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Twenty-year survivorship of tree seedlings in wind-created gaps in an upland hardwood forest in the eastern US

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Abstract
Wind is a common canopy disturbance in the upland oak (*Quercus*)- and hickory (*Carya*)-dominated stands of the Central Hardwood Region of the eastern US. Canopy openings range from small gaps, resulting from windthrow of single dominant trees, to occasional large gaps of many hectares formed by straight-line winds associated with severe thunderstorms and rare subtropical hurricanes. Vegetation regeneration response in small gaps and larger artificially created (i.e., timber harvested) gaps has been extensively studied, but little has been reported on naturally formed large gaps (> 6 trees) where a partial canopy typically remains from residual overstory and midstory trees. We investigated advance regeneration survivorship on a landscape scale within and around 12 large wind-felled gaps created by Hurricane Opal (October 1995) in a Southern Appalachian watershed. We hypothesized that survivorship would (1) change along a linear distance gradient from the unaffected forest towards gap center (2) vary in relation to categorical gap locations-within-gaps versus in the adjacent unaffected forest and (3) be affected by vegetation and environmental variables. In early 1996 we tagged tree seedlings in quadrats located along linear axes that extended from gap center into the unaffected forest and measured a variety of vegetation and environmental variables. Overall mean survivorship declined from 1997 (0.96) to 2016 (0.56). We found that survivorship was related to linear distance gradients for species rated intermediate in shade tolerance, such as red oaks, but not for shade intolerant, tolerant, and semi-tolerant species (e.g. white oaks). We found that survivorship increased on a linear distance gradient from gap center into the unaffected forest over the first 9 years of our investigation. By year 20 this relationship had reversed: survivorship increased from the unaffected forest to gap centers. Survivorship was also modeled as a function of categorical location of tagged seedlings within-gaps versus in the unaffected forest. Again, we found that survivorship of only intermediate shade tolerant species was related to categorical locations. Survivorship decreased in relation to time and cohort competition and increased with initial seedling height. Our 20-year investigation revealed changes in dynamics of regeneration that would not have been apparent in a short-term study. These results will enable resource managers to assess regeneration development in large gaps following windstorms in oak-dominated hardwood stands.

Keywords Canopy gap · Light gradient · Moisture regime · Regeneration · Site quality survivorship · Wind disturbance

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Introduction

The effects of wind on upland hardwood forest structure and composition have been studied mostly in the context of either small (1 or 2 tree death) openings (gap-phase disturbance) or in retrospective studies of past disturbances. Larger wind-created openings (> 0.1 ha) are common across US. Southern Appalachian landscapes of the Central Hardwood Region (CHR) (Greenberg and McNab 1998; McNab et al. 2004) and can be an important factor in shaping understory colonization, growth, and survival (Runkle 1985). Hardwood seedling survivorship and growth generally improve as midstory and overstory canopy cover decrease which increases light transmission to the forest floor (Dey and Parker 1997; Madsen and Larsen 1997; Buckley et al. 1998; Morrissey et al. 2010). However, most of the knowledge about this relationship is derived from man-made homogeneous manipulations in designed studies. Natural disturbances such as wind or ice storms which cause variable damage to canopy trees resulting in heterogeneous stand conditions have not been well studied.

Many gap disturbance tree seedling survivorship investigations have been limited to fewer than 5 years in duration, a time period often less than needed for hardwood regeneration to reach canopy closure, a critical life stage (Loftis 1989; Noble and Slatyer 1980). Also, most studies of survivorship in large gaps (> 6 trees) have utilized artificially created openings that may not mimic environmental conditions of naturally formed gaps, particularly where soils are disturbed by uprooted trees and other trees remain standing in the canopy thereby creating a mosaic of photosynthetically active radiation (PAR) at ground level (Clinton and Baker 2000).

Increases in light created by forest gaps change the dynamics of understory plants in response to changes in spatial and structural gradients (Swank and Vose 1988; Coates and Burton 1997). Light received at the forest floor gradually declines from gap center to exterior forest (Chen et al. 1995). Berg (2002) found that directly sensed PAR declined exponentially from wind-created gap centers to 40 ms beyond gap edge where PAR at ground level approximated that of the forest unaffected by wind damage. Forest tree advance regeneration survivorship may be proportional to a gradient of PAR. However, changes in seedling survivorship are not uniformly related to changes in gap light regimes and survivorship may vary substantially by species and its shade tolerance rating. For example, Puerta-Piñero et al. (2007) found that oak species seedling survivorship increased in low-light environments in relatively dry Mediterranean sites. In contrast, Motsinger et al. (2010) observed improvements in pin oak (*Quercus palustris*) seedling survivorship in response to increases in PAR from 3 to 15% of full sunlight over 3 years in Midwestern US bottomland sites. Berg (2002) found that hardwood seedling survivorship over 2 years in North Carolina upland hardwood sites was not related to overstory and midstory canopy cover and PAR imputed via hemispherical photography measured at 1.0 m above the forest floor. Brose and Rebbeck (2017) found no differences among acorn-origin northern red (*Quercus rubra* L.), chestnut (*Quercus montana* L.), white (*Quercus alba* L.), and black (*Quercus velutina* L.) oak seedling survivorship grown at 15, 40, and 75% of full sunlight (a range of light conditions often found in and around forest gaps) over 8 years. Vodde et al. (2015) found that mortality of alder (*Alnus glutinosa* L.) and birch species (*Betula pendula* Roth and *B. pubescens* Ehrh.) regeneration increased rapidly in sites with greater windthrow severity, but spruce (*Picea* abies) regeneration initially displayed lower mortality than the hardwoods but increased later in sites with high amounts of wind-felled coarse woody debris.

These findings on regeneration responses to received light may be strongly influenced by site quality, particularly available soil moisture, which may produce unique seedling survivorship responses within and around forest gaps (Coomes and Grubb 2000; Johnson et al. 2009). For example, Berg (2004) found that microsite available soil moisture, aliased by terrain shape index (McNab 1989), was negatively related to oak species survivorship in forest gaps, which aligns with extensive research that supports the hypothesis that lack of oak seedling survivorship through time is primarily a problem in high-quality mesic sites and not dry sites (Johnson et al. 2009). Although within-gap effects of variation in the soil moisture regime have been documented (Morrissey et al. 2010), less is known about long-term seedling survivorship in response to moisture variation among gaps. Particularly important is the long-term differential survivorship among gaps on a landscape scale where seedlings are responding not only to changes in the light regime, but also to effects of repeated stress from drought (Sanchez-Gomez et al. 2006).

Residual canopy trees are frequently left after gap formation; larger gaps are seldom clear-felled by natural disturbances (Berg 2002). Residual overstory and midstory trees reduce the amount of light reaching the forest floor and may change seedling survivorship probabilities. Schweitzer and Dey (2017) reported that oak seedling survivorship did not change over 12 years when midcanopy competition was reduced with individual stem herbicide injection and later shelterwood overstory removal in the Cumberland Plateau of the Southern US. Lhotka and Loewenstein (2009) found that removing all midstory trees from a riparian mixed mesophytic species site improved oak seedling survivorship over 7 years. Loftis (1990) reported that reducing midcanopy competitors through herbicide treatment improved northern red oak seedling survivorship on a cove site over 6 years. But residual tree canopies may also facilitate the survivorship of tree regeneration by inhibiting shade intolerant regeneration competition (Holmgren et al. 1997) and supporting the growth of mycorrhizal networks that could enhance tree seedling root acquisition of below-ground resources (Teste et al. 2009).

Generally, seedling survivorship and growth improve as gap size increases, particularly in the PAR-rich northern sides of gaps (Hibbs 1982; Ashton 1995; Gray and Spies 1996). Beckage and Clark (2003) found that planted northern red oak, yellow-poplar (*Liriodendron tulipifera* L.), and red maple (*Acer rubrum* L.) seedlings all exhibited superior survivorship within gaps compared to the untreated hardwood canopy forest, largely in response to higher PAR levels in gaps. Many investigators have linked tree seedling survivorship and growth with gap size and *categorical* position (gap center, gap edge, outside gap) within and around gaps (Yetter and Runkle 1986; Sipe and Bazzaz 1995; Van Der Meer et al. 1999). However, little is known about how hardwood seedling survivorship changes relative to *continuous* gradients of light within and around gaps.

Linear distance gradient from gap center can serve as a surrogate for continuous changes in light regimes and as a covariate related to plant colonization, survivorship, and growth (Berg 2002, 2004). Despite their utility we found few investigations dealing with linear distance gradients. Brown (1996) found that height growth of tropical hardwood seedlings decreased on a linear distance gradient from gap center to gap exterior. Berg (2004) found that 2-year advance regeneration survivorship increased on a linear distance gradient from wind-created gap centers into the unaffected forest. Of particular interest is how survivorship changes along linear distance gradients in the unaffected forest outside of gaps where gap sidelight may be sufficient for oaks and other species with intermediate shade tolerance to survive and grow (Fig. 1) (Johnson et al. 2009).

To answer land manager information needs for how forest gaps change hardwood regeneration survivorship over long time periods, we investigated the 20-year survivorship of advance

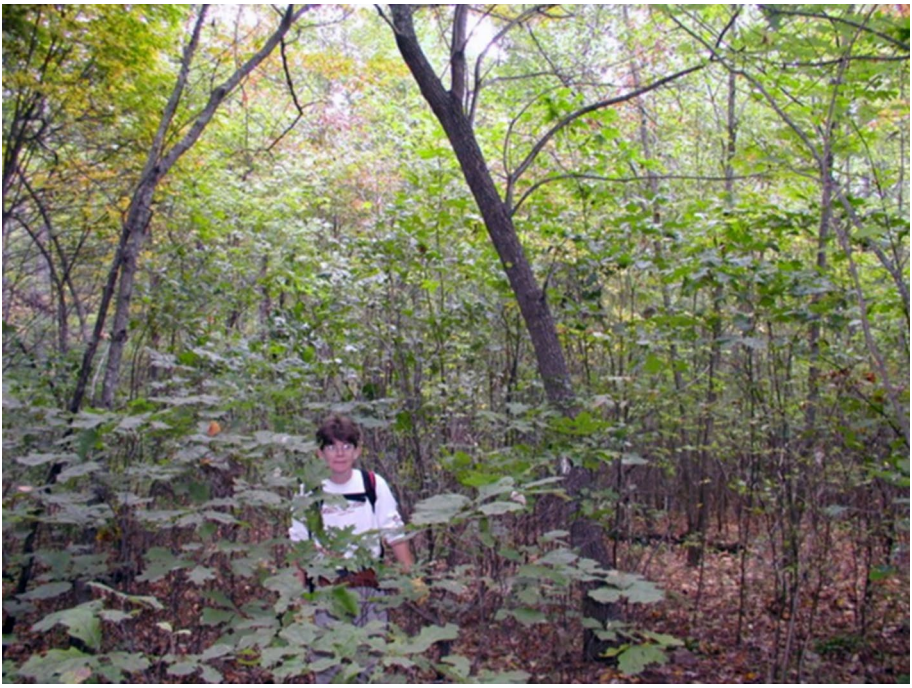

Fig. 1 Gap edge (at person) separating the unaffected forest (foreground) from the gap interior (background) which is supporting tall mixed-species regeneration. Oak regeneration at gap edge and in the unaffected forest has responded in height to increased side-light from the gap interior

hardwood regeneration located within and around gaps in a mixed species mesophytic upland forest created by a tropical hurricane (Hurricane Opal, October 1995) an uncommon type of large-scale disturbance in the Southern Appalachians. We tested three hypotheses: (1) 20-year advance regeneration survivorship would increase or decrease along linear distance gradients from gap center to edge within wind-created gaps and from gap edge into the unaffected forest, (2) 20-year regeneration survivorship would be greater or less by categorical gap locations (within-gaps versus outside gaps in the unaffected forest) based on varied gap-level available soil moisture and (3) 20-year survivorship would be related to vegetation and environmental variables.

Although effects of this hurricane disturbance were widespread (Clinton and Baker 2000), the scope of our study was limited by available resources and administrative control of experimental areas on the study site watershed and restricted to topography and forests that are typical of the Southern Appalachian Mountains area of the CHR. In this manuscript we report our findings of all arborescent species survivorship over 20 years. Knowledge of this and how survivorship varies by site quality could have practical implications for land managers.

Methods

Site description

The Bent Creek Experimental Forest is located about 16 km south of Asheville, NC (35.5°N, 82.6°W) in the Southern Appalachian region. It occupies most of a 2500 ha watershed characterized by two predominant ecosystems: (1) an intermountain basin of hilly terrain that is bordered by (2) steep highlands of mountainous topography (Fig. 2). The frost-free growing season extends from approximately May 1 to mid-October. Annual precipitation ranges from 120 cm at 670 m elevation to 150 cm at 850 m

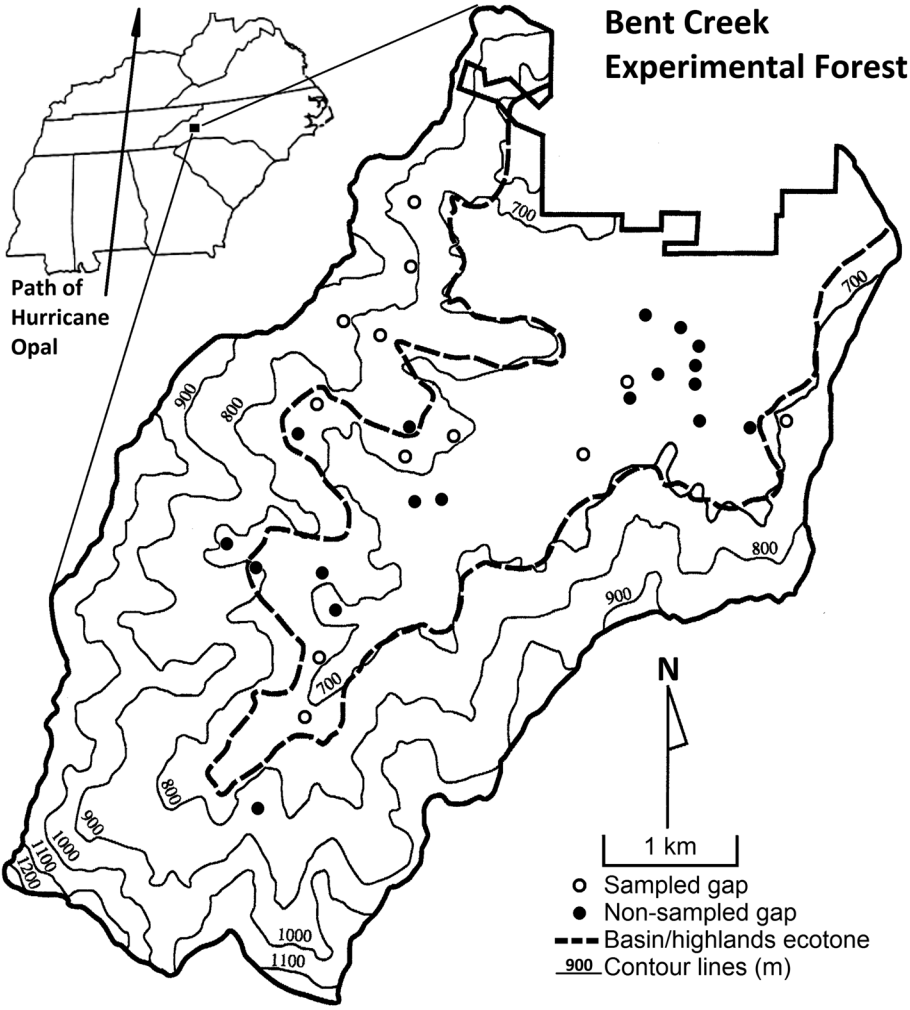

Fig. 2 Track of Hurricane Opal in the southeastern US, distribution of the 30 large canopy gaps in the Bent Creek Experimental Forest and the 12 gaps utilized in this study

elevation. Soils are derived from gneisses and schists, with occasional intrusions of mafic minerals found in amphibolite deposits. All soils are > 80 cm deep and acidic (pH < 5.2).

Originating in the Gulf of Mexico, Hurricane Opal made landfall in western Florida and moved rapidly northward through Alabama and central Tennessee (Fig. 2). On the morning of October 5, 1995, wind from Hurricane Opal struck the Bent Creek watershed. Sustained wind from Opal averaged 8.9 m/s, and maximum peak gusts of 25.9 m/s were recorded at the nearby Asheville airport. McNab et al. (2004) provide additional information on characteristics of this hurricane and the resulting landscape distribution of 30 multiple tree canopy gaps in the experimental forest (Fig. 2).

Gap selection

Single-tree gaps were most common and averaged 57 m^2; multiple-tree gaps averaged 117 m^2. Approximately one-third of the gaps were located in administrative areas not suitable for research activities or were harvested to salvage windthrown trees. Selected gaps for this investigation were restricted to the remaining openings that were at least 0.1 ha (1000 m^2) in size and contained at least 6 canopy trees that had fallen as a result of the hurricane. Beck (1988) commented on the 0.1-ha size as a reasonable minimum for the successful colonization and development of the most shade intolerant eastern hardwoods. By restricting this investigation to gaps > 0.1 ha, we ensured that all native species had sufficient light to colonize and grow successfully.

Twelve gaps meeting the above criteria were located October 1995 to June 1996 without regard to site environmental conditions. Runkle's (1992) definition of the extended gap was used to determine gap perimeters. Of the 12 gaps, seven were located in xeric-subxeric (dry) sites typically associated with the basin within oak-hickory vegetation communities on Ultisol soils, and five gaps were located in mesic-submesic (wet) sites common to the uplands within acidic and rich cove hardwoods on Inceptisols. Selected gap elevations ranged 670–850 m. Hurricane-created windfall trees mostly were uprooted and did not snap off from the bole. All selected gaps supported some residual hardwood overstory and midcanopy trees; residual tree distribution was highly variable. All gaps included varied densities and distributions of advanced, mostly hardwood species regeneration.

In 1996, measured tree basal area within-gaps (15.0 m^2/ha) was less than in the unaffected forest (20.5 m^2/ha); large tree (sapling and larger, > 3.8 cm diameter breast height) density was also less within-gaps (543.2 trees/ha) compared to the unaffected forest (686.2 trees/ha. Seedling density was essentially identical within-gaps (24.6 K/ha) compared with the unaffected forest (26.0 K/ha). Basal area and large tree density were generally higher on dry sites; regeneration density was higher on wet sites (Table 1). Total arborescent canopy cover (TOTALCOVER) (Table 2) averaged 0.68 within-gaps and 0.92 in the unaffected forest.

Advance regeneration included both from-seed and sprout cohorts that likely resulted from additional light transmission to the forest floor resulting from repeated disturbances such as ice storms, wind-throw and insect and pathogen caused mortality of canopy trees through time. These disturbance events provided the light needed for established regeneration to survive to the next disturbance when fresh pulses of light enabled small trees to again achieve their light compensation points (Johnson et al. 2009). Because these repeated canopy disturbances yielded highly variable light transmission through time and space advance regeneration varied greatly in age and species.

Table 1 Total samples and means of vegetation variables by gap position and landscape ecosystem classification (LEC) (Barnes et al. 1982) soon after forest disturbance by Hurricane Opal in the Bent Creek Experimental Forest

Position in gap	LEC class	Samples N	Tree basal area m^2/ha	Tree density N/ha (> 3.8 cm dbh)	Seedling density K/ha
Exterior[a]	Wet	62	14.6	541.8	33.7
	Dry	83	24.8	806.5	20.0
	All	145	20.5	693.3	26.0
Interior	Wet	65	15.9	414.2	29.3
	Dry	59	13.8	699.1	19.4
	All	124	15.0	549.8	24.6
All	Wet	127	15.3	476.5	31.4
	Dry	142	20.5	761.9	19.7

[a]Includes sample plots established at gap perimeters that separate interior from exterior positions

During May–July 1996 two perpendicular axes running north–south and east–west were located within 9 of the 12 gaps that were approximately circular in shape; axes intersected at gap center. Axis orientation was changed when realignment provided the opportunity to establish a gradient along the entire length of three of the 12 gaps that were elliptical in shape. Transect lines extended out from gap center along established axes in the cardinal directions. Sampling quadrats were located at: (1) gap center, (2) out from center along transects 7.3 m apart in gaps where distance from center to edge was < 30 m, and up to 10.67 m in larger gaps to until gap edge was reached, (3) at the north, south, east, and west gap edges, and (4) progressively outward beyond gap edges 7.3 m apart. The most extreme quadrats were installed where ground-level solar radiation approximated that of forests unaffected by windthrow. This resulted in 15–32 established 0.0013-ha quadrats per gap, totaling 269 quadrats. Figure 3 exemplifies the sampling scheme used in all 12 gaps (Fig. 2).

Tree regeneration measurements

Two regeneration sources (seed or sprout origin) ≤3.8 cm diameter breast height (if present) were selected at random within each of the 0.0013-ha quadrats and tagged for long-term identification and measurement, which provided a sample of 26 arborescent species and 474 tagged seedlings over the 12 gaps (Table 3). Regeneration species were rated as intolerant, intermediate or tolerant of shade according to Burns and Honkala (1990) (Table 3). However, in contrast to the Burns and Honkala intermediate rating, we identified the white oaks (*Q. alba, Q. prinus and Q.* stellata) as semi-tolerant. These species have consistently exhibited higher survivorship than the red oaks in sites with residual forest canopies in the mountains of western North Carolina (Loftis 1995). Tagged seedling

Table 2 Variable means, ranges and explanations

Variable	Mean (units)	Range or values	Explanation
GAPCAP	41.04 (degrees) in 1996, 38.9 in 2016	36.9–53.0	Gap aperture (Runkle 1992) from gap center: Angle from gap center to canopy tree tops along gap perimeters. The mean of 8 readings taken at 45-degree intervals
GAPPOS	5.80 (m)	− 29.27–95.31	Gap position: Linear horizontal distance from gap-edge to quadrat. Distances from edge towards gap center are positive, from edge to unaffected forest are negative
HECTARES	0.443 (ha) in 1996	0.104–1.262	Gap area
HT96	0.627 (m)	0.061–3.658	Initial seedling height: measured in 1996
LFI	0.191 (percent slope converted to decimal)	0.082–0.338	Landform index (McNab 1993)—the protection offered by the surrounding topography, expressed as the slope from gap center to the surrounding landscape horizon. The mean of 8 readings taken at 45 degree intervals. Higher values suggest greater mesoscale soil moisture
RESTRPOS	na	I = within gap E = outside gap	Categorical location of tagged advanced regeneration.
STATUS	15.28% of live tagged seedlings were overtopped throughout the 20 year investigation	dichotomous	Whether the subject seedling is overtopped or not overtopped. "Not overtopped" means that at least 50% of an imaginary cylinder, 1 m in height of the same diameter as the tree crown, positioned above the tagged-seedling, is free of competing vegetation. Measured at each time period
TIMECOUNT	(integer count)	0, 1, 2, 3, 5, 9, 20	Years from date of initial inventory (1996) to measurement
TIMECOUNT2	na	na	TIMECOUNT*TIMECOUNT quadratic term- to account for non-linearity of TIMECOUNT in logistic regression models
TOTALCOVER	0.858 (proportion) over 20 years	0.000–1.000	TOTALCOVER-cover expressed as a proportion: canopy cover of midstory and overstory trees. Measured with a go/no-go densitometer at 17 points within 3.6 m of each quadrat center. Based on 17 points in 1997 but was based on 5 points in 2003 and 2016. Differences in outcomes with the 17 versus 5 point systems were highly correlated (r = 0.71) and therefore both were judged satisfactory. The 1997 measured TOTALCOVER values were assigned to the 1997 and 1998 data vectors; the 2003 values were assigned to the 2001 and 2005 data vectors and the 2016 values were assigned to the 2016 vectors
TRANSASP	0.952 (unitless)	0.0–1.996	Transformed aspect-quadrat aspect modified with Beers transformation to give quadrats with aspect of 45 degrees highest; aspect of 225 degrees the lowest values. TRANSASP (Beers et al. 1966)
TSI	3.229 (%)	0.000–1.000	Terrain shape index (McNab 1989). Microsite topography, expressed as the ground surface percent slope within 15.24 m from quadrat center. The mean of 8 readings taken at 45 degree intervals. TSI is a surrogate for microsite soil moisture. Higher values suggest higher soil moisture content

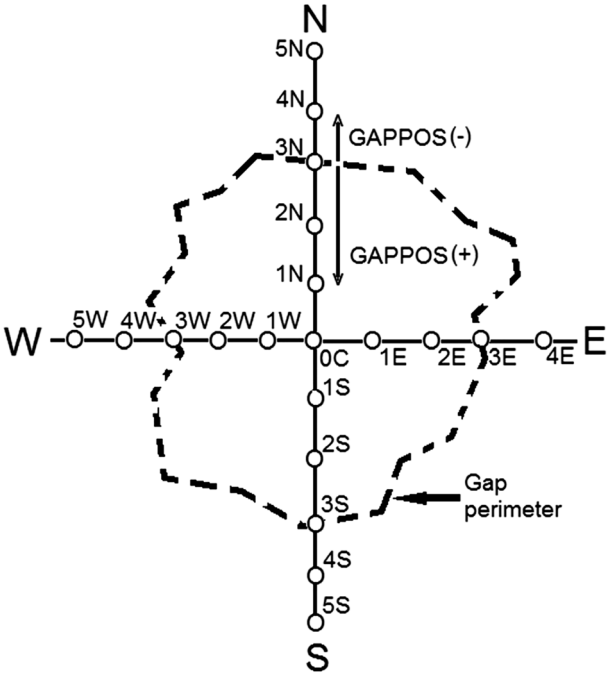

Fig. 3 Sampling scheme for the 12 windthrow canopy gaps created by Hurricane Opal in the Bent Creek Experimental Forest

survivorship was measured in 1997, 1998, 2001, 2005, and 2016. A wide array of variable types (Table 2) was measured and tested as covariates:

- Distance/gap attributes: these variables served as surrogates for light transmission to the forest floor.
- Cover: variables that quantified tree canopy, woody debris and tree-fall pits or mounds habitat.
- Site quality.
- Tree regeneration competition.
- Initial seedling size.

Data analysis

To test all three hypotheses, data were pooled across all 12 gaps (269 quadrats) and analyzed as random intercept multilevel (seedlings within-gaps), repeated measures logistic models. To test the hypothesis 1 that survivorship would change over time on linear distance gradients, we modeled survivorship $= f$ (linear distance from gap center into the unaffected forest, years since 1996 when seedlings were tagged). To address hypothesis 2 that survivorship would change with categorical location (within-gap or in unaffected forest), we modeled survivorship $= f$ (categorical locations, years since 1996) separately for wet (mesic and submesic) and dry (xeric and subxeric) site gaps. Next, for hypothesis 3 we investigated how survivorship varied by individual

Table 3 Shade tolerance group, scientific and common names of tagged tree seedlings, number of seedlings tagged, mean total height (m) at initial inventory in summer 1996 (HT96) and standard error (SE)

Tolerance group	Scientific names	Common names	N	HT96 (SE)
Intolerant	*Liriodendron tulipifera* L.	Yellow-poplar	19	0.56 (0.14)
	Robinia pseudoacacia L.	Black locust	16	0.65 (0.14)
Intermediate	*Betula lenta* L.	Sweet birch	1	1.83 (–)
	*Carya spp.**	Hickory	31	0.51 (0.12)
	Carya glabra (Mill.) Sweet	Pignut hickory	3	0.30 (0.10)
	Castanea pumila Mill.	Chinkapin	4	0.43 (0.14)
	Fraxinus americana L.	White ash	14	0.81 (0.15)
	Magnolia acuminata L.	Cucumber tree	1	0.21 (–)
	Prunus serotina Ehrh.	Black cherry	1	0.76 (–)
	Quercus coccinea Muenchh.	Scarlet oak	83	0.35 (0.06)
	Quercus falcata Michx.	Southern red oak	2	0.41 (0.11)
	Quercus rubra L.	Northern red oak	44	0.51 (0.06)
	Quercus velutina Lam.	Black oak	68	0.45 (0.05)
Sermi-tolerant	*Quercus alba* L.	White oak	46	0.58 (0.09)
	Quercus prinus L.	Chestnut oak	36	0.30 (0.04)
	Quercus stellata Wangenh.	Post oak	2	0.62 (0.05)
Tolerant	*Acer rubrum* L.	Red maple	61	1.25 (0.12)
	Acer saccharum Marsh.	Sugar maple	1	0.36 (–)
	Cornus florida L.	Flowering dogwood	9	2.86 (0.28)
	Diospyrous virginiana L.	Persimmon	2	0.24 (0.09)
	Ilex opaca Ait.	American holly	2	1.46 (0.43)
	Nyssa sylvatica Marsh.	Blackgum	1	0.37 (–)
	Oxydendrum arboreum (L.) DC.	Sourwood	8	1.35 (0.37)
	Pinus strobus L.	Eastern white pine	2	0.14 (0.05)
	Sassafras albidum (Nutt.) Nees	Sassafras	15	0.77 (0.14)
	Tsuga canadensis (L.) Carr.	Eastern hemlock	2	1.84 (0.96)

*Species (*C. glabra, C. tomentosa*) of hickory could not be identified

environmental variables that were generally not included in the hypotheses 1 and 2 models. The statistical relationships between survivorship and these individual variables were reported without full parameter estimate tables, instead we presented only the probabilities of finding a more extreme observation (p-values). Elapsed time since 1996 was included with the individual variables of interest; these "small" models were then survivorship $= f$ (individual variable, years since 1996).

Results

All hypotheses were tested with mixed models incorporating R-side random effects using SAS PROC GLIMMIX (SAS 2013) which produced pseudo-likelihoods that cannot be used to compare candidate models that differ in their data (SAS 2013). This made comparison of alternative models by information theoretic procedures (Burnham and

Anderson 2002) impossible and there are no widely-accepted metrics for such R-side model fit comparisons (Osborne 2015). We sought parsimony and added only essential variables that explained environmental effects previously shown to be important in explaining differences in survivorship (Burnham and Anderson 2002). We compared model results with varied covariance structures, including spatial power to accommodate varied time lengths between measurements, variance components (VC) and compound symmetry (CS). We adopted CS covariance for all models because it consistently yielded the lowest pseudo AICs (when comparing varied covariance structures for the same models pseudo AICs are appropriate—because the data parameterized is identical for each candidate model) and correct signs (±) of the parameters.

To address our hypothesis 1 that tagged seedling survivorship would vary by linear distance gradients, we parameterized separate survivorship models for each of the four regeneration shade tolerance groups: tolerant, semi-tolerant, intermediate and intolerant, because we suspected that survivorship would vary by species specific responses to changes in received light. We first tested the relationship of survivorship with time since disturbance (TIMECOUNT) and the variable GAPPOS which served as a surrogate for light received beneath the canopy and midcanopy as aliased by location along a linear distance gradient from gap edge.

We tested how well GAPPOS served as a surrogate for light received beneath the forest canopy by regressing the global site factor (GSF), the proportion of direct and indirect PAR received beneath versus above the canopy, versus GAPPOS. GSF was imputed by analysis of hemispherical photography using the program Hemiview (Delta-T Devices 1999) where the camera with fisheye lens was positioned 1.0 m above ground level at quadrat centers in 1998. We examined the relationship of GAPPOS to GSF with SAS PROC GLIMMIX (SAS 2013). Quadrats were nested within-gaps in a random intercept model; GAPPOS was related to GSF ($p = 0.054$). Imputed GSF was found to decline with distance from gap center.

We then progressively added variables to our hypothesis 1 model that characterized differences in site quality and regeneration size. For the intermediate group, covariates also included TIMECOUNT squared, to account for non-linearity, site quality represented by aspect (TRANSASP), and initial regeneration size characterized by seedling or sprout height in 1996 (HT96) plus the interactions TIMECOUNT*GAPPOS and HT96*TRANSASP (Table 4). Survivorship of intolerant, tolerant and semi-tolerant regeneration was not related to GAPPOS ($p > 0.28$); we therefor did not develop separate models for these species groups. The small sample size of the intolerant group (35) limited our ability to accurately relate survivorship to GAPPOS. Most within-gap and unaffected forest microsites provided insufficient light to foster the survival of shade intolerants. Because the pre-hurricane forests of the 12 selected gaps had not been disturbed by substantive man-made or natural manipulations for at least 30 years prior to our study we suggest finding light-demanding shade intolerant regeneration such as yellow-poplar immediately after Hurricane Opal would have been unlikely.

Overall survivorship (based on actual and not modeled data) of the 474 tagged seedlings declined from 1997 (0.96) to 2016 (0.56). Of the intolerant group, survivorship declined from 0.94 to 0.16, for the intermediates survivorship declined from 0.94 to 0.55 and survivorship dropped from 0.99 to 0.65 for shade tolerant seedlings (Fig. 4). Hypothesis 1 modeled survivorship of the shade intermediates increased more than 40% by year 9 from gap center to 30 m. inside the unaffected forest. However, the slope of this relationship reversed at year 20 (Fig. 5); survivorship then declined from gap center into the unaffected forest.

Table 4 Parameter estimates for multilevel (tagged seedlings within gaps) repeated measures (over 5 time periods) logistic regressions parameterized with SAS PROC GLIMMIX (SAS 2013)

Parameter		Estimate	SE	DF	t Value	Pr > |t|
All sites model—shade intermediate species—hypothesis 1		Covariance for random intercept (by gap) = 0.0642; n = 252				
Intercept		4.5478	0.5440	48.78	8.36	< .0001
TIMECOUNT		− 0.2861	0.0584	1349.00	− 4.90	< .0001
TIMECOUNT2		0.0046	0.0024	1264.00	1.89	0.0585
GAPPOS		− 0.0400	0.0115	481.00	− 3.48	0.0005
HT96		− 0.2879	0.5163	488.90	− 0.56	0.5773
TRANSASP		− 0.7765	0.3626	89.78	− 2.14	0.0349
HT96*TRANSASP		0.8233	0.4539	570.40	1.81	0.0703
TIMECOUNT*GAPPOS		0.0021	0.0007	1374.00	3.01	0.0027
Dry sites model–shade intermediate species—hypothesis 2	Level	Covariance for random intercept (by gap) = 0.1123; n = 137				
Intercept		5.0018	0.6799	114.40	7.36	< .0001
TIMECOUNT		− 0.3746	0.08694	731.80	− 4.31	< .0001
TIMECOUNT2		0.0064	0.0033	675.80	1.94	0.0526
RESTRPOS	I	− 2.2987	0.6171	238.50	− 3.72	0.0002
RESTRPOS	E	0.0000	–	–	–	–
TIMECOUNT*RESTRPOS	I	0.1184	0.03632	688.80	3.26	0.0013
TIMECOUNT*RESTRPOS	E	0.0000	–	–	–	–
Wet sites model—shade intermediate species—hypothesis 2		Covariance for random intercept (by gap) = 0.2568; n = 115				
Intercept		3.6009	0.4008	14.22	8.98	< .0001
TIMECOUNT		− 0.1736	0.0174	604.40	− 9.99	< .0001
RESTRPOS	I	0.2559	0.3803	182.70	0.67	0.5018
RESTRPOS	E	0.0000	–	–	–	–

The hypothesis 1 model was developed with pooled tagged seedling data from all 12 gaps and gap locations. For the hypothesis 2 dry (xeric and subxeric) and wet (mesic and submesic) sites models gaps were rated dry or wet based on available soil moisture for plant growth

Variables (Table 2): TIMECOUNT = number of years since study installation (1996); TIMECOUNT2 = TIMECOUNT quadratic term; GAPPOS = distance in meters from center to edge is positive and edge into the unaffected forest is negative; HT96 = seedling height in 1996 (m); TRANSASP = transformed aspect (Beers et al. 1966); RESTRPOS = categorical location, "I" = gap interior (the gap proper), "E" = gap exterior (the unaffected forest adjacent to the gap)

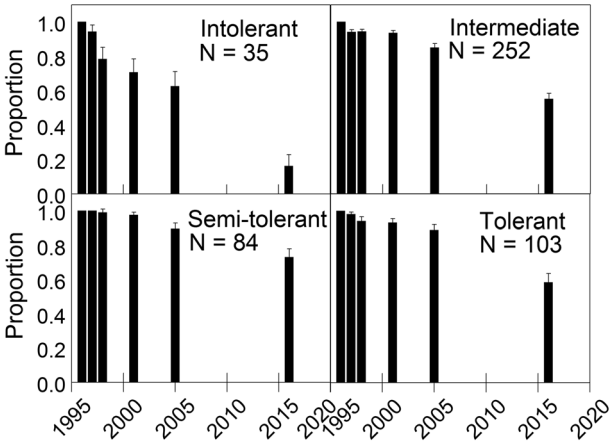

Fig. 4 Proportion of surviving advance regeneration by shade tolerance species group over 20 years

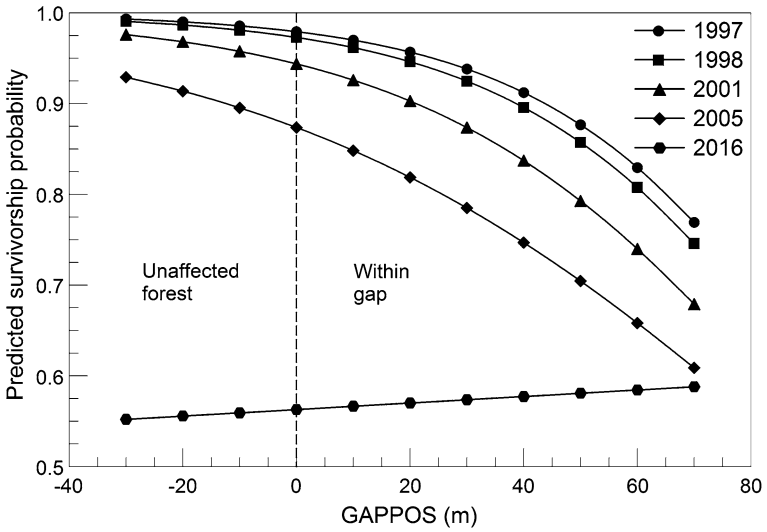

Fig. 5 Tagged shade intermediate regeneration survivorship versus distance from gap edge [GAPPOS (meters)]. Vertical dashed line is positioned at gap edge for reference

For the hypothesis 2 categorical gap-level hypothesis, we found that shade intermediate tagged seedlings located in dry site unaffected forest locations exhibited higher survivorship compared to seedlings located *within* dry site gaps (modeled with the categorical location variable RESTRPOS, Table 2). Survivorship of intermediate seedlings was not related to differences in categorical seedling locations in *wet* sites (Table 4, Fig. 6). Shade intolerant, tolerant and semi-tolerant regeneration survivorship was not related to categorical within-gap or outside-gap locations in either dry or wet sites ($p > 0.4$).

Overall goodness of fits for the multilevel logistic hypotheses 1 and 2 models cannot be judged with conventional metrics (Osborne 2015). However, the parameter estimates for all covariates remained stable as we progressively added more of them to our

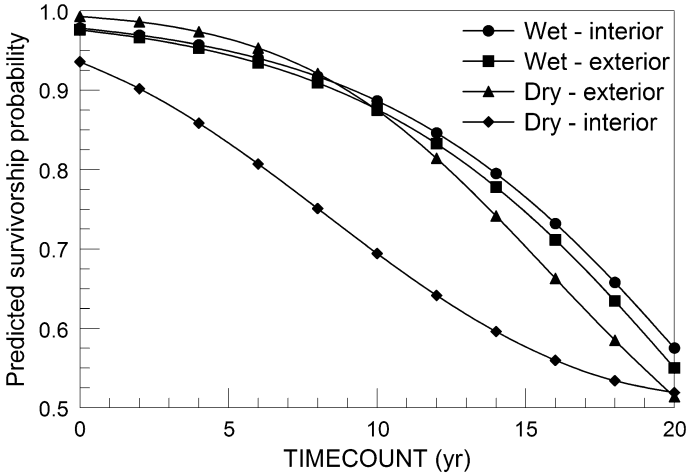

Fig. 6 Predicted tagged shade intermediate survivorship by categorical assignment of site quality (wet = mesic and submesic; dry = xeric and subxeric) (Barnes et al. 1982) and categorical gap position [gap interior and gap exterior (the unaffected forest adjacent to the gap)] by TIMECOUNT (years from study establishment)

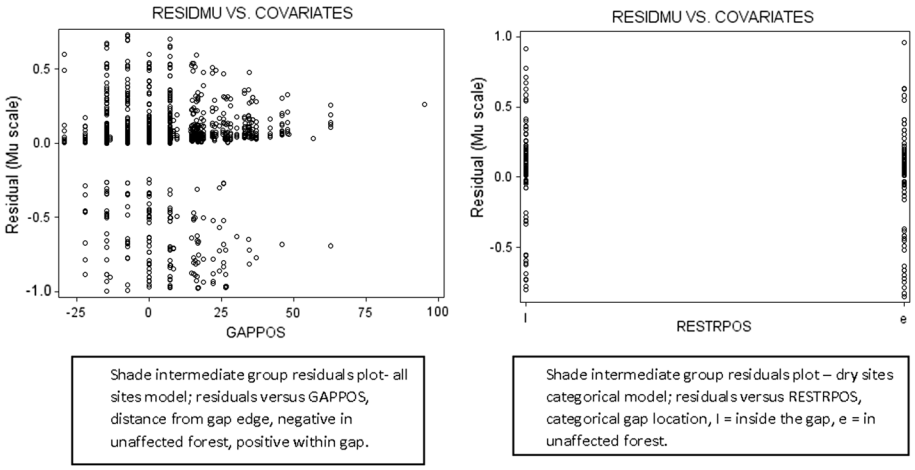

Fig. 7 Survivorship model residual plots

models, this was particularly noted for the hypothesis 1 model, suggesting our final models were robust. And the residuals plotted over key variables GAPPOS and RESTRPOS exhibited minimal heteroscedasticity (Fig. 7). Because survivorship of intolerant, tolerant and semi-tolerant species regeneration was not related to the essential hypothesis 1 linear distance gradient or hypothesis 2 categorical gap locations, we limited their findings in this manuscript. Additional study results pertain primarily to the intermediate species shade tolerance group.

To meet hypothesis 3, we tested the relationship of survivorship to individual environmental variables. Survivorship was strongly related to STATUS, whether or not the

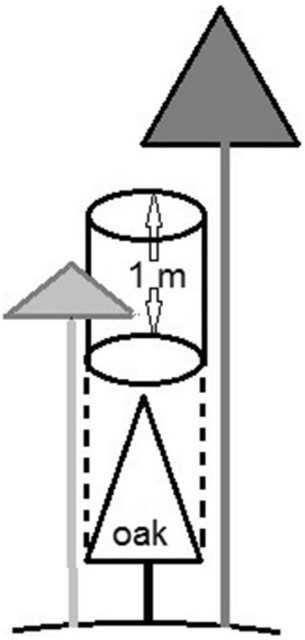

Fig. 8 Schematic of the variable STATUS: overtopped versus not-overtopped (Table 1). In the diagram the example oak tree is not-overtopped because less than 50% of the 1 m tall cylinder volume is competitor vegetation

seedling was overtopped by competing vegetation ($p < 0.0001$) (Fig. 8). For all seedlings the probability of a non-overtopped seedling surviving to 2016 was 0.72 compared to 0.44 for an overtopped seedling. And the probability of a seedling being overtopped declined with distance from gap center into the unaffected forest [STATUS $= f$ (GAPPOS), $p = 0.0001$]. The percentage of overtopped tagged seedlings increased from 9.4 in 1996 to 11.0 in 2001 to 20.9 in 2016. Because STATUS was strongly related ($p < 0.0001$) and collinear with GAPPOS, it could not be included in the hypothesis 1 intermediate species survivorship model. STATUS approximates cause and effect in explaining changes in the probability of tagged seedling survivorship because it directly relates to a threshold amount of PAR needed for most hardwood seedlings to achieve their light compensation points. Field crews measuring PAR with a ceptometer found that non-overtopped seedlings received at least 10–15% of full PAR, an amount sufficient to ensure the survivorship and growth of the oaks and other species groups rated intermediate in shade tolerance (Gottschalk 1985). This relationship of measured PAR to STATUS has not been fully tested and is therefore *ad-hoc*. Nonetheless, we suggest STATUS can serve to gauge the variability in seedling survivorship. Additionally, STATUS was strongly negatively (i.e., being overtopped) related to total tree canopy cover (TOTALCOVER) ($p = 0.0083$); canopy cover reduced the amount of transmitted PAR which reduced vegetative competition surrounding tagged seedlings. The vegetative competition indexed by STATUS largely consists of tree regeneration leaves and stems. TOTALCOVER increased from 0.68 in 1996 to 0.97 in 2016 in quadrats located in gap interiors and from 0.92 to 0.98 in unaffected forest locations. Survivorship was not related to TOTALCOVER ($p = 0.23$).

Survivorship was not related to the topographic variables landform index (LFI), terrain shape index (TSI), elevation, pit and mound seedling location microsites, and gap areal size

including ratios of gap perimeter to gap area. Gap center aperture, (GAPCAP) a surrogate for the amount of light received at gap center, declined from a mean of 41.6 degrees in 1996 to 38.9 degrees in 2016, supporting anecdotal crew observations that canopy trees at gap perimeters had fallen over the 20 year analysis period, effectively increasing gap areal size. Survivorship was negatively related to gap aperture, $p=0.04$.

Discussion

Compared to the unaffected forest, basal area and tree density within-gaps was reduced by about 25% following the hurricane. Taylor et al. (2017) reported similar results on stand structure following a hurricane in conifer-dominated stands in Nova Scotia. We found hardwood seedling density was not affected by the hurricane in the first year (1996) of our study, which was similar to findings of Beckage et al. (1999) in a study of artificial gaps and tree regeneration. The post-hurricane stand structures of "incomplete" (not clear felled by wind) canopy gaps in our study agreed with findings by Mitchell (2013) and Everham and Brokaw (1996) in comprehensive literature reviews of wind effects on forests.

We were surprised by the high tagged seedling survivorship for all regeneration (56%) at 20 years post-disturbance in our study. Most researchers have found much lower survivorship after less than even 10 years post-disturbance in CHR ecosystems (Johnson et al. 2009). In our study the shading effects of residual overstory and midstory trees suppressed competitor seedling growth and delayed seedling canopy closure, thereby facilitating tagged seedling survivorship. However, tree canopy shading also reduced tagged seedling diameter and height growth; few tagged seedlings advanced to sapling size by year 20.

Our finding that advance regeneration survivorship declined towards gap centers during the first 9 years after disturbance mirrors those of Berg (2002, 2004) and Sipe and Bazzaz (1995). Meiners et al. (2000) found that oak, ash (*Fraxinus americana* L.), and red maple (*Acer rubrum* L.) survivorship suffered in the subdued light environment found at gap edge, but seedling survivorship was enhanced near gap centers. Why is our finding of short-term (9 years) low survivorship towards gap center diametrically opposed to the results of other investigators such as Meiners? We suggest our findings stem from the interaction of TOTALCOVER with STATUS. Generally, seedling survivorship and growth increase as midstory and overstory canopy densities decrease (Buckley et al. 1998; Dey and Parker 1997). But our study was complicated by the highly variable distribution of residual midstory and overstory trees within-gaps. Scattered residual tree canopies reduced the quantity of transmitted PAR, thereby suppressing the growth of seedling competitors and reducing the probability that tagged regeneration would be overtopped, and so improving their chances of survival. Our finding that TOTALCOVER was negatively related to STATUS (being overtopped) supports this theory. However, the benefits of tree canopy cover likely declined with time. Since mean TOTALCOVER increased from 0.65 in 1996 to 0.82 in 2001 to 1.00 in 2016 within wet site gaps, we suggest that aggressive residual midstory and overstory tree crown expansion acted in concert with overtopping regeneration competition to reduce PAR needed for tagged seedlings to survive. These combined impacts became acute by 20 years after hurricane disturbance and were particularly detrimental to tagged seedlings located in the unaffected forest. As canopy cover increased, sidelight entering the unaffected forest likely declined, eventually depriving seedlings of sufficient light to enable them to achieve their light compensation points (Kramer and Kozlowski 1979).

Facilitation benefits conferred by canopy cover were therefore clearly time-dependent. Overall, the shading effects of residual canopy and midstory trees in gap interiors and the shading provided by canopy trees located at gap edge likely produced a gradient of reduced PAR from gap centers into the unaffected forest; this combination of shading impacts yielded our findings of short-term increased tagged regeneration survivorship from gap center into the unaffected forest. Results from the hypothesis 1 analysis suggest that the reversal in survivorship by GAPPOS likely started before the 20-year switch in survivorship seen in the hypothesis 1 shade intermediate species linear distance model (Fig. 5).

In contrast to the findings of others (e.g. Kathke and Bruelheide 2010) the role that gaps play in tree seedling survivorship in our study was substantive and persisted for the full 20 years of our study. Arborescent canopy cover likely facilitated survivorship of the intermediates for at least the first 9 years post-hurricane. And the change in this response by year 20 where survivorship increased from the unaffected forest towards gap center clearly show that gap-level disturbances are a major shaper of hardwood regeneration dynamics. Whereas Kathke and Bruelheide (2010) found that microsites contributed much more than within-gap or unaffected forest location to Norway spruce survivorship we found that intermediate hardwood species survivorship was strongly related to locations within and around gaps throughout the life of our investigation. However, we suspect differences in survivorship by environmental variables between these two studies may be strongly influenced by shade tolerance ratings and microsite regeneration requirements of varied species and fundamental site differences. Because our study subjects were largely advance regeneration hardwoods, differences in pit and mound topography and soils attributes made little difference in survivorship.

Tree seedling survivorship and growth generally improve as gap size increases because of solar radiation gains at ground level (Sipe and Bazzaz 1995). However, we found no difference in survivorship as a function of gap areal size. We suspect that having gaps in our study >0.10 ha diluted the effect of gap size on seedling survivorship. The literature on gap dynamics varies widely in the effects of gap size on survivorship, and Morrissey et al. (2010) found that although planted hardwood survivorship improved in large gaps (0.40 ha) compared to medium size (0.10 ha) gaps, no improvements in survivorship were found in small (0.02 ha) versus large gaps.

Our finding of a negative relationship of survivorship to gap aperture was problematic. Because intermediate species survivorship improved with higher total canopy cover in our investigation, we expected that survivorship would be positively related to gap aperture (i.e., that tall overstory trees at gap edges would shade-out competitor growth which should yield higher tagged seedling survivorship) and that this effect would be most acute in small area gaps with tall overstory trees at gap edge and attendant large gap aperture readings. This finding was complicated with the smaller aperture readings taken in 2016 compared to 1996-demonstrating that the 12 gaps were expanding in size as gap-edge trees progressively fell-down. As Kubota (2000) found, the interaction of gap expansion with gap formation is a major driver of tree regeneration dynamics.

Survivorship was not related to seedling locations on wind-created pits and mounds, in agreement with Clinton and Baker (2000). Because only a small fraction of gap areas was covered with pits and mounds and seedlings were tagged without regard to these habitats, any statistical relationship would have been improbable. Our findings of greater survivorship with large initial regeneration seedling height on sites with high available soil moisture concur with those of other investigators (Johnson et al. 2009). Oaks and many of the other species in this study such as hickory (*Carya*) are advance regeneration-dependent (Johnson et al. 2009; Loftis 1989). Probability of their survival and subsequent competitive

status is based on size, as represented by basal diameter or height (Loftis 1989). Having large initial size confers competitive advantages in high-density cohorts of regeneration.

Among the physical site variables we evaluated for relationships with regeneration survivorship, only aspect was significant. We found aspect significantly affected seedling survivorship as both a single variable regressor and as an interaction with initial height (HT96) in our hypothesis 1 model. As a single variable regressor, aspect predicted high survivorship on high-energy southerly facing slopes which may be related to lower arborescent regeneration competition on high-energy aspects. Although aspect is strongly associated with soil moisture regimes in the Southern Appalachians (Clinton et al. 1994), it is seldom reported as a factor affecting survivorship of regeneration, likely because most gap studies in temperate hardwoods are short-term and lack tagged seedling subjects needed to accurately measure survivorship through repeated measurements. Our finding that survivorship was higher on southerly aspects conflicted with Morrissey et al. (2010), who reported higher survival and better growth of planted oaks in artificial gaps on northerly sites compared to southerly sites in Indiana. Clinton et al. (1994) studied regeneration in relation to aspect and topographic position in small natural gaps of upland hardwood stands and found density of young seedlings (<5 years) was highest on dry upper slopes irrespective of direction.

The effects of aspect in our hypothesis 1 intermediate species model are most apparent in the highly significant interaction between aspect (TRANSASP) and initial height (HT96). This interaction demonstrates that large initial height confers substantial advantages to seedlings on low-energy aspects but not on high-energy aspects (Fig. 9); seedlings must grow quickly and gain dominance to survive within clumps of seedling competitors fostered by the abundant soil moisture found on low-energy sites (Loftis 2004). Competition for light is typically less severe on high-energy aspects so seedlings have less need of large initial size to survive.

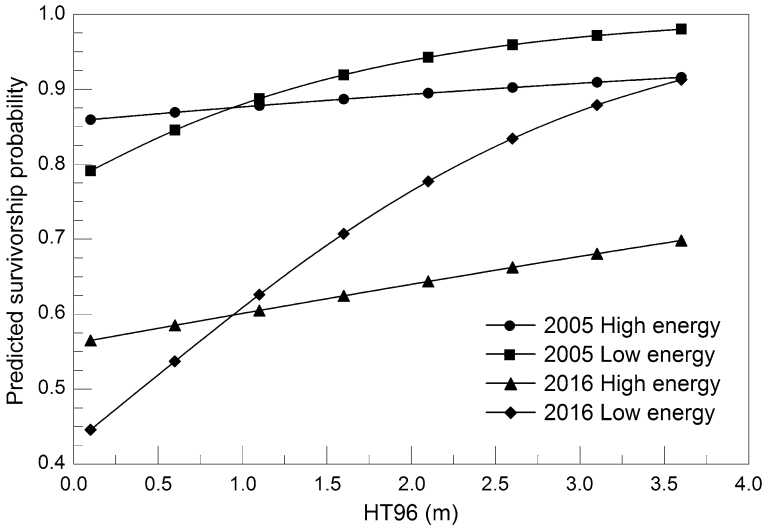

Fig. 9 Tagged seedling survivorship versus HT96 [initial seedling height (meters)] and transformed aspect (TRANSASP) interactions at years 9 (2005) and 20 (2016) measurements, expressed as TIMEASPECT (combinations of year and low or high energy aspects)

We were surprised that seedling survivorship was not related to microsite available soil moisture aliased by terrain shape index (TSI), at the 2001, 2005, or 2016 measurements. However, two-year survivorship (1996–1998) was strongly related to TSI (Berg 2002). TSI probably accounted for much of the moisture-related variation in regeneration survivorship associated with multiple years of severe drought that occurred prior to the hurricane disturbance in 1995. However, 3 years of above average precipitation immediately after Hurricane Opal likely allowed seedlings to respond more to changes in light and less to competition for moisture.

The relationship of shade tolerance group seedling survivorship with environmental variables generally followed a PAR-based gradient in our study. For example, only the intermediates' survivorship was related to location along a linear distance gradient from gap center into the unaffected forest. Both the tolerants and semi-tolerants require less light than do the intermediates, so their locations along distance gradients had little effect on their survivorship. And there was likely insufficient light in any gap location—within or outside gaps, to foster the survivorship of shade intolerants. Our findings may be confounded with advance regeneration age and because we did not inventory the ages of regeneration cohorts it would be impossible to relate survivorship to age. Kubota (2000) found that the varied ages of tree regeneration resulting from repeated disturbances had a substantial impact on regeneration dynamics.

The soil moisture variation among gaps characterized by categorical differences in site quality, wet versus dry, in our study provided an opportunity to examine watershed-scale variation of moisture regimes as an experimental factor, which differs from many well designed gap studies where site variation is minimized, such as the Shure et al. 2006 study of regeneration survivorship where gap location was controlled. On a categorical gap-level basis, we found slightly lower seedling survivorship, without regard to location on a linear gradient, on dry sites. Beckage et al. (1999) found a small increase in soil moisture within-gaps compared to outside gaps, but observed little effect of moisture on vegetation dynamics. Beckage and Clark (2003) reported that trenching in hardwood gaps had little effect on seedling survivorship in comparison to changes in other resources. Also, Finzi and Canham (2000) reported that moisture was not a limiting factor for seedling survivorship in gaps of hardwood forests. During periods of drought in gaps, Booth and Hoeksema (2010) reported that mycorrhizal networks can serve as conduits for moisture from deeper soil horizons and thereby affect seedling survivorship. Coomes and Grubb (2000) suggest that changes of soil moisture may interact with light tolerance of seedlings, thereby affecting survival and growth of certain species in canopy gaps. Our study demonstrates that long-term observations are needed to better understand the dynamics of competition for resources as vegetation matures.

Summary findings

- Modeled survivorship of intermediate shade tolerant seedlings on all gaps increased on a linear distance gradient from gap center into the unaffected forest over the first 9 years after study establishment. By year 20, this relationship had reversed and survivorship increased towards gap center. Intolerant, tolerant and semi-tolerant species survivorship was not related to a linear distance gradient.

- By categorical gap location, modeled survivorship of the shade intermediates was greater in unaffected dry site forest locations. For wet sites, intermediate species survivorship was not related to the location of tagged seedlings within-gaps or in the unaffected forest at any time. Intolerant, tolerant and semi-tolerant species dry or wet site survivorship was not related to categorical gap location.
- Large initial height conferred substantial survivorship benefits on low-energy aspects.

Conclusions

Changes in the relationship of survivorship to environmental variables through 20 years suggest that long-term investigations may be essential to understanding seedling survivorship dynamics. In particular, the reversal of the relationship of seedling survivorship by location in and around gaps 15–20 years post-study establishment highlights the need to provide additional light to seedlings through time to ensure survival. Theoretically, a suite of natural disturbances through time such as wind, ice, and insect and pathogen attacks on canopy trees would provide the light needed for seedling survival (Johnson et al. 2009). Regeneration survivorship and growth responses within and around forest gaps are complex and are subject to subtle changes in light regimes created by residual overstory and midstory trees. Clearly, long-term investigations of the effects of repeated disturbances that produce fresh pulses of light through time to promote regeneration are needed to inform land managers of the site conditions necessary to successfully grow hardwoods.

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