YELLOW-POPLAR AND OAK SEEDLING DENSITY RESPONSES TO WIND-GENERATED 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 small "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 important in shaping understory colonization, growth, and survival. On October 5, 1995, Hurricane Opal struck the Bent Creek Experimental Forest, creating a unique opportunity to investigate the effects of wind damage and wind-created large forest gaps on forest understory vegetation. We investigated the relationships of yellow-poplar (*Liriodendron tulipifera* L.) and oak (*Quercus* spp.) seedling densities to spatial and structural gradients in and around 12 large, Hurricane Opal–created gaps. Seedling densities were modeled with repeated measures regressions over 3 years (1996, 1997, and 1998). Oak seedling density was highest in the south end of gaps and on high-energy aspects. Oak densities were negatively correlated with hurricane-created crown debris cover and large woody debris. Yellow-poplar seedling density was positively related to distance from southern gap edge and predicted soil moisture, and negatively associated with time since disturbance and crown debris. Yellow-poplar density was highest in the light-rich north end of gaps. The oaks were better able to populate the south end of gaps where yellow-poplar competition was less. Forest managers should expect similar natural regeneration trends in manmade gaps, such as group selection openings.

INTRODUCTION

Hurricane-force winds create large gaps (> 0.1 ha) in eastern hardwood forests. These disturbances are important mechanisms for forest understory recruitment and density changes in the Southern Appalachians (Runkle 1985). Because hurricanes create unique understory plant microsites and massive amounts of tree debris in and around wind-created gaps, understory responses vary substantially from those of manmade gaps (Elliott and others 2002).

Understory recruitment and density generally increase as gap size increases, at the photosynthetically active radiation-rich (PAR) north end of gaps, and with reductions in forest canopy (Busing and White 1997, Ehrenfeld 1980). Several investigations have addressed the change in gap understory dynamics relative to categorical gap positions (center, edge, exterior) (Gysel 1951, Palik and Murphy 1990). However, few studies have focused on understory density changes along continuous linear distance gradients from gap exterior towards gap center (Matlack 1994). Knowledge of differential understory species densities along linear distance gradients would enable managers to predict gap partitioning for species of interest.

Hurricane Opal struck the Bent Creek Experimental Forest on October 5, 1995, creating a unique opportunity to investigate the effects of wind damage and resulting large forest gaps on forest understory vegetation. We developed predictive models relating yellow-poplar (*Liriodendron tulipifera* L.) and oak (*Quercus* spp.) seedling densities to spatial and structural gradients in and around the large gaps created by Hurricane Opal.

Our objectives were to test the hypotheses that yellow-poplar and oak seedling densities in and around wind-created gaps increase (1) on a linear distance gradient from outside gap towards gap center, (2) as gap size increases, (3) in the north end of gaps, (4) as tree canopy cover decreases, (5) as wind-created woody debris decreases, (6) as shrub cover decreases, and (7) with time.

METHODS

Sustained winds of 8.9 m/s and maximum peak gusts of 25.9 m/s were recorded at the Asheville, NC, airport during Hurricane Opal. Within a 259-ha surveyed parcel at Bent Creek, an average of 0.89 canopy gaps/ha were created by windfalls from Opal. Single-tree gaps were the most common type of opening, averaging 57±34 m^2. Multiple-tree gaps averaged 171±117 m^2 (Greenberg and McNab 1998).

Gap Selection

The gaps selected for our study were all in the 2400-ha Bent Creek Experimental Forest, located about 16 km south of Asheville, NC (35.5° N., 82.6 ° W.). We restricted our selection to openings at least 0.1 ha in size, with at least six canopy trees per gap downed by Hurricane Opal. Beck (1988) found the 0.1-ha size a reasonable minimum for the successful colonization and development of the most shade-intolerant eastern hardwoods. By selecting gaps > 0.1 ha in size for our study, we ensured that all native hardwoods had enough light to colonize and grow successfully.

Between October 1995 and June 1996 we located 12 gaps meeting the criteria; the selected gaps ranged from 0.13 ha to 1.26 ha in area. We used Runkle's (1992) definition of the extended gap to determine gap perimeters. Hurricane-created windfall trees were mostly uprooted and had not snapped off from their boles.

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All selected gaps supported some residual hardwood overstory and midcanopy trees; residual tree distribution was highly variable. Common overstory species included oaks, hickories (*Carya* spp.), and yellow-poplar. Common midstory species included dogwood (*Cornus florida* L.), sourwood [*Oxydendron arboreum* (L.) DC.], red maple (*Acer rubrum* L.), and blackgum (*Nyssa sylvatica* Marsh.).

Of the 12 gaps, 6 were located in dry oak-hickory vegetation communities, 4 in acidic coves, and 2 in rich coves (Schafale and Weakley 1990). Annual precipitation ranged from 120 cm at 670 m elevation to 150 cm at 850 m elevation. Area soils consisted of gneisses and schists, with occasional intrusions of mafic minerals found in amphibolite deposits. All soils were > 80 cm deep and acidic (pH < 5.2).

Study Design

Sampling points were installed May to July 1996. We located two horizontal perpendicular axes of north-south and east-west within each gap. Axes intersected at gap center. Transect lines extended out from center along the established axes in cardinal directions. We located sampling points at (1) gap center; (2) out from center along transects 7.3 m to 10.67 m apart 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 points were installed outside gaps where ground-level solar radiation approximated that of forests unaffected by windthrow.

This procedure 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.

Understory Vegetation Measurements

Yellow-poplar and oak seedlings (propagules of both sprout and seed origin) were censused three times: (1) July to September 1996, (2) September 1997, and (3) July to October 1998. All sprouts and seedlings $\leq$ 3.81 cm diameter at breast height (d.b.h.) within the 13-m^2 quadrats were censused by species, with only the dominant individual per sprout clump tallied. Because total counts were limited to propagules from seed plus the dominant individual per sprout clump, counted seedling density is in effect a "practical management density," not total density. Oak species counted included northern red (*Q. rubra* L.), chestnut (*Q. prinus* L.), black (*Q. velutina* L.), southern red (*Q. falcata* Michx.), and scarlet (*Q. coccinea* Münchh.).

Variables

We tested a wide array of variables as covariates, including

1. 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 tree tops at gap edge (Runkle 1992)
2. Cover: canopy cover of overstory, midstory, and total canopy
3. Solar radiation: direct, indirect, and total PAR received at 1 m aboveground. We used canopy photography to predict PAR
4. Debris and microtopography resulting from Hurricane Opal: crown debris, coarse woody debris, tree-fall pits or mounds
5. Site: slope, aspect, categorical estimates of soil moisture potential (xeric, subxeric, submesic, mesic), elevation, landform index (McNab 1993), and terrain shape index (McNab 1989)
6. Vegetative competition: shrub cover.

(Reference table 1 for the variables used in final vegetation density regression equations.)

Data Analysis

We used repeated measures regression techniques to test all hypotheses. Oak and yellow-poplar seedling densities were regressed against covariates across three time periods: time 1 (1996), time 2 (1997), and time 3 (1998). Data were pooled across all 12 gaps and 269 quadrats.

We used SAS PROC GENMOD (SAS Institute 2000) to model tree seedling densities. Specifically, the REPEATED feature found in GENMOD was used to model density changes with time as generalized estimating equations (Allison 1999). At first we used the Poisson distribution, but we found that variances were substantially higher than means, which violates a critical Poisson distribution assumption. To remedy this overdispersion problem, we modeled seedling densities with the negative binomial distribution. The negative binomial is a generalization of the Poisson and accounts for overdispersion by adding a disturbance term to the regular Poisson model (Allison 1999). The linearized-negative binomial model is:

$$\log \lambda_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + ... + \beta_k x_{ik} + \sigma\varepsilon_i$$

where

λ_i = the predicted tree seedling integer count

β s = the intercept and coefficients

x s = the covariates

$\sigma\varepsilon_i$ = the disturbance term.

There are no generally accepted goodness-of-fit measures for generalized estimating equations (GEE). The best overall metric of GEE model performance is a simple ratio of the model's deviance to error degrees of freedom (DF) (Allison 1999). Ideally, deviance to DF should equal 1.0. Using the negative binomial yielded density models with deviance to DF close to this desirable 1.0 ratio. Deviance to DF = 744.211:676 = 1.104 for the all-species model, 1.125 for oak, and 1.104 for yellow-poplar (table 2). Having these ratios close to 1.0 ensured reasonable estimates of parameter standard errors (Allison 1999).

Table 1—Variables used in vegetation density regression models

Variable	Mean	Range	Explanation
	units		
DS	36.1 (m)	-21.00 – 205.00	Distance from south: distance from south gap edge to quadrat. Positive values indicate quadrat is north of south edge; negative values indicate quadrat is south of south edge (Yoshida and others 1998).
YPOSN	1.2 (m)	-112.3 – 109.4	Distance north or south of gap center. Positive values indicate quadrat location north of center; negative values indicate south of center (Yoshida and others 1998).
PRO	3.8 (percent)	0.0 – 75.0	Coarse woody debris suspended aboveground level: ocular estimate of proportion of quadrat surface area covered by woody debris suspended aboveground that resulted from Hurricane Opal; recorded in 1996 on 13 m^2 quadrats.
CROWN	10.7 (percent)	0.0 – 95.0	Crown debris, as above.
YPTOTDEN	3.6 (integer count)	0 – 35	Yellow-poplar seedling density per quadrat; response variable.
OAKDEN	10.5 (integer count)	0 – 57	Oak seedling density per quadrat; response variable.
TRANSASP	0.967 (unitless)	0.0 – 1.996	Transformed aspect: quadrat aspect modified with Beers and others (1966) transformation to give quadrats with aspect of 45° highest values, 225° lowest values.
LFI	0.19 (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 eight readings taken at 45-degree intervals. LFI is an index of predicted soil moisture. Higher values suggest higher soil moisture content.
TIME	N/A	1 – 3	When seedling counts were conducted. Time 1 = 1996, time 2 = 1997, time 3 = 1998.

DS = distance from south gap edge; YPOSN = distance south or north of gap center; PRO = coarse woody debris; CROWN = hurricane-created crown debris cover; YPTOTDEN = yellow-poplar seedling counts; OAKDEN = oak seedling counts; TRANSASP = transformed aspect; LFI = landform index; TIME = when seedling counts were conducted.

RESULTS

We found that seedling densities were strongly related to cardinal direction within gaps. Oak seedling density was highest in the south end of gaps, as indicated by the negative slope of the distance south or north of center (YPOSN) parameter (table 2, fig. 1). Yellow-poplar density was highest in the north end of gaps, as evidenced by the positive distance from south gap edge (DS) parameter (table 2). These two distance gradient covariates are hybrids of cardinal direction and continuous linear distance.

Yellow-poplar densities were positively correlated with gap perimeter, a surrogate for gap size ($r = 0.30$, $P < 0.0001$). However, DS was so highly collinear with gap perimeter ($r = 0.68$, $P < .0001$) that both DS and gap perimeter could not be used in the density model. As the stronger covariate, DS was used in the final yellow-poplar model.

As expected, hurricane-created crown debris (CROWN) significantly reduced predicted seedling densities in both models (table 2, fig. 2). CROWN interacted significantly with time in the oak equation, testifying to the decline of crown debris coverage over the 3-year response period. CROWN also interacted significantly with large woody debris (PRO) in the oak model. This is not surprising. PRO resulted mostly from trees downed by the hurricane, and most downed trees contained live crowns.

Surprisingly, seedling density was not related to canopy cover or predicted solar radiation (table 2). We found no relationship of seedling density to shrub cover. Years 1996, 1997, and 1998 (TIME) was a significant covariate in both models, but time exhibited a meaningful negative trend only in the yellow-poplar model (table 2, figs. 1 and 2).

Physical site variables accounted for significant variation in both density models. Oak densities were highest on high-energy aspects, as evidenced by the negative slope of the transformed aspect (TRANSASP) parameter. Yellow-poplar was positively related to landform index (LFI) and TRANSASP (table 2).

Table 2—Predicted tree seedling counts[a]

Response variable	n	DF	Deviance	Pearson chi-square	Log likelihood	Covariate	Parameter estimate	Empirical standard error	Z value	Prob. > Z
OAKDEN	743	733	824.905	791.856	12,380.976	Intercept	2.8281	0.0782	31.78	< 0.0001
						YPOSN	-0.0057	0.0023	-2.49	0.0129
						TRANSASP	-0.2687	0.0753	-3.57	0.0004
						Time 1 (1996)	-0.2022	0.0326	-6.20	< 0.0001
						Time 2 (1997)	-0.2698	0.0316	-8.54	< 0.0001
						Time 3 (1998)	0.0000	0.0000	.	.
						YPOSN*CROWN	-0.0003	0.0001	-2.24	0.0252
						CROWN*PRO	-0.0012	0.0002	-4.76	< 0.0001
						CROWN*Time 1	-0.0081	0.0027	-3.03	0.0025
						CROWN*Time 2	-0.0044	0.0023	-1.90	0.0581
						CROWN*Time 3	-0.0027	0.0023	-1.19	0.2322
YPTOTDEN	743	737	605.3614	644.175	3,602.978	Intercept	-3.2543	0.3535	-9.21	< 0.0001
						TRANSASP*DS	0.0126	0.0010	12.24	< 0.0001
						CROWN	-0.0111	0.0048	-2.31	0.0211
						LFI	14.7085	1.4249	10.32	< 0.0001
						Time 1 (1996)	0.8707	0.1295	6.72	< 0.0001
						Time 2 (1997)	1.0368	0.1207	8.59	< 0.0001
						Time 3 (1998)	0.0000	0.0000	.	.

DF = degrees of freedom; OAKDEN = oak seedling counts; YPOSN = distance south or north of gap center; TRANSASP = transformed aspect; CROWN = hurricane-created crown debris cover; PRO = large woody debris cover; YPTOTDEN = yellow-poplar seedling counts; DS = distance from south gap edge; LFI = landform index.

[a] All species seedling counts per quadrat measured in 1996, 1997, and 1998. Data are from measurements of 269 quadrats in 1996, 1997, and 1998 taken on 12 Hurricane Opal-created gaps within the Bent Creek Experimental Forest.

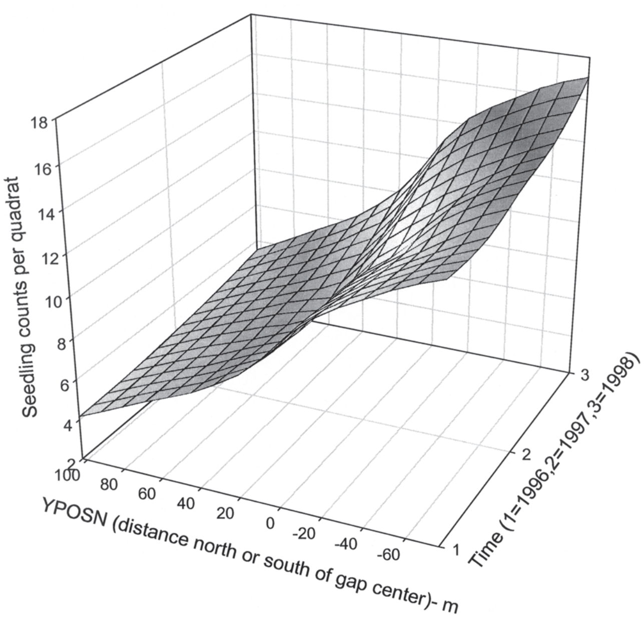

Figure 1—Oak seedling counts per 13-m^2 quadrat vs. YPOSN (distance north or south of gap center; positive values of YPOSN = north of center, negative values = south of center) and time.

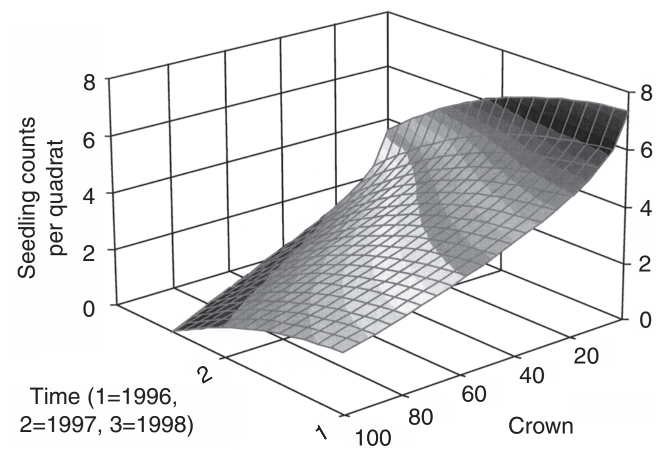

Figure 2—Yellow-poplar seedling counts per 13-m^2 quadrat vs. CROWN (percent crown debris cover) and time.

DISCUSSION

Density models exhibited surprisingly strong relationships over the brief 3-year response period. The significant positive DS covariate (expressed as an interaction term with TRANSASP) in the yellow-poplar seedling model supported the hypothesis that vegetation density would increase in the north end of gaps. However, the opposite was true for the oak density model, where the negative YPOSN parameter indicated higher oak seedling densities south of gap center (table 2). While both oak and yellow-poplar densities changed on continuous linear distance gradients, regression models for both species groups suggested that maximum densities were not reached at gap center. Final regression models supported our hypotheses that tree seedling densities increased as crown and woody debris decreased. We rejected the hypotheses that seedling densities would increase as gap size increased, as canopy cover decreased, and as shrub cover decreased.

Time showed consistent effects on vegetation density only in the yellow-poplar model, where density marginally decreased over 3 years (fig. 2). Because yellow-poplar seedlings were not tagged at the start of each of the three growing seasons, we can only speculate that the reduction in yellow-poplar seedling density through time is due to germinant mortality. Other investigators' findings of vegetation density change through time on disturbed sites vary widely. Tift and Fajvan (1999) discovered that red maple aggressively invaded small gaps, with substantial numbers of fresh recruits establishing each year for 10 to 15 years longer than other species. Beckage and others (2000) studied hardwood dynamics in the Southern Appalachian region and found that seedling densities remained relatively static for the first 3 years after artificial creation of 0.03-ha gaps. Fresh tree seedling recruits then increased substantially in years 4 and 5. Clinton and Boring's (1994) investigation of tree seedling density and shrub competition showed that although all-species richness declined with time, seedling density increased with time.

The density of shade-intolerant yellow-poplar seedlings increased in the light-rich north end of gaps in this study, concurring with findings of other investigators (Canham 1989, Poulson and Platt 1989). Oak densities followed just the opposite pattern; densities increased towards the south end of gaps. Oaks apparently take advantage of lower yellow-poplar competition in the south end of gaps; they are able to flourish in the reduced PAR environment found south of gap center where yellow-poplar is less successful. Our findings of distinct species and life-form density differences among gap locations support the gap-partitioning theory (Bazzaz 1996).

We did not find increases in oak and yellow-poplar seedling densities with increasing gap size, although most other investigators have found strong positive relationships between seedling density and gap size (Busing and White 1997, Collins and Pickett 1987). In particular, shade-intolerant species require larger gaps. Busing and White (1997) found that shade-intolerant arborescent recruitment depended on gaps > 0.04 ha. Beckage and others (2000) discovered that only red maple would successfully colonize 0.03 ha or smaller gaps. We suspect that selecting gaps > 0.1 ha diluted the effect of gap size on understory vegetation response in our study.

Increased understory density is often strongly correlated with increases in beneath-canopy PAR (Carvell and Tryon 1961, Crow and others 2002). For this study, however, oak and yellow-poplar seedling densities were not strongly related to PAR. There are several probable reasons for this. Arborescent seedling densities were mostly negatively correlated with PAR indices. These correlations were weak (r = -0.10 to -0.15 with P = 0.02 to 0.05) due to high variability in height, but indicated that dense vegetation was often taller than the 1-m measurement height and, therefore, covered the camera lens used to measure PAR. Hemispherical photos were taken in 1998, at the end of the response period. If the photos had been taken in 1996, the 1-m instrument height would probably have been above most tree seedlings, and predicted radiation may have been closely related to seedling density.

Unlike Peterson and others (1990), we found no relationship between vegetation density and pit or mound topography. We suggest that because only a small fraction of gap areas were covered with pits and mounds, few tree seedlings were located on these microsites, making any statistical relationships improbable.

Physical site variables facilitated a pooled-data approach for all 12 gaps. Oak densities were higher on high-energy aspects, as evidenced by the significant positive TRANSASP covariate in the oak model. We suggest that this is a competition-related phenomenon. In our experiment, yellow-poplar thrived on low-energy aspects and mesic sites and probably inhibited oak colonization. Oaks are able to capitalize on the lack of arborescent seedling competition found on more xeric sites and recruit successfully (Johnson and others 2002). These findings of higher oak densities on drier sites conform to those of Jenkins and Parker (2000) and Carvell and Tryon (1961).

Seedling densities exhibited surprisingly poor relationships to overstory and midstory canopy cover in our study. Other researchers have mostly found increases in vegetation density with reductions in canopy cover (Buckley and others 1997, Clark and others 1999, Jenkins and Parker 2000). In a previous investigation, seedling survivorship and growth were negatively correlated with canopy cover (Berg 2002).

Unlike other investigators, we found no relationship between tree seedling density and shrub cover (McKenzie and others 2000, Wetzel and Burgess 2001). We had expected substantial reductions in understory density with increasing shrub cover. This lack of relationship is probably due to the light overall shrub cover on our sites. Mean shrub cover among all 269 quadrats increased from just 9.3 percent in 1996 to 14.2 percent in 1998. There were few quadrats where shrub cover exceeded 30 percent. Further, few quadrats contained rhododendron (*Rhododendron maximum* L.), a species shown to substantially dampen tree seedling colonization (Baker and Van Lear 1998, Beckage and others 2000, Clinton and Boring 1994). Some quadrats on drier sites were covered with mountain laurel (*Kalmia latifolia* L.). As did Waterman and others (1995), we found that mountain laurel did not suppress tree seedling density.

Tree seedling densities were substantially diminished by hurricane-created crown debris (table 2). We suggest that crown debris probably eliminated growing space opportunities for new understory recruits and killed advance regeneration by crushing or smothering.

CONCLUSIONS

1. Yellow-poplar seedling densities increased in the north end of gaps; oak densities and herb species richness were greater in the south end of gaps; these findings support the gap-partitioning theory
2. Hurricane-created crown debris significantly retarded tree seedling density
3. Oak and yellow-poplar seedling densities were not related to canopy cover or shrub cover
4. Oak and yellow-poplar seedling densities were not related to gap size. Yellow-poplar density was positively related to gap perimeter length, but this relationship was eclipsed by a stronger, collinear covariate for distance from southern gap edge
5. Yellow-poplar seedling density decreased over the 3-year response period. Oak seedling density remained essentially unchanged through time
6. Physical site variables proved useful in explaining differences in tree seedling density.

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