeric oak forest at the Bent Creek Experimental Forest, Asheville, NC. Direction of windthrow was nonrandom in four of the five gaps, but differed among gaps suggesting that each was caused by an independent downburst. Windthrows reduced tree density by 19–39% and basal area (BA) by 30–53% within gaps. Most windthrows were uprooted (17–38% of all trees) versus broken below 1.8 m height (0–3%). Most species were uprooted in proportion to their abundance regardless of canopy position. Red oaks (*Quercus coccinea*, *Quercus rubra* and *Quercus velutina*) were disproportionately uprooted, while *Nyssa sylvatica* and *Acer rubrum* were resistant to uprooting. As a group, *Quercus* lost 27–47% of individuals and 41–50% of BA. *Q. coccinea* lost $\geq 44\%$ of trees and $>55\%$ of BA in sites where it occurred. Only minor shifts in canopy species dominance were evident. For several species, significantly more large-diameter individuals uprooted than their smaller counterparts. No relationship between dbh and number uprooted was detected for the red oaks, however. Canopy position appeared to have little bearing on this relationship. Uprooting disturbed 1.6–4.3% of the ground area and displaced 1 X-587 m³ of root-soil-rock masses (rootmasses) per gap. We suggest that episodic, high-intensity wind is not uncommon, and has a substantial influence on forest structure, species composition, regeneration and microtopography of the southern Appalachian mountains at variable scales. ©1998 Elsevier Science B.V.

Keywords: Windthrow; Gap dynamic; Treefall; Wind disturbance; Uproot; Soil disturbance

1. Introduction

In the southern Appalachians, gap formation by individual tree death is frequently cited as the dominant process of forest regeneration (Lorimer, 1980;

Runkle, 1982, 1985, 1990; White et al., 1985; Clinton et al., 1993, 1994; Battles et al., 1995). Although large-scale wind disturbance has been documented in the eastern U.S. (Spurr, 1956; Reiners and Reiners, 1965; Henry and Swan, 1974; Oliver and Stephens, 1977; Dunn et al., 1983; Canham and Loucks, 1984; Foster, 1988a,b; Peterson and Pickett, 1991; Putz and Sharitz, 1991; Peterson and Pickett, 1995), only scant information exists on the occurrence multiple-tree blowdowns caused by high-intensity wind in the

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southern Appalachian mountains (Lorimer, 1980; White et al., 1985; Busing and Pauley, 1994).

Most studies of wind damage describe small (usually $< 400 \text{ m}^2$) (Lorimer, 1980, 1989; Runkle, 1981, 1982, 1985; Romme and Martin, 1982; Runkle and Yetter, 1987; Clebsch and Busing, 1989) or very large areas (400–240,000 ha) (Spurr, 1956; Peterson and Pickett, 1991) of wind disturbance, while intermediate-sized gaps have received little attention. However, downbursts of wind may create gaps of variable size, often intermediate in scale between single-tree gaps or large forest openings created by catastrophic wind events (Canham and Loucks, 1984). While most descriptions depict 'neat' (e.g. Runkle, 1982; Foster, 1988b; Peterson and Pickett, 1991; Clinton et al., 1993), or complete gaps having distinct, treeless interiors and discrete forest boundaries, actual patterns and completeness of multiple-tree windthrow can be quite variable in nature (Spurr, 1956; Putz and Sharitz, 1991).

Much of the focus on single-tree gap dynamics to the virtual exclusion of larger-scale wind damage in the southern Appalachian mountains can be attributed to the assumption that severe wind damage is infrequent or localized (Lorimer, 1980; Runkle, 1990) in the region, and hence has a negligible impact on forest dynamics. In support of this assumption, stand-level studies of forest dynamics might easily miss large patches of windthrown trees, since such disturbance is patchy (Lorimer, 1980).

However, historical data tracing hurricane paths (compiled by Neumann et al., 1993) indicates that hurricane-related windstorms have recurred in the southern Appalachians fourteen times since 1871 at intervals ranging from 1–24 yr. Although they lose some velocity as they move inland, hurricane-related winds of 64–97 km/h have been recorded in the mountains of western NC since 1911 (Lorimer, 1980). Field inventories of four national forests in northeastern Georgia, western NC and eastern TN determined that approximately 2479 ha, or 0.28% of land within those national forests was damaged by winds during Hurricane Opal. Of the total, 0.18% was in intermediate to large areas of multiple treefalls (sold for salvage-logging); the remaining estimated 0.10% was scattered single or small groups of fallen trees and was not salvage-logged (B. Stansel, C. McGinnis, K. Compton, R. Aubuchon and E. Brown,

personal communication). If similar damage can be assumed to occur at an average of 8.3 ± 7.6 yr intervals (McNab and Greenberg, in review), approximately 6.8% (4.3% in intermediate to large patches of multiple treefalls, and 2.5% in single or small groups of treefalls) of the southern Appalachian landscape is affected by high-intensity wind within the (minimum) 200-yr generation span of many eastern forest trees.

High winds can cause uprooting or breaking of isolated individuals or large clusters of trees. Severity of damage depends upon stand characteristics such as age, structure, species composition and history; site factors such as soil properties, soil depth and topography (which, in turn influence species composition, rooting habit, size and other important stand features); and storm characteristics such as type, wind velocity, direction, duration and the amount of precipitation may also influence the type and extent of damage (Curtis, 1943; Ruth and Yoder, 1953; Gratkowski, 1956; Touliatos and Roth, 1971; Savill, 1983; Canham and Loucks, 1984; Foster, 1988a,b; Brokaw and Grear, 1991; Gresham et al., 1991; Hook et al., 1991; Conner, 1992; Attiwill, 1994; Battles et al., 1995). Uprooting of trees is a significant cause of soil turnover, contributing to natural microtopographic variation, and altering soil properties (Lutz, 1940; Lyford and MacLean, 1966; Meyers and McSweeney, 1995).

Storm events such as thunderstorm downbursts, hurricane-related winds or other intense wind events are important high-intensity disturbances that act at variable scales, and influence the age and size structure, and species composition of mesic eastern forests (Lorimer, 1980; Canham and Loucks, 1984). Although numerous studies address post-disturbance vegetation response, only a few (e.g., Foster, 1988b; Putz and Sharitz, 1991) characterize the direct and immediate impact of high winds on forest structure and composition. Yet, the features of disturbance such as numbers, biomass and identity of standing and fallen trees, the amount of soil disturbance and resulting microtopography may affect future forest composition, structure, and age distribution at multiple scales (Putz, 1983; Beatty and Stone, 1986; Lorimer, 1980). Further, an understanding of the specific features of the natural disturbance types that influence regional forest dynamics may be of utility

in designing management plans and silvicultural systems that are compatible with ecosystem processes (Lorimer, 1980).

The purpose of our study was to characterize the immediate effect of severe wind damage on stand structure, composition and ground disturbance at five intermediate-sized gaps created by Hurricane Opal within the Bent Creek watershed in the southern Appalachian mountains. Specific objectives were to: (1) determine spatial patterns of windthrow within and among gaps; (2) examine mode of windthrow and injury; (3) determine differential vulnerability among species; (4) establish relationships (if any) between tree diameter (dbh) and likelihood of windthrow within and among species; (5) examine changes in tree community composition due to windthrow; (6) quantify soil disturbance resulting from uprooted trees and; (7) determine relationships between tree dbh and rootmass area and volume.

Hurricane Opal made landfall on October 4, 1995 in the Florida panhandle as a category 3 intensity storm. The remnants of Opal passed approximately 240 km west of Asheville, NC on October 5. Precipitation attributable to Opal (October 3–6, 1995) was 15.1 cm at BCEF, and peak wind gusts reached 93 km/h at weather stations nearby the study area (Graumann et al., 1995).

The majority of gaps created by this windstorm were caused by single-tree windthrows (gap area $\leq 200 \text{ m}^2$) (McNab and Greenberg, in review). However, at least 21 larger gaps characterized by multiple-tree windthrows (uprooted and broken trees) within intermediate-sized (0.1–4 ha), discrete areas were apparently created by downbursts of wind (e.g., Fujita, 1985) associated with Hurricane Opal.

2. Study area

This study was conducted in the Bent Creek Experimental Forest (BCEF), a 2500 ha watershed within the Pisgah National Forest in Asheville, NC. Elevation ranges from 700–1070 m. Annual precipitation averages 120 cm and is evenly distributed throughout the year (Owenby and Ezell, 1992). Mean annual temperature is 12.9°C. Winters are short and mild and summers are long and warm. Dominant soil orders are Ultisols that have clay accumulations in the B horizon and are associated with intermontane basins, and Inceptisols associated with mountain slopes. Both soils are moderately deep (solums $> 80 \text{ cm}$).

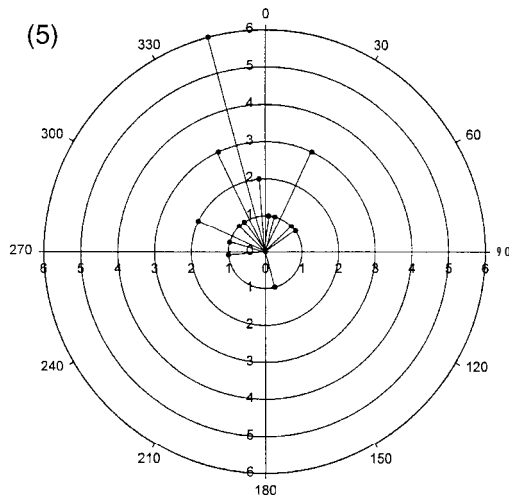
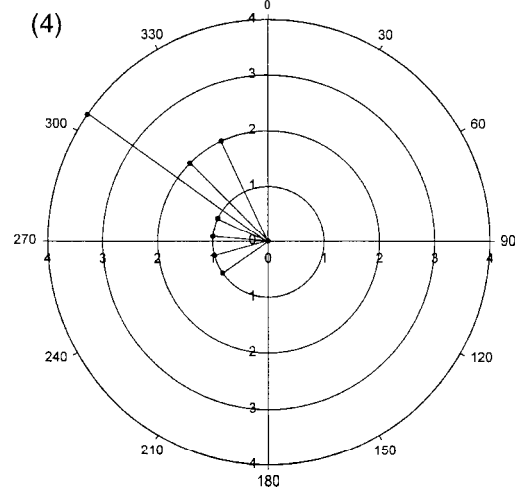
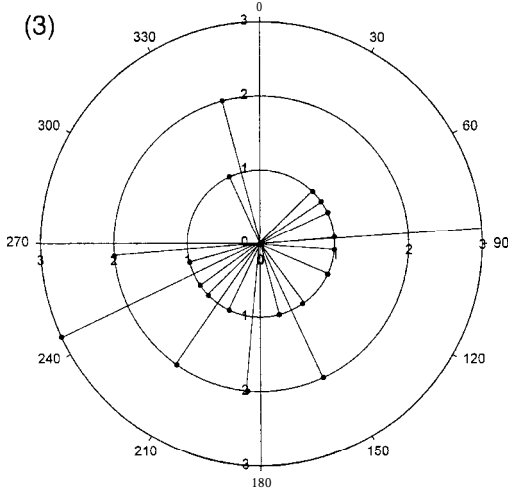
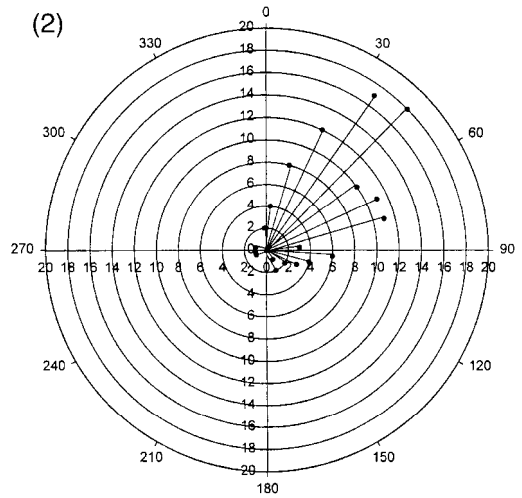
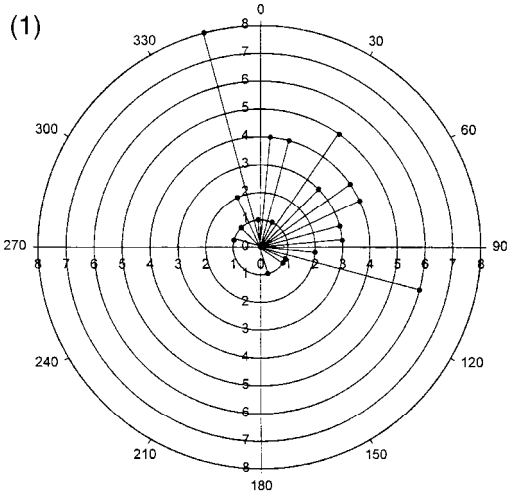
Common tree species on xeric sites include *Quercus coccinea* Muenchh., *Quercus prinus* L., *Quercus velutina* Lam., *Nyssa sylvatica* Marsh., *Oxydendrum arboreum* (L.) DC., and occasional *Pinus echinata* Miller and *P. rigida* Miller. On moist slopes and in coves *Liriodendron tulipifera* L. and *Quercus rubra* L. dominate. *Acer rubrum* L., *Carya* spp., *Cornus florida* L. and *Quercus ulbu* L. are common in all sites (McNab, 1996) (nomenclature follows Radford et al., 1968). Forests are 80–120 yr old in most of the BCEF watershed.

3. Methods

We selected five downburst-created gaps between 700–900 m elevation within the BCEF. All selected gaps had ≥ 10 treefalls and appeared representative of other multiple-treefall gaps within the study area. Gaps were defined to include the ground area within

Table 1
Topographic features and size of five downburst gaps, Bent Creek Experimental Forest, Asheville, NC

		Downburst gap				
		1	2	3	4	5
Slope (%)	range	18–56	25–71	15–52	8–17	22–3s
	mean \pm SD	42 \pm 8	44 \pm 12	33 \pm 10	13 \pm 1.5	30 \pm 4
Aspect (°)	range	20–154	36–197	58–244	153–210	230–280
Elevation	(m)	720	850	750	700	720
Gap Area	(ha)	1.1	1.1	0.3	0.2	0.5



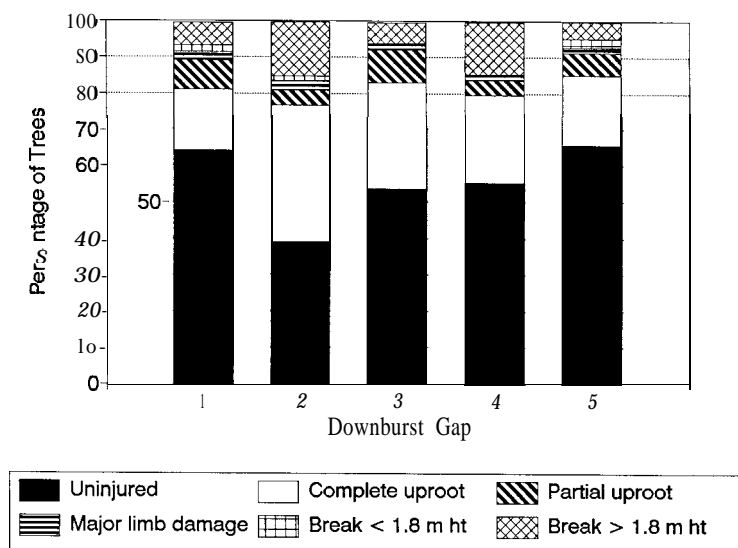


Fig. 2. Condition class of trees damaged during Hurricane Opal, Bent Creek Experimental Forest, Asheville, NC.

a canopy opening extending to the bases of dominant trees that were contiguous with a strip of forest canopy ≥ 25 m wide surrounding the opening (modified from Runkle, 1982). Hence, standing trees that were not contiguous with the surrounding forest canopy were included within gaps. Gap perimeters were mapped as polygons using the static mode of the Global Positioning System (GPS), and differentially corrected areas determined (Liu and Brantigan, 1995).

All standing and Opal-felled trees and snags ≥ 12.7 cm dbh were identified, measured at breast height and individually tagged. Recently uprooted trees were easily discerned from older treefalls by soil freshness on rootmasses, presence of tight bark and leaves on branches. Hence, pre-hurricane forest composition could be inferred.

Slope and aspect were recorded for all tree locations and direction of fallen trees was recorded. For discussion purposes trees were classified as: uninjured (including minor limb breakage or bark scrapes); completely uprooted; partially uprooted (including those with visible signs of root disturbance and leaning, unbroken trees); major limb breakage ($\geq 25\%$ of limbs broken); bole broken ≤ 1.8 m

height or; bole broken > 1.8 m height. We did not attempt to discern between treefalls that were directly versus indirectly (by other falling trees) wind damaged, nor whether fallen trees were hollow or weakened by disease. Length, width, and depth of exposed rootmasses (including roots, soil and associated rocks), and maximum depth of pits were measured.

3.1. Statistical analyses

We tested for uniformity in direction of fall for completely uprooted trees within gaps using the Rayleigh test (Zar, 1984). For common species ($n \geq 13$) we tested the null hypothesis that trees (all sites combined) were uprooted (completely or partially) in proportion to their abundance using log likelihood ratio analyses (G-tests) (Zar, 1984). The dbh of completely and partially uprooted trees versus broken and standing trees were compared (all sites combined) using t-tests (Statistical Analysis Systems Institute, 1989).

Rootmass is defined as the summed soil, rocks, and roots of individual trees and snags that were completely uprooted during Hurricane Opal. Root

plates rather than taproots (as often occurs in up-rooted southern pines) influenced rootmass shape in our study area. Data were analyzed to estimate mean rootmass volume (calculated most appropriately as elliptical cylinders), total individual rootmass volume per unit area, mean individual rootmass area (calculated as ellipses), percentage ground area disturbed, and mean maximum pit depth. 'Individual' rootmasses include both single-tree and contiguous, indiscernible rootmasses of > 1 tree. Relationships between independent variables dbh, slope and aspect, and dependent variables rootmass area and volume were explored using simple linear and stepwise mul-

multiple regression. We excluded Opal-felled snags and contiguous rootmasses of > 1 tree for regression analyses.

4. Results

The area of the downburst gaps studied ranged from 0.2–1.1 ha (Table 1). Gap shapes were **irregular** and a variable number of standing trees remained within all gaps. Rayleigh's test indicated that direction of windthrow was nonrandom in four gaps ($p < 0.001$ for gaps 1, 2, 4 and 5; $p < 0.20$ for gap

Table 2

Pre-/post-hurricane relative (percentage") basal area (top line) and density (bottom line) of trees ≥ 12.7 cm dhh in five downburst gaps, Bent Creek Experimental Forest, Asheville, NC (total basal area and density values at bottom)

Species	Downburst gap				
	1	2	3	4	5
<i>A. rubrum</i> L.	11/15 26/30	5/8 13/17	1/2 1/2	< 1/1 2/3	1/2 2/3
<i>Carya</i> spp.	1/1 3/3	3/3 5/6	4/7 7/10	11/15 18/22	1/2 1/1
<i>C. florida</i> L.	1/1 5/7	1/1 5/6	< 1/1 2/3	2; :	–
<i>Fraxinus americana</i> L.	4/4	2/1 –	– –	– –	–
<i>L. tulipifera</i> L.	5/7 5/6	32/34 31/29	5/8 9/11	< 1 2/3	– –
<i>N. sylvatica</i> Marshall	< 1 1/2	–	2/3 8/10	7/11 12/16	2/2 6/8
<i>O. arboreum</i> (L.) DC.	13/17 9/9	1/1 3/4	7/9 16/19	9/10 25/22	7/8 23/22
<i>P. echinata</i> Miller	< 1 < 1	–	6/4 5/3	–	10/14 10/12
<i>Q. alba</i> L.	9/10 7/8	14/11 8/7	22/28 21/23	35/18 18/11	17/24 20/23
<i>Q. coccinea</i> Muenchh.	42/27 23/14	–	20/17 7/3	–	40/28 20/14
<i>Q. falcata</i> Michaux	< 1 < 1	–	–	–	14/11 9/7
<i>Q. prinus</i> L.	13/18 16/19	25/24 18/17	11/11 8/8	19/30 10/14	2/2 4/4
<i>Q. rubra</i> L.	–	9/6 12/10	7/3	–	–
<i>Q. velutina</i> Lam.	4/2 3/2	4/4 3/3	14/6 9/3	18/15 10/8	6/7 5/5
Other	< 1/1 2/2	2/3 2/2	< 1/1 1/2	–	< 1 1/1
Total basal area (m ² /ha)	27/18	37/17	22/12	27/17	22/14
Total density	297/241	272/165	273/193	295/223	272/213

"Percentages may total < 100% due to rounding errors.

Table 3

Mean \pm SD dbh and number (in parentheses) of completely and partially uprooted versus standing or broken trees ≥ 12.7 cm dbh at five downburst gaps created by Hurricane Opal, Bent Creek Experimental Forest, Asheville, NC. p-Value < 0.05 denotes significantly different dbh's between condition classes

Species	Condition class		p-value
	Uprooted	Other	
<i>A. rubrum</i> L. ^a	8.4 \pm 2.6 (19)	8.4 \pm 3.6 (108)	0.9617
<i>Carya</i> spp.	14.0 \pm 7.5 (9)	8.6 \pm 2.5 (29)	0.0017
<i>C. Florida</i> L.	5.7 \pm 0.5 (7)	5.5 \pm 0.4 (29)	0.1972
<i>F. americana</i> L.	12.7 \pm 5.6 (6)	8.2 \pm 2.5 (7)	0.0813
<i>L. tulipifera</i> L. ^a	17.6 \pm 5.2 (43)	13.2 \pm 6.2 (77)	0.0001
<i>N. sylvatica</i> Marshall ^a	5.1 \pm n (1)	7.0 \pm 2.4 (24)	n/a
<i>O. arboreum</i> (L.) DC.	8.1 \pm 1.9 (22)	7.2 \pm 1.6 (71)	0.0338
<i>P. echinata</i> Miller	15.3 \pm 1.2 (5)	11.3 \pm 2.4 (13)	0.0025
<i>Q. alba</i> L.	19.4 \pm 6.7 (31)	12.2 \pm 6.1 (69)	0.0000
<i>Q. coccinea</i> Muenchh. ^a	17.5 \pm 4.6 (56)	17.1 \pm 6.3 (49)	0.6885
<i>Q. falcata</i> Michx.	15.4 \pm 4.7 (5)	13.7 \pm 2.9 (8)	0.4340
<i>Q. prinus</i> L.	18.8 \pm 6.6 (32)	12.8 \pm 6.5 (91)	0.0000
<i>Q. rubra</i> L. ^a	17.0 \pm 7.2 (20)	15.2 \pm 8.7 (13)	0.5254
<i>Q. velutina</i> Lam. ^a	17.6 \pm 4.2 (21)	15.1 \pm 5.0 (16)	0.1135

^aDenotes that the proportion of partially or completely uprooted trees is significantly different from the expected (based on the total proportion of uprooted trees) ± 3 I %, using log-likelihood ratio analysis (G-test) (Zar, 1984).

3). However, the general direction of windthrow differed for each gap (Fig. 1). Spatially discrete disturbed areas and among-gap differences in direction of windthrow suggest that gaps were caused by independent wind events or downbursts during Hurricane Opal.

The wide range of slope steepness and aspect within some gaps and among gaps (Table 1) suggests that topography played a small role in the location of

wind damage where downbursts occurred. However, McNab and Greenberg (in review) found that nearly all windthrows within a 259 ha survey area at BCEF occurred on upper or middle slopes.

Uprooting was the dominant mode of windthrow in all gaps with 17–38% of all live trees completely uprooted and an additional 4–9% partially uprooted (Fig. 2). Fewer than 3% of trees broke at or below 1.8 m, but an additional 5–15% broke above 1.8 m at each gap (Fig. 2), usually with the crown snapped off. Uprooted trees and trees broken ≤ 1.8 m reduced tree basal area (BA) by 30–53% and density by 19–39% in the five downburst gaps (Table 2). There was no evidence of defoliation. Some trees had shed leaves for winter, but most retained live or dead leaves.

A total of 28% of trees were completely or partially uprooted (31% of common species). Most species were uprooted in proportion to their abundance (based on the total proportion of uprooted trees, we 'expected' 31% of individuals within a tested species to be uprooted) regardless of whether they were canopy or understory species (Table 3). Significantly fewer *N. sylvatica* and *A. rubrum* were uprooted than expected. On average, both had small diameters in study gaps. However, several other co-occurring small-diameter species did not exhibit a similar resistance to uprooting (Table 3). Conversely, a disproportionate susceptibility of some species to windthrow was apparent (Tables 2 and 3). Significantly more red oaks (subgenus *erythrobalanus*), including *Q. coccinea*, *Q. rubra* and *Q. velutina* were uprooted than expected. *Q. coccinea* alone lost 44–67% of trees and > 55% of BA in the three sites where it occurred. Basal area of all *Quercus* spp.

Table 4

Rootmass and soil disturbance characteristics caused by trees uprooted during Hurricane Opal at five downburst gaps created by Hurricane Opal, Bent Creek Experimental Forest, Asheville, NC

Measurement	Downburst gap				
	1 (n = 51)	2 (n = 111)	3 (n = 27)	4 (n = 12)	5 (n = 27)
Total volume uprooted in site (m ³ /ha)	200.6	587.2	277	174.9	129.7
Mean (\pm SD) individual ^a rootmass volume (m ³)	4.3 \pm 3.3	6.0 \pm 5.1	3.4 \pm 3.1	2.4 \pm 1.9	2.2 \pm 2.0
Ground surface area disturbed (%)	1.9	4.3	2.7	2.4	1.6
Mean (\pm SD) individual ^a rootmass area (m ²)	4.1 \pm 2.4	4.4 \pm 3.0	3.4 \pm 2.4	3.3 \pm 2.8	2.7 \pm 1.8
Mean (\pm SD) pit depth (m)	0.7 \pm 0.3	1.0 \pm 0.4	0.6 \pm 0.2	0.6 \pm 0.2	0.5 \pm 0.3

^aIndividual^a rootmasses include both single- and multiple-tree rootmasses having contiguous, indiscernable rootmasses.

was reduced by 41–50% and density decreased by 27–47%. At downburst gap 2, where it was abundant, *L. tulipifera* lost 42% of individual trees and 51% of BA. However, for all sites combined it fell in proportion to its total abundance.

Although total BA and density decreased substantially, the relative BA and density of most species did not shift dramatically. Hence, only minor shifts in species dominance patterns were evident (Table 2).

Diameter at breast height was significantly larger ($p < 0.05$) for uprooted trees than non-uprooted trees in about half of the common tree species (Table 3). Despite similar mean dbh's among the canopy-domi-

nant oak species, significantly more large than small-diameter individuals of white oaks (subgenus *leptobalanus*) *Q. alba* and *Q. prinus* (two dominant species that fell in proportion to their abundance) were uprooted, while no such relationship was detected in the frequently-uprooted red oaks (*Q. coccinea*, *Q. rubra* and *Q. velutina*). Among understory species, significantly more large than small-diameter *O. arboreum* were uprooted, whereas no such relationship was detected uprooting-resistant *N. sylvatica* and *A. rubrum*, despite similar mean diameters.

The ground area disturbed by uprooted trees during Hurricane Opal ranged from 1.6–4.3% among the five gaps. Total soil-rock-rootmass volume up-

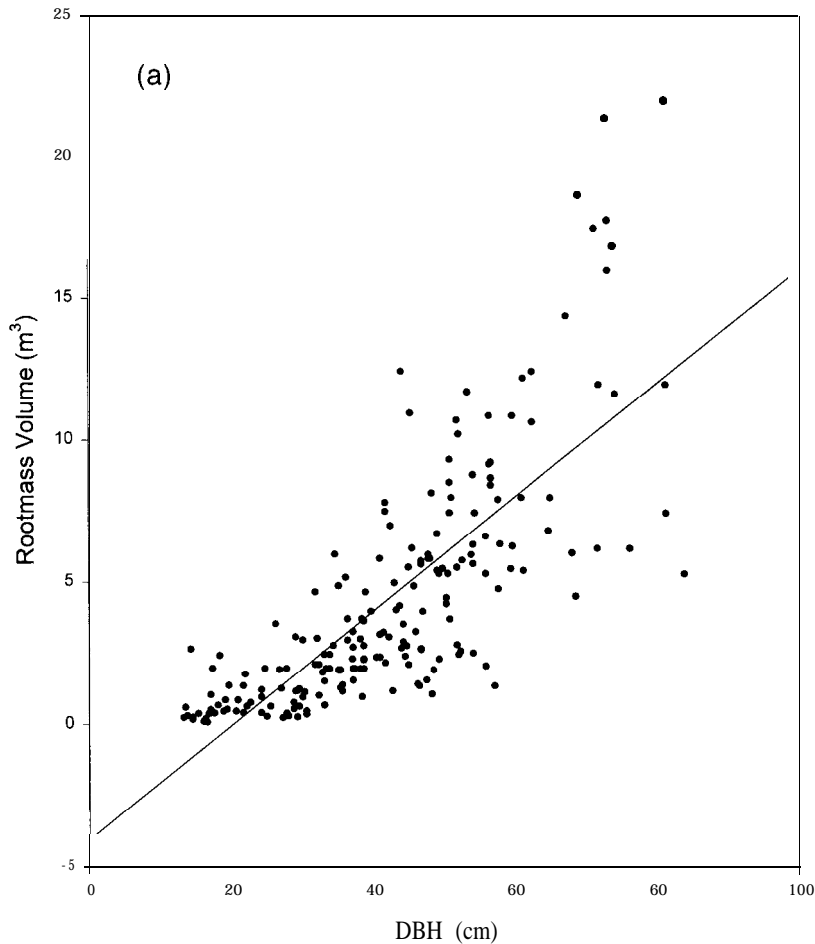


Fig. 3. Rootmass (a) volume (volume = $-4.01 + 20.07$ (dbh), $R^2 = 0.59$); and (b) area (area = $-1.46 + 12.55$ (dbh), $R^2 = 0.59$) as a function of tree diameter at breast height.

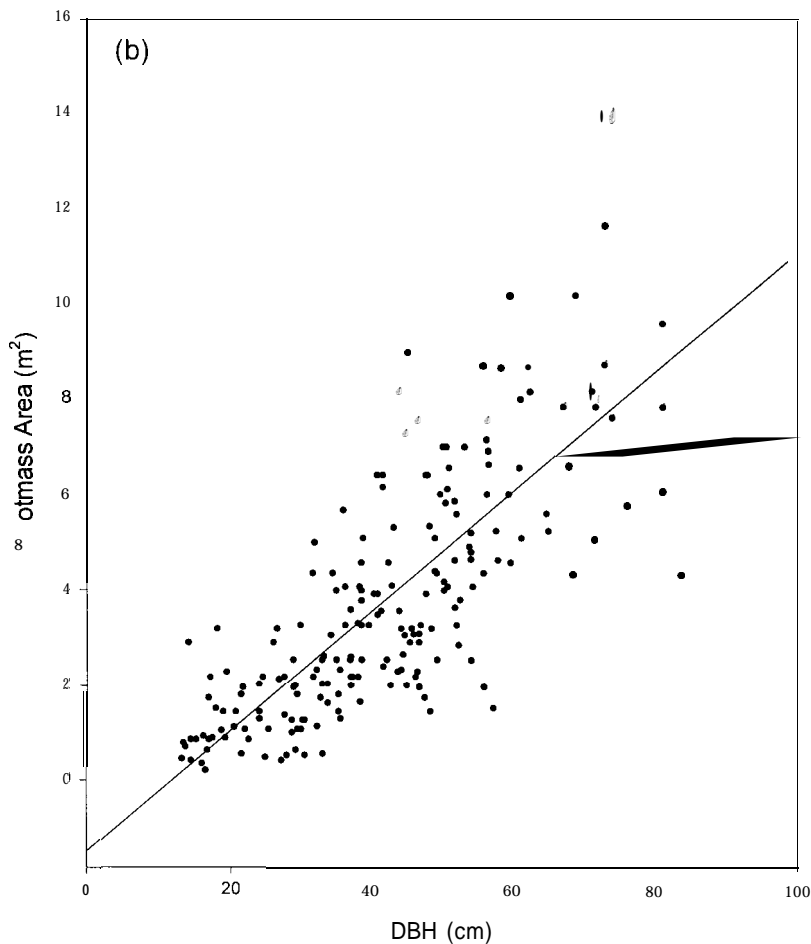


Fig. 3. (continued)

rooted ranged from 130–587 m³/ha (Table 4). Mean individual (including merged rootmasses of > 1 tree) rootmass area ranged from 2.7–4.4 m² among gap; mean individual rootmass volume ranged from 2.2–6.0 m³ among gaps.

Stepwise linear regression indicated that aspect was a significant and slope a nonsignificant predictor of rootmass area and volume. However, plotted data indicated that dbh and aspect were autocorrelated (e.g., tree size is greater on northeast-facing aspects), hence we did not employ aspect in predictive models. Both area and volume of rootmasses were significantly correlated with dbh ($p < 0.001$) (Fig. 3). Hence, simple linear regressions using dbh as the

independent variable were considered the most valid model.

5. Discussion

Among-gap differences in the direction of windthrows suggests that several independent wind events associated with Hurricane Opal occurred within the BCEF. Patterned direction of windthrow is evident of wind direction (Cratkowski, 1956; Falinski, 1978; Foster, 1988b). Air turbulence or secondary effects of neighboring windthrows may have caused some trees to fall in directions other than that of the prevailing wind (Falinski, 1978).

Shallow soils that necessitate spreading, shallow root systems can promote uprooting (Fraser, 1962). Since soil depth generally decreases with increasing slope (Putz et al., 1983) a higher incidence of uprooting might be expected on steeper slopes. However, a wide range of slopes within and among downburst study gaps, and moderately deep soils in each (USDA Forest Service, unpubl. ¹) suggest that these factors did not substantially influence incidence of tree uprooting at BCEF. Romme and Martin (1982) found little relationship between frequency of windthrow and slope position or landform. Cremeans and Kalisz (1988) reported that incidence of uprootings were related to topographic position but independent of soil depth.

Of the total 28% of trees that were windthrown in the five measured downburst gaps at BCEF, nearly all were uprooted. Both the proportion of windthrows and the ratio of uprooted versus broken trees reported in other studies on hurricane-related damage (Foster, 1988b; Gresham et al., 1991; Hook et al., 1991; Peterson and Pickett, 1991; Putz and Sharitz, 1991; Duever and McCollom, 1992) and 'background' tree death in eastern hardwood forests (Romme and Martin, 1982; Runkle, 1982; DeWalle, 1983; Harcombe and Marks, 1983; Clinton et al., 1993) is highly variable.

The mode of windthrow may be influenced by wood properties, architectural and morphologic features such as height:dbh ratios, bole taper, buttressing, rooting depth and crown shape. However, reported differences in *Q. coccinea* windthrows among studies suggest that factors other than wood and architectural properties influence how trees are windthrown. Nearly all windthrown *Q. coccinea* in our study area were uprooted. In contrast, Cremeans and Kalisz (1988) noted a high incidence of breaking or death prior to falling by *Q. coccinea* due to heartrot. Romme and Martin (1982) reported that *Q. coccinea* were 90% more likely to be broken than uprooted in a Kentucky hardwood forest. This suggests that wind and site characteristics play an important role in how trees are windthrown.

Numerous authors report interspecific differences in vulnerability to wind damage (Touliatos and Roth, 1971; Brewer and Merritt, 1978; Glitzenstein and Harcombe, 1988; Gresham et al., 1991; Putz and Sharitz, 1991; Duever and McCollom, 1992; Sharitz et al., 1992), and especially high vulnerability of *Quercus* (Romme and Martin, 1982; DeWalle, 1983; Foster, 1988b; Putz and Sharitz, 1991; Duever and McCollom, 1992; Sharitz et al., 1992). However, only oaks of the red oak group (*Q. coccinea*, *Q. rubra* and *Q. velutina*) were especially vulnerable to uprooting in our study (while no oaks were resistant to uprooting, the white oaks fell in proportion to their abundance). Clinton et al. (1993) reported that *Q. coccinea* created 44% of gaps at the Coweeta Hydrologic Laboratory near Franklin, NC, although it composed only 6% of stand density.

The 'oak decline' disease complex is a possible explanation for the disproportionately high incidence of windthrow in the red oak group at BCEF. Oak decline results from interaction of age, predisposing abiotic stress factors (such as poor site conditions or drought) and the root fungus *Armillaria mellea* Vahl ex Fr. or secondary insect pests to weaken trees. The red oak group, especially *Q. coccinea* and *Q. velutina* are more susceptible to oak decline than the white oak group (Oak et al., 1988, 1996). Several studies suggest a positive relationship between dbh and susceptibility to uprooting of hardwoods (Reiners and Reiners, 1965; Lugo et al., 1983; Putz et al., 1983; Foster, 1988b; Gresham et al., 1991; Hook et al., 1991; Reilly, 1991; Walker, 1991; Sharitz et al., 1992; Sheffield and Thompson, 1992). Peterson and Pickett (1991) found intermediate dbh size classes most likely to uproot. We found that more large-diameter individuals were uprooted than their smaller-diameter counterparts, but only in about half of the common species. Many canopy-dominant species, including the oaks that were especially vulnerable to uprooting (*Q. coccinea*, *Q. rubra* and *Q. velutina*) exhibited no such relationship. Among understory species, *O. urboreum* was commonly uprooted, and significantly more larger-dbh individuals fell than smaller ones. However, *N. sylvatica* and *A. rubrum*, both having similar dbh's to *O. urboreum*, were especially resistant to uprooting, and no relationship between dbh and uprooting was evident.

The prevalence of uprooting in both canopy and

¹ Soil survey of Bent Creek Experimental Forest. On file with: US Department of Agriculture Forest Service, Asheville, NC, 28806.

understory species alike suggests that vulnerability to uprooting was not related to canopy position, but may instead be related to unmeasured architectural or morphological features such as wood strength and rooting depth, and/or to storm characteristics such as wind properties and precipitation.

Such interspecific differences in wind-related mortality can have a profound influence on community composition and structure in areas prone to severe windstorms (Foster, 1988b; Putz and Sharitz, 1991; Sharitz et al., 1992). Despite considerable loss of the dominant *Q. coccinea* in gaps where it occurred only minor shifts in species dominance (relative BA and density) were apparent. However, future species composition will in part depend upon canopy replacement 'by regeneration.

Persistent and cumulative effects of tree uprooting can result in high percentages of land area covered by pit and mound topography (Denny and Goodlett, 1956; Lyford and MacLean, 1966; Armson and Fessenden, 1973; Skvortsova and Ulanova, 1977; Vene-man et al., 1984; Cremeans and Kalisz, 1988). Lyford and MacLean (1966) reported 48% of the ground surface disturbed at a site in Canada. Cremeans and Kalisz (1988) reported $\leq 2.4\%$ of the ground surface disturbed at a site on the Cumberland Plateau in Kentucky. Our study reveals that a single wind event can disturb up to 4.3% of the ground within small areas.

Site and soil factors that influence species composition and rooting habit may affect rootmass area, volume and likelihood of uprooting, hence the proportion of pit and mound topography. Other studies report individual rootmass areas ranging from 0.5–40 m² and pit/mound areas as great as 40 m² (Brewer and Merritt, 1978; Falinski, 1978; Shubayeva and Karpachevskiy, 1983; Beatty and Stone, 1986; Cremeans and Kalisz, 1988). Cremeans and Kalisz (1988) and Putz (1983) report a positive relationship between tree dbh and both rootmass volume and ground area disturbed.

The disturbance regime and driving force in forest regeneration of the Southern Appalachians has been characterized as small-scale gap formation by individual tree death (e.g., Lorimer, 1980; Romme and Martin, 1982; Runkle, 1982; Clinton et al., 1993). This study documents intermediate-sized gaps created by multiple treefalls during a single storm event.

While high-intensity wind events are less frequent and more widely dispersed across the landscape than background individual tree death (Romme and Martin, 1982), they impact a considerable area of the Appalachian landscape within the generation span of most common tree species.

We suggest that wind disturbance acts at a continuous scale in the southern Appalachian mountains. High-intensity winds create forest openings ranging in size from single-tree gaps to several ha or more, with sufficient temporal and spatial frequency to affect a sizeable portion of the southern Appalachian mountain landscape. While single-tree gap dynamics may be a primary and constant disturbance process at the stand scale, multiple-tree openings become apparent at a larger spatio-temporal scale. Further, the 'completeness' of forest openings is variable, and ranges from small, treeless gaps to 'incomplete' gaps where numerous trees remain standing. We suggest that episodic, high-intensity wind events act at variable scales and have a substantial influence on forest structure, species composition, regeneration and microtopography of the southern Appalachians.

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