SURVIVORSHIP AND GROWTH OF OAK REGENERATION IN WIND-CREATED GAPS

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Abstract—The effects of wind on upland hardwood forest structure and composition have been studied mostly in the context of either one to two tree mortality gap-phase openings or in retrospective studies of ancient disturbances. Larger (> 0.1 ha) wind-created openings are common across Southern Appalachian landscapes and can be an important factor in shaping understory colonization, growth, and survival. I investigated the relationships of oak seedling survivorship and growth to spatial and structural gradients in and around large hurricane-created gaps on the Bent Creek Experimental Forest. I related 2-year tagged-seedling survivorship to distance from gap edge and physical site through logistic regression. Seedling survivorship declined progressively on a linear distance gradient from gap exterior to gap center. Survivorship also declined as microsite soil moisture increased. I used multiple nonlinear regressions to relate 2-year tagged-seedling basal diameter growth and height growth to distance from gap edge, initial seedling height, canopy cover, and physical site. Basal diameter growth increased as midstory canopy cover declined, at gap positions close to gap center, as initial seedling height increased, and as microsite soil moisture increased. Seedling height growth increased with decreasing overstory canopy cover, at locations near gap center, as initial seedling height increased, and as microsite soil moisture increased.

INTRODUCTION

Hurricane-force winds frequently initiate forest structural and compositional changes in the Southern Appalachians. The effects of wind on upland hardwood forest structure and composition have been studied mostly in the context of either small gap-phase openings, or in retrospective studies of ancient disturbances. Larger (> 0.1 ha) wind-created openings, which are common across Southern Appalachian landscapes (Greenberg and McNab 1998), can be an important factor in shaping understory colonization, growth, and survival (Runkle 1985).

Increases in light created by wind-generated gaps change the dynamics of understory plants. Generally, seedling survivorship and growth improve as gap size increases, as canopy cover decreases, and in the photosynthetically active radiation (PAR)-rich north end of gaps (Ashton 1996, Chen and others 1995, Dale and others 1995). PAR and attendant plant growth and survivorship gradually decline from gap center to exterior forest (Chen and others 1995). 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 (Sipe and Bazzaz 1995). Analyzing understory vegetation as a function of categorical covariates is attractive to many investigators, because these discrete approaches yield easily understood mean responses. However, continuous variables lend themselves to predictive equations that enable managers to understand where responses take place along a gradient of change. If managers could predict survivorship and growth along linear distance gradients, they could then also predict the extent of gap partitioning for arborescent species of interest.

Windstorms create massive amounts of woody debris in hardwood forests (Greenberg and McNab 1998). This debris may either enhance or hinder seedling survivorship and growth. Hurricane Opal, which struck the Bent Creek Experimental Forest on October 5, 1995, provided a firsthand opportunity to evaluate the effects of wind damage, particularly large area gaps, on forest understory vegetation. I investigated the relationships of oak (*Quercus*) seedling survivorship and growth to spatial and structural gradients in and around large Hurricane Opal-created gaps.

OBJECTIVES

My objective was to test the hypotheses that 2-year oak seedling survivorship and growth increase as gap size increases, on a linear distance gradient toward gap center, in the north end of gaps, and as hurricane-created woody debris decreases.

METHODS

Hurricane Opal struck Bent Creek on the morning of October 5, 1995. Opal created sustained winds of 8.9 miles per second and maximum peak gusts of 25.9 miles per second at the nearby Asheville, NC, airport. Within a 259-ha surveyed parcel at Bent Creek, an average of 0.89 canopy gaps/ha were created by Opal-generated windfalls. Single-tree gaps were the most common opening, averaging 57 ± 34 m^2. Multiple-tree gaps averaged 171 ± 117 m^2 (Greenberg and McNab 1998).

Gap Selection

Selected gaps are located within the 2 400-ha Bent Creek Experimental Forest, about 16 km south of Asheville, NC (35.5° N, 82.6° W) in the Southern Appalachian Mountains. Gaps were restricted to openings at least 0.1 ha in size. Also, at least six canopy trees per gap must have fallen as a result of Hurricane Opal. Beck (1988) commented on the 0.1-ha size as being a reasonable minimum for the successful colonization and development of the most shade-intolerant eastern hardwoods. By restricting gap areas to > 0.1

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ha, I ensured that all native hardwoods had enough light to colonize and grow successfully.

Using Runkle's (1992) definition of the extended gap to determine perimeters, I located 12 gaps meeting the above criteria ranging from 0.13 to 1.26 ha from October 1995 to June 1996.

Project Site

Of the 12 gaps, 6 are located in dry oak-hickory vegetation communities, 4 in acidic coves, and 2 in rich coves (Schafale and Weakley 1990). 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 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).

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.

Gap Sampling Design

Sampling points were installed during May to July 1996. Two horizontal perpendicular axes were located within each gap: north-south and east-west. Axes intersected at gap center. Axis orientation was changed when realignment allowed a gradient along the entire length of a gap. Transect lines extended from center along established axes in the cardinal directions. Sampling points were located at:

1. gap center
2. out from center along transects 7.3 to 10.67 m apart until gap edge was reached
3. at the north, south, east, and west gap edges
4. progressively outward beyond gap edges 7.3 m apart.

The most extreme points were installed outside gaps where ground-level solar radiation approximated that of forests unaffected by windthrow.

This design resulted in 15 to 32 sampling points per gap and 269 points among all 12 gaps. Established sampling points formed the centers of 13 m^2 circular quadrats.

Tree Seedling Measurements

One or two oak seedlings ≤ 3.81 cm in diameter at breast height were selected at random within each of the 13 m^2 circular quadrats and tagged for long-term identification and measurement. Tagged oaks included 54 northern red (*Q. rubra* L.), 38 chestnut (*Q. prinus* L.), 69 black (*Q. velutina* L.), 2 southern red (*Q. falcata* Michx.), and 73 scarlet (*Q. coccinea* Muenchh.).

Tagged oaks were pooled into one analysis group, because survivorship rates, growth, and response to disturbance are similar for these species (Personal communication. 2000. David Loftis, Project Leader, USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, Asheville, NC 28806). Seedlings were measured twice: June to October 1996 and October to November 1998.

Variables

A wide array of variables were measured and tested as covariates (see table 1 for detailed descriptions of covariates used in final models):

Variables that directly relate to hypotheses:

- distance/gap attributes: gap area, gap perimeter, ratios of gap length to width, distance from gap center to edge, distances from north and south gap edges to center, cardinal direction from center, and gap aperture (angle from gap center to canopy treetops at gap edge (Runkle 1992)
- cover: canopy cover of overstory, midstory, and total canopy
- debris resulting from Hurricane Opal: crown debris, coarse woody debris, tree-fall pits or mounds.

Covariates that help explain background variability:

- site: slope, aspect, categorical indices of soil moisture potential (xeric, subxeric, submesic, mesic), elevation, landform index (McNab 1993), and terrain shape index (McNab 1989)
- vegetative competition: overtopped vs. not-overtopped (dichotomous estimate of subject seedling position relative to surrounding vegetation), shrub coverage, tree seedling densities
- tagged seedling condition: sprout vs. seed origin, broken vs. whole seedling top, microtopography where the seedling is located, initial height, and initial basal diameter.

Data Analysis

I used regression analysis to test all hypotheses.

Seedling survivorship—I employed logistic regression to test the seedling survivorship hypothesis.

The logistic model (Hosmer and Lemeshow 2000) is

$$P = \frac{\exp(b_i X_i)}{1 + \exp(b_i X_i)}$$

where

P = predicted probability of seedling survivorship

b_i = vector of regression coefficients

X_i = vector of independent variables

exp = base of the natural logarithm.

Data were pooled across all 12 gaps and 269 quadrats and analyzed with SAS PROC LOGISTIC (SAS Institute 2000).

Basal diameter and height growth—I tested seedling basal diameter and height growth hypotheses with nonlinear regression, using SAS PROC NLIN (SAS Institute 2000).

I regressed basal diameter growth against covariates using the exponential function, $\beta_0(e^{\beta_1 x_1 + \beta_2 x_2 \ldots \beta_n x_n})$. I modeled height growth with another exponential function, $\beta_0 + e^{\beta_1 x_1 + \beta_2 x_2 \ldots \beta_n x_n}$.

Table 1—Variables used in oak seedling survivorship and growth regression models: data from 12 Hurricane Opal-created gaps within the Bent Creek Experimental Forest

Variable	Mean	Range	Explanation
	units		
GAPPOS (fig. 1)	5.64 (m)	-29.27 – 95.30	Gap position: Linear horizontal distance from gap-edge to quadrat center. Distances from edge towards gap interior are positive, from edge to gap exterior are negative.
MIDCOVER	0.6 (decimal)	0.0 – 1.0	Midcanopy cover: Canopy cover of midcanopy trees. Canopy cover was measured with a go/no-go densitometer (Geographic Resource Solutions 1997) at 17 points within 3.6 m of each quadrat center. The GRS device is essentially a small periscope with level vials and center point for dichotomous calls as to whether or not there is arborescent vegetation overhead. Positive "hits" were then summed and divided by 17 to yield the fraction of the area with overhead canopy.
OVERCOV	0.5 (decimal)	0.0 – 1.0	Overstory cover: Canopy coverage of true canopy species, such as the oaks. Measured as above.
LFI	.19 (decimal)	.08 – .34	Landform Index (McNab 1993): The degree of protection offered by the surrounding topography, expressed as the percent slope from gap center to the surrounding landscape horizon. The mean of 8 readings taken at 45-degree intervals. LFI is a surrogate for soil moisture. Higher values suggest higher soil moisture content.
TSI	3.0 (decimal)	-8.6 – 36.6	Terrain Shape Index (McNab 1989): Microsite topography, expressed as the percent slope parallel to ground surface within 15.24 meters from gap 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.
SURV	0.9 (decimal)	0.0 – 1.0	Survivorship between 1996 and 1998: Dichotomous response variable.
BDGROW98	0.3 (cm)	-4.3 – 2.5	Basal diameter growth between 1996 and 1998; response variable.
HT96	0.6 (m)	0.1 – 3.7	Initial seedling height: measured in 1996.
HTGROW98	0.2 (m)	-1.5 – 2.5	Height growth between 1996 and 1998; response variable.

GAPPOS = gap position; MIDCOVER = midstory canopy cover; OVERCOC= overstory cover; LFI = landform index; TSI = terrain shape index; SURV = 2-year survivorship probability; BDGROW98 = 2-year basal diameter growth; HT96 = initial height; HTGROW98 = 2-year height growth.

These functions are modifications of the Mitcherlich equation, commonly used to model vegetation growth (Myers 1990). Other investigators have used similar functions to model tree diameter and height growth (Vanclay 1994).

RESULTS

Survivorship

Based on the results of my logistic model (table 2), I rejected the hypothesis that survivorship should increase as gap size increases, toward gap center, in the north end of gaps, and as hurricane-created debris declines.

Oak seedling survivorship declined toward gap center and on high-moisture microsites as indexed by terrain shape index (TSI) (fig. 1). The negative slope of the TSI parameter in the survivorship model makes sense; oak survivorship is superior on drier sites, probably because arborescent seedling competition is less than that of mesic sites (Johnson and others 2002).

My predictive model is weak; standard error of the gap position (GAPPOS) parameter is roughly half the parameter estimate (table 2). The low rescaled pseudo-R^2 of 0.11 bears evidence that my survivorship model has poor goodness-of-fit. Classification accuracy is poor, as evidenced by the area under the ROC curve (Hosmer and Lemeshow 2000) of 0.774 (1.0 = perfect classification; 0.5 = no classification benefit; < 0.7 generally indicates poor classification) (fig. 2). Also, my model exhibited declining percent correct classifications with increasing cut point values (94 percent at cut point of 0.50 to 83.3 percent at cut point of 0.90), suggesting poor classification ability.

Topography (seedling location: pit, mound, or near large woody debris) was not correlated with seedling survivorship (table 1). Because only a small fraction of gap areas were covered with pits and mounds, few tagged seedlings were located on these microsites, making any statistical relationships improbable. I found no relationship of oak seedling survivorship to hurricane-created debris, including crown debris and log debris > 8 cm in diameter.

Oak seedling survivorship was not related to cardinal direction within gaps or gap size. I found no relationship of

Table 2—Logistic model[a]: 2-year oak seedling survivorship

Response variable	n	Likelihood ratio	Prob. > chi-square	Pseudo-R^2	Maximum rescaled pseudo-R^2	Correct classifications (cut point)
						percent
SURV	234	9.532	.0085	.04	.11	94.0 (.50) 83.3 (.90)

Covariate	Parameter estimate	Standard error	Chi-square	Prob > chi-square
INTERCEPT	3.392	.410	68.53	<.0001
GAPPOS	-.029	.016	3.16	.08
TSI	-.101	.042	5.95	.01

[a] SURV = 2-year survivorship probability; BDGROW98 = 2-year basal diameter growth; HTGROW98 = 2-year height growth; MIDCOVER = midstory canopy cover; OVERCOC: overstory cover; GAPPOS = gap position; HT96 = initial height; LFI = landform index; TSI = terrain shape index (table 1).

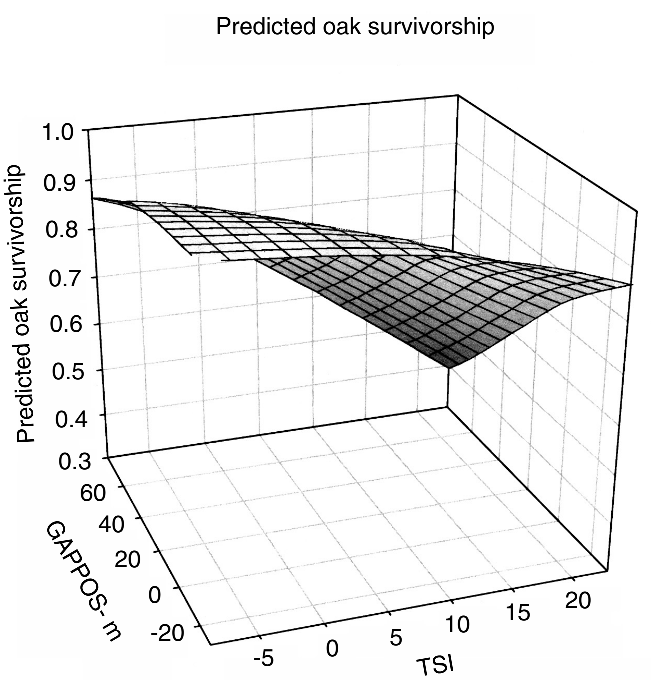

Figure 1—Two-year oak survivorship vs. GAPPOS and TSI. GAPPOS = gap position; TSI = terrain shape index (table 1).

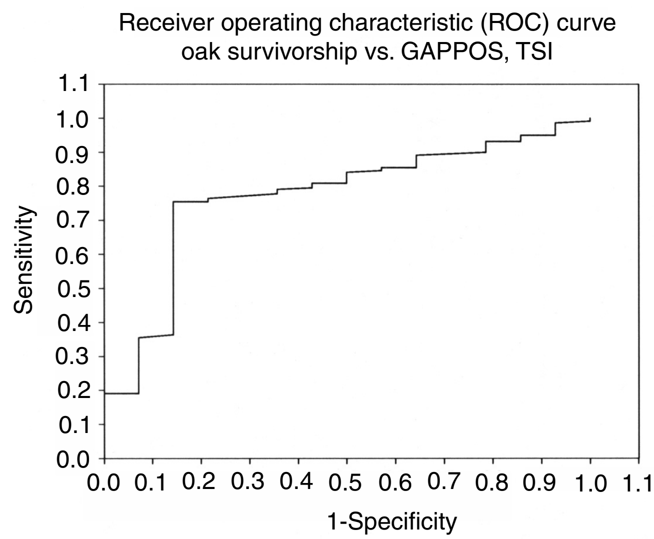

Figure 2—Two-year oak survivorship vs. GAPPOS and TSI: ROC curve (45° diagonal plot suggests poor model accuracy; straight line = perfect accuracy). Area under curve = 0.774 (0.5 = no classification benefit; 1.0 = perfect classification).

survivorship to surrounding arborescent seedling competition, gap aperture, canopy cover, or tagged seedling condition, including initial seedling height, seedling origin (sprouts vs. propagules from seed), or amount of seedling top damage.

Growth

I encountered significant problems with outliers in all growth analyses. In particular, negative growth observations created enormous modeling problems. Negative basal diameter and height growth are not unusual; oak seedlings frequently lose their tops to herbivory or weather damage (Johnson and others 2002). New tops usually develop after resprouting, but the new growth may not make up for increment lost over the 2-year measurement period. Some of these negative growth observations in larger diameter stems created high influence points that actually reversed the sign of initial height (HT96) parameter slopes. I solved this problem by deleting all negative growth observations.

My analyses supported my hypotheses of increased oak basal diameter and height growth toward gap center (table 3, figs. 3 and 4). However, data analyses did not support my hypotheses that growth would increase in larger gaps, in the north end of gaps, and as hurricane-created debris decreased.

Table 3—Nonlinear growth models: 2-year oak seedling basal diameter and height growth[a]

Response variable	n	Mean square error	Computed F statistic	Prob. > F	Nonlinear R^2	Covariate	Parameter estimate	Standard error
BDGROW98	169	.09	77.52	<.0001	.31	INTERCEPT	0.463	.065
						MIDCOVER	-1.01	.256
						GAPPOS	0.01	.004
						HT96-LFI	2.24	.260
HTGROW98	169	.0518	12.0	<.0001	.23	INTERCEPT	-.8143	.041
						HT96	.1192	.041
						GAPPOS	.00256	.001
						OVERCOV	-.1702	.001
						HT96-TSI	.0110	.005

[a] BDGROW98 = 2-year basal diameter growth; HTGROW98 = 2-year height growth; HT96 = initial height; GAPPOS = gap position; MIDCOVER = midstory canopy cover; OVERCOC: overstory cover; LFI = landform index; TSI = terrain shape index (table 1).

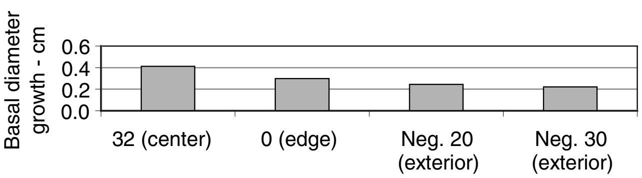

Figure 3—Two-year oak basal diameter growth vs. GAPPOS, HT96, TSI, and MIDCOVER.

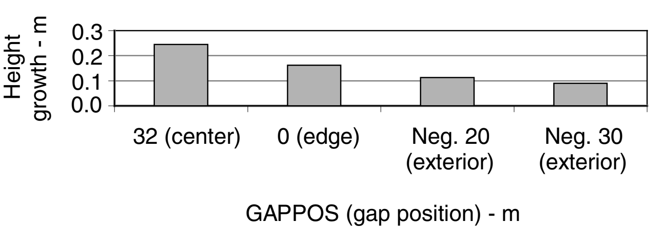

Figure 4—Two-year oak height growth vs. GAPPOS, HT96, TSI, and OVERCOV.

Seedling basal diameter and height growth were highly variable. Basal diameter growth mean square error was 0.09 with mean of 0.3 cm; height growth mean square error was 0.0518 with mean of 0.2 m. Accordingly growth relationships are weak; the basal diameter growth model R^2 is 0.31, and the height growth model R^2 is 0.23. Also, the distance gradient covariate GAPPOS explained little of the variability in growth, as evidenced by high GAPPOS standard errors relative to parameter estimates in both the basal diameter and height growth models (table 3).

HT96 contributed substantially to explaining variability in basal diameter and height growth (table 3). Basal diameter and height growth correlated with seedling origin (sprouts vs. propagules arising from seed). However, initial height was so highly collinear with origin that origin had to be eliminated from all models.

Site variables, TSI, and landform index (LFI) explained much of the variation in growth (table 3). I have no rational explanation why LFI proved valuable in the basal diameter growth model as opposed to TSI in the height growth model. The positive slopes of TSI and LFI (HT96-LFI in the basal diameter growth model, and HT96-TSI in the height growth model) make sense; growth of surviving seedlings should be superior on mesic sites.

Both overstory canopy cover (OVERCOV) and midstory canopy cover (MIDCOVER) (table 1) were negatively correlated with oak seedling height growth. However, OVERCOV was much more strongly related to height growth than was MIDCOVER. In fact, MIDCOVER was not significant in the presence of OVERCOV when both variables were included in the height growth model.

The interaction terms HT96-LFI in the basal diameter growth model and HT96-TSI in the height growth model include covariates not included as main effects in the nonlinear functions (table 3). This contradicts recommendations of some statisticians to always include main effects in “hierarchically well formulated models” (Glantz and Slinker 1990). However, including both interaction and all main effect terms created substantial collinearity, so I deleted problematic main effects from both the basal diameter growth and height growth models.

DISCUSSION

Survivorship declined toward gap center and increased at gap edge and in microsites up to 20 m beyond gap edge in the unaffected forest (fig. 1). My results of higher seedling survivorship in microsites closer to gap edge than gap center mirror those of McNab (McNab, W.H. 2002. Poor American chestnut seedling survivorship in gap-centers. Unpublished data analysis. U.S. Department of Agriculture, Forest Service, Southern Research Station) and Sipe and Bazzaz (1995). Meiners and others (2000) found that oak, ash (*Fraxinus americana L.*), and red maple (*Acer rubrum L.*) survivorship suffered in the subdued light environment at gap perimeters; seedling survivorship was enhanced near gap centers**.** Why are my findings of low survivorship toward gap center diametrically opposed to the results of other investigators such as Meiners and others (2000)? Perhaps seedling competition increases toward gap center, which may be contributing to early oak seedling death. This trend may reverse through time for seedlings near gap center that are able to attain dominance. Eventually, oak seedlings outside gaps probably will die at an increasing rate, because they will not be able to acquire sufficient sunlight to achieve their compensation points (Kramer and Kozlowski 1979).

My findings of increasing basal diameter and height growth along a linear distance gradient toward gap center are consistent with those of Brown (1996). He found that height growth of tropical hardwoods increased linearly on a distance gradient from gap exterior to gap center. Brown's study is one of few relating seedling performance to linear distance gradients.

Tree seedling survivorship and growth generally improve as gap size increases because of solar radiation gains at ground level (Sipe and Bazzaz 1995). However, improvements in growth often attenuate beyond thresholds in gap size. For example, Coates (2000) found substantial seedling growth enhancement as gap size increased up to 0.1 ha but discovered no growth improvements in sizes beyond 0.1 ha to 0.5 ha. However, I found no correlations of oak seedling survivorship or growth with gap size. I suspect that having my gaps > 0.1 ha in size diluted the effect of gap size on oak survivorship and growth.

The lack of relationship of oak survivorship and growth to hurricane-created crown debris is surprising. Crown debris intercepts substantial solar radiation and should be negatively correlated with survivorship and growth. Crown debris was heavily distributed throughout gaps as a result of windthrown trees. I suspect that one reason for this lack of correlation is deterioration of crown debris over the 2-year measurement period. Crown debris coverage declined from a mean of 10.6 percent in 1996 to 0.7 percent in 1998.

Generally, tree seedling survivorship and growth increase as midstory and overstory canopy densities decrease (Buckley and others 1998, Dey and Parker 1997). As expected, I found that seedling growth was negatively correlated with cover. Why did I not find a significant negative relationship of seedling survivorship to canopy cover? I suggest that the tagged seedlings had sufficient carbohydrate reserves to sustain life over the 2-year response period, even under residual tree canopies. However, the answer eludes me, because my logistic model only measured the dichotomous response of live vs. dead, not physiological condition.

Most surprising is the lack of relationship between oak survivorship and initial size (Johnson and others 2002). Oaks are advance-regeneration-dependent (Johnson and others 2002, Loftis 1989). Probability of their survival and subsequent competitive status is based on size, as represented by basal diameter or height (Battaglia and others 2000, Loftis 1990). Having large initial size confers competitive advantages in high-density cohorts of regeneration. My findings of no survivorship relationship with initial size may be because my analysis includes only 2 years of response time. Many authors suggest that oak survivorship is quite high for the first few years after disturbance before severe competition takes place (Johnson and others 2002).

Topographic factors can serve as surrogates of available soil moisture (Vanclay 1994). TSI and LFI apparently captured important differences in soil moisture across all 12 gaps to explain much of the variability in survivorship and growth (tables 2 and 3).

This study validates the use of LFI and TSI to explain site difference impacts on seedling survivorship and growth. Previously, these indices had been used solely in site classification studies (Hutto and others 1999) (W.H. McNab. 1995. Field guide to site classification in the Bent Creek Experimental Forest. Unpublished manuscript. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station). Because many forestry investigations are better analyzed with regression than through agricultural-style field-blocked studies, physical site variables such as LFI and TSI are invaluable in explaining vegetation response by differing site qualities.

CONCLUSIONS

1. Oak seedling survivorship declined on a continuous horizontal distance gradient from gap exterior to gap center.
2. Seedling basal diameter and height growth increased on a continuous horizontal distance gradient from gap exterior to gap center.
3. Arborescent overstory cover proved useful in explaining reductions in seedling height growth; midcanopy cover substantially reduced basal diameter growth. Seedling survivorship was not related to cover.
4. Hurricane-created debris had no discernible effect on seedling growth or survivorship.
5. Gap size did not affect 2-year oak seedling survivorship or growth in the range of gap sizes investigated (0.1 to 1.3 ha).
6. Gap-edge effects on oak seedling survivorship and growth persisted at least 20 m into the unaffected forest.
7. Physical site variables enable oak seedling growth and survivorship comparisons among a wide variety of sites.

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