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Landscape distribution and characteristics of large hurricanerelated canopy gaps in a southern Appalachian watershed

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Abstract

Hurricane-related winds are a major source of disturbance in coastal ecosystems of the southern United States, but their effects on forests in the southern Appalachian Mountains, >400 km inland, have seldom been documented. In October 1995, remnant winds of Hurricane Opal caused windthrow of individual and patches of trees throughout the mountainous region of western North Carolina. USA. The 2-day storm event was accompanied by over 150 mm of precipitation and gusty, predominantly southeasterly winds with peak velocities at low elevations of up to 26 m/s; peak velocities were over 40% greater at high elevations. In a landscape-scale case study, we spatially located the population of large canopy gaps (groups of ≥10 windthrown trees) within a 2400 ha watershed to determine frequency of occurrence on basin and highland landscape types, dimensions, association with topographic features, and direction of treefall as a measure of wind vectors. The distribution of large gaps was not random within the watershed and occurred at an average density of 1 per 39 ha in the basin (elevation < 700 m), which is characterized by hills of low relief and soils with high clay content. In comparison, gap density averaged 1 per 192 ha on the surrounding highlands (elevation >700 m) of high relief and soils with low clay content. Gaps on both landscape types occurred with greater frequency on sites of southeasterly aspect. Sizes of large canopy gaps ranged from 0.1 to 3.9 ha (average 0.7 ha) and were not correlated with landscape type or topography. Gap shape tended to be linear and averaged 2.3 times longer than wide. Direction of mean treefall among gaps was predominantly northwesterly and was strongly associated with aspect on highland, but less so in basin landscape types. Variation in mean treefall direction among gaps suggests that gaps were created by individual gusts of high-velocity, linear winds. A logistic discriminant model based on elevation, azimuth, and slope gradient correctly classified 78% of the study sites. However, gap size and association with topographic features were similar between basin and highland landscapes. Although the southern Appalachian Mountain region is over 400 km from the Gulf of Mexico and the Atlantic Ocean, results from our study suggest that strong winds from hurricane remnants can influence forest structure, with greater impacts on basin than highland landscapes. © 2004 Elsevier B.V. All rights reserved.

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1. Introduction

Remnants of subtropical hurricanes are a relatively rare large-scale form of disturbance to forests of the

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southern Appalachian Mountain region that occur about once every 10–20 years (Nelson and Zillgitt, 1969; Boose et al., 1994; Greenberg and McNab, 1998). This region is situated over 400 km from the coasts of the Atlantic Ocean and Gulf of Mexico, where subtropical hurricanes make landfall. High-velocity winds associated with hurricanes usually dissipate quickly as the storms move inland from

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the coast (Janiskee, 1990; Kaplan and DeMaria, 1995; Bosart et al., 2000). Inland hurricane-related disturbances result primarily from large amounts of precipitation that can produce localized flooding and debris avalanches (Williams and Guy, 1973; Eschner and Patric, 1982). However, reports of extensive tree windthrow from two recent hurricanes-Hugo in September 1989 (Doggett, 1993) and Opal in October 1995 (Greenberg and McNab, 1998; Clinton and Baker, 2000)—indicate that wind associated with remnants of subtropical hurricanes may also be an important and recurring influence on the canopy structure of southern Appalachian forests. In the absence of exogenous disturbances, forests in the southern Appalachians are relatively homogeneous in structure consisting of a multi-aged, multi-strata, closed canopy with occasional small gaps resulting from single-tree mortality (Lorimer, 1980; Barden, 1981; Runkle, 1981).

Periodic hurricanes have been shown to have a strong influence on the structure, composition, and development of forest vegetation in the northern Appalachian Mountains of New England, about 150 km from the Atlantic coast (Foster, 1988; Boose et al., 1994). The differential susceptibility of species to hurricane winds (Parresol and Alemany, 1998) has resulted in conversion of pinelands to hardwooddominated forests in mountainous terrain of New England (Foster, 1988). Greenberg and McNab (1998) have also reported differential susceptibility of tree species to windthrow in southern Appalachian forests. Clearly, high-intensity winds can alter forest canopy structure. Associated changes in microsites such as the formation of pit and mound micro-topography (Clinton and Baker, 2000), higher light levels, or the accumulation of more coarse woody debris can influence bird (Greenberg and Lanham, 2001) and herpetofaunal (Greenberg, 2001), promote invasion of exotic plant species such as oriental bittersweet (Celastrus orbiculatus) (McNab and Loftis, 2002), increase vegetation diversity (Elliott et al., 2002) and influence forest regeneration (Berg, 2002). Previous studies of hurricane effects in the southern Appalachian Mountains have focused on wind-related disturbance within canopy gaps; the spatial distribution, physical characteristics, and topographic association among canopy gaps have never been examined at a landscape scale.

Physiography of the southern Appalachian region consists predominantly of two types of landscapes: (1) low-relief intermontane basins, and (2) high-relief mountainous highlands (Hack, 1982; McNab, 1996). An earlier study revealed that climate, topography, soils, and vegetation differ between basin and highland landscapes (McNab, 1996). That study, however, did not speculate on how the effects of large-scale disturbance events such as catastrophic windstorms might differentially affect the forest structure of the two landscapes. Higher elevation sites should experience greater rates of disturbance due to higher windspeed (Finnigan and Brunet, 1995). Yet, casual observations following Opal indicated the opposite: areas of intense disturbance appeared to occur with greater frequency at lower elevations. Differences in the distribution, frequency, and severity of wind disturbance between basins and highlands would logically be expected to have far-reaching different effects on ecosystem processes between the two types of landscapes.

For this case study, we used a southern Appalachian watershed to examine at a landscape scale the spatial distribution and characteristics of canopy gaps created by hurricane-related winds. Our objectives were to: (1) examine the spatial distribution, frequency of occurrence, and relationship with topographic factors of the population of large canopy gaps occurring in basin and highland landscapes; (2) determine the relationship between canopy gap size, treefall vectors, and topographic factors; and (3) develop a classification model to examine the relative importance and combined influence of topographic factors associated with the occurrence of large canopy gaps on specific sites in the watershed. Other studies have documented the ecological effects of selected canopy gaps formed by Opal (Greenberg and McNab, 1998; Clinton and Baker, 2000; Greenberg, 2001; Greenberg and Lanham, 2001; Berg, 2002; Elliott et al., 2002; Yeakley et al., 2003): ours examines the spatial distribution and characteristics of the *population* of large canopy gaps formed in a single watershed.

Hurricane Opal originated in the southern Gulf of Mexico and made landfall in western Florida on 4 October 1995, with sustained winds of 180 km/h (Graumann et al., 1995). Remnants of Opal moved rapidly northward the next day and the poorly defined center passed over the hilly central Tennessee region

with a sustained wind speed of about 5 km/h near the center. About 240 km to the east, however, in the mountainous region of western North Carolina, winds were strong and variable. There, sustained velocity averaged 27 km/h from the southeast with gusts of up to 93 km/h recorded at a National Weather Service meteorological station (NCDC, 1995) near Asheville. Precipitation associated with the storm in this region occurred over 3 days (October 3–5) and amounted to 15.1 cm.

Our visual assessment suggested a continuous range of canopy damage caused by hurricane-related winds. Although the storm occurred late in the growing season, leaf fall from the deciduous arborescent species, predominantly oaks (Quercus) had not begun. We grouped forest disturbance into two categories: (1) uprooting or stem breakage of scattered single or several trees in a random and unapparent pattern across the landscape or (2) relatively discrete, obvious areas where many trees were uprooted or broken, creating large canopy gaps. Individual windthrows were common throughout the watershed (about 1 per 0.5 ha), and occurred with no obvious pattern from valley floor to ridge top. Large canopy gaps, however, were relatively infrequent and appeared to occur mainly at lower elevations. Less conspicuous tree damage included limb breakage and partial canopy defoliation. A similar pattern of disturbance was documented throughout the Appalachian Mountain region of North Carolina, with disturbance decreasing from southern to northern latitudes (FEMA, 1996).

2. Methods

2.1. Study area

We conducted the study in the Bent Creek Experimental Forest (35.5°N, 82.6°W), a 2400 ha field research facility of the US Forest Service, located in the southern Appalachian Mountains 16 km southwest of Asheville, North Carolina. The Bent Creek watershed drains to the northeast; elevations range from about 600–1200 m. The climate is characterized by cool winters (mean January temperature is 2.3 °C) and warm summers (mean July temperature is 22.3 °C). Annual precipitation averages about

1200 mm at lower elevations and, except for peaks in March and August, is evenly distributed throughout the year. Geologic formations consist of metamorphosed Precambrian gneisses and schists that have weathered to form a maturely dissected relief. Upland soils are generally well-drained, relatively deep (>80 cm), acidic (pH < 5.5), and range from fine to coarse textured. The experimental forest occupies most of the Bent Creek watershed and is situated on two predominant landscape types—the Asheville basin and the Pisgah Mountains highland (Hack, 1982; McNab, 1996). The basin is characterized by low hills with gentle to moderately steep slopes and occupies about 36% (860 ha) of the experimental forest; the highland is mountainous with moderate to steep slopes. The indistinct boundary between the basin and highland is variable and occurs between approximately 700-800 m elevations with a transition that is somewhat associated with slope gradient. Except for lesser maximum elevations, physical features of the Bent Creek watershed are typical of the southern Appalachian Mountain region.

Unmanaged forests of the Bent Creek watershed are characterized by a closed, deciduous canopy that averages about 30 m in height and about 25 m²/ha basal area with multiple sub-strata. Species of Quercus (alba, coccinea, montana, velutina) dominate the overstory on drier sites of slopes and ridges. Mesic valleys and floodplains are dominated by Liriodendron tulipifera. Mid-canopy species include Oxydendron arboreum, Cornus florida, and Nyssa sylvatica. Acer rubrum occurs throughout as a midstory or canopy species. Conifers (Pinus strobus, P. rigida) are minor components of some stands, particularly on sites of less mesic moisture relationships. The shrub stratum consists of evergreen shrubs (Kalmia latifolia on xeric sites, Rhododendron maximum on mesic sites) and tree saplings. Mature forest stands tend to be multi-aged, with the overstory canopy averaging about 125 years of age. In the absence of exogenous disturbance, single-tree mortality creates small canopy gaps for tree recruitment.

2.2. Canopy gaps

Our study design consisted of locating all (i.e. the population) large areas of intense forest disturbance caused by Hurricane Opal in the Bent Creek

watershed. The total census of large gaps was achieved by ground reconnaissance and large-scale (1:12,000) aerial photography. A blowdown site was classified as a large gap if ≥ 10 canopy trees in a contiguous, relatively discrete area were directly or indirectly affected by wind that resulted in uprooting or stem breakage. The 10-tree threshold of a large gap was based on intensive ground survey in several areas of the watershed where all occurrences of n > 1 windthrown trees were inventoried to determine a natural break between extensive and intensive disturbance. An unavoidable consequence of our study design was the potentially small number of large canopy gaps available to characterize and model. An advantage of our study design of mapping all large gaps in the watershed is that estimates of gap frequency as a function of areal sample size may be determined by simulation.

We classified six topographic or shape features of each gap:

- 1. Landscape location was classified in two groups (basin, sites typically <700 m elevation and on hilly terrain with slope gradient <20%; highland, sites usually >700 m elevation and on mountainous terrain with slope gradient >20%).
- 2. Aspect was classified in four quadrants of 90° each (north = $316\text{--}45^{\circ}$, east = $46\text{--}135^{\circ}$, south, west).
- 3. Slope gradient was classified in three categories of steepness (gentle <20%, moderate 20–40%, steep >40%).
- 4. Land form was classified by three types (ridge, slope, or cove).
- 5. Land surface shape was classified by three curvatures (convex, planar, or concave).
- 6. Gap shape was classified in two groups (linear, if the ratio of length to width was ≥ 2 , non-linear, if ratio of length to width was ≤ 2).

In addition, elevation, aspect, and slope gradient of sites where gaps occurred were measured as continuous variables that we later used to develop a classification model. Soil order was determined from a map of soil units (Woodruff, 1991). A geographic positioning system was used to determine the area and reference geographic coordinates at the approximate center of each gap. A Kolmogorov–Smirnov goodness of fit test was used to determine if gap areas were distrib-

uted uniformly from the minimum to maximum sizes inventoried (Zar, 1996).

We measured the direction of treefall ($n \le 15$ trees per gap) at each gap to estimate wind vectors (Wakimoto and Black, 1994). The mean direction of tree windthrow and 95% confidence limits were calculated for each gap (Zar, 1996). This metric may be problematic for some uprooted trees, however, because root system structure and strength may vary among sites in relation to slope gradient, soil physical properties, and prevailing winds, all of which can influence direction of fall (Goodge, 1983; Cannell and Coutts, 1988).

2.3. Gap spatial analysis

We calculated the distance from each gap to its nearest neighboring gap using plotted locations on a topographic map as a simple measure of dispersion. We tested the hypothesis that gaps were distributed randomly throughout the watershed using Ripley's K(d) (Ripley, 1981), a second-order spatial analysis that quantifies point pattern at multiple scales. We replaced K(d) with L(d), a square root transformation that stabilizes the variance and has an expected value of zero (Moeur, 1993). We compensated for edge effects by using a weighting factor according to Moeur (1999). We followed the common convention of restricting the analysis to distances of half the smallest dimension of the 5 km × 6 km study area (Moeur, 1999). An envelope of 95% confidence boundaries of L(d) was determined from deviations of observations from 200 Monte Carlo simulations for distances of 0-2.5 km at intervals of 0.025 km. The observed distribution was considered as clustered when L(d)exceeded the 95% confidence envelope of the Monte Carlo simulations. We used the "RipK" (Moeur, 1999) computer program to calculate L(d).

Finding non-randomly distributed gaps (clustered) for the entire watershed led us to test our second hypothesis that gaps were randomly distributed within each of the two landscape types. We made separate tests for gaps occurring in the basin and for gaps on the highland using an incremental search radius of 0.025 km. We chose a maximum distance of 2.0 km for the basin analysis because that portion of the watershed is generally confined to a $4.0 \text{ km} \times 4.5 \text{ km}$ area. We employed a maximum distance of

2.5 km for the highlands gaps because they were bounded within the same area as the entire watershed.

2.4. Topographic analysis

We used two-way contingency tables and chisquare to initially test for independence of gap frequencies classified by landscape type against categorical topographic variables and gap shape. Because gap frequency and topographic classifications were not dependent on landscape type, we pooled the two data subsets to increase sensitivity (i.e. from greater N) in subsequent tests for the entire watershed. One-way frequency tables of topographic and gap shape categories were tested with chi-square under the assumption of hypothesized equal ratios. We used correlation analyses to determine the relationship of gap size with the topographic variables. Treefall direction was tested for independence with landscape types and categorized topographic variables. Variables expressed as circular, angular units (e.g. treefall direction) were transformed as the cosine of the measured azimuth to obtain a continuous metric for analysis. For developing a classification model, we transformed measured aspect of the site where the gap occurred as a function of an "optimum" aspect (i.e. [cosine (optimum - measured) + 1]). Optimum aspect was the mean azimuth of the population of gap sites occurring in the watershed, which is analogous to selecting northeast as the optimum aspect for tree growth in the northern hemisphere (Beers et al., 1966). The significance level $P \le 0.05$ was used for inclusion of variables in the model. Correlation and regression were used to test for relationships of treefall direction with the continuous topographic variables measured on each canopy gap site. The significance level $P \le 0.05$ was used for chi-square tests of independence.

We used multiple logistic regression to develop a model for examining the collective influence of topographic variables on gap formation and for application as a means of estimating the probability of disturbance at a particular site in the watershed. We used stepwise, backward elimination of variables (Zar, 1996) for model development. Because logistic analysis depends on a binary dependent variable (i.e. occurrence or non-occurrence), an unbiased set of sites without disturbance was obtained using a geographic

information system to sample random non-gap points in the watershed. The number of non-gap sites equaled the number of gap occurrences.

3. Results

3.1. Gap distribution

A total of 30 gaps occurred in the Bent Creek watershed (Fig. 1). Of the 30 gap sites, 22 (73%) occurred in the basin portion of the watershed and 8 (27%) gaps occurred in the highland. Among all gaps, distance to the nearest neighbor averaged 319 m $(\pm 162 \text{ m})$ and ranged from 152 m to 823 m. Graphical analysis of L(d) for all 30 gaps present in the combined basin and highland landscape types of the Bent Creek watershed clearly indicated that gaps were clustered, except at landscape scales less than 0.3 km, where gaps were randomly distributed (Fig. 2, panel A). We found significant differences in gap spatial distribution by landscape type. The 22 gaps within the basin were clustered, except at small and large-scale distances (Fig. 2, panel B). Highland gaps were generally not clustered (Fig. 2, panel C). Our results should be considered conservative (i.e. underestimation of non-random spatial dispersions) because we did not use the improved L(d) estimator developed by Ward and Ferrandino (1999).

3.2. Canopy gap dimensions and soil characteristics

Sizes of the 30 gaps ranged from 0.1 to 3.9 ha and most (21) gaps were 0.5 ha or less; only two were larger than 1.5 ha (Fig. 3). The Kolmogorov–Smirnov test indicated gaps were not uniformly distributed by size (P < 0.001). Mean area of all 30 gaps averaged 0.69 ha (S.E. = 0.16 ha) and did not differ significantly (P = 0.450) between basin and highland landscapes (Table 1). Length of gaps averaged 98.4 m (range 44–196 m) and width averaged 46.7 m (range 21–120 m). The ratio of length to width averaged 2.3 (range 1.2–3.8). Gap area was not significantly correlated with elevation (r = -0.112, P = 0.556), aspect (r = -0.044, P = 0.818), or gradient (r = -0.210, P = 0.265). Soil characteristics were similar between basin and highland gaps, but the latter had sandy loam

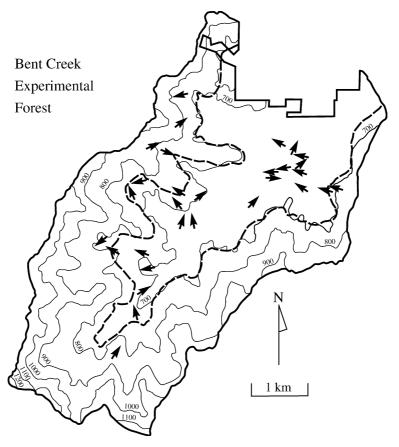


Fig. 1. Distribution of the population of 30 large canopy gaps formed by Hurricane Opal in the Bent Creek watershed in the southern Appalachian Mountains. Arrow symbols indicate the location and mean direction of windthrown trees at each gap site. The dashed line indicates the approximate boundary between basin and highland landscape types.

soil texture and lacked clay accumulation in the B-horizon. The remnants of Hurricane Opal created a total of 13.5 ha of large canopy gaps in the basin (mean density of 1 per 39 ha) and 7.1 ha in the highland (mean density of 1 per 192 ha).

3.3. Canopy gap topographic characteristics and frequency

Two-way contingency tests indicated that gap occurrence was independent of landscape type and quadrant direction (P = 0.399), steepness (P = 0.101), landform (P = 0.062), or surface shape (P = 0.518) (Table 2). We then pooled the basin and highland data sets to test for differences of gap occurrence in relation to topographic variables for the watershed as a whole. On the combined landscapes,

chi-square analysis indicated that gap occurrences were not distributed uniformly among four categories of aspect (P = 0.002), and occurred more frequently on east- or south-facing sites (n = 24) than on sites facing north or west (n = 6). Similarly, gaps occurred more frequently on slope or cove landforms than on ridges (P = 0.002), and on planar surface shapes compared to convex or concave surfaces (P = 0.001) (Table 2). In addition, gap shape was independent of landscape type (P = 0.207), but tended to be linear (P = 0.028) when pooled across the combined basin and highland landscapes.

3.4. Direction of damaging winds

We inventoried 402 windthrown trees (297 in the basin and 105 on the highland) at the 30 gaps.

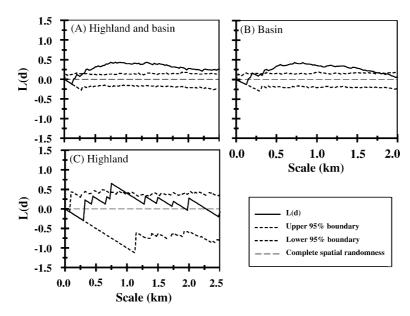


Fig. 2. Ripley's L(d) results for the analysis of spatial distribution of the population of large canopy gaps associated with Hurricane Opal in: (A) combined highland and basin landscapes, (B) basin landscapes only, and (C) highland landscapes only of the Bent Creek watershed. Significant clustering is indicated by a deviation of L(d) above the confidence envelope; repulsion is indicated below.

The quadrant of mean treefall direction at the gap sites was independent of landscape type (P = 0.0399), which allowed pooling of the basin and highland data sets. Using pooled landscapes, a test of equal ratios

indicated that direction of treefall among gaps was significantly greater (P = 0.002) to the north and west quadrants (n = 25) than to the south and east quadrants (n = 5). Regression analysis indicated that the

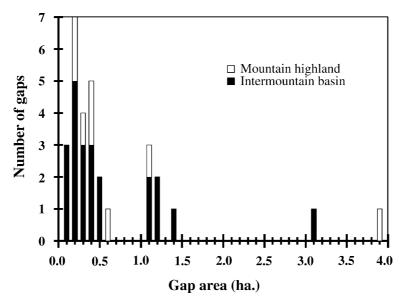


Fig. 3. Distribution by size and landscape type of the population of large canopy gaps associated with Hurricane Opal in the Bent Creek watershed.

Table 1 Means (\pm S.E.) and associated *t*-test statistics of physical and soil characteristics of the population of large canopy gaps formed by Hurricane Opal in basin and highland landscapes of the Bent Creek watershed, North Carolina

Characteristics	Basin	Highland	t-Value	<i>P</i> -value ^a 0.011
Gap sites, n	22	8	6.533	
Length (m)	91.2 ± 11.9	109.1 ± 22.6	-0.766	0.457
Width (m)	52.0 ± 10.6	38.8 ± 5.1	0.954	0.358
Length to width ratio	2.0 ± 0.27	2.70 ± 0.30	-1.602	0.133
Area (ha)	0.61 ± 0.1	0.89 ± 0.4	-0.765	0.450
Perimeter (m)	397 ± 66	494 ± 132	-0.717	0.479
Predominant soil family ^b	Hapludults	Dystrudepts	na	na
Solum thickness range (cm) ^b	36–168	41–180	na	na
Depth to clay horizon (cm) ^b	13-132	na ^c	na	na
Predominant soil texture ^b	Clay loam	Sandy loam	na	na

^a t-Test of hypothesized equal ratios of counts or difference between basin and highland means.

cosine transformed mean treefall direction of gaps was not associated with transformed site azimuth on the highland ($r^2 = 0.162$, P = 0.323), basin ($r^2 = 0.007$, P = 0.718), or combined landscapes ($r^2 = 0.015$,

P=0.522). The plotted 95% confidence limits of the mean windthrow direction at a gap typically encompassed azimuths of approximately 60° , indicating relatively little variability in direction of treefall

Frequency by topographic categories and landscape type of the population of large canopy gaps created by Hurricane Opal in the Bent Creek watershed, North Carolina

Topographic or shape class	Landscape type ^a		P-value	Combined landscapes ^b	P-value
	Basin	Highland			
Aspect quadrant					
North	1	0	0.399	1	0.002
East	8	4		12	
South	9	3		12	
West	4	1		5	
Slope steepness class					
Gentle	12	1	0.101	13	0.273
Moderate	7	4		11	
Steep	3	3		6	
Landform class					
Ridge	1	1	0.062	2	0.002
Slope	10	0		10	
Cove	11	7		18	
Surface shape class					
Convex	4	1	0.518	5	0.001
Planar	16	5		21	
Concave	2	2		4	
Gap shape class					
Linear	14	7	0.207	21	0.028
Non-linear	8	1		9	

^a Two-way test of cell counts.

^b Obtained from map and soil unit descriptions.

^c Not applicable.

^b One-way test of hypothesized equal ratios.

within gaps. The standard deviation of individual treefall azimuth within gaps was similar ($\pm 16.0^{\circ}$) between basin and highland (P=0.858) landscapes.

3.5. Probability model

We developed a logistic function to estimate the probability of major canopy disturbance as a function of common topographic variables. Earlier analyses indicated that gap frequency was significantly associated with classes of landscape type and easterly to southerly quadrants, which is apparent from a scatter plotting of gap occurrence in relation to elevation and aspect (Fig. 4). A number of multiple logistic models were evaluated to determine the combined effect of the measured variables on the probability of occurrence of a canopy gap. The most parsimonious and highly significant formulation for predicting the probability of a canopy gap at a particular site was a combination of three continuous topographic variables:

$$\begin{split} \text{logit}_{G} &= 10.590 - 0.020 (\text{ELE}) \\ &+ 1.684 (\cos[143\text{-ASP}] + 1) \\ &+ 0.078 (\text{GRAD}) + \epsilon \end{split} \tag{1}$$

where $logit_G$ is the logit form of the probability of a canopy gap, ELE the site elevation (m), cos[143-ASP]

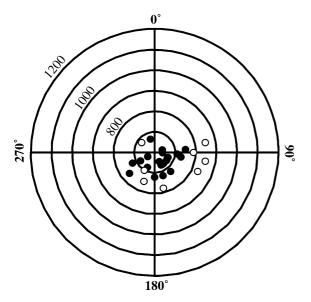


Fig. 4. Occurrence of the population of large canopy gaps in relation to elevation and site azimuth in basin (●) and highland (○) landscapes in the Bent Creek watershed.

the cosine of site aspect with an optimum of 143° (explained earlier as the mean aspect of all gap sites), GRAD the site slope gradient (%), and ε the error consisting of unexplained variation. All variables in the model were highly significant (P < 0.003) except for GRAD (P < 0.032); interactions were not significant.

A plot of sensitivity versus 1 – specificity for all cutpoints indicated an optimum probability cutoff of about 0.53. Area under the receiver operating characteristic curve was 0.87, which suggests the model has excellent discrimination (Hosmer and Lemeshow, 2000), Application of the model to the site data from the 30 gaps resulted in an overall classification accuracy of 78%. Model sensitivity (sites with gaps) was 83%; specificity (sites without gaps) was 73%. Application of the model to a hypothetical site in the Bent Creek watershed with values of topographic variables equal to the means of the 30 gaps (elevation = 712 m, aspect = 143°, gradient = 26%) resulted in a probability value of 0.851. Solving the logistic model for selected values of aspect and elevation, with gradient held constant at its mean value, indicates that the potential probability of large gap occurrence is greatest at lowest elevations and for easterly to southerly aspects (Fig. 5). The estimated probability of gap occurrence is reduced as gradient decreases, as illustrated in Fig. 5 for two selected values on sites of north aspects.

4. Discussion

Remnant winds associated with Hurricane Opal created relatively few large canopy gaps in the 2400 ha watershed. The watershed-level probability of a hurricane-related, large canopy gap occurring at a random site was low: <1 in 100 (i.e. 20.6 ha of gaps/2400 ha in watershed). Gaps, however, occurred with disproportionately greater frequency in basin compared to highland landscapes. Approximately 36% of the watershed consists of basin landscapes, but 73% of the gaps occurred there. None of the large gaps on the highland landscape occurred on upper slopes or ridges; most were situated at lower elevations near the basin transition zone. Other observations (data on file) of numerous single windthrown trees on slopes and ridges at high elevations (>1000 m)

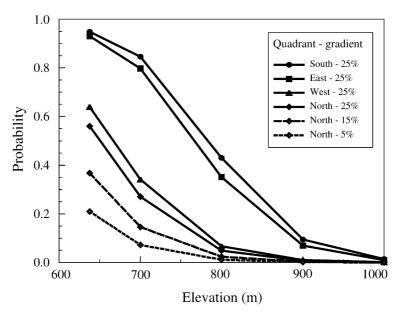


Fig. 5. Estimated probability of occurrence of large canopy gaps associated with Hurricane Opal in relation to elevation, midpoints of four quadrant classes (i.e. north = 0°), and selected slope gradients in the Bent Creek watershed. The estimated probabilities are derived from Eq. (1).

suggest that strong winds occurred throughout the watershed. However, the absence of patches of intense disturbance at high elevations in the study area, where velocities were estimated as about 40% greater than at lower elevations (Grant Goodge, November 1998, pers. commun.), suggests that the background wind velocity alone was not the cause of large gaps.

Average gap size was not correlated with any of the measured topographic variables, which suggests that wind characteristics were the primary controlling mechanism of disturbance. Gaps in the Bent Creek study area ranged up to 3.9 ha, which were smaller than gaps caused by Opal in similar mountainous terrain of the Coweeta watershed, about 100 km southwest of Bent Creek where wind velocity was higher (Graumann et al., 1995). At Coweeta, winds from Opal formed gaps ranging from single tree to 10 ha (Elliott et al., 2002). In the Nantahala National Forest, adjacent to Coweeta, about 15% of the forested area was severely affected (William Culpepper, pers. commun. in Clinton and Baker, 2000).

The differential rate of gap occurrence, 1 per 39 ha in the basin and 1 per 192 ha in the highlands, resulted in a greater heterogeneity of forest canopy structure at lower elevations of the watershed. Most studies of

hurricane damage to forests in relation to topography have been designed to characterize the range of disturbance—not the spatial relationship—of the areas of severe damage. Our results generally agree with those of Reilly (1991) and Foster and Boose (1992), who found greater hurricane disturbance to vegetation at lower elevations. Others, however, have found that hurricane damage can occur throughout the landscape (Bellingham, 1991; Brokaw and Grear, 1991) and varies by species (Parresol and Alemany, 1998). We, too, observed hurricane-related disturbance at higher elevation in the Bent Creek watershed, but canopy gaps were small and consisted primarily of one- and two-tree blowdowns.

The logistic regression analysis indicated that the probability of gap formation was strongly associated with site topographic characteristics, particularly direction of exposure. Eighty percent of gaps associated with Opal in the study area occurred on east and south facing slopes, which is consistent with wind fields generated by the counterclockwise rotation of winds around the low-pressure center of the storm that passed west of the study area. Similar findings were reported for Opal-related disturbance in the Coweeta watershed (Clinton and Baker, 2000; Elliott et al.,

2002; Yeakley et al., 2003). Other studies of hurricane effects on forests have also found increased damage on windward slopes compared to leeward slopes (Bellingham, 1991; Reilly, 1991; Foster and Boose, 1992).

A minor limitation of our case study of the population of gaps in the Bent Creek watershed is the inability to estimate the probability of their areal occurrence. Because we neither sampled replicated areas of specific sizes in the watershed nor examined other watersheds of varying size in the region, our model is not appropriate for estimating the probability of gap occurrence as a function of unit area. Gap occurrence in relation to area examined could be studied, however, by using the spatially defined data set from the watershed to simulate various sampling schemes.

Treefall direction provided evidence of the direction of damaging winds within the watershed. In the study area, treefall was predominantly to the west and north, indicating that damaging winds originated from the east and south: in the Bent Creek watershed, these are the areas bounded by higher ridgelines. Examination of the wind vectors at the gap sites suggests high variability in source direction of the damaging winds. Some treefall vectors, however, could have been affected by root system characteristics, which can influence the direction of treefall (Goodge, 1983; Cannell and Coutts, 1988). The somewhat higher correlation of treefall direction with aspect of gap sites on the highland suggests that some damaging winds originated at higher elevations or were modified by land forms. We suggest that embedded cells of high-velocity winds at higher elevation developed turbulence when encountering a ridgeline and caused windthrow in the aspect direction as wind traveled down the opposite slope. We found opposing mean direction of treefall at several adjacent gaps, particularly in the basin landscape (Fig. 1), which suggests that individual wind events were responsible for the disturbances, confirming our previous observations on a small subsample of study sites (Greenberg and McNab, 1998).

In a previous study, we used the term "downburst" when referring to causes of intense disturbance in the study area (Greenberg and McNab, 1998). However, the wind phenomena that caused the disturbance at the study sites were unlike conventional downbursts (Fujita, 1985; Goodge, 1983) that typically originate

from summer thunderstorms. The variable and localized intense forest disturbance we observed has been reported elsewhere, particularly in association with hurricane damage near coasts (Foster, 1988; Brokaw and Grear, 1991; Putz and Sharitz, 1991; Wakimoto and Black, 1994; Platt et al., 2000). Fujita (1993) described as microbursts the "...damage causing peak winds ... that were far stronger than ordinary peak gusts experienced along the path of [Hurricane] Andrew." Platt et al. (2000) concluded that microbursts associated with Hurricane Andrew (as it encountered forests in extreme southern Florida) created numerous, variable-sized linear patches of windtrees. Wakimoto and Black hypothesized that surface winds of hurricanes are slowed by friction with Earth's surface, which allows cells of higher speed winds in the upper atmosphere to reach ground level and cause local disturbances. Observations by Wurman and Winslow (1998) of intense small-scale (sub-kilometer) linear groundlevel turbulence in the eyewall of Hurricane Fran tend to support the conclusions of Wakimoto and Black (1994), and are similar to the scale of disturbances we observed. Clearly, additional observations and data are needed to improve our understanding of the localized turbulent wind cells that appear to be associated with remnants of some hurricanes.

What makes our study unique among investigations of landscape-scale damage to forests from hurricanes is that we examined only the discrete areas of intensive disturbance that were embedded within a large watershed exhibiting extensive disturbance. Others have noted differential levels of forest disturbance within hurricane-affected areas, but have examined damage to vegetation in relation to topography using randomly located plots for quantifying the range of disturbance severity (Bellingham, 1991; Brokaw and Grear, 1991; Putz and Sharitz, 1991; Reilly, 1991), or a subset of disturbed sites that extended over a range of small to large sizes (Clinton and Baker, 2000). We can, therefore, make few specific comparisons with results of other studies. Also, most studies of hurricane damage in relation to mountainous terrain have been made on Caribbean islands where soils and vegetation species were very different, and where wind velocity was much greater than we observed (Brokaw and Walker, 1991). It seems clear, however, that the complex mountainous terrain of the study area was an

important contributing factor to the pattern of landscape damage in the Bent Creek watershed.

In summary, wind damage to forests resulting from remnants of subtropical hurricanes is a relatively rare landscape-scale disturbance in the southern Appalachian Mountains. Our study focused on the size distribution and landscape location of large canopy gaps in the Bent Creek watershed that were formed by the windthrow of >10 contiguous trees during the distant passage of Hurricane Opal, in early October 1995. Storm-related disturbance in the study area was manifested by blowdown ranging from single trees throughout the watershed to formation of a small number (n = 30) of large gaps ranging in size from 0.1 to 3.9 ha. In many large gaps, their linear shape and consistent direction of treefall suggests that blowdown was caused by a single gust of high-velocity winds, similar to the straight-line winds characteristic of microbursts. However, mean treefall direction varied among gaps, suggesting multiple, individual episodes of microburst-like winds. Gaps were not randomly distributed across the landscape, but occurred with greater frequency on southeast-facing slopes at low elevations. Gap size was not associated with topographic variables. Limited implications for management can be gleaned from this case study, but when combined with results of other hurricane-related investigations in the Bent Creek watershed on coarse woody debris (Greenberg and McNab, 1998), reptile and amphibian dynamics (Greenberg, 2001), bird assemblages (Greenberg and Lanham, 2001), and forest regeneration (Berg, 2002) it becomes apparent that wind is a landscape-scale form of disturbance in forest ecosystems of the southern Appalachians that warrants greater study.

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References

- Barden, L.S., 1981. Forest development in canopy gaps of a diverse hardwood forest in the southern Appalachians. Oikos 37, 205–209
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. For. 64, 691–692.
- Bellingham, P.J., 1991. Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. Biotropica 23, 427–439.
- Berg, E., 2002. Hurricane effects on forest understory vegetation in the southern Appalachians. PhD Dissertation. Clemson University, Clemson, SC, 111 pp.
- Boose, E.R., Foster, D.R., Fluet, M., 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecol. Monogr. 64, 369–400.
- Bosart, L.F., Velden, C.S., Bracken, W.E., Molinari, J., Black, P.G., 2000. Environmental influences on the rapid intensification of Hurricane Opal (1995) in the Gulf of Mexico. Mon. Weath. Rev. 128, 322–352.
- Brokaw, N.V.L., Grear, J.S., 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. Biotropica 23, 386–392.
- Brokaw, N.V.L., Walker, L.R., 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23 (4a), 442–447.
- Cannell, M., Coutts, M., 1988. Growing in the wind. New Sci. 117, 42–46.
- Clinton, B.D., Baker, C.R., 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. For. Ecol. Manage. 126, 51–60.
- Doggett, C.A., 1993. A method to assess large-scale forest damage: a case study. S. J. Appl. For. 17 (4), 197–199.
- Elliott, K.J., Hitchcock, S.L., Krueger, L., 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. J. Torrey Bot. Soc. 129 (1), 48–59.
- Eschner, A.R., Patric, J.H., 1982. Debris avalanches in eastern upland forests. J. For. 80 (60), 343–347.
- Federal Emergency Management Agency (FEMA), 1996. Hurricane Opal fuels management assessment. Unpublished report prepared in response to Major Disturbance Declaration FEMA-1073-DR North Carolina, February 22, 1996, 34 pp. with 4 appendices.
- Finnigan, J.J., Brunet, Y., 1995. Turbulent airflow in forests on flat and hilly terrain. In: Coutts, M.P., Grace, J. (Eds.), Wind and Trees. Cambridge University Press, Cambridge, pp. 3–40.
- Foster, D.R., 1988. Species and stand response to catastrophic wind in central New England, USA. J. Ecol. 76, 135–151.
- Foster, D.R., Boose, E.R., 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. J. Ecol. 80, 79–98.

- Fujita, T.T., 1985. The Downburst: Microburst and Macroburst. Report of Projects NIMROD and JAWS. Satellite and Mesometeorology Research Project, Research Paper Number 210. University of Chicago.
- Fujita, T., 1993. Damage survey of Hurricane Andrew in south Florida. Storm Data 34 (8), 25–29.
- Goodge, G.W., 1983. Tornado or "microburst". The State Climatologist 7 (3) 23–31. National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC.
- Graumann, A., Kobar, J., Lott, N., Ross, D., Ross, K., Ross, T.,
 Sittel, M., 1995. Hurricane Opal. General Technical Report 95US Department of Commerce, National Oceanic and Atmospheric Administration, National Climatic Data Center,
 p. 18.
- Greenberg, C.H., McNab, W.H., 1998. Forest disturbance in hurricane-related downbursts in the Appalachian Mountains of North Carolina. For. Ecol. Manage. 104, 179–191.
- Greenberg, C.H., 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. For. Ecol. Manage. 148, 135–144.
- Greenberg, C.H., Lanham, J.D., 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. For. Ecol. Manage. 154, 251–260.
- Hack, J.T., 1982. Physiographic divisions and differential uplift in the Piedmont and Blue Ridge, Geological Survey Professional Paper No. 1265. US Department of Interior. Geological Survey, Washington, DC, p. 49.
- Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, 2nd ed. Wiley, New York, NY, p. 373.
- Janiskee, R.L., 1990. Storm of the century: Hurricane Hugo and its impact on South Carolina. Southeast. Geogr. 30, 63–67.
- Kaplan, J., DeMaria, M., 1995. A simple empirical model for predicting the decay of tropical cyclone winds after landfall. J. Appl. Meteorol. 34, 2499–2512.
- Lorimer, C.G., 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61 (5), 1169–1184.
- McNab, W.H., 1996. Classification of local- and landscape-scale ecological types in the southern Appalachian Mountains. Environ. Monitor. Assess. 39, 215–229.
- McNab, W.H., Loftis, D.L., 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian Mountains, USA. For. Ecol. Manage. 155, 45–54.
- Moeur, M., 1993. Characterizing spatial patterns of trees using stem-mapped data. For. Sci. 39, 756–775.
- Moeur, M., 1999. User's Manual for Ripley's K Analysis. USDA Forest Service, Rocky Mountain Research Station, Unpublished.

- National Climatic Data Center (NCDC), 1995. Local Climatological Data, Asheville, NC (Asheville Regional Airport).
 October 1995. US Department of Commerce, National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC.
- Nelson, T.C., Zillgitt, W.M., 1969. A Forest Atlas of the South. USDA Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, p. 27.
- Parresol, B.R., Alemany, S., 1998. Analysis of tree damage from Hurricane Hugo in the Caribbean National Forest, Puerto Rico.
 In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference, Clemson, SC, February 25–27, 1997. General Technical Report SRS-20. US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 599–603.
- Platt, W.J., Doren, R.F., Armentano, T.V., 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, 43–50.
- Putz, F.E., Sharitz, R.R., 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. Can. J. For. Res. 21, 1765–1770.
- Reilly, A.E., 1991. The effects of Hurricane Hugo in three tropical forests in the US Virgin Islands. Biotropica 23, 414–419.
- Ripley, B.D., 1981. Spatial Statistics. Wiley, New York, p. 252.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62, 1041–1051.
- Wakimoto, R.M., Black, P.G., 1994. Damage survey of Hurricane Andrew and its relationship to the eyewall. Bull. Am. Meteorol. Soc. 75, 189–200.
- Ward, J.S., Ferrandino, F.J., 1999. New derivation reduces bias and increases power of Ripley's L index. Ecol. Modell. 116, 225–236.
- Williams, G.P., Guy, H.P., 1973. Erosional and depositional aspects of Hurricane Camille in Virginia, 1969. US Geological Survey Professional Paper 804, p. 80.
- Woodruff, J., 1991. Soil map of a portion of the Pisgah District of the Pisgah National Forest. Unpublished report and map (1:12,000) on file at: US Department of Agriculture, Forest Service, Pisgah National Forest, Asheville, NC.
- Wurman, J., Winslow, J., 1998. Intense sub-kilometer-scale boundary layer rolls observed in Hurricane Fran. Science 280, 555–557.
- Yeakley, J.A., Coleman, D.C., Haines, B.L., Kloeppel, B.D., Meyer, J.L., Swank, W.T., Argo, B.W., Deal, J.M., Taylor, S.F., 2003. Hillslope nutrient dynamics following upland riparian vegetation disturbance. Ecosystems 6, 154–167.
- Zar, J.H., 1996. Biostatistical Analysis, 3rd ed. Prentice-Hall, Upper Saddle River, NJ, p. 662.