

# Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses

Barton D. Clinton\*, Corey R. Baker

USDA Forest Service Southern Research Station, Coweeta Hydrologic Laboratory 3160 Coweeta Lab Road, Otto, NC 28763, USA

Received 30 October 1998; accepted 12 February 1999

---

## Abstract

We characterized pit and mound (PM) topography resulting from catastrophic wind in the Coweeta Basin, and located 48 **PMs** across a variety of forest types. Our measurements included pit length, width, and depth; and mound height, thickness, and width. Species of fallen trees were identified, and DBH (diameter at breast height, 1.37 m) was measured for biomass determination. We identified five distinct microsites at each PM: mound face, mound top, pit bottom, pit-wall, and intact forest floor. On each microsite, we measured photosynthetically active radiation (PAR), soil temperature, and soil moisture, and took soil samples from four microsites (intact forest floor, pit wall, pit bottom, mound top) to determine carbon and nitrogen concentrations.

**Treefall** direction was marginally non-random. Three PM dimensions were significantly related to fallen tree biomass: mound width; mound height; and pit width. Other relationships failed because (1) rooting depth of the fallen tree was not necessarily proportional to tree size; and (2) trees that fell striking other trees often slid back into the pit, altering its dimensions. PAR was highest at mound top ( $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and lowest in pit bottom ( $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Mean soil temperature varied  $\approx 3^\circ\text{C}$  across microsites, and soil moisture ranged from 24% on the mound top and mound face to 34% in the pit bottom. Nitrogen and carbon concentrations were significantly higher on the forest floor ([N] = 0.23%; [C] = 4.73%) than on the other three microsites ([N] = 0.08-0.10%; [C] = 1.4-2.2%). Over time, soil nutrition and microsite instability, due to erosion and settling, may be the most influential factors determining rates of vegetative establishment in **PMs**.

We characterized initial vegetative recovery in 27 **blowdown** sites. Trees were placed in one of two damage classes: direct wind damage (direct); and damage due to the fall of another tree (indirect). Basal and/or bole sprouting, and live or dead crowns were noted. **Blowdown** areas ranged from 181 to 4043  $\text{m}^2$  and averaged 1175  $\text{m}^2$ . Mean diameter of indirectly damaged trees was 50% of the mean for trees directly damaged, but both had similar minimum diameters. Overall, the biomass of indirectly damaged trees accounted for <10% of total biomass but 33% of the total number of stems. Of the indirectly damaged trees, 38% were topped, 82% exhibited basal or bole sprouting, and 21% had live crowns. By contrast, of the directly damaged trees, only 5% were topped, <50% were sprouting, and only 11% had live crowns. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Microtopography; Pits and mounds; Windthrow; Microclimate; Forest disturbance; Succession

---

\*Corresponding author. Tel.: +1-828-524-2128 ext. 124; fax: +1-828-369-6768.

E-mail address: [bclinton@sparc.ecology.uga.edu](mailto:bclinton@sparc.ecology.uga.edu) (B.D. Clinton)

## 1. Introduction

Forest communities, in part due to disturbance, are heterogeneous at both large and small scales, and these differences influence plant community development (Bazzaz, 1983; Halpern et al., 1990). Disturbance takes a variety of forms and occurs at varying temporal and spatial scales. At large spatial scales, wind is one primary agent of natural disturbance in many forest ecosystems, although the frequency and magnitude of wind events vary among and within forest types. For example, in a Costa Rican rain forest, Lawton and Putz (1988) found that 80% of forest openings were wind-induced. Similarly, Barden (1981) found that wind contributed to 97% of canopy gap formation in a mature mixed-mesophytic forest (see Braun, 1950) in the southeastern USA. Clinton et al. (1993), however, found that in a mature southern Appalachian mixed hardwood forest, wind accounted for only 11% of tree mortality.

Uprooting, or treefall, is a major source of disturbance in most forest ecosystems (Cooper, 1913; Stearns, 1949; Webb, 1958; Wright, 1974; Pritchett, 1979); and, in both temperate and tropical forests, is an important process in the creation of micro-topographic variation (Peterson et al., 1990). It has a substantial influence on the immediate physical environment by moving large rocks (Lutz, 1960), inverting soil horizons (Mueller and Cline, 1959; Schaetzl, 1986; Beatty and Stone, 1986), exposing buried seeds (Putz, 1983; Putz and Appanah, 1987), and forming areas of pit and mound PM topography (Lyford and Maclean, 1966). Micro-topographic variation provides important micro-sites for plant establishment (Sousa, 1984; Pickett and White, 1985; Belsky, 1986; Uhl et al., 1988). However, there is conflicting information in the literature about which microsites provide the most suitable conditions. For example, Goodlett (1954) and Lyford and Maclean (1966) reported that in hardwood forests of the northeastern US, and in spruce forests of Canada, respectively, regeneration in pits almost never occurs. Conversely, Peterson and Pickett (1990) found the greatest species richness, total biomass, and stem density in pit microsites following hurricane damage in the northeast US. Certainly, these observed differences are forest-type and disturbance-intensity dependent, i.e. some species are better adapted to or tolerant of a variety of microsite conditions.

Compared to the surrounding forest, PMs are relatively small; although they can play key roles in determining a regenerating forest community's composition and structure (Beatty, 1984). The variation in soil moisture and temperature between pit and mound, alone, can influence forest composition (Smallidge and Leopold, 1984). In addition, pit characteristics can affect plant development and species dispersal (Thompson, 1980). The presence of pits increase the localized area's potential for seasonal flooding, increase litter accumulation, elevate concentrations of nutrients, increase soil moisture levels; but it may moderate pH levels and lower potential for frost heaving (Smallidge and Leopold, 1984; Beatty and Stone, 1986). Pits, mounds, and downed trees all provide protection of regenerating plant species against harsh microclimatological conditions, e.g. desiccating winds, and browsing where there are high densities of mammalian herbivores (Peterson and Pickett, 1995).

Historical analysis of hurricane paths and other windstorms in the southern Appalachians (Greenberg and McNab, 1998, *sensu* Neumann, see p. 4) suggests that since 1971, 14 storms have occurred in the region at intervals of 1-24 years. The most recent significant event was Hurricane Opal, which affected the region on October 4-5, 1995, and caused extensive disturbance to both the canopy and forest floor in the Coweeta Basin. Creation of PM micro-sites was widespread across the region and in places resulted in areas of blowdowns sometimes many hectares in size. As much as 15% of the Wayah Ranger District of the Nantahala National Forest was severely affected by this storm (district silviculturist B. Culpepper, personal communication). The purpose of this study was to: (1) describe gaps created by windfall (e.g., overall size, species involved); (2) characterize features of PM disturbance; (3) quantify the microclimate of distinct microsites within PM; and (4) characterize initial sprout responses on blowdown sites.

## 2. Methods

### 2.1. Study site

This study was conducted at the Coweeta Hydrologic Laboratory, in the Blue Ridge physiographic

province of western North Carolina... The Coweeta basin is  $\approx 2100$  ha, ranges in elevation from 700 to 1600 m, and has steep terrain. Mean annual precipitation ranges from 1800 mm at low elevations to over 2300 mm at high elevations;  $<5\%$  falls as snow or ice. Mean annual temperature is  $13^{\circ}\text{C}$  and typically ranges from  $-4^{\circ}\text{C}$  in January to  $19^{\circ}\text{C}$  in July and August (Swank and Crossley, 1988). The basin contains three main ridges running generally in an east-west direction. The storm track of Hurricane Opal was northerly, and the center passed within 180 km west of the basin (Mayfield, 1995). Total rainfall through September for 1995 was only slightly more than the long term mean through September, but rainfall for August and September prior to the storm was 20% higher than the long term totals for those months. In addition, 107 mm of rain fell during the 24 h immediately prior to the storm. Officials at nearby National Oceanographic and Atmospheric Administration (NOAA) stations recorded wind gusts at  $26\text{ m s}^{-1}$  at low elevations and at  $37\text{ m s}^{-1}$  at high elevations (Graumann et al., 1995). Locally, sustained wind damage occurred between 1100 h on October 4 and 0900 on October 5, 1995.

## 2.2. Pit and mound measurements

In the summer of 1996, we randomly selected 48 uprooted trees within the Coweeta basin. On most sites, the PM had resulted from the fall of a single tree. On a few, however, several uprooted trees formed a single PM. For each PM we recorded aspect (degrees), slope (degrees), and relative slope position (ridge, mid-slope, cove). We measured for tree-fall direction (degrees), DBH (cm), pit length (m), pit width (m), pit depth (m), mound height (m), mound width (m), mound thickness (m), and the slope (degrees) at which root-mat leans into or out of the pit. Mound height and slope measurements were taken relative to the deepest point in the pit. The pit-depth value is a vertical distance measured from the deepest point in the pit to the highest point on the surrounding pit wall. Locations of pit length, pit width, pit depth, and mound height measurements were flagged to ensure that future measurements are taken at the same place within each PM. We used the initial characterization measurements as a means of relating PM size to tree biomass. We identified trees ( $>2.5$  cm DBH) to spe-

cies and recorded DBH (cm) for biomass estimation using species-specific allometric equations (Clark and Schroeder, 1986).

## 2.3. Pit and mound microclimate

Within each PM, we measured soil moisture, soil temperature, and photosynthetically active radiation (PAR; 400-700 nm). These measurements were taken at pit bottom, pit wall, mound top, mound face, and adjacent forest floor. Volumetric soil water content was estimated to 15 cm using time domain **reflectometry** (TDR). We quantified incident PAR at 20 cm above each microsite using a Sunflext Ceptometer (Decagon Instruments), and measured soil temperature to a depth of 10 cm using a digital thermocouple/probe thermometer (**Barnant** Instruments). We took soil samples at a depth of 5 cm from all microsites except the mound face. Samples were dried at  $50^{\circ}\text{C}$  for 48 h and analyzed with a Perkin-Elmer 20400 CHN elemental analyzer for percent total nitrogen (N) and total carbon (C). No corrections were made for ash content.

## 2.4. Vegetation responses within blowdowns

Blowdowns are areas of wind damage inclusive of **PMs** and all other related damage therein. We selected 27 blowdowns for study. Area ( $\text{m}^2$ ) was calculated using the formula for the area of an ellipse (i.e.,  $[\pi(L \times W)]/4$ ). Tree species were recorded, and DBH was measured to determine biomass. We considered damaged trees as being in one of two damage classes: direct and indirect. Direct damage resulted from wind-induced uprooting or snapping-off. Indirect damage occurred when a tree was uprooted or otherwise damaged by the fall of another tree. Within damage classes, we noted whether trees had been uprooted or snapped-off; whether there was sprouting at the base or along the bole, and if the crowns were alive or dead. We estimated biomass using species-specific allometric equations (Clark and Schroeder, 1986).

## 2.5. Statistical analyses

Using Pearson correlation (PROC **CORR**; SAS Institute Inc., 1991), we analyzed PM dimensions in terms of their relationship to fallen-tree biomass. A

chi-square goodness-of-fit test was conducted on fall direction to test for randomness. Microclimatic conditions for five microsites within each PM were compared using analysis of variance (PROC ANOVA; SAS Institute Inc., 1991). We used Duncan's multiple-range test to separate means, and Pearson correlation (PROC CORR; SAS Institute Inc., 1991) to determine the significance of relationships among microclimatic variables (i.e., soil moisture, soil temperature, and PAR). We also used analysis of variance (PROC ANOVA; SAS Institute Inc., 1991) to compare percent soil C and N among microsites, and Duncan's multiple-range test to separate means.

### 3. Results

#### 3.1. Pit and mound characteristics

We identified 14 tree species involved in PM formation. Often, more than one stem of a species was associated with the formation of an individual PM. As a result, when conducting analyses of mean biomass per plot for tree species, we pooled trees to form five species groups. The red oak group included *Quercus rubra* L. (northern red oak), *Quercus velutina* Lam. (black oak), and *Quercus coccinea* Muenchh. (scarlet oak); the white oak group included *Quercus prinus* L. (chestnut oak) and *Quercus alba* L. (white oak). The

'others' group was composed of non-oak species found at two or fewer PM plots. Species pooled to form the latter included *Betula lenta* L. (black birch), *Carya glabra* Sweet (pignut hickory), *Magnolia fraseri* Walter (Fraser magnolia), *Oxydendrum arboreum* D.C. (sour-wood), *Prunus serotina* Ehrh. (black cherry), and *Robinia pseudoacacia* L. (black locust). There was a sufficient number of plots containing *Acer rubrum* L. (red maple) and *Liriodendron tulipifera* L. (yellow poplar) to warrant analyzing these species individually. Mean DBH was highly variable within and among species and species groups (Table 1).

Treefall direction (i.e., the eight cardinal directions) was marginally non-random ( $\chi^2 = 2.31$ ;  $p < 0.05$ ). That is, of the 48 PMs, 14 fell in a NNE direction, while the number of treefalls in the other seven directions were similar (median = 5).

Regression analysis of biomass and pit size indicated that three of the six PM dimensions were influenced by tree biomass (Fig. 1). Mound height ( $r^2 = 0.40$ ,  $p = 0.0001$ ), mound width ( $r^2 = 0.37$ ,  $p = 0.0001$ ), and pit width ( $r^2 = 0.34$ ,  $p = 0.0001$ ) all had a significant correlation with biomass of the fallen trees that formed them. However, there was a weak correlation between pit length and mound height ( $r = 0.36$ ,  $p = 0.01$ ), and no correlation was found between tree biomass and pit length (Fig. 1). In addition, mound thickness and pit depth were not significantly related to tree biomass (Fig. 1).

Table 1

Tree species identified in pit and mound formation. Species are in rank order by total number of trees

Species	PM frequency <sup>a</sup>	Total trees	Mean DBH (cm)	DBH range (cm)
<i>Acer rubrum</i> (red maple)	11	26	20.4	5.2-46.5
<i>Quercus coccinea</i> (scarlet oak)	10	26	47.1	18.8-71.4
<i>Quercus prinus</i> (chestnut oak)	12	18	39.8	9.5-73.0
<i>Liriodendron tulipifera</i> (yellow poplar)	9	18	29.1	13.0-55.8
<i>Quercus rubra</i> (northern red oak)	7	11	34.5	17.3-60.0
<i>Oxydendrum arboreum</i> (sourwood)	8	10	26.3	10.3-42.0
<i>Magnolia fraseri</i> (Fraser magnolia)	2	7	15.7	5.0-30.0
<i>Robinia pseudoacacia</i> (black locust)	2	5	16.3	4.0-34.0
<i>Quercus alba</i> (white oak)	3	5	49.6	40.0-60.0
<i>Betula lenta</i> (sweet birch)	5	4	18.8	13.0-25.1
<i>Quercus velutina</i> (black oak)	4	4	50.9	40.0-57.5
<i>Prunus serotina</i> (black cherry)	1	3	28.2	21.3-33.2
<i>Carya</i> spp. (hickories)	5	3	47.8	13.3-85.0
<i>Tsuga canadensis</i> (eastern hemlock)	1	1	8.4	—

<sup>a</sup> Pit/mound and frequency indicates the number of PMs a given species is associated with.

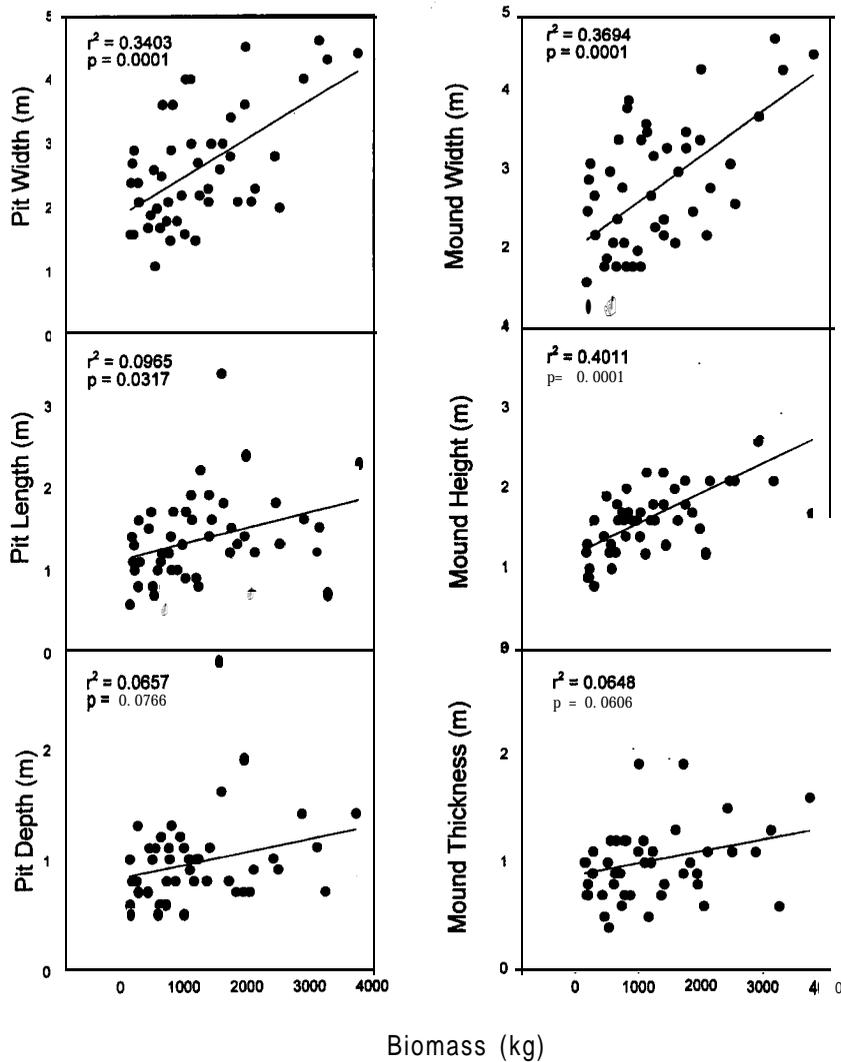


Fig. 1. Scatter plot of pit and mound dimensions and biomass of the fallen tree. Where pit and mound plots were formed by more than one stem of a species, biomass was summed for all trees.

### 3.2. Pit and mound microclimate

Among the five microsites (Fig. 2), microclimate conditions were substantially different. The largest difference in PAR, soil temperature, and soil moisture occurred between mound top and pit bottom. Across all plots, the pit microsite had the lowest mean values for PAR ( $66.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and soil temperature ( $17.5^\circ\text{C}$ ); while the highest mean values for these variables,  $272.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $19.9^\circ\text{C}$ , respectively, were found on the mound top. Conversely, soil

moisture was highest in the pit (34%) and lowest on the mound top (23%). Concentrations of N and C were significantly higher in the intact forest floor than in all other microsites; however, C : N was not significantly different among microsites (Table 2).

### 3.3. Blowdown and damage characteristics

Table 3 summarizes number of trees, DBH, biomass, and area disturbed in 27 blowdown sites. Within those sites, total number of damaged trees

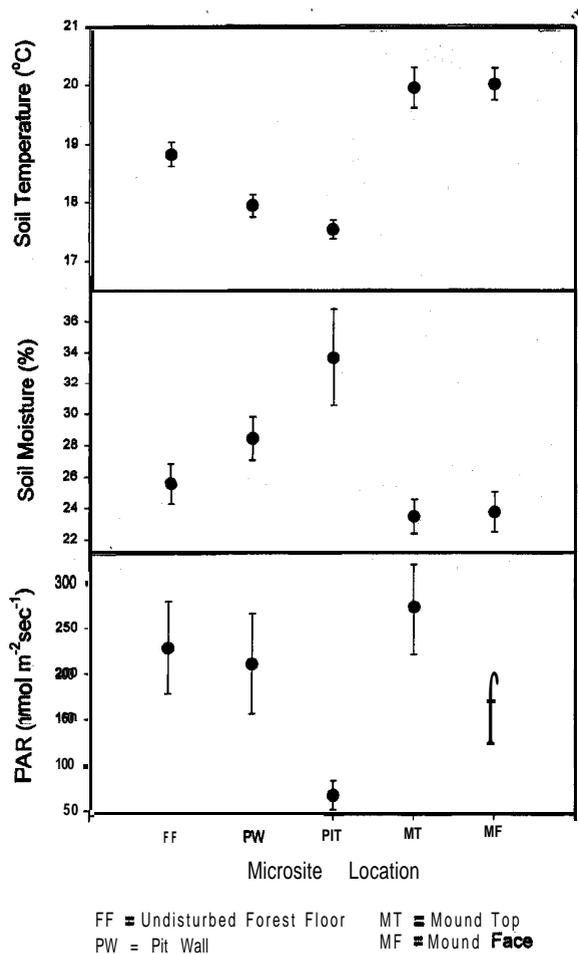


Fig. 2. Plot of microclimatic variables and pit and mound microsites. Individual points represent means for a given variable across plots, Error bars represent one standard error.

(both classes) ranged from 1 to 35. **Blowdown** area ranged from 181 to 4043 m<sup>2</sup>, with a mean of 1175 m<sup>2</sup> (Table 3). Mean diameter of indirectly damaged trees was 50% of the mean for those directly damaged (Fig. 3), but both had similar minimum diameters. Over all plots, the biomass of indirectly damaged trees accounted for <10% of total biomass, but 33% of total number of trees. Of indirectly damaged trees, 38% were topped, 82% exhibited basal or bole sprouting, and 19% had live crowns. By contrast, of the directly damaged trees, only 6% were topped, <50% were sprouting, and 11% had live crowns (Table 4). Fig. 4 shows the diameter distribution of uprooted and snapped-off trees in both damage classes. The

Table 2

Soil carbon (C) and nitrogen (N) concentrations and C : N ratio for four microsites

Microsite	c (%)	N (%)	C:N
Forest floor	4.73a (0.32)	0.23a (0.02)	21.8a (0.81)
Pit wall	2.11b (0.25)	0.10b (0.01)	20.2a (0.66)
Pit bottom	1.42b (0.23)	0.08b (0.01)	26.5a (4.49)
Mound top	2.15b (0.29)	0.10b (0.01)	21.2a (1.12)

Note: Values in parentheses are standard errors. Column means with the same letters are not significantly different ( $\alpha = 0.05$ ).

Table 3

Mean, minimum and maximum **blowdown** area (m<sup>2</sup>), stem DBH (cm), biomass (kg), and number of trees for hurricane Opal blowdowns evaluated in this study

	Mean	Minimum	Maximum
<b>Blowdown</b> area	1175 (74.4)	181	4043
DBH	27.2 (1.2)	3.5	85.0
Biomass per plot	5956 (1557)	194	27803
Trees per plot	8 (1.6)	1	35

Values in parentheses are standard errors.

likelihood of resprouting was strongly related to damage type, i.e., direct or indirect (Table 4). For example, all species and species groups were, overall, twice as likely to sprout if damaged indirectly than if damaged directly. On a species basis, oaks were the least likely to sprout in either damage class. **Sourwood**, yellow poplar, and red maple all were likely to sprout regardless of damage class, particularly those damaged indirectly, all of those species sprouted (Table 4).

## 4. Discussion

### 4.1. Pit and mound characteristics

Much of the damage from Hurricane Opal occurred on upper-slope positions and ridges where older trees with large crowns and full foliage acted as sails in the high winds; a combination of high leaf area, shallow soil, and saturated conditions rendered these sites particularly vulnerable to windthrow. **Treefall** direction was evenly distributed in all but one of the eight cardinal directions. Prevailing winds were from the

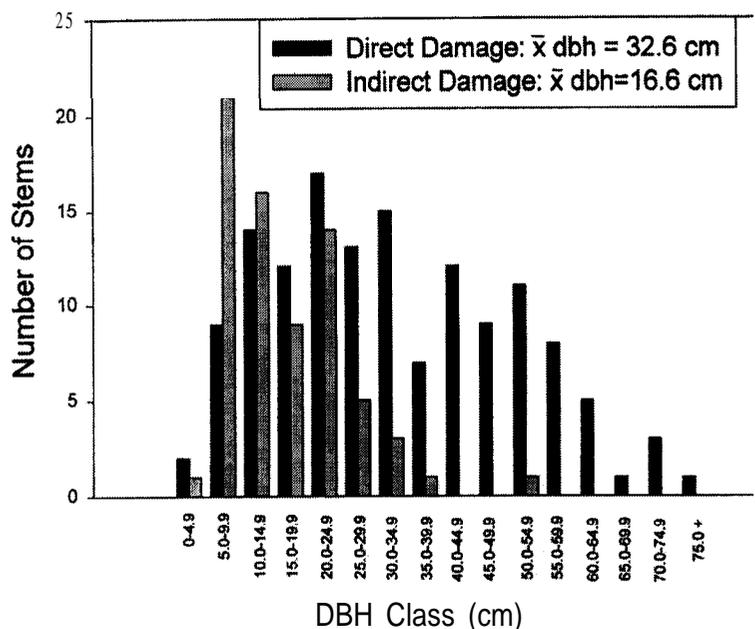


Fig. 3. Diameter distribution of trees within blowdowns. Direct damage represents wind-induced **treefall** and indirect damage represents trees that were damaged by the fall of another stem.

southeast, but during the height of the storm in this area, because of local topography and possibly spawned microbursts, wind direction varied considerably. At a high elevation climatic station at Coweeta, wind direction was consistently SSE ( $163.1 \pm 1.8^\circ$ ). By contrast, wind direction was consistently NW ( $316.6 \pm 3.3^\circ$ ) at low elevations. Clearly, turbulent winds felled trees in all directions, and the direction of fall may have been caused as much by trees

rebounding from wind gusts as by the prevailing winds.

PM dimensions varied greatly, and not all were proportional to tree size. Some variation can be explained by observations of the manner in which many of the trees fell. The PM relationships that failed when regressed with tree biomass were pit length, pit depth, and mound thickness. We observed that many of the trees struck others as they fell and, in many

Table 4

Distribution (%) of direct and indirect damage, sprouting, and live crowns by species and major species groups, and total for all trees during the first growing season following hurricane Opal. In some cases, trees were both sprouting and had live crowns

	Others	Red Maple (%)	Y. Poplar (%)	Sourwood (%)	White oaks (%)	Red oaks (%)	Total
Direct							
Sprout	23	73	78	70	17	17	48
Live crown	10	4	17	20	13	7	11
Topped	7	8	0	10	4	10	6
Up-rooted	93	92	100	90	96	90	94
In-direct							
Sprout	57	100	100	100	50	50	82
Live crown	10	24	0	34	10	0	19
Topped	38	48	25	50	50	50	38
Up-rooted	62	52	75	50	50	50	62

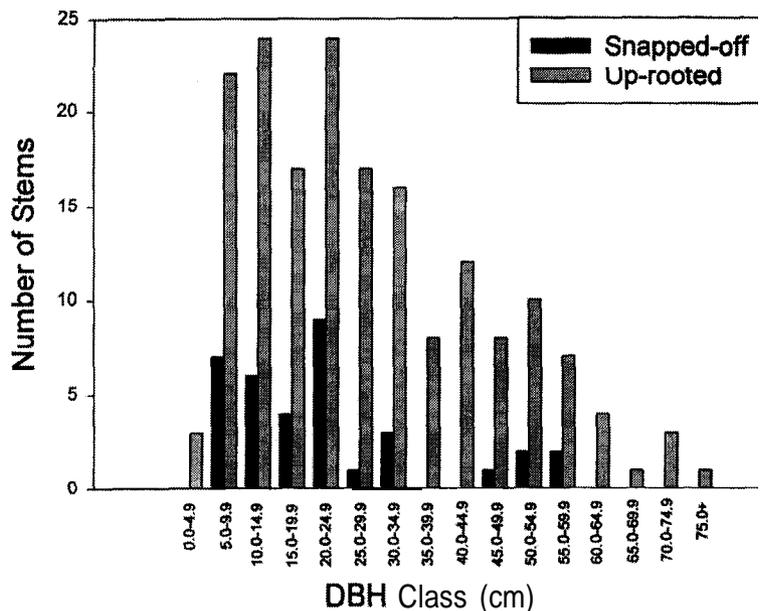


Fig. 4. Diameter distribution of snapped-off (below the live crown) versus uprooted trees for all damaged trees within blowdowns.

cases, were pushed back into the pit, producing a 'ball and socket' PM type (see Beatty and Stone, 1986). This pattern of *treefall* helps explain why the pit length versus biomass relationship failed and the mound height versus biomass relationship did not.

Pit depth and mound thickness were not proportional to tree biomass, because the majority of trees causing PMs were shallow-rooted, either by habit or by chance. Often, impervious subsurface layers were exposed in pits, and in some cases parent material was visible. Hence, pit depth and mound thickness were more a function of edaphic conditions than tree size. It is possible that this characteristic alone rendered most trees more susceptible to windthrow.

#### 4.2. Microclimate

PAR, soil moisture, and soil temperature were all highly variable among the five microsites. Overall, the greatest differences were found between pit bottom and the mound top. Mean values for each of the five microsites indicated that the pit generally had the least amount of light and the lowest soil temperatures, while having the highest soil moisture (Fig. 2). By contrast, mound tops had the highest mean soil temperature and PAR values, and the lowest soil moisture.

Soils on the mound top were generally nutrient poor, primarily because the exposed, lower soil layers contain little or no organic material. However, no significant differences were found in percentage of N among pit, pit wall, and mound top. Warmer soil temperatures on mound tops could result in higher seed germination rates; however, seed deposition there is lower than in the pit, so this microsite will probably support fewer new germinants. In addition, the mound top is a site of rapid erosion, resulting in a physically unstable substrate. The combined effect of potentially low seed deposition and soil instability make vegetation establishment on the mound top problematic. Beatty and Stone (1986) observed that few seedlings survive a mound top's eventual collapse. Further, the inherent infertility of mound tops, as well as pit bottoms, also reduce chances for successful vegetative establishment. Continued monitoring of these sites for changes in PM geometry and vegetative establishment will validate or refute these posits.

#### 4.3. Vegetation recovery

Treefalls are typically violent, site-altering events and may cause extensive vegetative damage. Damage to smaller, understory trees, although fewer and even

less significant in terms of overall biomass, may contribute substantially to vegetation recovery. In this study, indirectly damaged trees exhibited more sprouting and had more live crowns following disturbance than larger, uprooted trees. Hence, sprouts from indirectly damaged trees in the pre-storm understory may influence future stand composition to a greater degree than vegetative responses associated with blown down trees. The contribution to vegetation recovery made by new seedlings on these sites has yet to be evaluated. In large openings, however, there is a strong likelihood that colonization by new seedlings will play an important role in the long-term recovery of these sites.

#### 4.4. Treefall versus standing dead snags

Natural disturbance plays an important role in determining the structure and composition of forests. The type and scale of disturbance determine the degree to which plant and animal species respond to the redistribution of light, moisture, nutrients, and cover or protection (Putz et al., 1983). Mineral soil exposed by treefalls constitutes a distinctly different set of microsites than pathogenically induced tree mortality, by which snags are created. In the latter case, the forest floor is disturbed only by small, periodic additions of coarse woody debris and the eventual fall of the main stem, which may take decades. Windthrow produces important classes of microhabitats not produced by snags. For example, the lack of a pulse addition of coarse woody debris, typical of wind-induced tree mortality, may reduce regeneration opportunities for species such as sweet birch (*Betula lenta* L.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), and rosebay rhododendron (*Rhododendron maximum* L.), whose reproductive strategies include 'nurse logs' as fresh substrate for seed germination (Fowells, 1965).

#### 5. Conclusion

Numerous and widespread PMs throughout the Appalachians represent past catastrophic wind events. Many are conspicuously devoid of vegetation that can be directly linked to the disturbance itself (B. Clinton, personal observation). Most large historic blowdowns have recovered and now support mature vegetation,

much of which can be linked to the disturbance itself. Conversely, small individual blowdowns may not provide the necessary increase in available resources to support regenerating species. Thus, like small-scale standing dead snags, individual blowdowns are more likely to recover vegetatively through ingrowth, i.e. sprouts, advance regeneration, or canopy closure.

Large-scale forest disturbance caused by catastrophic wind, although infrequent in this region, may have more long-term effects than more frequently occurring individual standing dead snags in terms of determining future forest structure and composition. The former create opportunities for the most shade intolerant species, whereas the latter offers no such opportunity for that class of plant species. The prolific sprouting exhibited by indirectly damaged trees reflects faster vegetative recovery than occurs from propagules alone. Moreover, understory composition prior to disturbance may offer insight into future post-disturbance forest composition, given that vegetative responses in the indirectly damaged 'predisturbance' understory is favored over responses in the directly damaged overstory. With continued monitoring of these PMs, we would gain important information about tree replacement in the southern Appalachians and contributions by wind-induced disturbances to this process.

#### Acknowledgements

This project was partially funded through the National Science Foundation's Long Term Ecological Research REU program and the U.S. Forest Service. The authors would like to thank Bill Culpepper of the Wayah Ranger District of the Nantahala National Forest for providing helpful information on storm damage extent. The authors would also like to thank Drs. Katherine Elliott and Cathryn Greenberg for helpful and timely reviews.

#### References

- Barden, L.S., 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. *Oikos* 37, 205-209.
- Bazzaz, EA., 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. In:

- Mooney, H.A., Godron, M. (Eds.), *Disturbance and Ecosystems, Components of Response*. Springer-Verlag, New York. pp. 259-276.
- Beatty, S.W., 1984. Influence of microtopography and canopy species on spatial patterns of forest **understory** plants. *Ecology* 65, 1406-1419.
- Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. *Can. J. For. Res.* 16, 539-548.
- Belsky, A.J., 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* 74, 419-437.
- Braun, E.L., 1950. *Deciduous forests of eastern North America*. Hafner, New York, New York, USA.
- Clark, A., Schroeder J.G., 1986. Weight, volume, and physical properties of major hardwood species in the southern Appalachian mountains. USDA Forest Service SFES Res. Paper SE-253. U.S. Government Printing Office, Washington DC, pp. 63.
- Clinton, B.D., Boring, L.R., Swank, W.T., 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta basin. *Ecology* 74(5), 1551-1558.
- Cooper, W.S., 1913. The climax forest of Isle Royale, Lake Superior, and its development. I. *Bot. Gaz.* 55, 1-44.
- Fowells, H.A., 1965. *Silvics of forest trees of the United States*. U.S. Department of Agriculture, Agricultural Handbook No. 271.
- Goodlett, J.C., 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. *Harvard For. Bull.*, pp. 25.
- Graumann, A., Kobar, J., Lott, N., Ross, D., Ross, K., Ross, T., Sittel, M., 1995. Hurricane Opal. National Climatic Data Center, Research Customer Service Group, Gen. Tech. Rep. 95-02.
- Greenberg, C.H., McNab, W.H., 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *For. Ecol. Man.* 104, 179-191.
- Halpern, C.B., Frenzen, P.M., Means, J.E., Franklin, J.F., 1990. Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington. *J. Veget. Sci.* 1, 181-194.
- Lawton, R.O., Putz, F.E., 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69(3), 764-777.
- Lutz, H.J., 1960. Movement of rocks by uprooting of forest trees. *Am. J. Sci.* 258, 752-756.
- Lyford, W.H., Maclean, D.W., 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper No.* 15.
- Mayfield, M., 1995. Preliminary report, Hurricane Opal, 27 September-6 October 1995. National Hurricane Center, pp. 14.
- Mueller, O.P., Cline, M.G., 1959. Effects of mechanical soil barriers and soil wetness on rooting of trees and soil mixing by blow-down in central New York. *Soil Sci.* 88, 107-111.
- Peterson, C.J., Pickett, S.T.A., 1990. Microsite and elevation influences on early forest regeneration after catastrophic **windthrow**. *J. Veget. Sci.* 1, 657-662.
- Peterson, C.J., Carson, W.P., McCarthy, B.C., Pickett, S.T.A., 1990. Microsite variation and soil dynamics within newly created **treefall** pits and mounds. *Oikos* 58, 39-46.
- Peterson, C.J., Pickett, S.T.A., 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76(3), 763-774.
- Pickett, S.T.A., White, P.S. (Eds.), 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, Florida, pp. 472.
- Pritchett, W.L., 1979. *Properties and management of forest soils*. Wiley, New York.
- Putz, F.E., 1983. **Treefall** pits and mounds, buried seeds, and the importance of soil disturbance to pioneer tree species on **Barro Colorado Island**, Panama. *Ecology* 64, 1069-1074.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A., 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. *Can. J. For. Res.* 13, 1011-1020.
- Putz, F.E., Appanah, S., 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. *Biotropica* 19, 326-333.
- SAS Institute Inc., 1991. *SAS user's guide: statistics*. 1991 edition, SAS Institute Inc., Cary, NC.
- Schaetzl, R.J., 1986. Complete soil profile inversion by tree uprooting. *Phys. Geogr.* 7, 181-189.
- Smallidge, P.C., Leopold, D.J., 1984. Watershed liming and pit and mound topography effects on seed banks in **the Adirondacks**, New York. *For. Ecol. Manage.* 72, 273-285.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353-391.
- Stearns, F.W., 1949. Ninety years of change in a northern hardwood forest in Wisconsin. *Ecology* 30, 350-358.
- Swank, W.T., Crossley, D.A. (Eds.), 1988. *Forest hydrology and ecology at Coweeta*. Springer-Verlag, New York, pp. 469.
- Thompson, J.H., 1980. Treefalls and colonization patterns of temperate forest herbs. *Am. Midl. Nat.* 104, 176-184.
- Uhl, C., Clark, K., Dezzio, N., Maquino, P., 1988. Vegetation dynamics in Amazonian **Treefall** gaps. *Ecology* 69, 751-763.
- Webb, L.J., 1958. Cyclones as an ecological factor in tropical lowland rainforests, North Queensland. *Aust. J. Bot.* 6, 220-228.
- Wright, H.E., 1974. Landscape development, forest fires, and wilderness management. *Science* 186, 487-495.