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Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging[1]

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ELLIOTT, K. J. (USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Rd., Otto, North Carolina 28763), S. L. HITCHCOCK AND L. KRUEGER (Furman University, Greenville, South Carolina 29613). Vegetation response to large-scale disturbance in a Southern Appalachian forest: Hurricane Opal and salvage logging. J. Torrey Bot. Soc. 129: 48–59. 2002.—Disturbance such as catastrophic windthrow can play a major role in the structure and composition of southern Appalachian forests. We report effects of Hurricane Opal followed by salvage logging on vegetation dynamics (regeneration, composition, and diversity) the first three years after disturbance at the Coweeta Hydrologic Laboratory in western North Carolina. The objective of this study was to compare species composition and diversity of undcrstory and groundlayer species in a hurricane + salvage logged (H+S) forest to an adjacent undisturbed forest. Abundance of groundlayer species was much higher in the H+S forest than in the undisturbed forest, and abundance increased over time. Percent cover, density, and species richness were significantly higher in the H+S forest than in the undisturbed forest. In addition, percent cover increased by approximately 85% between 1997 and 1999 in the H+S plots.

Shannon's index of diversity (H') based on percent cover was significantly higher in the H+S forest than the undisturbed forest by the third year after disturbance. However, there was no significant difference in H' based on density between H+S forest and the undisturbed forest in either year. In the undisturbed forest, 59 species and 50 genera represented 30 families. By 1999 (the third year after disturbance), the H+S forest retained 93 species. 72 genera and 42 families. The Asteraceae and Liliaceae had the highest number of species in both sampled forests, with more species of Liliaceae in the H+S plots. Micro-relief created from pit and mound topography from uprooting of windthrown trees, shade from the slash-debris left on site from the salvage logging, and shade from the remaining overstory trees created a mosaic of environmental conditions. This environmental heterogeneity could be responsible for the mix of early (shade intolerant) and late (shade tolerant) successional herbaceous species, and a higher species richness and diversity than the undisturbed forest.

Key words: hurricane, windthrow, treefall, regeneration, herbaceous species

Wind is the primary cause of treefalls in the mesic forests of eastern North America, causing a spatial gradient of disturbances, from small gaps (Runkle 1981, 1982; Hibbs 1983; Pickett and White 1985) to large blowdowns (Bormann and Likens 1979; Dunn et al. 1983; Foster 1988; Matlack et al. 1993; Peterson and Pickett 1995; Foster et al. 1998; Peterson 2000). Although uncommon, large blowdowns generated from inland hurricanes provide an opportunity to study the effects of catastrophic windfall. Historical analysis of hurricane paths and other windstorms in the southern Appalachians (Greenberg and McNab 1998) suggests that since 1971, 14 storms have occurred in the region at intervals of 1-24 years. On October 5, 1995, the center of Hurricane Opal passed over southeastern Tennessee causing high winds and heavy rainfall in much of the southern Appalachians (U.S. Depart. Commerce, 1996) including the Coweeta Basin, southwestern North Carolina. The unusual size and strength of Opal, unlike other storms in this region, had a considerable effect on inland forest communities resulting in large-scale tree damage and subsequent salvage logging operations. As much as 15% of the Wayah Ranger District of the Nantahala National Forest was severely affected by this storm (B. Culpepper, silviculturalist, pers. comm.), and much of this forest was subsequently salvage logged.

We examined community regeneration after catastrophic windthrow followed by salvage log-

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ging of a high elevation, mixed-hardwood forest in the Coweeta Basin, western North Carolina. Little is known about how these southern Appalachian forests will respond to catastrophic windthrow and salvage logging. In addition, information on herb responses to gaps is scarce relative to that for trees (Collins et al. 1985; Moore and Vankat 1986; Collins and Pickett 1988a, 1988b). The objective of this study was to compare overstory, understory, and groundlayer richness, diversity (H'; Shannon index), evenness (J'), and composition in a hurricane+salvage logged (H+S) forest to that in an adjacent undisturbed forest. Whereas other studies in the Coweeta Basin have documented regeneration following disturbance (e.g., Boring et al. 1988, Elliott and Swank 1994, Clinton et al. 1994, Elliott et al. 1997, Elliott et al. 1999), this is the first study to examine the effects of catastrophic windthrow and salvage logging on regeneration and vegetation dynamics.

Methods. HURRICANE OPAL. Hurricane Opal began as a tropical storm that emerged from the west coast of Africa on September 11, 1995. It made landfall near Pensacola Beach, Florida, as a marginal category 3 hurricane on the Saffir-Simpson Hurricane Scale, causing extensive storm surge damage to the immediate coastal areas of the Florida Panhandle. Most of the severe structural damage occurred at the coastline, primarily as a result of the storm surge and waves (U.S. Depart. Commerce 1996). However, strong winds caused damage up to several hundred kilometers inland.

On October 5, a peak gust of 130 km hr was recorded atop a 1317 m mountain located just east-southeast of Asheville, North Carolina. Large-scale tree damage was common in many locations of the southern Appalachians where sustained winds averaged 64 km hr with frequent gusts of 96 km hr (U.S. Depart. Commerce 1996). At Coweeta Hydrologic Laboratory, highest wind speeds were recorded at the mid-elevation (~990 m) climate station (CS-28). Wind speed averaged 39 km hr for an 8-hr period (0300 hr to 1100 hr EDT) (Coweeta Hydrologic Laboratory, unpub. data). Torrential rains associated with Opal began over land about 12 hrs before landfall. The rainfall ranged from maximum amounts of 20 to 40 cm across parts of Alabama. Georgia, nnd much of the Florida Panhandle to S-13 cm over the Ohio Vulley and New England. Rains in South Carolina averaged 5 to 10 cm. while in North Carolina, 8 to 13 cm were common. Robinson Creek (Jackson County, North Carolina) measured 23 cm (U.S. Depart. Commerce 1996). At Coweeta, rainfall was 11 cm on October 4, and 9 cm on October 5, 1995. The saturated soils from the heavy rainfall followed by high windspeeds caused substantial blowdown in the Coweeta Basin and in much of the southern Appalachians. Although rare, hurricane-caused blowdowns of this scale are not unprecedented in the Coweeta Basin. In 1835, a major hurricane struck Jones Creek to the north and blew down much of the timber in the Cowecta Basin (Douglass and Hoover 1988).

STUDY AREA. The study area is an approximutely IO ha windthrow located in the Coweeta Basin (35°04' latitude, 83°26' longitude) near Franklin, North Carolina. The Coweeta Basin is in the Nantahala Mountains-part of the Blue Ridge province in the Southern Appalachians. The study area has a southeast-facing aspect and ranges in elevation from 1220 to 1370 m. The mean annual temperature is 13 C and mean annual precipitation is 183 cm (Swift et al. 1988). Slopes range from 50 to 90 percent. Soils in the area are an Edneyville-Chestnut complex, described as coarse-loamy, mixed, mesic Typic Dystrochrepts (Thomas 1996).

SAMPLING DESIGN. Twelve 20 X 40 m plots were established in January 1997 following the completion of the salvage logging in Fall, 1996. Diameter of all standing live trees ≥5.0 cm diameter at breast height (dbh, 1.37 m above ground) was measured to the nearest 0.1 cm. To recreate the stand composition and structure prior to disturbance, cut stumps and windthrow trees not salvaged were identified to species and basal diameter was measured to the nearest 0.1 cm.

In fall 1999, a 5 X S-m subplot was established in the NE corner of each 20 X 40-m plot to measure regeneration of woody sprouts and seedlings (understory layer). Basal diameter of all woody species (6.0 cm dbh, > 1.0 m height) was measured to the nearest 0.1 cm. In June 1997 (one growing season after disturbance) and June 1999 (three growing seasons after disturbance), groundlayer species (all herbs + woody species < 1.0 m height) were measured in four 1.0 X 1.0-m subplot located in the corners of each 20 X 40-m plot. Percent cover was visually estimated and density was determined by counting all groundlayer species. To compare the hur-

Table 1. Average density, average basal area, and importance value (IV = (relative density + relative basal area)/2) of overstory trees in the undisturbed forest and the hurricane + salvage logged (H + S) forest; precut (reconstructed from measurements of cut stumps, standing live trees, and blowdown trees) and residual stand (postcut).

	Density (stems ha-‘)			Basal area (m^2 ha^{-1})			IV		
	Undis-	H + S		Undis-	H + S		Undis-	H + S	
Species	turbed	Precut	Postcut	turbed	Precut	Postcut	turbed	Precut	Postcut
Acer rubrum	145.0	40.6	3.1	4.3	1.3	0.2	17.15	6.73	4.26
Carya spp.	122.5	153.1	26.0	3.1	8.9	2.2	13.69	30.55	36.74
Quercus rubra	57.5	18.8	6.2	27.0	2.7	1.1	12.89	5.90	12.91
Quercus alba	55.0	11.4	3.1	5.0	3.2	0.3	12.10	5.64	5.01
Quercus prinus	40.0	9.4	3.1	5.1	0.4	0.2	11.25	1.74	3.59
Liriodendron tulipifera	90.0	45.8	1.3	13.9	6.8	0.8	10.84	14.58	11.79
Robinia pseudoacacia	35.0	21.9	0	1.6	2.0	0	5.13	5.34	
Quercus velutina	25.0	22.9	3.1	1.5	6.8	0.3	4.15	11.84	4.59
Oxydendrum arboreum	15.0	2.1	0	0.5	<0.1	0	1.91	0.30	
Nyssa sylvatica	15.0	3.1	1.0	0.2	0.1	0.1	1.29	0.48	1.22
Acer saccharum	10.0	6.2	3.1	0.2	0.1	0.1	1.22	0.93	3.02
Amelanchier arborea	15.0	2.1	0	0.1	0.1	0	1.22	0.33	—
Acer pensylvanicum	5.0	6.2	0	0.1	0.1	0	0.47	0.90	
Betula lenta	5.0	11.5	0	0.1	0.3	0	0.46	1.74	—
Cornus florida	5.0	13.5	1.0	<0.1	0.1	<0.1	0.38	1.81	0.85
Fraxinus americana	2.5	14.6	1.0	<0.1	0.5	0.1	0.21	2.47	1.36
Castanea dentata	0	3.1	0	0	<0.1	0		0.41	—
Prunus serotina	0	21.9	7.3	0	4.0	1.1	—	8.00	14.34
Sassafras albidum	0	1.0	0	0	0.1	0		0.28	—
Total	720.0	413.5	66.7	30.3	37.6	6.5			
	(111.8)	(42.7)	(11.8)	(2.8)	(2.9)	(1.1)			

Note: Species are ranked by IV of the undisturbed forest. Standard errors for total values are in parentheses. Species nomenclature follows Brown and Kirkman 1990.

ricane blowdown + salvage logged forest (H+S) to an undisturbed forest, an additional six 20- X 40-m plots were established in the spring of 1997 in an adjacent forest, similar in aspect, elevation, and forest composition. Sampling of overstory, understory, and groundlayer was conducted in 1997 and 1999 in this undisturbed forest in a similar manner as the H+S forest. Species nomenclature for trees follows Brown and Kirkman (1990) and species nomenclature for shrubs and herbs follows Gleason and Cronquist (1991).

DATA ANALYSES. Importance values (IV) were calculated as (relative density + relative basal area)/2 for overstory and understory woody species, and as (relative density + relative percent cover)/2 for groundlayer species. Relative density, relative basal area, and relative percent cover were calculated as proportion of total abundance of species *i*. Species diversity of the groundlayer was calculated on a per plot basis and a per site basis (Magurran 1988) for comparison with other studies. The Shannon index of diversity (H′) (Shannon and Weaver 1949), and Pielou's (1966) evenness index (J') were used to compare the diversity of the H+S forest, one (1997) and three (1999) growing seasons after salvage logging, to an adjacent mature (75+ year-old), undisturbed forest. The Shannon index was calculated on the basis of density ($H'_{density}$), basal area ($H'_{basal\ area}$), and importance value (H'_{IV}) for understory species and on the basis of density ($H'_{density}$) and percent cover (H'_{cover}) for groundlayer species. Because H' alone fails to show the degree that each factor contributes to diversity, we calculated a separate measure of species evenness (J'). H' was calculated as: $-\Sigma p_i \ln p_i$, where p_i = proportion of total abundance of species *i*, with abundance of woody species = stem density (stems ha-‘) or basal area (m^2 ha-‘); and abundance of groundlayer species = density (plants m^{-2}) or percent cover. Species evenness was calculated as: J' = $H'/H'max$; where H'max = maximum level of diversity possible within a given community = ln(S), and S = species richness. We used t-tests (Magurran 1988) to compare the differences in H' calculated on a per site basis between the H+S forest and the undisturbed forest in the two years (1997 and 1999). We used a two-factor analysis of variance (PROC GLM, SAS Institute Inc. 1996),

Table 2. Average density, average basal area, and importance value (IV = (relative density + relative basal area)/2) of shrub layer species in the undisturbed forest and the hurricane + salvage logged (H t S) forest (postcut 1999).

	Density (stems ha^{-1})		Basal area (m^2 ha^{-1})		IV	
	Undisturbed	H + S	Undisturbed	H + S	Undisturbed	H + S
Castanea dentata	1333	3733	0.37	1.20	9.70	5.99
Smilax spp.	1933	3500	0.06	0.07	7.39	2.33
Carya spp.	467	1700	a0.25	0.39	5.06	2.23
Acer rumbrum	800	2700	0. 16	0.66	4.93	3.66
Kalmia latifolia	267		0.16		3.15	
Sassafras albidum	667	300	0.09	0. I 3	3.54	0.60
Liriodendron tulipifera	600		0.09		3.29	
Aristolachi macrophylla	733	2267	0.05	0.20	3.24	1.99
Rhododendron calendula	333	200	0.14	<0.01	3.04	0.13
Prunus serotina	533	3767	0.05	0.74	2.5 1	4.56
Amelanchier arboreum	200	233	007	0.0 1	1.64	0. I 8
Fraxinus americana	267	I067	0.05	0.29	1.61	1.53
Acer pensylvanicum	267	767	0.04	0.1 1	1.52	0.8 1
Quercus rubra	133	467	0.02	0.07	0.76	0.49
Robinia pseudoacacia	133	900	0.02	0.33	0.76	1.57
Nyssa sylvatica	67	200	0.02	0.05	0.52	0.28
Rubus allegheniensis	67	12933	<0.01	1.57	0.24	12.68
Calycanthus florida	—	8367		1.32		9.16
Rubus odorata		3867		1.07		5.65
Hydrangea arborescence		1033	—	0.18		1.18
Vitis sp.	—	533	—	0.17		0.84
Cornus florida		267	—	0.02		0.24
Quercus alba		300	—	0.02		0.23
Cornus alternifolia		233	—	0.02	—	0.22
Tilia Americana		33	—	0.02		0.09
Quercus velutina		100	—	0.02	—	0.07
Symplocus tinctoria		33	—	0.01		0.05
Acer saccharum		67		co.0 1		0.04
Betula lenta		67		<0.01		0.04
Oxydendron arboreum		33		co.0 1		0.02
Vaccinium staminium	—	33		<0.01		0.02
Total	8,800a	49,700b	1.66a	+8.66b		
H′	2.48a	2.47a	+2.45a	2.47a		
J′	0.87	0.73	0.86	0.73		
S	17	29				

Note: Species are ranked by IV of the undisturbed forest. Total density, basal area, and diversity (H') between the undisturbed forest and the hurricane + salvage logged forest followed by different letters are significant at the $p \leq 0.05$ level. Species nomenclature follows Gleason and Cronquist 1991

where the two factors were disturbance and year, to compare differences in density and basal area of the understory species; density and percent cover of the groundlayer species; and diversity of the groundlayer calculated on a per plot basis between the Hi-S and undisturbed forests in 1997 and 1999.

Results. OVERSTORY. Before disturbance. the H+S forest had a similar composition of dominant species, with the exception of' *Prunus serotina*, to the adjacent, undisturbed forest (Table 1). This high-elevation mixed-hardwoods forest was dominated by *Carya* spp., *Quercus velutina*, and *Liriodendron tulipifera* with a considerable basal area of *Prunus serotina*, *Quercus alba*, and *Quercus rubra* (Table 1). The salvage logging operation rernoved 344 sterns/ha and 3 1.1 m^2 ha of basal area, leaving an average residual density of 65.7 sterns/ha and a basal area of 6.46 m^2/ha. This type of' harvest is similar to a two-aged shelterwood cut, a practice that is becoming more common on the National Forests of this region (Bill Culpepper, pers. comm.).

Alter the salvage logging, density in the H+S forest was reduced by 84% and basal area was reduced by 83%. Species that were no longer represented in the overstory after hurricane and salvage cutting were *Robinea pseudoacacia*, *Betula lenta*, *Acer pensylvanicum*, *Castanea dentata*, *Amelanchier arborea*, *Oxydendron arboreum*, and *Sassafras albidum*.

Table 3. Frequency (Freq = percentage of plots where species occurred). average density (plants m^{-2}), average percent cover, and importance value (IV = (relative density + relative percent cover)/2) of groundlayer species found in the undisturbed plots in 1999 and the hurricane + salvage logged (H + S) forest in 1997 and 1999.

	Undisturbed				H + S							
	1999				1997				1999			
Species	Freq	Density	Cover	IV	Freq	Density	Cover	IV	Freq	Density	Cover	IV
Trees												
Acer pensylvanicum	8	0.08	0.08	0.26					2	0.02	0.00 l	0.01
Acer rubrum	25	0.33	0.46	1.29	21	0.64	1.27	1.30	27	0.44	1.27	0.80
Carya spp.	4	0.04	0.12	0.30	8	0.3 I	0.33	0.40	21	0.35	3.02	1.61
Castanea dentate	12	0.2 I	1.25	2.82	25	0.64	2.85	2.60	8	0.17	0.23	0.18
Cornus florida	—		—		2	0.04	0.21	0.19				
Fraxinus Americana	4	0.04	0.00 1	0.04	6	0.12	0.69	0.6 l	14	0.2 l	l.oo	0.57
Liriodendron tulipifera	4	0.25	0.04	0.33	29	0.06	0.47	0.29	17	0.25	0.19	0.20
Nyssa sylvatica	—				2	0.10	0.08	0.1 1	6	0.06	0.14	0.10
Prunus serotina	17	0.29	0.29	0.90	4x	1.44	1.86	2.12	46	1.10	1.44	1.16
Quercus alba	—				6	0.08	0.06	0.09	12	0.2 1	0.60	0.38
Quercus prinus	—				6	0.08	0.02	0.05	2	0.08	0.10	0.08
Quercus rubra	46	0.88	1.29	3.56	29	1.19	1.27	1.53	25	1.46	4.2 l	2.65
Quercus velutina	42	1.46	1.08	3.70	17	0.25	0.33	0.3X	14	0.21	0.38	0.27
Robinia pseudoacacia	12	0.21	0.17	0.55	12	0.33	0.73	0.73	6	0.08	0.12	0.09
Sassafras albidum	17	0.33	1.08	2.59	6	0.10	0.67	0.59	4	0.06	0.12	0.09
Symplocos tinctoria	—				2	0.02	0.02	0.02	2	0.04	0.08	0.06
Shrubs												
Calycanthus florida									2	0.04	0.08	0.06
Gaylassacia baccata					2	0.06	0.10	0.1 I				
Hydrangea arborescence	4	0.12	0.33	0.82					2	0.04	0.10	0.07
Kalmia latifolia	17	0.42	0.50	1.46	2	0.08	0.10	0.12	2	0.04	0.21	0.12
Rubus allegheniensis	4	0.04	0.04	0.13	14	198	2.92	3.21	29	1.12	3.27	2.06
Rubus odorata	—				4	0.10	0.52	0.47	2	0.52	2.08	1.23
Vaccinium spp.*	—				2	0.06	0.3 l	0.28	6	0.23	1.21	0.68
Vines												
Aristolochia macrophylla	46	0.83	1.13	3.17	29	0.79	1.98	1.95	35	0.62	2.54	1.49
Clematis verticillaris					21	1.60	4.69	4.50	19	1.27	4.62	2.78
Dioscorea villosa	8	0.12	0.04	0.21	25	0.35	0.48	0.54	21	0.31	0.58	0.42
Ipomoea pandurata					2	0.04	0.04	00.5	8	0.19	0.52	0.33
Lonicera japonica					2	0.10	0.04	0.08				
Parthenocissus quinquefolia	17	4.79	3.00	10.98	67	13.29	8.38	12.38	71	17.17	IS.79	14.9
Smilax spp.	58	1.54	0.50	2.57	23	1.31	1.25	1.57	40	1.33	2.77	1.91
Toxicodendron radicans					2	0.50	0.62	0.72	4	0.79	0.83	0.74
Vitis sp.					17	0.46	0.60	0.68	23	0.56	2.56	1.48

Table 3. Continued

Species	Undisturbed				H + S							
	1999				1997				1999			
	Freq	Density	Cover	IV	Freq	Density	Cover	IV	Freq	Density	Cover	IV
Ferns												
Botrychium virginianum					6	0.14	0.14	0.18	14	1.50	1.17	1.20
Dennstaedtia punctilobula	4	0.96	0.21	1.38								
Dryopteris intermedia	4	0.21	0.12	0.47								
Polystichum acrostichoides	12	0.83	0.50	1.86	2	0.44	0.10	0.27	4	0.81	0.62	0.65
Thelypteris hexagonoptera	4	0.67	0.21	1.09	2	0.44	0.06	0.23	2	0.29	0.10	0.17
Thelypteris noveboracensis	4	0.04	0.04	0.13	2	0.42	0.02	0.19				
Herbs												
Agrimonia rostellata					4	0.25	0.06	0.16	6	0.27	0.12	0.18
Amphicarpa bracteata				—	6	017	0.08	0.14	2	0.04	006	0.05
Angelica triquinata					4	0.12	0.06	0.10	2	002	0.001	0.01
Arisaema triphyllum	21	1.92	0.38	2.67	58	3.98	0.77	2.29	58	7.12	2.06	4.04
Asclepias exaltata					2	0.06	0.04	0.06	12	0.2 1	0.25	0.21
Aster divaricatus	17	0.33	0.13	0.59	25	1.31	0.62	1.06	35	1.46	1.21	1.21
Aster spp.	4	0.04	008	0.22	8	0.17	0.10	0.15	19	0.50	0.46	0.43
Carex spp.	17	0.79	0.12	1.04	6	0.33	0.12	0.24	2	0.02	0.08	0.05
Caulophyllum thalictroides					6	0.2 1	0.33	0.36	8	0.12	0.56	0.32
Chimaphila maculata	12	0.38	0.04	0.46		—			2	002	0.001	0.01
Cimicifuga racemosa	4	0.38	0.04	0.46	40	1.56	1.81	2.13	42	0.99	4.23	2.46
Coreopsis major	4	0.04	0.04	0.13	2	0.02	004	004	2	002	0.04	0.03
Desmodium nudiflorum	50	2.25	1.21	4.74	29	1.23	0.54	0.96	38	1.50	1.96	1.59
Erigeron strigosus					2	0.02	0.02	002	2	0.04	0.001	0.02
Eupatorium rugosum	25	0.62	0.58	1.83	71	19.19	4.19	1 1.43	58	5.44	2.25	3.41
Galium lanceolatum	17	0.67	0.04	0.74	31	3.58	0.8 1	2.16	46	9.35	3.27	5.57
Gillenia trifoliata					2	0.02	0.04	004	2	0.04	0.2 1	0.12
Helianthus sp.							—		2	0.06	0.02	0.04
Hieracium paniculatum	8	0.08	0.04	0.17								—
Houstonia purpurea	17	1.25	0.38	2.01	14	2.52	1.33	2.14	8	0.50	0.14	0.28
Hypericum sp.	8	0.08	0.04	0.17	2	0.02	0.001	0.0 1	2	0.04	0.02	0.03
Impatiens capensis					19	2.46	3.14	3.59	40	9.25	5.73	6.72
Lysimachia quadrifolia	37	1.21	0.58	2.41	21	0.79	0.44	0.69	29	1.17	0.96	0.96
Medeola virginiana					2	0.04	0.02	0.03	4	0.14	0.31	0.2 1
Monarda clinipodia					19	1.04	1.17	1.39	27	2.23	0.83	1.35
Oxalis stricta	4	0.38	0.12	0.63	17	1.35	0.15	1.18	8	1.92	1.67	1.62
Panicum spp.*	42	8.29	1.71	11.73	25	2.79	0.88	1.88	35	7.17	2.04	404
Phytolacca americana			—		4	0.08	0.06	0.08	2	0.02	0.02	0.02
Poa spp.	21	3.79	0.54	4.87	13	4.25	0.69	2.33	10	1.62	0.35	0.86

Table 3. Continued

	Undisturbed				H + S							
	1999				1997				1999			
Species	Freq	Density	Cover	IV	Freq	Density	Cover	IV	Freq	Density	Cover	IV
Podophyllum peltatum					2	0.04	0.04	0.05	14	0.48	0.90	0.64
Poligonatum biflorum	4	0.04	0.04	0.13	31	0.81	0.48	0.73	54	0.75	0.94	0.77
Potentilla canadensis	17	0.29	0.002	0.29		—			21	1.02	0.56	0.71
Prenanthes trifoliolata	4	0.08	0.001	0.04	2	0.47	0.25	0.39	6	0.35	0.20	0.24
Pycnanthemum incanum					21	0.54	0.52	0.65	19	1.62	1.98	1.65
Ranunculus sp.									4	0.06	0.06	0.06
Sanguinaria canadensis					48	2.21	0.71	1.50	54	3.23	2.15	2.42
Smilacina racemosa	50	2.33	1.92	6.30	27	1.21	1.10	1.41	44	2.42	6.50	4.17
Smilax herbacea	8	0.25	0.25	0.77	8	0.14	0.25	0.26	17	0.58	0.60	0.54
Solidago spp.*	50	1.46	0.92	3.35	50	5.04	2.81	4.40	54	2.79	2.27	2.29
Stachys sp.	4	0.08	0.04	0.17	4	0.17	0.02	0.02				
[illegible]					3	0.38	0.10	0.24				
Tiarella cordifolia	4	0.12	0.21	0.56	2	0.06	0.001	0.03	4	0.25	0.21	0.21
Tradescantia virginiana	4	0.25	0.17	0.59	4	0.06	0.02	0.04	4	0.08	0.10	0.08
Trillium sp.	8	0.08	0.08	0.26	42	0.75	0.48	0.70	25	0.60	0.73	0.61
Uvularia perfoliata	12	2.38	0.62	3.64	12	0.85	0.33	0.62	4	0.48	0.21	0.30
Veratrum parviflora		—			17	0.27	0.56	0.57	21	0.35	0.67	0.47
Viola spp.*	38	5.79	0.96	7.70	75	31.06	2.48	14.99	71	17.50	3.81	9.31

Note: * *Solidago* spp. include *arguta* and *curtissi* found on the undisturbed and H + S plots, and *erecta*, and *lancifolia* found only on the H + S plots; Viola spp. include *cucullata* and *rotundifolia* found on the undisturbed and H + S plots, and *blanda, hastata,* and *palmata* found only on the H + S plots. *Panicum* spp. include *dichotomum* and *commutatum* on the undisturbed and H + S plots. Aster spp. include mostly undulatus with a few small Aster sp. that could not be identified to the species level. Nomenclature follows Brown and Kirkland (1990) for tree species and Gleason and Cronquist 1991 for shrub and herbaceous species,

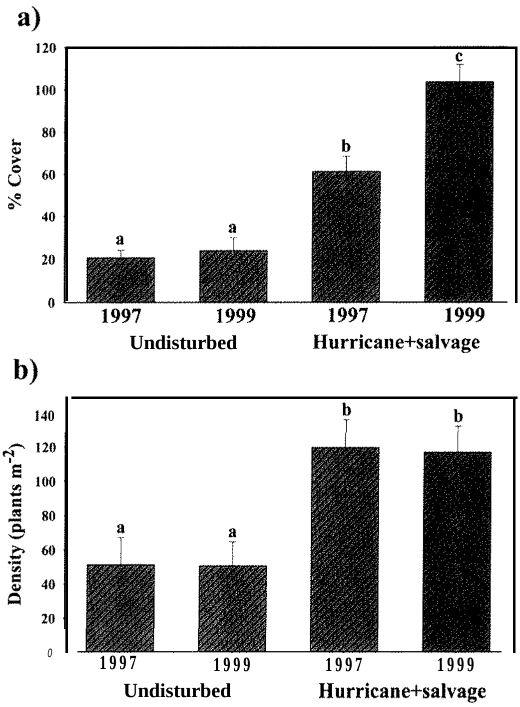

FIG. 1 Average percent cover (a) and density (b) of groundlayer species (all herbaceous species + woody species < 1.0 m height) in the undisturbed forest and the hurricane + salvage logged forest in the Coweeta Basin, western North Carolina; 1997 (one year following completion of the salvage logging) and 1999 (three years following completion of the salvage logging). Bars with different letters are significantly different at $p \leq 0.05$.

UNDERSTORY LAYER. Only 3 years after disturbance (1999), basal area was almost 9 m^2 ha^{-1} and density was almost 50,000 stems ha^{-1} in the understory layer (Table 2). In addition, species richness was higher in the H+S forest (S = 29) than the undisturbed forest (S = 17). Conversely, $J'_{density}$ and $J'_{basal\ area}$ were lower in the H+S forest than the undisturbed forest. No differences were found for $H'_{density}$ or $H'_{basal\ area}$ between the undisturbed forest and the H+S forest. The maximum diversity ($H'_{max} = \ln S$) with 29 species present would be 3.37; whereas, H'_{max} in the undisturbed forest with 17 species would be 2.83. Thus, for the undisturbed forest, woody species were more evenly distributed (i.e., higher J’) than in the H+S forest and the additional 12 species accounted for only 2.3% of the IV. Some species that were not represented in the overstory layer after salvage cutting were regenerating in the understory layer, such as *R. pseudoacacia*, *A. pensylvanicum*, *C. dentata*, and *S. albidum* (Table 2).

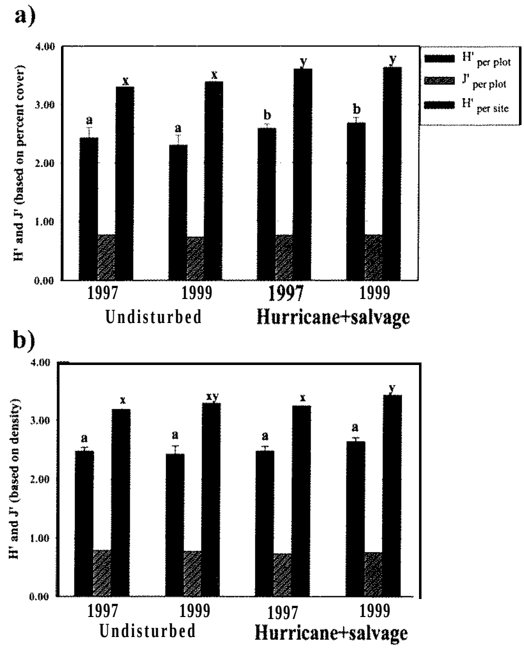

FIG. 2. Diversity (H’ per plot and H’ per site) and evenness (J’ per plot) based on percent cover (a) and based on density (b) of groundlayer species (all herbaceous species + woody species ≤ 1.0 m height) in the undisturbed forest and the hurricane + salvage logged forest in 1997 (one year following completion of the salvage logging) and 1999 (three years following completion of the salvage logging). Bars with different letters are significantly different at $p \leq 0.05$.

GROUNDLAYER. Percent cover and density were higher in the H+S forest than in the undisturbed forest and percent cover increased over time in the H+S forest (Fig. 1a, 1b). Percent cover increased by approximately 85% between 1997 and 1999 in the H+S forest. H'_{cover} was significantly higher in the H+S forest than the undisturbed forest in both years (Fig. 2a) whether it was calculated as H’ per plot or H’ per site. However, there was no significant difference in $H'_{density}$ between the H+S forest and the undisturbed forest in either year, but $H'_{density}$ increased in the H+S forest between 1997 and 1999 when calculated as H’ per site (Fig. 2b). In the H+S forest, species ranked *Parthenocissus quinquefolia* > *Eupatorium rugosum* > *Viola cucullata* > *Clematis verticillaris* > *Viola rotundifolia* in 1997; and *P. quinquefolia* > *Impatiens capensis* > *Galium lanceolatum* > *Viola cucullata* > *Smilacina racimosa* in 1999. In the undisturbed forest, species ranked *P. quinquefolia* > *Viola rotundifolia* > *Panicum commutatum* > *Smilacina racemosa* > *Poa* spp. in 1999.

Table 4. Groundlayer species richness (S_{sp} = number of species per m^2; S_p = number of species per plot; S = number of species per site), number of genera and families found on the undisturbed and hurricane + salvage logged (H + S) forest in 1997 and 1999. Standard errors are in parentheses.

	Undisturbed	H + S	
	1999	1997	1999
S_{sp} (number of species/m^2)	9.5 (1.0)	12.2 (0.6)	14.5 (0.7)
S_p (number of species/plot)	23.3 (3.8)	29.5 (1.7)	33.3 (1.9)
S (total number of species/site)	59	85	93
Number of genera	so	69	75
Number of families	30	41	42

In the undisturbed forest, 59 species and SO genera represented 30 families (Table 4). By 1999, the H+S forest contained 93 species, 72 genera and 42 families (Table 4). The Asteraccae and Liliaceae had the highest number of species in both sampled areas, with more species of each family in the H+S plots (Table 5). More herbs, both early and late successional species, were found in the H+S forest than in the undisturbed forest (Table 5). In addition, some late successional species that were found in both forests were more abundant in the H+S forest; these included *Arisaema triphyllum*, *Cimicifuga racemosa*, *Galium lanceolatum*, *Oxalis stricta*, and *Viola* spp. (Table 3). Fewer fern species were found in the H+S forest than the undisturbed forest, with the exception of *Botrychium virginianum*, ferns were also more abundant in the undisturbed forest. More woody species (trees, shrubs, and vines) were also found in the groundlayer of the H+S forest than in the undisturbed forest. For trees species, *L. tulipifera*, *P. serotina* occurred more frequently and had higher IV in the H+S forest than the undisturbed forest; conversely, Q. *rubra* and Q. *velutina* occurred less frequently and were less abundant than the undisturbed forest (Table 3).

Discussion. Typical of southern Appalachian forests following disturbance, the H+S forest was regenerating quickly (Boring et al. 1988). Tree species that were not present in the overstory layer after salvage logging were regenerating in the understory layer. For example, some ovcrstory tree species, such as *Carya* spp., *Prunus serotina*, and *Fraxinus americana* were abundant in the understory layer three years after disturbance. The potential recovery of the overstory in the H+S forest by natural regeneration is substantial. Within 3 years following disturbance, regrowth of woody species in the understory layer was rapid; density was 5.6 times higher and basal area was 5.2 times higher in the H+S forest than the 75+ year old, undisturbed forest. However, this initiation phase of stand development (Oliver and Larson 1996), where many small woody stems contribute to total stand basal area, may last only a few more years. For example, in a low elevation, clcarcut forest in the Coweeta Basin, the stem exclusion stage of stand development (Oliver and Larson 1990) that coincides with canopy closure occurred between 8 and 17 years following disturbance (Elliott et al. 1997).

In the understory layer, species that contributed the most to total understory basal area were *Castanea dentata* > *Rubus* spp. (allegheniensis and odorata) > *Calycanthus florida* > *Prunus serotina* > *Acer rubrum*. *Rubus allegheniensis* had the highest IV in the H+S forest, yet was a minor species in the undisturbed forest. *Rubus allegheniensis* is an opportunistic species that increases in abundance after canopy opening (Collins and Pickett 1988a; Boring et al. 1988; Roberts and Dong 1993; Cooper-Ellis et al. 1999) and will decrease with canopy closure (Elliott et al. 1997). It is considered very shade intolerant and has a seed bank strategy for reproduction (Peterson and Pickctt 1995). Thus, it is not surprising that *R. allegheniensis* is more abundant in the H+S forest than the undisturbed forest.

Abundance of groundlayer species was higher in the H+S forest than in the undisturbed forest; further, abundance increased over time in the H+S forest. In the H+S forest, more species were represented by the various growth forms (trees, shrubs, vines, and herbs) than in the undisturbed forest. More species were represented by late (shade-tolerant) and early (shade-intolerant) successional categories in the H+S forest than in the undisturbed forest. Not only were species richness and diversity higher in the H+S forest than in the undisturbed forest, genera richness and family richness were also higher.

The H+S forest had a considerable amount of slash left from the logging, and pit and mound

Table 5. Number of species representing the families found in the groundlayer of the undisturbed forest and the hurricane + salvage logged (H + S) forest.

Family	Succession*	Number of species Undis-turbed	H + S
Aceraceae	Late	2	2
Anacardiaceae	Early		1
Apiaceae	Late		1
Araceae	Late	1	1
Aristolochiaceae	Early	1	1
Asclepiadaceae	Early		1
Aspidiaceae	Late	4	3
Asteraceae	Early	9	13
Balsaminaceae	Early		1
Berberidaceae	Late		2
Calycanthaceae	Early		1
Caprifoliaceae	Early	—	1
Commelinaceae	Late	1	1
Convovulaceae	Early		1
Cornaceae	Late		1
Cyperaceae	Early	1	2
Dioscoreaceae	Late	1	1
Ericaceae	Early	3	4
Fabaceae	Early	2	3
Fagaceae	Late	3	5
Hypericaceae	Late	1	1
Juglandaceae	Late	1	1
Lamiaceae	Early	1	3
Lauraceae	Early	1	1
Liliaceae	Late	6	11
Magnoliaceae	Late	1	1
Nyssaceae	Early		
Ophioglossaceae	Late		1
Oleaceae	Late	1	1
Orchidaceae	Late	1	—
Oxalidaceae	Early	1	1
Papaveraceae	Late	—	1
Phytolaccaceae	Early		1
Primulaccae	Late	1	1
Poaceae	Early	4	4
Pteridaceae	Late	1	—
Ranunculaceae	Early	2	4
Rosaceae	Late	3	6
Rubiaceae	Late	2	2
Saxifragaceae	Late	1	2
Symplocaceae	Early		1
Violaceae	Late	2	5
Vitaceae	Early	1	2

Note: * successional status refers to the time when most of the species within a family are likely to be most abundant; criteria for early (0-10 yrs after disturbance) is shade-intolerant or open canopy species, criteria for late (>20 yrs after disturbance) is shade-tolerant species that can thrive in the understory of a closed canopy forest.

topography was created from the blowdown of large trees. In the Coweeta Basin, Clinton and Baker (1999) measured considerable variation in soil characteristics (carbon, nitrogen, and C:N ratio), light (PAR; photosynthetically active radiation), soil moisture, and soil temperature within pit and mound microsites created by treefall. The micro-relief of pit and mound topography from uprooting of windthrown trees (Beatty 1984; Peterson and Campbell 1993; Foster et al. 1997), shade from the slash-debris left on site from the salvage logging, and shade from the remaining overstory trees created a mosaic of environmental conditions. This environmental heterogeneity could be responsible for the mix of early (shade intolerant) and late (shade tolerant) successional herbaceous species, and a higher species richness and diversity than the undisturbed forest.

In other forest types, partial cutting methods, such as shelterwood cutting or strip-cutting, resulted in higher plant diversity than clearcutting (Gove et al. 1992; Hannerz and Hånell 1997; Bråkenhielm and Liu 1998). In a boreal pine forest, Bråkenhielm and Liu (199X) found that H' declined the tirst five to eight years after harvest, with the time depending on treatment. H' then started to increase, with the increase earlier on plots with slash than on those without In a mixed deciduous forest, Gove et al. (1992) compared diversity trends after strip-cutting and clearcutting; strip-cutting had higher diversity both one and ten years after harvesting. In a central Appalachian hardwood forest, Gilliam (in press) found that clearcutting with herbicide treatment appeared to have minimal effects on species richness or diversity of the groundlayer -20 yr after cutting. In contrast, Hammond et al. (1998) found that clearcutting in mixed-oak forests of Virginia resulted in more species change than other harvest techniques such as group selection and shelterwood cutting.

Although overstory residual density and basal area were low after harvest, the H+S disturbance regime and the resulting species composition and diversity differ strikingly from diversity patterns following clearcutting in this region (Elliott and Swank 1994; Elliott et al. 1997; Elliott et al. 1998). For example, in a nearby clearcut forest (Elliott et al. 1997) many more ground flora species were present in all communities before clearcutting than in years 1 through 17 after clearcutting, and the abundance of late successional species was higher before than after clearcutting. In contrast, H' was much higher in the H+S forest than in the clearcut forest the first few years following disturbance. Many factors accounted for the dramatic difference in H' and richness of groundlayer flora between the nearby clearcut forest and the H+S forest of this study. The scale of disturbance was much larger in the clearcut forest compared to the H+S forest (57 ha vs. 10 ha of this study); intensity of disturbance was greater in the clearcut forest compared to the H+S forest (complete clearcut with all stems >2.5 cm cut vs. partial cut of this study); microsite variability was lower in the clearcut forest compared to the H+S forest (i.e., pit and mound topography plus partial shade from remaining overstory trees created a mosaic of microsite conditions in the H+S forest); difference in aspect resulted in higher solar radiation after cutting in the clearcut forest compared to the H+S area (the clearcut forest is a south-facing watershed vs. the east-facing aspect of the H+S forest). However, even among clearcut watersheds within the southern Appalachians, other factors were also responsible for the differences in diversity patterns (see Elliott et al. 199X), such as community type, elevation, aspect, and patterns of cutting.

In the southern Appalachians, high-intensity winds create forest openings ranging in size from single-tree gaps to several hectares or more, with sufficient temporal and spatial frequency to affect a sizeable portion of the landscape (Greenberg and McNab 1998). While high-intensity wind events are less frequent and more widely dispersed across the landscape than individual tree death, they impact a considerable area of the Appalachian landscape as exemplified by Hurricane Opal in 1995. After wind disturbance, managed forests are generally salvaged to minimize economic losses. This combination of blowdown and salvage logging creates a heterogeneous microenvironment contributing to high plant diversity with both early and late successional species regenerating after disturbance.

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