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Long-term recovery dynamics following hurricane-related wind disturbance in a southern Appalachian forest

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ABSTRACT

Wind disturbance affects thousands of km^2 annually in eastern temperate forests, yet few studies address long-term recovery. Here, I assess changes in forest structure and composition before (pre-Opal), immediately after (Y0), and 21 years after (Y21) Hurricane Opal in 0.166–1.08 ha gaps created by microbursts, and undisturbed controls. In gaps, an average of 24.0% of trees (41.1% BA) were windthrown and 1.0% of trees (1.1% BA) died standing during Opal; scarlet and black oak were disproportionately windthrown. Subsequent windthrow or standing tree mortality rates did not differ between treatments. By Y21 an average of 32.2% (49.5% BA) of trees were windthrown in gaps and 3.2% (2.4% BA) in controls; 7.2% (7.6% BA) died standing in gaps and 12.0% (11.7% BA) in controls. Pit depth and windthrown rootmass area decreased by 63% by Y21. Total snag density differed over time (23.8–38.8/ha in controls; 6.7–19.7/ha in gaps); "new" snag (e.g., died after Opal) density did not differ between treatments. Disproportionately more scarlet oak, shortleaf pine, and hickory but fewer yellow-poplar, red maple and sourwood died standing. By Y21 live tree density and (marginally) basal area recovered to pre-Opal levels in gaps but remained lower than controls. In gaps, hurricane-related mortality of trees 38.1–50.7 cm dbh was heaviest, and density of this size-class remained lower by Y21; density of trees 50.8–63.4 cm was also lower in gaps in Y21. Trees grew faster in gaps than controls but stand-level gains in average dbh were smaller in gaps due to a greater increase in small trees (ingrowth) by Y21. Initial hurricane-related mortality changed relative importance (average of relative abundance and relative BA) of species in gaps; differences in mortality and growth rates among species contributed to subsequent shifts by Y21, especially in gaps. Post-Opal gains in shade-intolerant yellow-poplar importance were small but significant by Y21; shade-tolerant generalist species such as red maple and sourwood also increased, whereas scarlet and black oak decreased. Cumulatively, small changes by multiple species resulted in decreased (−19.9%) importance of the oak-hickory group and a corresponding increase in "other"; this trend was also evident in controls at a much smaller scale (−5.6%). Results indicate that a wind-related "pulse" of heavy mortality unevenly distributed among species – in this case scarlet and black oak - can alter stand structure and relative importance of species for decades, with accelerated loss of the oak-hickory group and replacement largely by shade-tolerant generalist species.

1. Introduction

Wind may be the most impactful agent of natural disturbance across eastern hardwood forests (Peterson et al., 2016), affecting thousands of square kilometers annually (Oldfield and Peterson, 2019) and causing pulses of tree mortality and changes to forest structure that are irregularly distributed at spatial and temporal scales (Harmon and Pabst, 2019). Potentially damaging winds are associated with a variety of storm types in the eastern US, including tornadoes, derechos, hurricanes, and tropical storms. The severity and mode (e.g., uprooting versus trunk breakage) of damage can vary with wind characteristics including speed, direction, duration, and travel path, as well as topography, soil characteristics including depth (Platt et al., 2000), and saturation due to rainfall before and during storms (e.g., Peterson and Rebertus, 1997; Greenberg and McNab, 1998; Rebertus and Meier, 2001; Xi et al., 2008a; Cowden et al., 2014; Peterson et al., 2016). Damage can also vary with tree species, size, architecture, root structure, and age but may be inconsistent among sites (Greenberg and McNab, 1998; Leach, 2003; Xi et al., 2008a; Busing et al., 2009; Holzmueller et al., 2012; Peterson et al., 2016).

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Differences in wind-related tree mortality among species and greater vulnerability of larger trees to windthrow (Greenberg and McNab, 1998; Peterson, 2007; Xi et al., 2008a; Busing et al., 2009; Holzmueller et al., 2012) can result in canopy dominant trees and species being disproportionately removed, altering the distribution of size-classes and relative abundance of species (Peterson et al., 2016). Several studies show only slight changes in canopy tree species diversity after moderate wind damage (e.g., Greenberg and McNab, 1998; Leach, 2003; Holzmeller et al., 2012; Cowden et al., 2014); others show decreased diversity after high-severity wind damage (Peterson and Rebertus, 1997; Peterson et al., 2016). Most studies of wind disturbance focus on immediate impacts to forest composition and structure, with far less attention given to longer-term processes of delayed tree mortality, regeneration, growth rates of residual live trees, and shifts in size-class distributions and species composition (Everham and Brokaw, 1996; Webb, 1999; Busing et al., 2009; Xi and Peet, 2011).

Oak trees play a central role in forest ecology (Rodewald, 2003) and economics (Patterson, 2004) of the Central Hardwood Region. Acorns (oak seeds) – an important wildlife food – are a "keystone" to biological diversity by affecting populations of rodents that in turn are prey to raptors and carnivores, and populations of white-tailed deer (*Odocoileus virginianus*) that alter forest structure and composition through browsing (Feldhamer, 2002). The sustainability of eastern oak-dominated forests is threatened by high oak mortality rates and widespread regeneration failure – the failure of seedlings and saplings to attain canopy status, especially on higher quality mesic sites (Loftis et al., 2011; Dey, 2002). Several studies report that shade-tolerant species are likely to replace oaks in small (single-tree) gaps (e.g., Taylor and Lorimer, 2003; Hart and Grissino-Mayer, 2009) and intermediate-severity wind disturbance (Cowden et al., 2014; White et al., 2015; Xi et al., 2019), eventually leading to decreased oak dominance in upland hardwood forests. Successional trajectories are at least partially dependent on pre-disturbance successional phase and species composition of large (>1.4 m ht), already established advance reproduction (Xi et al., 2019). Increasing emphasis on forest management modeled on the range of variation by natural disturbance regimes (Greenberg et al., 2016) highlights the need to quantify longer-term dynamics of both structural and compositional forest recovery.

On 5 October 1995 the remnants of Hurricane Opal (hereafter Opal) brought heavy precipitation (>15 cm between 3 and 6 October) and wind gusts up to 93 km/hr to the Bent Creek Experimental Forest, Pisgah National Forest (BCEF), Asheville, North Carolina. The tropical storm caused wind damage to forests throughout the southern Appalachians; approximately 0.28% of the land area within four southern Appalachian national forests was damaged (Greenberg and McNab, 1998). Damage within the 2500 ha BCEF included multiple single-tree windthrows (canopy gaps $\leq$ 200 m^2), and 30 larger gaps created by microbursts, characterized by multiple-tree windthrown trees within discrete, intermediate-sized (0.1–3.9 ha; median 0.4 ha) areas (McNab et al., 2004).

Greenberg and McNab (1998) characterized the immediate effect of these wind microbursts on stand structure and composition (Pre-Opal forests were inferred from newly fallen trees), and ground disturbance within five of these intermediate-sized gaps. Nonrandom but differing direction of windthrow among gaps indicated that each was created by an independent microburst. Microbursts reduced tree density (19–39%) and basal area (BA) (30–53%), and most windthrows were uprooted, versus snapped. Red oaks (*Quercus coccinea*, *Q. rubra*, and *Q. velutina*) were disproportionately uprooted, whereas *N. sylvatica* and *A. rubrum* were resistant to uprooting; the incidence of uprooting increased with tree diameter. Uprooted trees created pits ranging in average depth from 0.5 to 1.0 m among gaps. Tree mortality resulted in minor shifts in canopy species dominance (Greenberg and McNab, 1998).

I subsequently (1996) established a plot in undisturbed forest of similar age and species composition adjacent to each of four original study gaps, to serve as paired controls under a replicated Before-After/Control-Impact paired model (BACIP; Smith, 2002). Study gaps and their paired controls were periodically revisited through 2016 (21 years post-Opal) to assess longer-term tree mortality and growth. This replicated BACIP approach was used to experimentally assess changes in forest structure and composition before (pre-Opal), immediately after (Y0), and 21 years after (Y21) Opal in wind-disturbed gaps and undisturbed forested controls. I also examined whether tree mortality rates and modes (windthrown or standing) differed between gaps and controls, and how the abundance of pre-Opal (died before Opal), new (died after Opal), and total standing snags changed over time. My objective was to examine long-term recovery of forest structure and composition in gaps created by hurricane-related wind downbursts by comparison with forest structure and composition prior to Opal and with undisturbed forested controls. Specific questions include: (1) Will structural attributes such as tree density and BA increase more in gaps than controls over time following initial reductions in gaps by Opal, due to greater tree growth and ingrowth? (2) Will tree size-class distributions in gaps recover to pre-Opal or control distributions within the 21-year study period, given initial heavy loss of larger trees during Opal? (3) Will relative importance of tree species and the oak-hickory group in particular shift more in gaps than controls or pre-Opal, given initial heavy oak-hickory losses, ongoing oak decline, and regeneration dynamics?

2. Methods

2.1. Study area and land use history

This study was conducted at the Bent Creek Experimental Forest (BCEF), a 2500 ha watershed within the Southern Appalachians in Pisgah National Forest, Buncombe County, North Carolina. Elevations within BCEF ranged from 700 m to 1070 m. Average annual precipitation was 140 cm and was evenly distributed year-round. Monthly average temperatures range -4.2° to 8.6 °C in January, to 16.0° to 28.9 °C in July (Owenby and Ezell, 1992). Common tree species in this upland hardwood forest included black oak, chestnut oak (*Q. montana*), scarlet oak, white oak (*Q. alba*), sourwood (*Oxydendrum arboreum*), red maple (*Acer rubrum*), dogwood (*Cornus florida*), and interspersed shortleaf pine (*Pinus echinata*). Common shrub species included mountain laurel (*Kalmia latifolia*) and deerberry (*Vaccinium stamineum*) (McNab et al., 2004). Average site index (base age 50) was 20.6 $\pm$ 0.6 (range 14.9–32.3) within the BCEF study area (Greenberg et al., 2014); xerophytic species composition on study plots indicated they were less productive sites (McNab and Keyser, 2020).

Study sites were undisturbed by humans for 80–120 years at study establishment. Beginning around 1795 early settlers cleared about 25% of the watershed (mostly less-steep topography) for subsistence farming; the rest was open woodlands created by high-grade harvesting of trees for sale, firewood cutting, livestock grazing, and nearly annual burning (Nesbitt and Netboy, 1946). Fields were abandoned and anthropogenic disturbances, including fire, discontinued between 1900 when George Vanderbilt began purchasing tracts for his estate, and 1914 with the purchase of BCEF by the US Forest Service (Nesbitt and Netboy, 1946). Old fields generally succeeded to southern yellow pines (primarily shortleaf pine, but also some pitch pine (*P. rigida*) and Virginia pine (*P. virginiana*)) on drier sites, or yellow-poplar on more productive moister sites, then to mixed hardwoods or mixed pine-hardwoods (Nesbitt and Netboy, 1946; Hoffman and Anderson, 1945). Subsequently, the non-native chestnut blight (*Cryphonectria parasitica*) (starting around 1926 in western North Carolina) eliminated the once-dominant mature American chestnut (*Castanea dentata*) (Elliott and Swank, 2008), and at least two southern pine beetle outbreaks (1974–1976; 1997–2003) killed many yellow pines (Nowak et al., 2016).

2.2. Study design

All standing and Opal-felled trees and snags ≥ 12.7 cm dbh were identified, measured diameter at breast height (dbh), and individually tagged in four downburst-created gaps between 700 and 900 m elevation within the BCEF watershed during late fall 1995, immediately after Opal. Recently fallen trees were easily distinguished from older treefalls by freshness of soil on rootmasses (if windthrown) or breakage (if snapped), tight bark on boles, and leaves on branches; recent snagfalls were distinguished from older coarse woody debris by evidence of decomposition (loose or absent bark, decomposing wood, and usually absence of branches and twigs) and freshness of soil on rootmasses (if windthrown) or breakage (if snapped). This allowed inferential reconstruction of pre-Opal forest structure and composition. Gaps were defined to include the ground area within a canopy opening extending to the bases of dominant trees that were contiguous with a strip of undisturbed forest canopy ≥ 25 m wide surrounding the opening (modified from Runkle, 1982); residual (surviving) standing trees were included within gaps if they were not contiguous with the surrounding forest canopy. Study gap areas were measured as polygons with the Global Positioning System (GPS), and ranged from 0.166 to 1.08 ha. The following year (1996) the same measurements were made in 0.2 ha plots randomly established in undisturbed forest of similar age and composition (controls) adjacent to (and paired with) each gap. I saw no evidence of hurricane-related damage in controls and therefore considered both post-Opal (late 1995) measurements in gaps and 1996 measurements in controls measurements as Y0. Gaps and controls were re-inventoried in 2000 (Y5), 2006 (Y11), 2012 (Y17), and 2016 (Y21) (5, 11, 17, and 21 years post-hurricane) to assess post-Opal tree mortality, and whether pre-Opal and new snags were still standing. In 2016 dbh was remeasured and ingrowth (live trees growing into the ≥12.7 dbh size-class since study establishment) was inventoried. In controls, ingrowth was measured in the 0.2 ha plots; in gaps, it was measured in randomly located variable-sized subplots ranging from 0.1 to 0.2 ha to accommodate their irregular sizes and shapes. Pit depth and rootmass area were remeasured for a subsample of windthrown trees in gaps to determine the amount of pit infilling and rootmass decay over 21 years.

2.3. Statistical analysis

I used repeated measures ANOVAs (PROC MIXED; SAS 9.3) in a randomized block design to compare density/ha and BA/ha of common species, the oak-hickory group (OH), "other" (non-oak-hickory; OTH), and total live trees, and importance values (the average of relative abundance and relative BA) of common species, OH, and OTH between gaps and controls pre-Opal, Y0, and Y21. I also compared average stand-level dbh and diameter size-classes (SC; 12.7 cm increments) of live trees between gaps and controls during those three time periods. Ingrowth of new (untagged) live trees that grew from <12.7 cm to ≥12.7 cm dbh between 1995 and 2016 was included in Y21 estimates. Repeated measures ANOVAs were also used to compare tree mortality (windthrown, standing, and total) between gaps and controls directly due to Opal (Y0), and subsequently at periodic intervals (Y5, Y11, Y17, and Y21), and to compare the number of standing snags (pre-Opal, new, and total) in gaps and controls at any given "snapshot" in time (pre-Opal, Y0, Y5, Y11, Y17, and Y21). My primary interest was in ANOVA treatment × year interaction effects as indicators that mortality rate, forest structure and species composition differed between gaps and controls over time. A non-significant treatment × year interaction indicated that that there was a consistent difference between treatments across years. Treatment, year, or treatment × year interaction differences were considered significant with an overall experimental α of <0.05. When significant interaction effects were present, I identified treatments or years warranting further examination ($p < 0.05$ in tests of effect slices) and used the least square means for partitioned F-tests (SLICE option) in PROC MIXED (SAS 9.4) to examine the significance of treatment differences within identified years, and among-year differences within identified treatments. Count data were square-root transformed and percent data were arcsine square-root transformed (Zar 1998) for ANOVAs to reduce heteroscedasticity.

I used chi-square tests to examine whether species differed in likelihood of windthrow during Opal (gaps only) based on the proportion of windthrown trees for all species combined ("expected"), and in likelihood of dying standing after (not including direct effects) Opal based on the proportion of trees that died standing for all species combined ("expected"; gaps and controls combined). I used t-tests to compare change (Y0-Y21) in dbh and BA of individual (not stand-level) live trees by species between gaps and controls (trees pooled across sites within treatments). I used paired t-tests to test whether average dbh differed between windthrown and non-windthrown trees during Opal, and to compare BA growth/ha of original tagged trees still living in Y21, as well as differences in density and BA of live ingrowth between gaps and controls. I also used paired t-tests to examine differences (1995–2016) in pit depth and rootmass area (calculated as an ellipse) for a subsample of live trees uprooted by Opal within gaps.

3. Results

3.1. Tree mortality

Total tree mortality resulting directly from Opal (1995) averaged 25.0% of trees (42.2% BA) in gaps; adjacent forested controls were undisturbed (Table 1; Figs. 1, 2). Cumulative (Y0-Y21) total mortality averaged 39.4% of trees (57.1% BA) in gaps, and 15.1% of trees (14.1% BA) in controls (Fig. 2a). Total tree mortality was marginally greater in gaps than controls, and greater in Y0 than Y21. A treatment × year interaction effect indicated that total tree mortality was greater in gaps than controls in 1995, and greater in Y0 than subsequent years; within controls, total mortality was greater in Y5, Y11, and Y17 than Y0. Total BA mortality was greater in gaps than controls and greater in Y0 than subsequent years. A treatment × year interaction effect indicated that total BA mortality was greater in gaps than controls in Y0; within gaps BA mortality was greater in Y0 than subsequent years, and within controls BA mortality was lower in Y0 than Y17 (Fig. 2a).

Most tree mortality was due to windthrow during Opal (uprooting or snapping <1.8 m ht); on average, 24.0% of trees (41.1% BA) was windthrown in gaps, but none in adjacent controls (Fig. 2b). Average dbh of windthrown trees (38.7 ± 1.1 cm) was larger than non-windthrown trees (25.7 ± 0.7 cm) ($t = 12.35$; $p = 0.0011$). Species differed in vulnerability, with scarlet and black oak especially prone to windthrow during Opal (Fig. 3); see Greenberg and McNab (1998) for greater detail. In gaps, an additional 8.2% (8.4% BA) of trees were windthrown over the next 21 years for a cumulative mortality of 32.2% of trees (49.5% BA); in controls a total of 3.1% of trees (2.4% BA) were windthrown over the 21-year study period (Fig. 2b). The number and BA of windthrown trees was greater in gaps than controls and greater in Y0 than subsequent years. Treatment × year interaction effects indicted the number of windthrown trees was greater in gaps than controls in Y0 and greater in Y0 than subsequent years in gaps (Fig. 2b); total BA of windthrown trees was greater in gaps than controls in Y0 and Y5.

Standing tree mortality (STM) resulting directly from Opal (1995) averaged 1.0% of trees (1.1% BA) in gaps, and none in adjacent controls (Fig. 2c). Cumulative (Y0-Y21) STM averaged 7.2% of trees (7.6% BA) in gaps, and 12.0% of trees (11.7% BA) in controls (Fig. 2c). STM did not differ between gaps and controls and was greater in Y0 than Y5; a treatment × year interaction effect indicated that STM was greater in Y5, Y11, and Y17 than Y0 in controls. STM BA did not differ between treatments and was marginally lower in Y0 than Y5; no treatment × year interaction effect was detected. Scarlet oak, black oak, shortleaf pine, and hickory died standing more than expected (based on the proportion of all trees that died standing), whereas yellow-poplar, red maple and sourwood died standing less than expected in the years following Opal

Table 1
Mean (±SE) number and BA (m^2) of live trees (≥12.7 cm dbh)/ha before, immediately after (1995–1996), and 21 years after (2016; including ingrowth) Hurricane Opal in gaps (G) and undisturbed controls (C), and results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects on common species[1] and all species combined (total), Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. Data were square-root transformed for analyses to reduce heteroscedasticity.

Species	Trt	Pre-Opal	Post-Opal	2016	p_{trt}	p_{yr}	p_{trtxyr}	Pre-Opal	Post-Opal	2016	p_{trt}	p_{yr}	p_{trtxyr}
		Number live trees/ha						Basal area (m^2/ha)					
ARUB	C	42.5 ± 15.5	42.5 ± 15.5	48.8 ± 13.3	0.1057	0.0024	0.0434	1.45 ± 0.64	1.45 ± 0.64	2.29 ± 0.74	0.2267	<0.0001	0.3164
*	G	21.5 ± 16.3	21.0 ± 15.9	44.0 ± 16.9				0.86 ± 0.65	0.85 ± 0.65	1.77 ± 0.72			
BLEN	C	2.5 ± 1.4	2.5 ± 1.4	2.5 ± 1.4	—	—	—	0.08 ± 0.05	0.08 ± 0.05	0.13 ± 0.08	—	—	—
	G	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 1.3				0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.03			
CARY	C	15.0 ± 5.4	15.0 ± 5.4	8.8 ± 2.4	0.6150	0.6469	0.3699	0.45 ± 0.21	0.45 ± 0.21	0.28 ± 0.17	0.1232	0.3804	0.3018
	G	20.6 ± 11.7	17.6 ± 8.9	18.6 ± 5.5				1.09 ± 0.66	0.91 ± 0.49	0.90 ± 0.36			
CFLO	C	5.0 ± 3.5	5.0 ± 3.5	3.8 ± 2.4	—	—	—	0.12 ± 0.07	0.12 ± 0.07	0.13 ± 0.07	0.9056	0.1251	0.1093
	G	6.3 ± 2.7	6.1 ± 2.5	10.6 ± 6.1				0.09 ± 0.04	0.09 ± 0.04	0.23 ± 0.12			
FGRA	C	2.5 ± 2.5	2.5 ± 2.5	2.5 ± 2.5	—	—	—	0.10 ± 0.10	0.10 ± 0.10	0.16 ± 0.16	—	—	—
	G	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0				0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			
ILOP	C	0.0 ± 0.0	0.0 ± 0.0	2.5 ± 1.4	—	—	—	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.02	—	—	—
	G	0.2 ± 0.2	0.2 ± 0.2	1.9 ± 1.6				<0.01 ± <0.01	<0.01 ± <0.01	0.03 ± 0.02			
LTUL	C	15.0 ± 10.2	15.0 ± 10.2	15.0 ± 10.2	0.8849	0.0070	0.0070	0.68 ± 0.42	0.68 ± 0.42	0.96 ± 0.53	0.8678	0.0002	0.0268
	G	11.2 ± 5.4	9.4 ± 4.1	22.2 ± 9.8				0.61 ± 0.33	0.54 ± 0.30	1.34 ± 0.51			
NSYL	C	3.8 ± 2.4	3.8 ± 2.4	13.8 ± 5.2	0.0142	0.0444	0.2722	0.06 ± 0.04	0.06 ± 0.04	0.29 ± 0.11	0.0616	0.0223	0.8164
	G	20.3 ± 6.1	20.3 ± 6.1	23.6 ± 2.0				0.68 ± 0.40	0.68 ± 0.40	0.82 ± 0.16			
OARB	C	81.3 ± 22.8	81.3 ± 22.8	92.5 ± 21.7	0.1936	0.0151	0.3530	2.58 ± 0.69	2.58 ± 0.69	3.82 ± 0.89	0.0736	<0.0001	0.3905
	G	50.3 ± 10.0	39.6 ± 6.8	66.8 ± 17.4				1.48 ± 0.33	1.15 ± 0.25	2.18 ± 0.42			
PECH	C	27.5 ± 20.2	27.5 ± 20.1	20.0 ± 16.8	0.4531	0.0215	0.6069	3.17 ± 2.48	3.17 ± 2.48	2.93 ± 2.51	0.3367	0.1370	0.5000
	G	9.7 ± 6.0	7.1 ± 4.9	6.0 ± 4.5				0.85 ± 0.51	0.53 ± 0.38	0.52 ± 0.46			
PRIG	C	1.3 ± 1.3	1.3 ± 1.3	0.0 ± 0.0	—	—	—	0.06 ± 0.06	0.06 ± 0.06	0.00 ± 0.00	—	—	—
	G	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0				0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			
PSTR	C	21.3 ± 21.3	21.3 ± 21.3	27.5 ± 25.9	—	—	—	0.55 ± 0.55	0.55 ± 0.55	1.12 ± 1.05	—	—	—
	G	0.0 ± 0.0	0.0 ± 0.0	11.9 ± 4.5				0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.09			
PVIR	C	1.3 ± 1.3	1.3 ± 1.3	1.3 ± 1.3	—	—	—	0.10 ± 0.10	0.10 ± 0.10	0.10 ± 0.10	—	—	—
	G	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0				0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00			
QALB	C	61.3 ± 19.5	61.3 ± 19.5	53.8 ± 16.9	0.3983	0.0585	0.1582	6.59 ± 1.71	6.59 ± 1.71	7.39 ± 2.18	0.2320	0.0727	0.1048
	G	46.2 ± 8.3	32.5 ± 6.8	36.4 ± 11.1				4.91 ± 1.59	2.48 ± 0.37	3.94 ± 0.91			
QCOC	C	21.3 ± 8.3	21.3 ± 8.3	15.0 ± 8.9	0.6917	0.0018	0.0802	3.36 ± 1.47	3.36 ± 1.47	3.46 ± 2.38	0.7959	0.0145	0.0631
	G	34.9 ± 15.4	16.2 ± 8.5	11.4 ± 5.9				5.97 ± 2.40	2.21 ± 1.13	1.86 ± 0.89			
QFAL	C	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	—	—	—	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	—	—	—
	G	6.1 ± 5.8	4.0 ± 3.7	4.1 ± 4.1				0.63 ± 0.62	0.40 ± 0.39	0.34 ± 0.34			
QMON	C	70.0 ± 23.2	70.0 ± 23.2	60.0 ± 19.4	0.2229	0.7909	0.5687	6.26 ± 2.68	6.26 ± 2.68	8.11 ± 3.67	0.3467	0.0044	0.9441
	G	26.4 ± 7.7	25.2 ± 7.6	26.4 ± 6.1				2.64 ± 1.00	2.52 ± 1.03	3.40 ± 1.03			
QRUB	C				—	—	—				—	—	—

(continued on next page)

Table 1 (*continued*)

Species	Trt	Pre-Opal	Post-Opal	2016	p_{trt}	p_{yr}	p_{trtxyr}	Pre-Opal	Post-Opal	2016	p_{trt}	p_{yr}	p_{trtxyr}
		Number live trees/ha						Basal area (m^2/ha					
		1.3 ± 1.3	1.3 ± 1.3	1.3 ± 1.3				0.03 ± 0.03	0.03 ± 0.03	0.07 ± 0.07			
	G	4.9 ± 4.6	1.8 ± 1.5	1.8 ± 1.5				0.48 ± 0.47	0.13 ± 0.12	0.21 ± 0.18			
QVEL	C	15.0 ± 7.4	15.0 ± 7.4	10.0 ± 5.4	0.8760	0.0003	0.0068	1.46 ± 0.78	1.46 ± 0.78	1.61 ± 0.97	0.9306	0.0029	0.0022
	G	18.6 ± 5.4	6.6 ± 2.1	4.4 ± 1.2				2.58 ± 0.89	0.74 ± 0.23	0.59 ± 0.22			
RPSE	C	2.5 ± 1.4	2.5 ± 1.4	0.0 ± 0.0	—	—	—	0.13 ± 0.11	0.13 ± 0.11	0.00 ± 0.00	—	—	—
	G	1.5 ± 0.9	1.5 ± 0.9	2.0 ± 2.0				0.04 ± 0.02	0.04 ± 0.02	0.03 ± 0.03			
SALB	C	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	—	—	—	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	—	—	—
	G	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0				<0.01 ± <0.01	<0.01 ± <0.01	0.00 ± 0.00			
TCAN	C	2.5 ± 2.5	2.5 ± 2.5	6.3 ± 6.3	—	—	—	0.04 ± 0.04	0.04 ± 0.04	0.13 ± 0.13	—	—	—
	G	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2				0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02			

[1] ARUB = *Acer rubrum* (red maple); BLEN = *Betula lenta* (sweet birch); CARY = *Carya* spp. (hickory); CFLO = *Cornus florida* (flowering dogwood); FGRA = *Fagus grandifolia* (American beech); ILOP = *Ilex opaca* (American holly); LTUL = *Liriodendron tulipifera* (yellow-poplar); NSYL = *Nyssa sylvatica* (blackgum); OARB = *Oxydendrum arboreum* (sourwood); PECH = *Pinus echinata* (shortleaf pine); PRIG = *P. rigida* (pitch pine); PSTR = *P. strobus* (white pine); PVIR = *P. virginiana* (Virginia pine); QALB = *Quercus alba* (white oak); QCOC = *Q. coccinea* (scarlet oak); QFAL = *Q. falcata* (southern red oak); QPRI = *Q. montana* (chestnut oak); QRUB = *Q. rubra* (northern red oak); QVEL = *Q. velutina* (black oak); RPSE = *Robinia pseudoacacia* (black locust); SALB = *Sassafras albidum* (sassafras); TCAN = *Tsuga canadensis* (eastern hemlock).

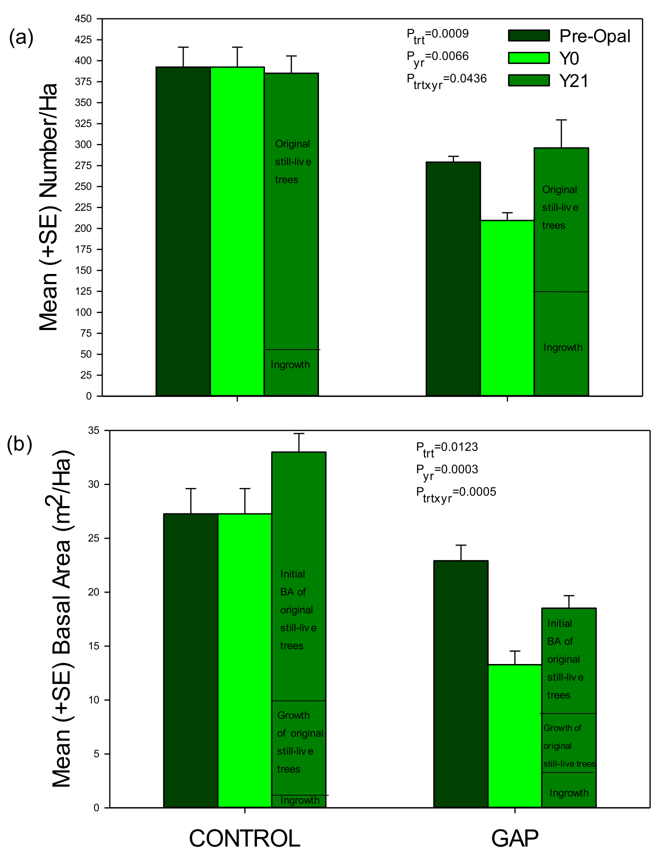

Fig. 1. Mean (±SE) total (a) number/ha, and (b) BA ($m^{2/}$/ha) of live trees (≥12.7 cm dbh) pre-Opal, immediately after (Y0), and 21 years after (Y21) Hurricane Opal in gaps and undisturbed controls, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects. Contributions of ingrowth and growth of still-living, original tagged trees are noted for Y21.

(Fig. 4).

3.2. Standing snags, pit depth, and rootmass area

Average total snag (dead standing trees that died before or after Opal) density was marginally greater in controls than gaps, ranging from 23.8 to 38.8/ha in controls 6.7–19.7/ha in gaps at any given "snapshot" in time (Fig. 5a). Total snag density was greater in Y5 than Y21; no treatment × year interaction effect was detected. Pre-Opal snag density was greater in controls than gaps and decreased over time within both treatments, with more pre-Opal than subsequent years, and more in Y0 and Y5 than Y17 and Y21; no treatment × year interaction effect was detected (Fig. 5b). New (e.g., post-Opal STM) snag density ranged from 13.8 to 26.3/ha in controls and 2.7–11.0/ha in gaps at any given "snapshot" in time (Fig. 5c) and did not differ between treatments. Fewer new snags were present in Y0 than subsequent years; a treatment × year interaction effect indicated there were fewer new snags in Y0 than subsequent years in controls, and more in controls than gaps in Y21 (Fig. 5c).

Depth of pits created by live windthrown trees (n = 81) was greater ($t = 16.90$; $p < 0.0001$) in Y0 (0.68 ± 0.03 m) than Y21 (0.25 ± 0.02 m). Similarly, rootmass (n = 89) area was greater ($t = 12.63$; $p < 0.0001$) in Y0 (3.94 ± 0.26 m^2) than Y21 (1.43 ± 0.11 m^2).

3.3. Stand structure and growth

Total live tree density was greater in controls than gaps and differed marginally among years (Table 1; Fig. 1a). A treatment × year interaction effect indicated that live tree density was greater in Y21 and (marginally; slice p = 0.0852) pre-Opal than Y0 in gaps; density was greater in controls than gaps pre-Opal and Y0 but did not differ in Y21. Total live tree BA (Fig. 1b) was greater in controls than gaps, and greater pre-Opal and Y21 than Y0. A treatment × year interaction effect indicated that BA was greater in Y21 than pre-Opal and (marginally; slice p = 0.0526) Y0 in controls; within gaps BA was lower in Y0 and marginally (slice p = 0.0883) lower in Y21 than pre-Opal. BA was greater in controls than gaps in Y0 and Y21. Ingrowth and growth of

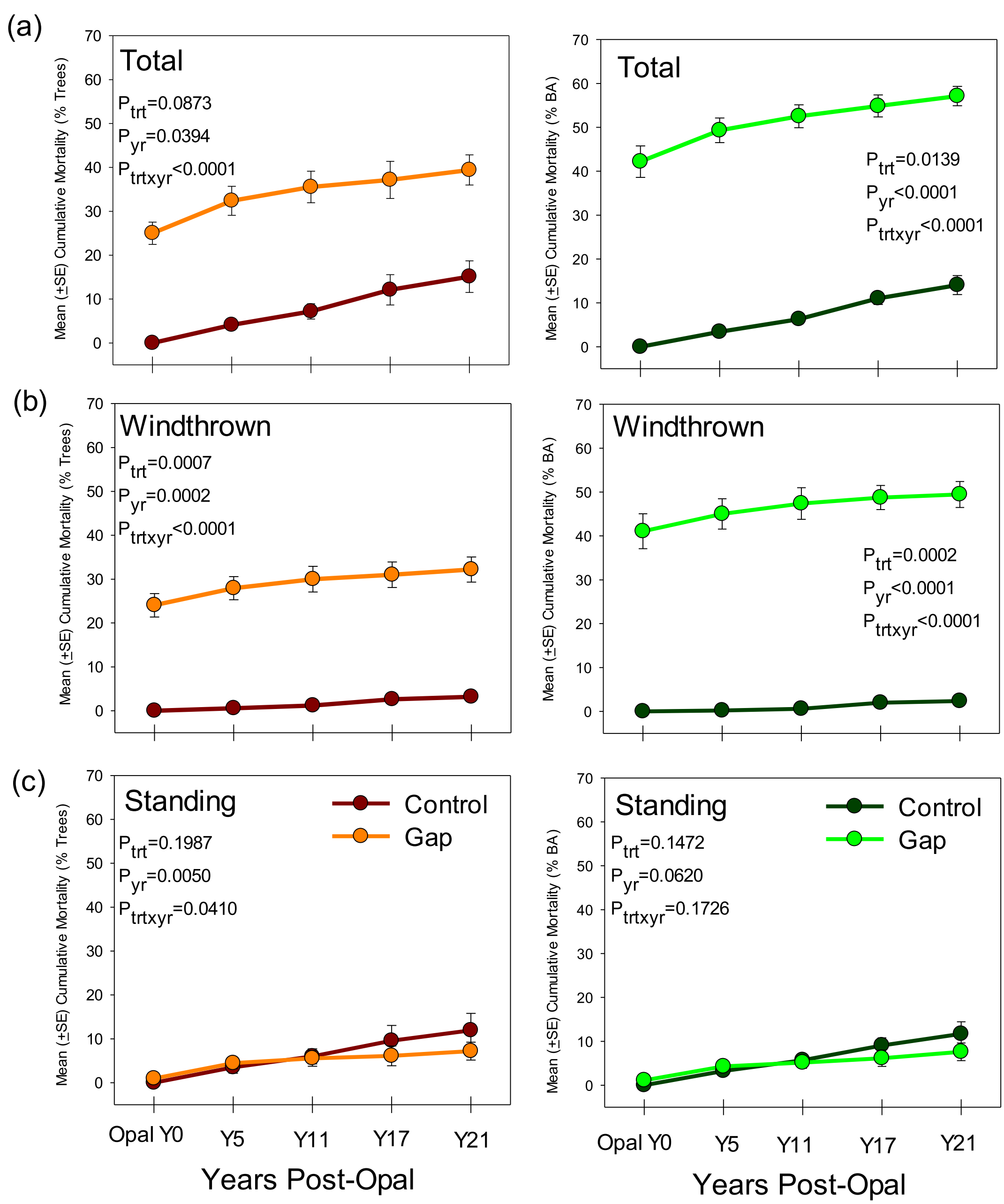

Fig. 2. Mean (±SE) cumulative percentage of number and BA of (a) total; (b) windthrown, and; (c) standing tree (≥12.7 cm dbh) mortality resulting directly from wind downbursts associated with Hurricane Opal (Y0) and 5, 11, 17, and 21 years after Hurricane Opal, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects.

still-living tagged trees contributed to gains in live tree density and BA by Y21 (Fig. 1a, b). Paired t-tests indicated total ingrowth (trees growing into SC ≥ 12.7 cm dbh) stems/ha was greater in gaps than controls ($t = 3.41$; $p = 0.0422$); total ingrowth BA/ha did not differ between the treatments. Dbh and BA growth of total individual trees was greater in gaps ($n = 361$) than controls ($n = 266$) (Fig. 6). However, total stand-level (per ha) BA gains by still-living tagged trees was greater in controls (where tree density was greater) than gaps ($t = -5.57$; $p = 0.0114$) (Fig. 1b).

Average stand-level dbh of living trees did not differ between gaps and controls and was lower in Y0 than pre-Opal or Y21 (Fig. 7). A treatment × year interaction effect indicated that average dbh was greater in Y21 than pre-Opal or Y0 in controls; in gaps, dbh was greater pre-Opal than Y0, and marginally (slice $p = 0.0544$) greater in Y21 than Y0. Density of SC 1–4 (12.7–63.4 cm) trees was greater in controls than gaps; density of trees ≥ 63.5 cm (SC 5+) did not differ between treatments (Fig. 8). Density of SC 3 (38.1–50.7 cm) trees was greater in Y21 than Y0 and lower than pre-Opal; density of trees ≥ 63.5 cm (SC 5 +) was greater in Y21 than Y0 and marginally (slice $p = 0.0759$) greater than pre-Opal. Treatment × year interaction effects were detected for SC 1, 3, and 4. In gaps, density of SC 1 (12.7–25.3 cm) trees was greater in Y21 than Y0 and marginally greater than pre-Opal; pre-Opal and Y0 density was greater in controls than gaps. In gaps SC 3 tree density was lower in Y0 and Y21 than pre-Opal; in Y0 it was greater in controls than gaps. In Y21, SC 4 (50.8–63.4 cm) tree density was greater in controls than gaps.

3.4. Species composition and relative importance of species

Among tested species (Table 1), density and BA of live red maple and

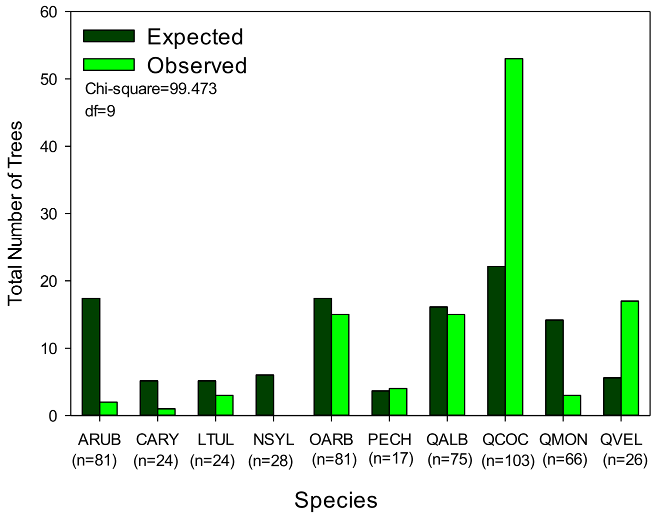

Fig. 3. Total expected versus observed windthrow frequency of common species during Hurricane Opal (1995) in gaps, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA, and results of Chi-square tests. Expected frequencies were calculated based on the percentage of total (all species combined) windthrown trees in gaps (21.5%). See Table 1 for full species names.

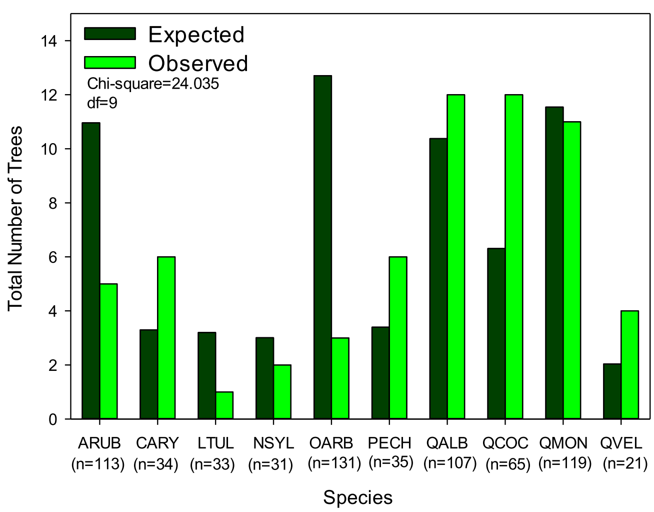

Fig. 4. Total frequency (raw number) of expected versus observed trees of common species that died standing after Hurricane Opal (1995–2016) in gaps and controls combined, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA, and results of Chi-square tests. Expected frequencies were based on the percentage of total (all species combined) live trees that died standing during the 21 years following hurricane Opal (9.7%). See Table 1 for full species names.

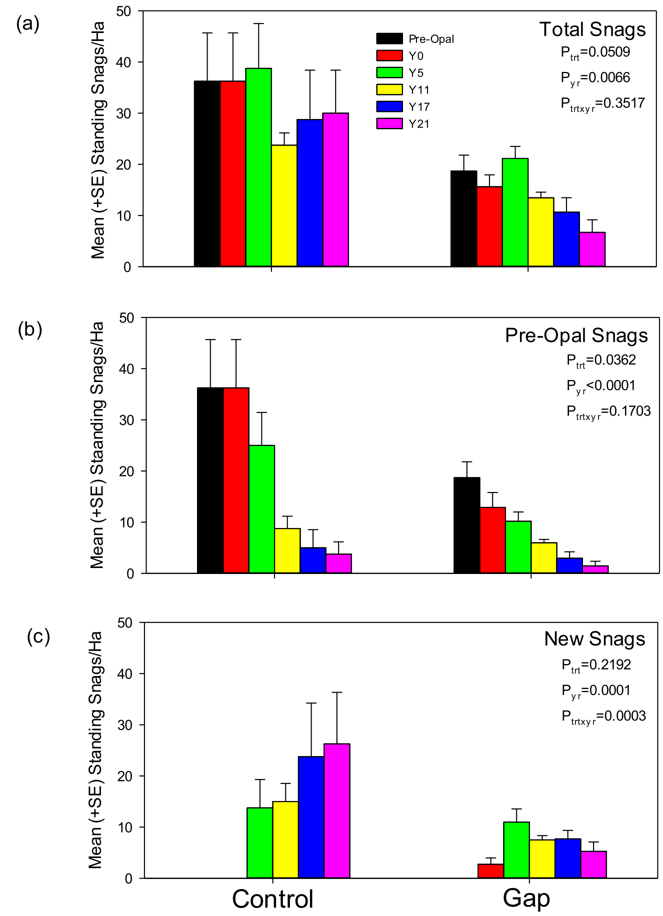

Fig. 5. Mean (±SE) (a) total; (b) pre-Opal (died before Opal), and; (c) new (died during or after Opal) standing snag (≥12.7 cm dbh and > 1.8 m ht) density (number/ha) pre-Opal, immediately after (Y0), and 5, 11, 17, and 21 years after Hurricane Opal, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects.

yellow-poplar did not differ between gaps and controls and was greater in Y21 than pre-Opal or Y0. Treatment × year interaction effects indicated that density of both species and yellow-poplar BA was greater in Y21 than pre-Opal or Y0 within gaps. Density and BA of sourwood, shortleaf pine, white oak, and chestnut oak did not differ between gaps and controls and no treatment × year interaction effect were detected. Sourwood density was greater in Y21 than Y0, and sourwood and chestnut oak BA was greater in Y21 than pre-Opal or Y0; shortleaf pine and white oak (marginally) density were lower in Y21 than pre-Opal, and white oak BA was marginally lower in Y0 than pre-Opal. Blackgum density was marginally lower in controls than gaps, and greater in Y21 than pre-Opal or Y0; no treatment × year interaction effect was detected. Scarlet oak density and BA did not differ between gaps and controls and were greater pre-Opal than Y0 or Y21; marginal treatment × year interaction effects indicated that density and BA were greater pre-Opal than Y0 or Y21 in gaps. Black oak density and BA did not differ between gaps and controls and was greater pre-Opal than Y0 or Y21; treatment × year interaction effects indicated that density and BA were greater pre-Opal than Y0 or Y21 in gaps. No treatment, year, or treatment × year interaction effects were detected for hickory spp. (Table 1).

Density of OH did not differ between treatments but was greater pre-Opal than Y0 or Y21; BA was greater in controls than gaps and greater pre-Opal than Y0 (Fig. 9). Treatment × year interaction effects indicated that OH density and BA were greater pre-Opal than Y0 or Y21 in gaps, and BA was greater in controls than gaps immediately in Y0 and Y21. Conversely, density of OTH was marginally greater in controls than gaps and greater in Y21 than pre-Opal and Y0. A treatment × year interaction effect indicated that density of OTH was greater in Y21 than pre-Opal or Y0; in Y0 density was greater in controls than gaps. BA of OTH was marginally greater in controls than gaps, and greater in Y21 than pre-Opal or Y0 (Fig. 9). Paired t-tests indicated ingrowth density of OTH was greater in gaps than controls ($t = 3.54$; $p = 0.0385$), but no differences were detected for OH or any tested species. Ingrowth BA/ha of OH, OTH, or tested species did not differ between the treatments. T-tests indicated that dbh growth of yellow-poplar, white oak, chestnut oak, and hickory spp. (Fig. 6a), and BA growth of yellow-poplar, white oak, and hickory spp. was greater in gaps than controls (Fig. 6b) but did not differ between treatments for other tested species.

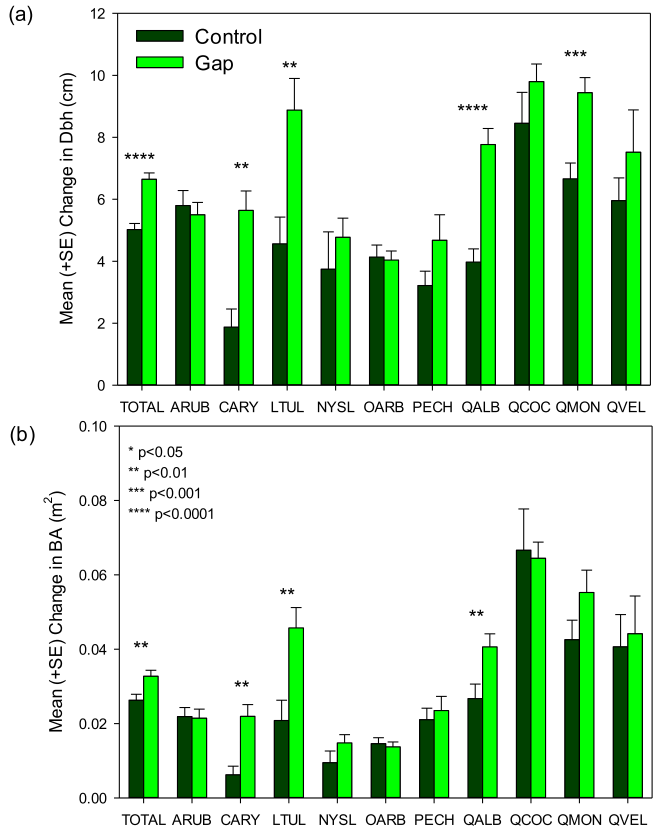

Fig. 6. Mean (+SE) 21-year change in (a) dbh and (b) basal area of individual (not stand level) live tagged trees (≥12.7 cm dbh) in gaps (n = 361 trees) and controls (n = 266 trees) for common species and all species combined, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects. See Table 1 for full species names.

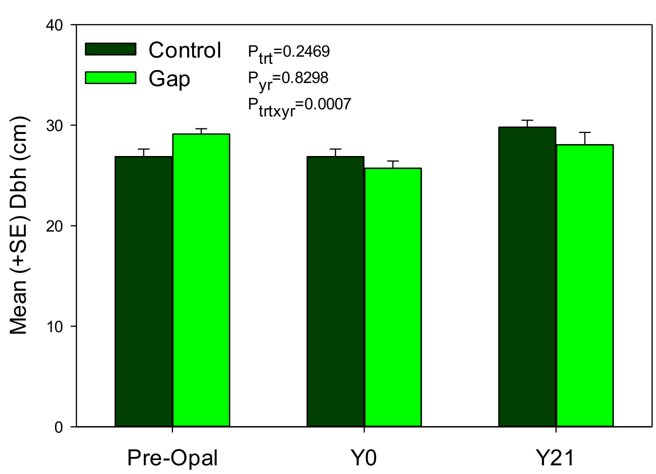

Fig. 7. Mean (±SE) stand-level live tree diameter (≥12.7 cm dbh) in gaps and undisturbed controls (n = 4 each) pre-Opal, immediately after (Y0), and 21 years after (Y21) Hurricane Opal, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. Mean diameters for Y21 include ingrowth. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects.

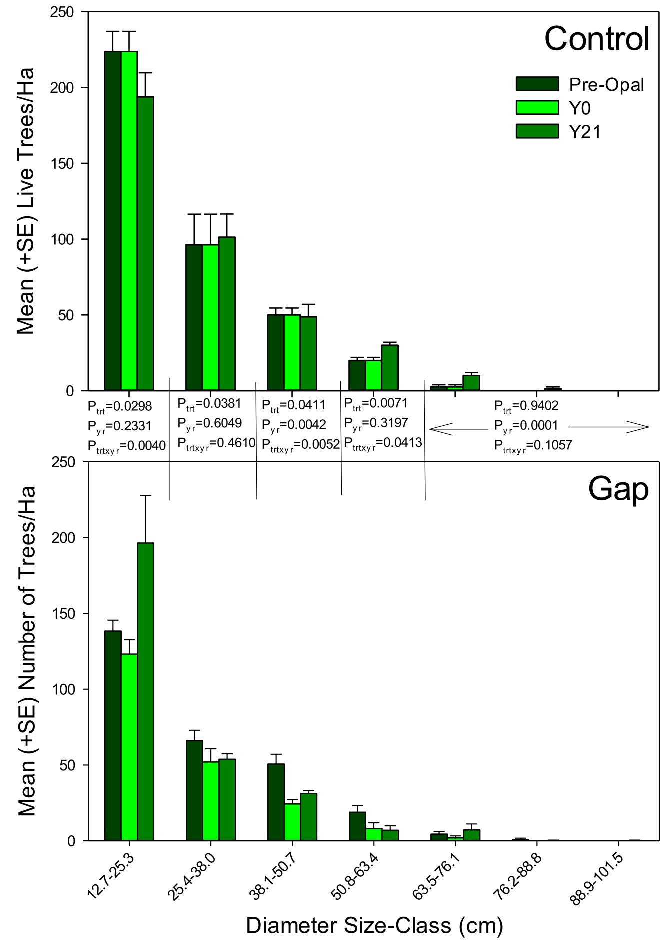

Fig. 8. Mean (+SE) diameter distribution of trees (≥12.7 cm dbh) in gaps and controls (n = 4 each) pre-Opal, immediately after (Y0) and 21 years after (Y21) Hurricane Opal, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. Means for Y21 include ingrowth. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects.

Importance values (IV) did not differ between gaps and controls for most species or OH, but year and (or) treatment × year interaction effects were detected for several (Table 2). Blackgum IV was greater in gaps than controls and marginally greater in Y21 than pre-Opal. Red maple and yellow-poplar IV were greater in Y21 than pre-Opal or Y0; treatment × year interaction effects indicated that IV of both species was greater in Y21 than pre-Opal or Y0 in gaps. IV of sourwood was greater in Y21 than pre-Opal or Y0, whereas shortleaf pine IV was marginally lower in Y21 than pre-Opal or Y0. Scarlet oak IV was lower in Y21 than pre-Opal or (marginally) Y0; a marginal treatment × year interaction effect indicated its IV was marginally (slice p = 0.0906) greater pre-Opal than Y0, and lower in Y21 than pre-Opal in gaps. Similarly, black oak IV was lower in Y21 than pre-Opal or marginally Y0, and greater pre-Opal than Y0; a treatment × year interaction effect indicated its IV was greater pre-Opal than Y0, and lower in Y21 than pre-Opal in gaps. Chestnut oak IV was greater in Y0 than pre-Opal; a treatment × year interaction effected indicated that IV was greater in Y0 and Y21 than pre-Opal in gaps. IV of OH was lower in Y21 than pre-Opal or Y0 and greater pre-Opal than Y0. A treatment × year interaction effect indicated that within both controls and gaps, OH IV was lower in Y21 than pre-Opal or Y0, and in gaps (only) greater pre-Opal than Y0. Conversely, the IV of OTH was greater in Y21 than pre-Opal or Y0, and lower pre-Opal than Y0; a treatment × year interaction effect indicated that OTH IV was greater in Y21 than pre-Opal or Y0 in both controls and gaps, and in gaps (only) lower pre-Opal than Y0.

4. Discussion

Our results illustrate 21 years of change in upland hardwood forest

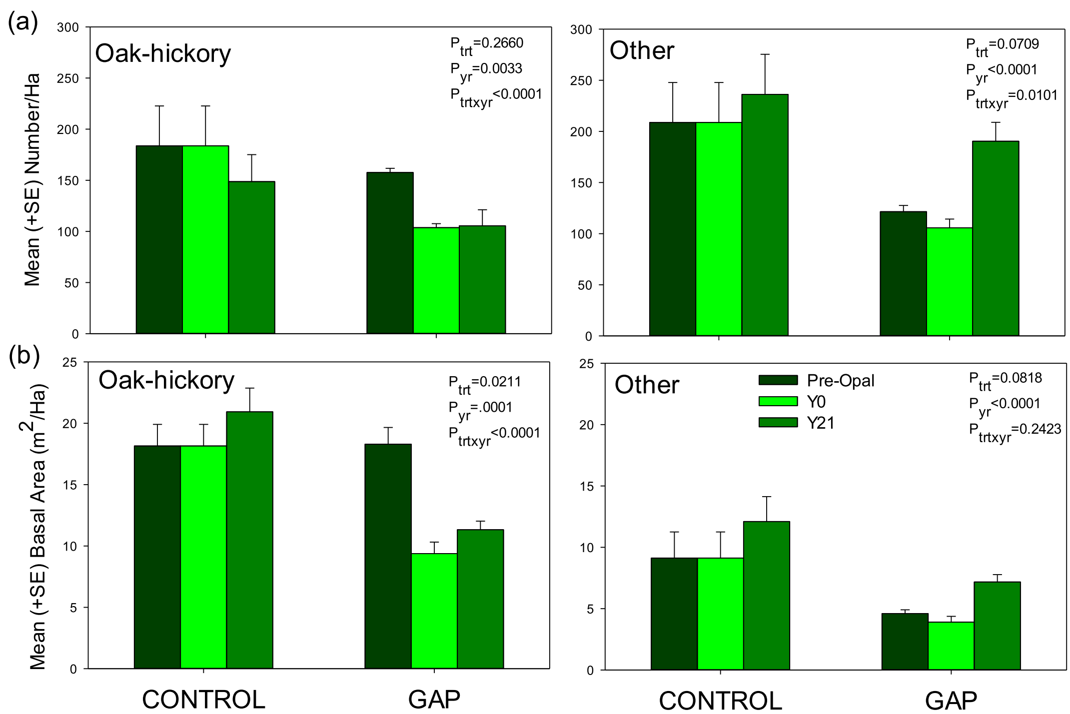

Fig. 9. Mean (±SE) total (a) number/ha, and (b) BA (m^2/ha) of live oak-hickory and "other" (non-oak-hickory) trees (≥12.7 cm dbh) pre-Opal, immediately after (Y0), and 21 years after (Y21) Hurricane Opal in gaps and undisturbed controls, Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. P-values are results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects.

structure and composition in undisturbed forest and gaps created by microbursts associated with Hurricane Opal in 1995. In gaps, initial changes in forest structure were dramatic, with 25.0% of trees and 42.2% of BA killed, mostly by windthrow (see Greenberg and McNab, 1998 for more detail on immediate impacts). In general, rates of tree mortality by windthrow were similar in gaps and controls over the next 21 years, although slightly greater BA fell in gaps than controls during the first five years after Opal; these were mainly individuals that had been partially uprooted by wind or other falling trees during Opal. High winds associated with two hurricane-related tropical storms (Frances and Ivan) in September 2004 toppled many trees within the study area (Greenberg et al., 2011) but did not substantially increase windthrow rates within study plots. Cumulatively, an average of 32.2% of live trees (49.5% BA) were windthrown in gaps, but only 3.1% of trees (2.4% BA) in controls over the 21-year study period. STM (snapped > 1.8 m ht) during Opal was negligible (1% of trees; 1.1% BA). Rates of STM varied over time but did not differ between gaps and controls; an average of 7.2% (7.6% BA) and 12.0% (11.7% BA) of trees died standing in gaps and controls, respectively over the 21-year study period. Xi et al. (2008b) reported delayed tree mortality twice the rate of "background" (pre-hurricane) mortality during the first five years after Hurricane Fran in a Piedmont upland hardwood forest. Harmon and Pabst (2019) found that substantial mortality of trees damaged by windthrow, breakage, or being struck by other falling trees, can occur for decades after wind events. In contrast, these long-term results indicate that overall, tree mortality was not accelerated in gaps following the initial "pulse" of hurricane-related mortality.

Results indicated that scarlet oak and shortleaf pine were more likely to die standing than other common species (18.5% and 17.1% of live standing trees in Y0, respectively). Throughout the Central Hardwood Region including BCEF, mature scarlet oak and black oak are especially prone to oak decline - a gradual crown dieback that often results in eventual death. Oak decline is often incited by drought, whereas advanced tree age and low site quality are considered predisposing factors, and armillaria root fungi (*Armillaria mellea*) or bark beetles contributing factors to already-declining trees (see Oak et al., 2016). Although less abundant than oak within the BCEF study area, shortleaf pines were heavily impacted by an outbreak of southern pine beetles (*Dendroctonus frontalis*) (1997–2003) (see Nowak et al., 2016) that likely contributed to higher than expected mortality rates.

In this study, 17.0% of the 755 trees still living after Opal (gaps and controls combined) died by windthrow (7.3%) or standing (9.7%) over the following 21 years for an average of 0.8% total mortality per year. This mortality rate corroborates other estimates of tree mortality and small (most < 200 m^2) gap formation frequency (0.5–2.0%) in central hardwood forests (Runkle, 1982; see Hart, 2016). This study illustrates the contrast between ongoing "background" mortality due to age, competition, insects, disease, wind, or drought (Lorimer, 1980) creating a fine-scale patchwork mosaic of structural heterogeneity and microsites, and infrequent higher-severity wind disturbance that substantially reduce the forest canopy in discrete, larger-scale patches across the landscape (Lorimer, 1980; McNab et al., 2004; Hart, 2016).

Results showed that live tree density and BA in gaps generally recovered to pre-Opal levels within 21 years, but the distribution of size-classes differed between gaps and controls 21 years after Opal. In gaps, hurricane-related mortality of trees 38.1–50.7 cm dbh (SC 3) was heaviest, and density of trees within this size-class remained lower by Y21; density of trees 50.8–63.4 cm (SC 4) was also lower in gaps than controls by Y21. Medium-sized (e.g., SC 2) trees were not substantially impacted by Opal, possibly due to a buffering effect by larger trees. In contrast, the density of small trees (12.7–25.3 cm; SC 1) increased in gaps by Y21 as seedlings, stump sprouts, or advance reproduction grew into tree size-classes (≥12.7 cm dbh). Peterson (2000) also reported heavier tornado-caused uprooting in intermediate-sized (40 cm) in a hemlock-hardwood stand in Pennsylvania, although a different tornado showed a linear relationship between size-class and uprooting, illustrating the range of potential effects of wind disturbance on tree diameter size-class distributions. Results here illustrate how intermediate-severity wind disturbance can alter tree diameter size-class distributions for decades.

Pits and mounds created by windthrow are important in "soil mixing" by moving rocks and soil (Lutz, 1960; Beatty and Stone, 1986) and

Table 2
Mean (±SE) importance value (average of relative abundance and relative BA) of live trees (≥12.7 cm dbh) before, immediately after (1995–1996), and 21 years after (2016; including ingrowth) Hurricane Opal in gaps (G) and undisturbed controls (C), and results of mixed-model ANOVAs comparing treatment, time, and treatment × time interaction effects on common species, the oak-hickory group (OH), and "other" (non-oak-hickory; OTH), Bent Creek Experimental Forest, Pisgah National Forest, North Carolina, USA. Percentage data were arcsine square-root transformed for analyses. See Table 1 for full species names.

Species	Trt	Pre-Opal	Post-Opal	2016	p_{trt}	p_{yr}	p_{trtxyr}
		Number live trees/ha					
ARUB	C	8.1 ± 3.1	8.1 ± 3.1	9.6 ± 2.4	0.6558	0.0006	0.0232
	G	5.7 ± 4.3	7.6 ± 5.5	11.9 ± 4.4			
CARY	C	2.7 ± 0.9	2.7 ± 0.9	1.5 ± 0.5	0.1500	0.2239	0.3600
	G	5.8 ± 3.2	7.6 ± 3.6	5.8 ± 2.0			
LTUL	C	3.2 ± 2.0	3.2 ± 2.0	3.2 ± 1.9	0.4519	0.0048	0.0070
	G	3.4 ± 1.6	4.4 ± 2.1	7.1 ± 2.3			
NSYL	C	0.7 ± 0.4	0.7 ± 0.4	2.4 ± 1.0	0.0328	0.0965	0.2526
	G	5.0 ± 1.7	7.4 ± 2.6	6.3 ± 0.6			
OARB	C	15.5 ± 4.3	15.5 ± 4.3	18.1 ± 4.4	0.7498	0.0107	0.5337
	G	12.2 ± 2.2	14.0 ± 2.4	17.9 ± 4.7			
PECH	C	8.5 ± 6.4	8.5 ± 6.4	7.2 ± 6.2	0.4416	0.0572	0.9365
	G	3.9 ± 2.4	4.1 ± 2.8	2.6 ± 2.2			
QALB	C	19.1 ± 4.5	19.1 ± 4.5	17.9 ± 5.0	0.8997	0.4356	0.9454
	G	18.7 ± 3.8	17.8 ± 3.8	16.7 ± 3.5			
QCOC	C	8.7 ± 3.6	8.7 ± 3.6	7.1 ± 4.5	0.3470	0.0027	0.0542
	G	20.1 ± 8.2	12.1 ± 6.1	7.1 ± 3.5			
QMON	C	22.2 ± 9.8	22.2 ± 9.8	21.2 ± 9.1	0.5188	0.0297	0.0157
	G	10.1 ± 3.9	14.6 ± 4.4	13.3 ± 3.1			
QVEL	C	4.3 ± 2.1	4.3 ± 2.2	3.5 ± 1.9	0.5968	0.0003	0.0019
	G	8.8 ± 2.6	4.4 ± 1.2	2.4 ± 0.7			
OH	C	57.1 ± 6.8	57.1 ± 6.8	51.5 ± 5.7	0.5364	<0.0001	<0.0001
	G	68.1 ± 2.1	60.2 ± 2.1	48.2 ± 0.8			
OTH	C	42.9 ± 6.8	42.9 ± 6.8	48.5 ± 5.7	0.5373	<0.0001	<0.0001
	G	31.9 ± 1.3	39.8 ± 2.1	51.9 ± 0.8			

creating microsites for plant establishment (Peterson and Pickett, 1990) and wildlife (Greenberg, 2002). Over time, effects of uprooting result in a substantial proportion of land area covered by pit and mound topography (e.g., Lyford and McLean, 1966); this process is accelerated by wind disturbances events such as Opal (Greenberg and McNab, 1998). In this study, rootmass area decreased by 63.7% during the 21 years after windthrow as roots decayed. Soil infilling reduced average pit depth by 63.2% within 21 years of tree uprooting. Peterson et al. (1990) reported a higher rate of infilling the first year (about 0.04 m) than the second (about 0.02 m) after recent windthrows, mainly by soil eroding from rootmasses and pit slopes. This study suggests that microtopography created by uprooting was reduced but still evident 21 years after Opal. Estimates in this study are likely conservative, as many fallen trees and associated pits were not found during 2016 measurements, often due to heavy decay (Robert J. Eaton, *unpubl. data*; pers. obs.) and possibly complete infilling of pits.

Although individual trees grew faster in gaps than controls, smaller stand-level gains in average dbh in gaps was likely due increased abundance of ingrowth (largely trees 12.7–25.3 cm dbh; SC 1). In controls, density changed little over time, as ingrowth (52.5 stems/ha) offset low levels of background tree mortality, but BA increased. In gaps, ingrowth (127.4 stems/ha) contributed to recovery of live tree density. Variability in ingrowth BA likely contributed to lack of statistical differences between gaps and controls, but nonetheless contributed 3.0008 m^2/ha to increases in BA/ha in gaps versus 0.9558 m^2/ha in controls within 21 years. Faster growth of residual (original, tagged trees) trees in gaps than controls also contributed to BA recovery in gaps, but BA gains were nonetheless greater in controls where a greater number of original, tagged trees also continued to grow. Small reproduction (e.g., seedlings, saplings, or stump sprouts) was not measured, but data nonetheless indicate that release of existing advance reproduction (saplings) and recruitment and growth of new reproduction (seedlings and stump sprouts) into larger size-classes (e.g., ingrowth), as well as growth of residual trees (see Everham and Brokaw, 1996; Mitchell, 2013) all contributed to forest structural recovery in gaps over the 21 years following substantial canopy reduction by Opal.

In this study, total snag density at any given "snapshot" in time ranged from 23.8 to 38.8/ha in controls and 6.7–19.7/ha in gaps and varied over time. A marginally higher density of pre-Opal snags (trees that died standing before Opal) - occurred in controls at study establishment; densities of new snags (trees that died standing in the years following Opal) did not differ between gaps and controls. Pre-Opal snags fell over time but were replaced by new snags at similar rates in both treatments. Snag density estimates in old growth southern Appalachian forests range from 10 to 70/ha (≥10 cm dbh) (McComb and Muller, 1983; Martin, 1992; Greenberg et al., 1997). Differences in species composition and size, in conjunction with interspecific differences in mortality, decay, and longevity rates influence snag densities among forests (Fassnacht and Steele, 2016). The wide range of snag densities among measurement periods in this study illustrates how snag abundance varies temporally regardless of wind disturbance, even within a single forest.

Small sample sizes and different snag longevities among species precluded statistical analyses on snag composition by species. However, it was notable that black oak (18.8%), shortleaf pine (17.2%), black locust (17.2%), scarlet oak (15.6%) and white oak (9.4%) composed a large proportion of identifiable (n = 64) pre-Opal snags (n = 71; all sites combined). This corresponds with results showing that many of these species were more likely to die standing than expected over the 21-year study period, and likely reflects their vulnerability to oak decline (oaks) or southern pine beetle attack (shortleaf pine). The prevalence of pre-Opal shortleaf pine and black locust snags – and a dearth of live trees - may additionally be artifacts of past land use within the BCEF watershed (Nesbitt and Netboy, 1946; Hoffman and Anderson, 1945; see Section 2.1). Both species commonly "pioneer" abandoned old fields and cutover forests; frequent burning by early inhabitants likely also facilitated conditions required for shortleaf pine regeneration. I was unable to precisely determine snag longevity due to long intervals between measurement periods. However, 8 (11.3%) pre-Opal snags remained standing for at least 21 years and included black locust (5), shortleaf pine, white pine, and scarlet oak (1 each). No new snags remained standing for more than 17 years, and most fell within less than 12 years.

Shifts in the relative importance of species occurred immediately after Opal and over the 21-year study period and were most evident in gaps where hurricane-related mortality was high and unevenly distributed among species. Other studies also show that high-severity wind disturbance can alter the relative abundance of trees and reduce diversity by removing forest canopy dominants (see Peterson et al., 2016).

In this study, initial sharp reductions in scarlet oak (−8.0%) and black oak (−4.4%) importance in gaps were driven by disproportionately heavy windthrow during Opal (Greenberg and McNab, 1998); by Y21 their importance had further declined from pre-Opal levels in gaps (−13.0% and −6.4% respectively), partly due to oak decline-related mortality.

Differences in growth rates of trees and reproduction (to tree-size), and mortality among species also contributed to shifts in relative importance among species over time, especially in gaps. For example, red maple and yellow-poplar importance showed small (+6.2 and +3.7%, respectively) but significant increases in gaps over the 21-year study period, in part due to their resistance to windthrow and (or) ability to grow rapidly in the higher-light environment. Density and (or) BA of chestnut oak and sourwood increased in both controls and gaps, contributing to their increased importance (+3.2 and +5.7% in gaps, respectively) by Y21. Conversely, the importance of shortleaf pine decreased in both gaps and controls (−1.3% for both) with decreasing density over time, likely due to pine beetle-related mortality and absence of regeneration. Although changes in the importance of most species were small, the cumulative effect resulted in a substantial (−19.9%) decrease in the importance of OH and a corresponding increase in OTH in gaps between pre-Opal and 2016. A similar 21-year trend of decreasing OH importance (−5.6%) and increasing importance of OTH was evident in controls, but at a much smaller scale.

Several studies show that both gap size (see Everham and Brokaw, 1996) and the severity of wind disturbance (see Peterson et al., 2016) are important determinants of future canopy composition (Wilder et al., 1999; Taylor and Lorimer, 2003) by affecting the understory light environment and recruitment of reproduction to larger size-classes (see Hart, 2016). Peterson et al. (2016) proposed that low- to moderate-intensity wind damage releases later-successional subcanopy and sapling stems by removing some canopy dominants, whereas high severity damage promotes the establishment and growth of shade-intolerant early successional species after substantial canopy and subcanopy removal. In the southern Appalachians, yellow-poplar is a fast-growing pioneer species that commonly establishes new seedlings after heavy canopy reduction by natural or silvicultural disturbances, often out-competing slower-growing species – particularly on moist, intermediate to high-quality sites (Loftis et al., 2011). In contrast, most southern Appalachian tree species, including oak and hickory, are mid- or highly tolerant of shade and depend on release of already-established advance reproduction and stump sprouts to grow into canopy positions after disturbances (Loftis et al., 2011).

The relatively large gaps studied here with about 75% of pre-disturbance trees (57.8% BA) remaining are best characterized as resulting from intermediate-severity wind disturbance (Peterson et al., 2016). A small increase yellow-poplar was evident, but establishment and growth were likely impeded by shade from residual canopy and subcanopy trees and relatively drier, lower-quality sites (e.g., Loftis et al., 2011). Cowden et al. (2014) also reported minimal response by yellow-poplar after intermediate-severity wind disturbance in an upland oak-dominated forest. In their study (Cowden et al., 2014), increased post-disturbance light at breast height was ephemeral (<3 years), as canopy reduction released existing advance reproduction and midstory stems, promoting crown expansion that soon reduced light on the forest floor.

In this study total ingrowth density was greater in gaps than controls, but no differences in the density of any species or OH were detected between gaps and controls, indicating that canopy reduction in gaps did not substantially promote regeneration of OH or any species in particular. In contrast, ingrowth of OTH was greater in gaps than controls and included red maple, sourwood, and other shade-tolerant species (Berg et al., 2019). Berg et al. (2019), studied 20-year seedling survival along transects from forest to gap centers within the same four study gaps used here and additional similar gaps created by Opal microbursts within the BCEF. Their results showed that seedling survival of mid-tolerant species (scarlet oak, black oak, and hickory) on subxeric sites decreased from forest to gap center but survival of shade-tolerant species such as red maple, sourwood, and blackgum did not differ along transects (Berg et al., 2019). Their findings (Berg et al., 2019) support results here showing that that whereas canopy reduction released reproduction, it did not substantially promote shade-intolerant species, nor the recovery of OH after its heavy loss during Opal.

5. Conclusions

The results of this study indicate that a wind-related "pulse" of heavy mortality unevenly distributed among species can alter stand structure and the relative importance of species for decades. Hurricane-related mortality followed by 21 years of low-level "background" mortality – both disproportionately concentrated in scarlet oak and black oak, growth of residual trees, and growth of reproduction to tree-size (ingrowth) contributed to shifts in species' importance and stand structure. Cumulatively, small changes by multiple species resulted in decreased (−19.9%) importance of OH and a corresponding increase in OTH; this trend was also evident in controls, but at a much smaller scale (−5.6%). Results indicate that intermediate-severity wind disturbance in upland hardwood forest may accelerate loss of mid-tolerant OH and replacement largely by shade-tolerant generalist species.

There is a growing emphasis on forest management modeled on the range of variation in natural disturbance regimes (Greenberg et al., 2016), especially on public lands. This study illustrates one example of forest structure among many across a continuum of area affected and levels of canopy removal created by different types and severities of wind-disturbance in the Central Hardwood Region (Hart et al., 2016; Peterson et al., 2016). Hurricane Opal created landscape-level heterogeneity with the BCEF watershed (McNab et al., 2004) and throughout much of the southern Appalachians (Greenberg and McNab, 1998; Clinton and Baker, 2000; Elliott et al., 2002) by creating a "perforated" forest of single- or multiple-tree, variably-sized gaps such as those described in this study. Structural heterogeneity was also created within gaps by reducing the number of canopy trees while retaining vertical structure; these changes were still evident more than two decades later. Silvicultural methods such single-tree selection (Keyser and Loftis, 2012) could be used to mimic this particular forest structure, but shade-tolerant species may eventually replace oak and hickory as canopy dominants.

Forest management for structural attributes modeled on natural disturbances must be balanced with other management objectives, such as sustaining eastern oak-dominated forests through successful oak regeneration. Results of this study corroborate others showing that oaks are often replaced by shade-tolerant species in small natural (e.g., Taylor and Lorimer, 2003; Hart and Grissino-Mayer, 2009) and experimentally-created (Dietze and Clark, 2008; Lhotka, 2013; Forrester et al., 2014) gaps as well as those created by intermediate-severity wind disturbance (Cowden et al., 2014; White et al., 2015; Xi et al., 2019).

Successful oak regeneration depends on development of seedlings to larger advance reproduction size that can compete with faster-growing species after release by canopy removal; this usually requires an interim moderate overstory or midstory reduction that increases light (Loftis et al., 2011; Berg et al., 2019). In this study, partial canopy reduction by Opal increased light, at least in the short-term (Greenberg and Lanham, 2001; Berg, *unpubl. data*) but did not favor OH regeneration over more shade-tolerant species. Further, this natural disturbance event was not followed several years later by canopy removal to release advance reproduction of OH and other mid-tolerant species that may have developed. This combined with heavy oak mortality during (windthrow) and after (oak decline) Opal is resulting in a successional trajectory of shade-tolerant species that will replace oak as a canopy dominant, even on subxeric sites where yellow-poplar was not a major competitor.

Sustainable disturbance-based forest management may require deviations from actions designed to mirror natural disturbances such as intermediate-severity wind disturbance if regeneration of oak and other mid-tolerant species is a management goal. Silvicultural treatments that alter the light environment at the forest floor, such as shelterwoods with reserves or the oak shelterwood system using midstory removal (Loftis et al., 2011) are unlikely to promote oak or other mid-tolerant species without multiple steps spanning several years, including seed production (e.g., acorns; hickory nuts), seedling establishment, their development into large advance reproduction, and finally release by overstory removal (Arthur et al. 2012); even then, several studies have demonstrated highly variable success in promoting oak regeneration using these methods (Loftis et al, 2011; Parrott et al., 2012; Schweitzer and Dey, 2017; Craig et al. 2014). Other studies have demonstrated that survival, growth, and density of advance reproduction by several species, including oak, increases near higher-light (e.g., Patterson, 2017) forest edge environments of gaps (Chen et al., 1992; Berg et al., 2019) or clearcuts (Lhotka and Stringer, 2013). Recent (Patterson, 2017) and current (Forester et al., 2019) research is addressing whether regeneration of oak and other mid-tolerant species in central hardwood forests can be promoted using an irregular group shelterwood reproduction method, or Femelschlag (Seymour, 2002; Raymond et al., 2009). The Femelschlag seeks to capitalize on gap edge effects to promote the development of competitive advance reproduction of mid-tolerant species in artificially-created gaps, and later (ca. 10 years) release by expanding gap perimeters during subsequent entries. This disturbance-based silvicultural system is designed to create a complex, multi-cohort forest structure and diverse species composition that includes mid-tolerant species. Wind and other natural disturbances are unlikely to sustain eastern oak-dominated forests without silvicultural intervention.

6. Author statement

The author (Cathryn H. Greenberg) has no conflict of interest regarding the submitted manuscript entitled *Long-term recovery dynamics following hurricane-related wind disturbance in a southern Appalachian forest.*

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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