

PATTERNS OF COMPETITION AND INSOLATION ALONG A CANOPY DISTURBANCE
SEVERITY GRADIENT: IMPLICATIONS FOR THE *QUERCUS* BOTTLENECK

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ABSTRACT

Regeneration failure of *Quercus* has been widely reported throughout the Central Hardwood Forest of the eastern United States across all but the most xeric site types. *Quercus* seedlings are often abundant in upland hardwood stands, but typically fail to recruit to larger size classes (i.e. the *Quercus* bottleneck). The goal of my study was to investigate the competition with small-sized *Quercus* stems to elucidate what variables may cause resistance or facilitation of *Quercus* recruitment. I established a 2 ha plot in the Sipsey Wilderness, AL that was subdivided into 5 x 5 m quadrats to encompass the entire extent of damage caused by an EF1 tornado in 2011.

The study area encompassed a range of damage (light, moderate, severe), starting from the center of the tornado tract and ending in an undamaged area (control). The canopy disturbance provided a range of light conditions in the understory (0.5–91.0% full sunlight). In each quadrat, the height of all small-sized *Quercus* stems (≥ 0.5 m in height to >5 cm DBH) were measured and recorded. The nearest neighbor was identified by species and measured for height and distance from the focal *Quercus* stem. Photosynthetically active radiation was quantified at 1.4 m above the forest floor. *Quercus*' competition was largely interspecific and the majority of competitors were shade-tolerant species such as *Acer saccharum* and *Ostrya virginiana*. Competitive indices of *Quercus*' primary competitors were significantly different ($p < 0.01$) revealing the relative competitive ability amongst species within the plot. Disturbance neighborhoods had no significant ($p > 0.01$) effect on the competitive ability of species. Spatial

patterns of *Quercus* stems, their nearest neighbor, and percent full sunlight were analyzed at 5 x 5 m, 10 x 10 m, and 20 x 20 m. Analysis at a fine-scale resolution revealed spatial patterns which would otherwise not be apparent at coarser scales. Creative and flexible silvicultural techniques may need to be implemented at finer scales to optimize the recruitment of *Quercus* spp.

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1.0 INTRODUCTION

Quercus species are common and widespread throughout the Eastern Deciduous Forest Formation of North America (Johnson et al., 2009). Indeed, the majority of the eastern United States landscape is characterized by forests either dominated by *Quercus* or in which *Quercus* is a component (Braun, 1950; Abrams, 1996; Dyer, 2006; Smith et al., 2009). Paleoecological analyses indicate that *Quercus* has been the dominant genus in forests of the eastern United States throughout much of the Holocene (Delcourt, 1979; Delcourt and Delcourt, 2000; Abrams, 2002). However, a widespread pattern of forest composition change is evident throughout the eastern United States. *Quercus* regeneration failure has been reported in *Quercus*-dominated systems across a range of site types throughout the region. The sapling and small-tree size classes in many *Quercus* stands are devoid of *Quercus* stems and are instead comprised of species with greater shade-tolerance, especially *Acer rubrum* L. and *Acer saccharum* Marsh. (Fei and Steiner, 2007; Nowacki and Abrams, 2008; Fei et al., 2011; McEwan et al., 2013; Hanberry, 2013). Based on the abundance of quantitative data reported from sites throughout the region, many researchers have concluded that this pervasive composition change from *Quercus*-to-*Acer* is inevitable over millions of hectares across the eastern United States (Lorimer, 1984; Abrams, 1992; Abrams, 2005; Nowacki and Abrams, 2008; McEwan et al., 2011). Unequivocally, the successional replacement of *Quercus* by more shade-tolerant species will present challenges to the management of wildlife populations, forest commodities, and other ecosystem goods and

services (McShea et al., 2007; Nowacki and Abrams, 2008; Alexander and Arthur, 2010; Dey, 2014).

Quercus seedlings are often abundant in mature *Quercus*-dominated stands, but these seedlings typically fail to recruit to sapling and small-tree size classes even following canopy disturbances that modify the sub-canopy light regime (Lorimer, 1984; Abrams, 1992; Abrams and Nowacki, 1992; Loftis and McGee, 1993; Lorimer, 1993; Smith, 1993; Hart and Grissino-Mayer, 2008; Nowaki and Abrams, 2008; Johnson et al., 2009; Fei et al., 2011; Richards and Hart, 2011). This phenomenon, often referred to as the *Quercus* bottleneck, has been documented in stands throughout the eastern United States (e.g. Crow, 1988; Abrams and Downs, 1990; Nowaki et al., 1990; Abrams and Nowacki, 1992; Abrams, 2003). The sapling and small-tree size classes in these stands often support an abundance of shade-tolerant stems, especially *A. rubrum* and *A. saccharum* (Lorimer, 1984; Abrams, 1998; Nowacki and Abrams, 2008; Fei and Steiner, 2009; Hart et al., 2014). Abrams (1996) hypothesized that in the absence of competition from shade-tolerant stems in lower forest strata, *Quercus* trees are relatively tolerant of understory conditions. Without competition from shade-tolerant stems in the understory and midstory, *Quercus* spp. have the physiological potential to survive beneath a closed canopy for decades and may be considered a gap-phase genus as they may persist in low light conditions (< 20% full sunlight) and maintain the ability to respond rapidly to increased growing space following canopy disturbance (Orwig and Abrams, 1995; Abrams, 1996; Rentch et al., 2003; Hart et al., 2012; Hart et al., in press). Even in the presence of competition, *Quercus* seedlings that begin with a height disadvantage can potentially grow faster than many of their competitors and eventually dominate the stand (Bey, 1964; Oliver, 1978; Lorimer, 1983; Clatterbuck and Hodges, 1988; Lockhart et al., 2006; Lockhart et al., 2012). However, the

density of shade-tolerant stems in the understory can impede the recruitment of *Quercus* from seedling to sapling size classes (Lorimer et al., 1994).

Canopy disturbance and subsequent increases in the quantity and quality of understory insolation is critical for the regeneration of *Quercus* (Lorimer, 1993; Johnson, 2004). Without receiving increased photosynthetically active radiation (PAR) from that which would occur under a closed canopy, *Quercus* seedlings are not able to recruit to the sapling size class and mortality rates are high. In stands with an abundance of shade-tolerant stems in sub-canopy strata, increased light caused by canopy disturbance may be restricted from reaching *Quercus* seedlings near the forest floor. As canopy disturbance is required for *Quercus* regeneration, *Quercus* advanced reproduction in stands may exhibit clumped or clustered patterns as a result of canopy openings (Rogers, 1985). Thus, silvicultural systems in *Quercus* stands are largely developed around managing the light regime (Watt et al., 1973; Gottschalk, 1983; Dey, 2002).

Stands represent the fundamental unit of silviculture. The concept of delineating stands as uniform operational units was developed to maximize management efficiency (O'Hara and Nagel, 2013). The stand concept was created to employ silvicultural methods that were based on stand-average density metrics initially designed to generate homogeneous stands, which may be relatively easier to manage than mixed species and/or multiaged stands (Puettmann et al., 2009). However, by using stand-level averages of metrics such as basal area and stem density intra-stand patterns, which may be highly variable, may not be revealed (O'Hara and Nagel, 2013). Adjusting our management approach to account for intra-stand variability requires the reevaluation of the stand concept (Puettmann et al., 2009; Churchill et al., 2013; O'Hara and Nagel, 2013). Natural disturbances can create variable patches because of temporal variation in disturbance intensity, local variation in tree size, species susceptibility, and topographic

variations among other factors (Runkle, 1985; Pickett and White, 1985; Canham et al., 2001; Hanson and Lorimer, 2007; Hart and Kupfer, 2011).

Studies conducted at multiple spatial scales where size (i.e. size of the observational unit) and extent (i.e. size of the entire study area; Wiens, 1989) are independent of one another may identify the best resolutions of domains, patterns and the determinants of the relationships among scales. This study used a continual plot sampled at a fine-spatial scale (5 x 5 m) to reveal more detail about the biological mechanisms (competition and PAR) that drive the variable patterns of *Quercus* advanced regeneration after a disturbance at the intra-stand level. The data set provided an opportunity to evaluate the relationship between *Quercus* spp. and neighboring stems (labeled competitors in the analysis) along a canopy disturbance severity gradient that modified the sub-canopy light regime. The specific objectives of this study were to (1) document the species, height and distance of all stems nearest *Quercus* advanced reproduction to provide information on neighboring stems in the regeneration layer, (2) to quantify spatial patterns of insolation in the understory and (3) to analyze patterns of *Quercus*, their nearest neighbor, and light levels at multiple spatial scales along a disturbance gradient. My results have implications for silvicultural operations in upland hardwood stands designed to promote *Quercus* regeneration.

2.0: STUDY AREA AND METHODS

2.1 Study Area

My study was conducted in the Sipsey Wilderness, which occurs on the William B. Bankhead National Forest in northern Alabama (34°20'N, 87°25'W). The Sipsey Wilderness is a 10,085 ha reserve managed by the USDA Forest Service (Figure 1). The reserve occurs on the southern Cumberland Plateau section of the Appalachian Plateau physiographic province (Fennemen, 1938). Pennsylvanian Pottsville formation bedrock underlies this region and the geology is predominantly comprised of sandstone with lesser amounts of siltstone, varying levels of stratified shale, and thin layers of discontinuous coal (Smalley, 1979; Szabo et al., 1988). The southern Cumberland Plateau is strongly dissected and is characterized by complex topography (Fennemen, 1938). Regionally, soils are coarse to medium textured, somewhat shallow, well to excessively drained, and typically acidic (USDA, SCS 1959).

The regional climate is humid mesothermal characterized by long, hot summers and short, mild winters (Thorntwaite, 1948). The mean annual temperature is 16 °C (January mean: 5 °C; July mean: 26 °C) and the frost-free period spans approximately 220 days from late-March to early-November (Smalley, 1979). Precipitation rates are evenly distributed throughout the year with no distinct dry season. Mean annual precipitation is 1390 mm with a January average of 135 mm and a July average of 113 mm (PRISM Climate Group, 2011). Thunderstorms occur on average 75 days year⁻¹ (Burt and Stroud, 2007) and result from convective lifting and low-pressure centers (Smalley, 1979). Based on Braun's (1950) forest classification, the southern

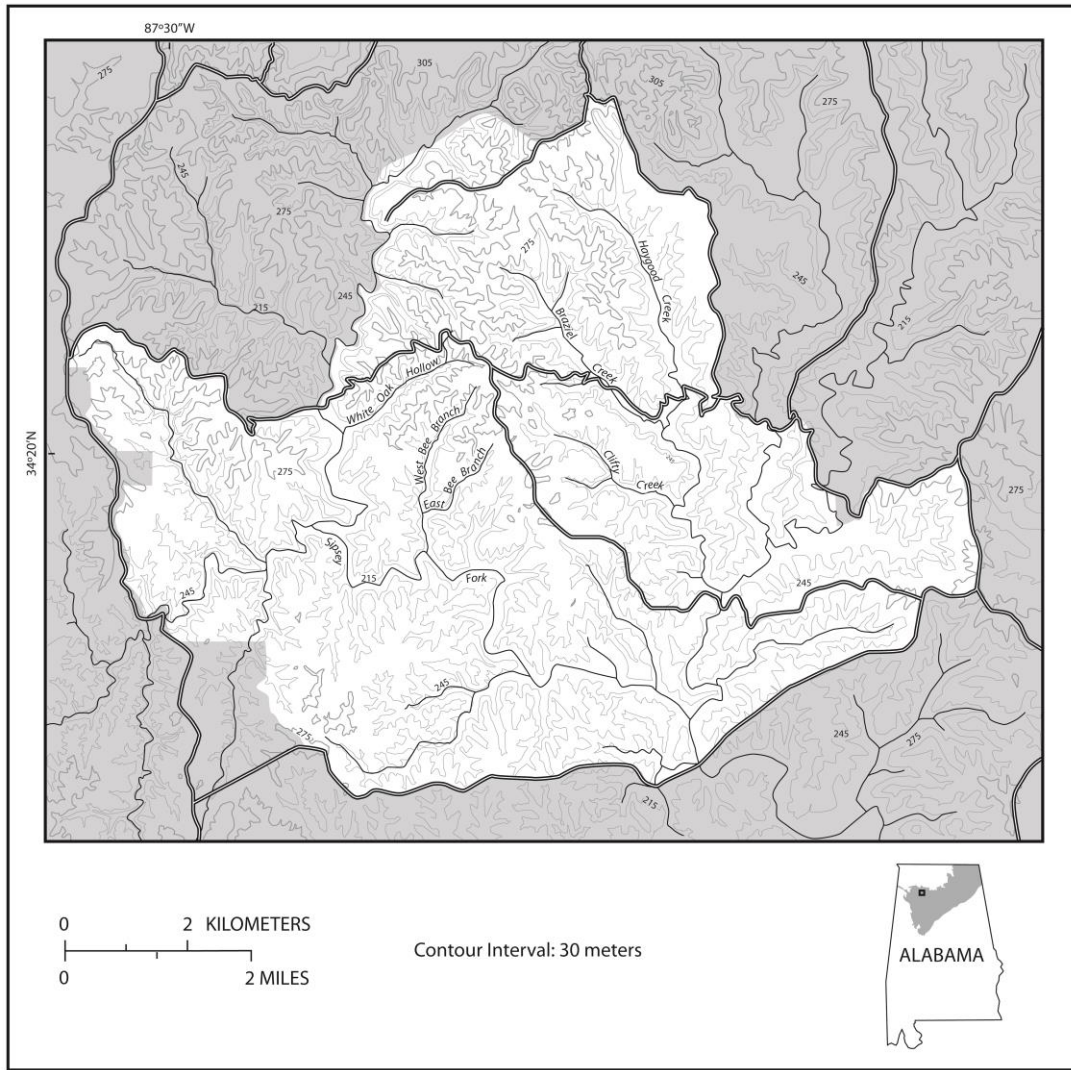


Figure 1. Sipsey Wilderness on the Bankhead National Forest in Alabama, USA (34°20'N, 87°25'W). Shaded portion on Alabama inset map is the Cumberland Plateau physiographic province.

Cumberland Plateau region represents a transitional zone between the Mixed Mesophytic Forest Region to the north and the *Quercus-Pinus* Forest Region to the south. Forest communities on the Cumberland Plateau are noted for high species richness and species composition is strongly influenced by topography and soil water availability (Hinkle, 1989; Clatterbuck et al., 2006). Zhang et al. (1999) classified 14 ecological communities based on dominant overstory species throughout the Sipsey Wilderness. Ridges and upper slope positions are often dominated by *Pinus taeda* L. and *Pinus echinata* Mill. Over a distance of less than 100 m along a topographic gradient, stands may transition to support stronger components of hardwood species (Zhang et al., 1999; Parker and Hart, 2014). Middle and lower slope positions are characterized by mesic hardwood stands that include strong components of *Fagus grandifolia* Ehrh., *Liriodendron tulipifera* L., and *Magnolia macrophylla* Michx. (Hardin and Lewis, 1980; Martin et al., 2008; Zhang et al., 1999; Richards and Hart, 2011; Parker and Hart, 2014). Zhang et al. (1999) found that *Quercus* was the most abundant genus in the Sipsey Wilderness and occurred in almost all 14 delineated community types.

On 20 April 2011 a long-lived, quasi-linear convective system developed in north-central Mississippi and tracked eastward through north Alabama (National Weather Service, 2011). A bow echo with a strong meso-vortex produced damaging straight-line winds across a five county region in north Alabama. The system also produced an EF1 tornado that tracked ca. 5 km and directly damaged portions of the Sipsey Wilderness. A wake low developed after the storms, which produced a short period of damaging non-thunderstorm winds in the area. Wind gusts of 152 km hr⁻¹ were recorded with the wake low system. Storm damage was most severe in the tornado path and decreased in severity of disturbance with distance from the main storm track (Cowden et al., 2014; White et al., 2015). Windstorms of this severity occur frequently across

the United States. From 1991–2010, approximately 1,215 EF0, EF1, and EF2 tornadoes occurred annually (this accounted for 95% of all tornado events) in the contiguous United States (NCDC, 2013).

2.2 Field Methods

I established a 2 ha (100 m x 200 m) permanently marked rectangular plot within a single stand that met the following criteria: (1) *Quercus alba* L. dominated, (2) fully contained within the Sipsey Wilderness, (3) establishment date circa 1900, (4) directly affected by the April 2011 tornado, and (5) without official records or observations indicating past exogenous disturbances effecting stand development. Candidate stands were located using geo-referenced data provided by the USDA Forest Service, data from previous studies in the area (Richards and Hart, 2011; Cowden et al., 2014; White et al., 2015), and field reconnaissance. The plot location was determined in situ with the use of topographic maps and visual reconnaissance. The plot was subjectively located to minimize topographic variation (3.7% slope) and to provide at least a 25 m buffer from the adjacent stands to avoid immediate changes in environmental factors and species composition. The long axis of the plot was oriented perpendicular to the swath of the tornado to incorporate varying magnitudes of canopy disturbance resulting from the storm to collect an inventory of post-disturbance biophysical conditions across the canopy disturbance gradient.

Data were collected in summer 2014 during the fourth growing season post-disturbance. The 2 ha plot was subdivided into 5 x 5 m quadrats to allow for analyses at a fine spatial resolution. In each quadrat I recorded species and diameter at breast height (DBH) of every live stem ≥ 5 cm DBH. Dead stems (≥ 5 cm DBH) rooted within the plot were measured for diameter

at 1.4 m about the root collar (estimated standing DBH), classified to the lowest taxonomic level possible, categorized as snag, uprooted, or snapped stem (Clinton et al., 1993; Yamamoto, 2000; Richards and Hart, 2011). Dead stems were placed into a decay class (Fraver et al., 2002; Hart and Grissino-Mayer, 2008) to determine the amount of basal area removed by the windstorm event. Decay classification was based on Fraver et al. (2002) and included decay class 1 (wood was sound, bark was intact, small to medium branches were still present); decay class 2 (wood was sound to slightly rotten, bark maybe attached, large branch stubs were present, log maintained round shape); decay class 3 (wood was substantially rotten, wood texture was moist, bark was barely attached, bole was oval shaped and partially buried in duff); decay class 4 (wood was rotten, branch stubs rotted, bark was detached, log was oval shaped and largely buried by duff). In each quadrant, all woody stems ≥ 1 m height, < 5 cm DBH (hereafter referred to as saplings), were tallied by species and placed into one of four height classes (A = 1–2 m height; B = 2–3 m height; C = 3–4 m height; D = 4 m height– < 5 cm DBH). For all *Quercus* stems ≥ 0.5 m height and < 5 cm DBH (hereafter referred to as small-sized *Quercus* stems), I measured the total stem height and documented the species. For each of these *Quercus* stems I also documented the distance to the nearest neighboring stem ≥ 0.5 m height, < 5 cm DBH as well as the species and stem height. The *Quercus* nearest neighbor had no qualification besides being alive, proximity, and size. *Quercus* stems ≥ 0.5 m were not analyzed because they are often poor competitors attributed to slow shoot growth and have high mortality rates of within a couple of years (Sander, 1972). *Quercus* seedlings may fail to recruit after canopy disturbance if they are shorter than surrounding stems. Thus, I focused on small-sized *Quercus* stems that had a higher probability of being competitive after a canopy disturbance. At these heights, the *Quercus* stems and neighboring stems were directly competing (crown touching; Zenner et al., 2012) or maintaining

a distance (> 1.8 m) where *Quercus* have the ability to obtain a competitive advantage if conditions are suitable (Clatterbuck, 1985; Lockhart et al., 2006).

Photosynthetically active radiation ($\mu\text{mol m}^{-2}\text{s}^{-1}$) was measured with two synchronized ceptometers (AccuPAR LP-80, Decagon Devices, USA) to quantify the amount of canopy intercepted solar radiation. One ceptometer was placed in full sunlight, while the second simultaneously recorded PAR levels within each 5 x 5 m quadrat. The quadrat ceptometer measurements were taken in a logarithmic spiral pattern (80 total readings per quadrat), starting at the center of the quadrat and spiraling outward to the edge. The 80 readings for each quadrat were averaged to provide a singular value. The mean quadrat value was divided by the readings simultaneously collected from the full sun ceptometer and converted to determine the percent of full sunlight for each quadrat.

2.3 Analytical Methods

All live stems ≥ 5 cm DBH were analyzed using standard descriptors. I calculated frequency (number of quadrats present), relative frequency (percent of quadrats where present), density (number of stems ha^{-1}), relative density (contribution to total trees), dominance (basal area $\text{m}^2 \text{ha}^{-1}$), relative dominance (contribution to total basal area), and relative importance (average of relative density and relative dominance) of each species. For saplings ≥ 1 m height, < 5 cm DBH I calculated density at three spatial resolutions (5 x 5 m, 10 x 10 m, 20 x 20 m) to identify the spatial patterns of the stems to determine the scale at which these patterns manifest.

Based on the time since canopy disturbance, I assumed that trees killed by April 2011 storm event were in decay class I. To assess the gradient of canopy disturbance, I categorized damage severities by averaging basal area lost over a 20 x 20 m area. This spatial resolution was

chosen based on Krajicek et al.'s (1961) maximum crown width equation for *Quercus* spp. in the Central Hardwood Region ($CW_{\max} = 3.12 + 1.829D$, where D is DBH in inches). The maximum crown width of the largest decay class I *Q. alba* stem was 17 m. Therefore, I deemed 20 x 20 m an appropriate size to classify damage severity based on the potential extent of damage created by the windthrown tree. The average amount of basal area removed (i.e. trees killed) from the natural mortality of individual trees (sensu Runkle, 1982) in the control plots was used as a surrogate for background mortality in study stands within the Sipse Wilderness. The value for average basal area removed from control plots was acquired from Cowden et al. (2014) because of proximity of study plots within the Sipse Wilderness. To account for downed trees post-disturbance, I subtracted the background rate of mortality, which was calculated as the average basal area (m^2) lost from control plots, from the basal area lost in each 20 x 20 m plot to estimate the basal area removed (decay class 1 stems/live stems + decay class 1) by the moderate-severity disturbance event. I then used the estimate of basal area removed by the April 2011 storm event to categorize each 20 x 20 m plot into one of four disturbance class neighborhoods following the criteria of Hanson and Lorimer (2007): control = 0–10% basal area removed, light disturbance = 11–30% basal area removed, moderate disturbance = 31–60% basal area removed, and severe disturbance = >60% basal area removed. The control neighborhood (i.e. undamaged areas) was assumed to be representative of pre-disturbance conditions and therefore used as a space-for-time substitution in this study.

Statistical analysis was only performed on small-sized *Quercus* stems and their competitors that were within the 0.5 m to 5.5 m height class because of the greater potential for the two stems to have competitive effects between one another. A modification of Hegyi's (1974) distance-weighted competitor index ($CI_i = (h_j/h_i)/DIST_{ij}$; where CI_i = competition index

of the i th focal tree, h_j = height of competitor stem, h_i = height of focal stem, $DIST_{ij}$ = distance between focal tree i and the j th competitor) was used to analyze the competitive ability of the *Quercus* stem's nearest neighbor on the focal *Quercus* stem (Lorimer, 1983; Holmes and Reed, 1991; Cole and Lorimer, 1994; Weber et al. 2008). All statistical analysis was performed in SAS v. 9.4. Data used for the comparison of means were statistically analyzed and visually assessed for normality and homoscedasticity. Variables that did not meet these criteria were log-, square root- or rank-transformed. To examine significant differences among the three disturbance classifications (i.e. light, moderate, and severe), one-way analysis of variance (ANOVA) was performed for *Quercus* stem height, nearest neighbor height, number of *Quercus* per quadrat, number of primary nearest neighbor stems per quadrat (i.e. the most commonly occurring nearest neighbor species: *A. saccharum* and *Ostrya virginiana* (Mill.) K. Koch.) and percent full sunlight. If a statistically significant difference was found among the four disturbance classes ($p < 0.05$), a Tukey-Kramer post-hoc test was conducted to identify which groups were different. Pearson correlation tests were used to assess the relationships between the *Quercus* stem height, nearest neighbor height, and distance from *Quercus* stem to the neighboring stem ($n = 553$). At the plot level, Pearson correlations were used to assess the relationship of percent of full sunlight, number of small-sized (0.5 to 5.5 m in height) *Quercus* stems per quadrat, and number of primary nearest neighbors per quadrat. Analyses of plot-level correlations were performed at three spatial resolutions (5 x 5 m, 10 x 10m, and 20 x 20 m). To test for differences in competitive ability, species were pooled into three functional groups (*Quercus*, *A. saccharum*, and *O. virginiana*) and then a group of 'others.' Competition indices were analyzed using a 4 x 4 factorial ANOVAs, with one factor being disturbance class and one factor being the functional

groups, with Student-Newman-Keuls post-hoc test to determine which variables were significantly different ($p < 0.01$).

Geo-referenced maps were created and analyzed in ArcMap v. 10.2 (Environmental Systems Research Institute, USA). Locations of small *Quercus* stems, their primary nearest neighbors (other *Quercus* taxa, *A. saccharum*, and *O. virginiana*.), and percent full sunlight were mapped, visually assessed, and then spatially analyzed with Global Moran's I to determine spatial dependence. *Acer rubrum* was not a primary nearest neighbor, but was a species of interest (i.e. part of the '*Quercus*-to-*Acer*' transition) therefore it was also analyzed to determine its spatial dependence. Getis-Ord G_i^* was used to find the extent to which each feature was surrounded by similar high or low values to determine patterns of distribution (i.e. clusters). All spatial data were examined at three resolutions: 5 x 5 m, 10 x 10 m, and 20 x 20 m, to observe how patterns changed among the different spatial scales.

3.0: RESULTS

3.1 Effects on Composition

Basal area of all live stems ≥ 5 cm within the plot was $20.6 \text{ m}^2 \text{ ha}^{-1}$ (Table 1). The five most dominant species based on basal area were *Q. alba*, *F. grandifolia*, *O. virginiana*, *A. saccharum*, and *Carya ovata* (Mill.) K. Koch. The species with the highest densities were *O. virginiana*, *Q. alba*, *A. saccharum*, *F. grandifolia*, and *Cornus florida* L. The most frequent species were *O. virginiana*, *Q. alba*, *A. saccharum*, *F. grandifolia*, and *C. florida*. The estimated basal area lost (removed by the wind disturbance event) was $5.9 \text{ m}^2 \text{ ha}^{-1}$. The most common species damaged based on relative densities of dead stems were *Q. alba*, *O. virginiana*, *Juniperus virginiana* L., *A. saccharum*, and *C. ovata*.

Of the 800 5 x 5 m quadrats sampled, 206 quadrats contained one or more *Quercus* species: *Q. alba*, *Q. rubra* L., *Q. prinus* L., *Q. muehlenbergii* Engelm., and *Q. falcata* Michx. In total, I documented 606 *Quercus* stems throughout the 2 ha study area, but only 553 stems were between 0.5 and 5.5 m height and used for analyses of competitive ability. *Quercus* stems of this size represented only 4% of all live woody stems of this size class in the plot ($n = 14,675$).

3.2 Effects of Competition on Small-Sized *Quercus* Stems

The average height of small-sized *Quercus* stems (0.5–5.5 m height) was 1.33 ± 0.80 m (SD; Table 2). The 553 stems (nearest neighbors) competing with small-sized *Quercus* stems represented 37 different species. The average competitor height was 1.70 ± 0.98 m (SD).

Average height of *Quercus* stems and average height of nearest neighboring stems (including

Table 1. Density and dominance measures for all live stems ≥ 5 cm DBH in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama. Species are ranked according to importance value (relative density + relative dominance).

Species	Density (stems/ha ⁻¹)	Relative Density (%)	Dominance (m ² /ha ⁻¹)	Relative Dominance (%)	Importance Value
<i>Quercus alba</i>	115.5	16.0	11.5	56.1	72.1
<i>Ostrya virginiana</i>	280.0	38.8	1.4	6.6	45.5
<i>Fagus grandifolia</i>	52.5	7.3	1.4	6.6	13.9
<i>Acer saccharum</i>	60.0	8.3	1.0	5.1	13.4
<i>Nyssa sylvatica</i>	32.5	4.5	0.4	1.7	6.2
<i>Cornus florida</i>	32.5	4.5	0.1	0.7	5.2
<i>Carya glabra</i>	15.0	2.1	0.5	2.7	4.7
<i>Ulmus alata</i>	15.0	2.1	0.4	1.8	3.9
<i>Fraxinus americana</i>	9.5	1.3	0.5	2.4	3.8
<i>Carya tomentosa</i>	8.5	1.2	0.5	2.3	3.5
<i>Carya ovata</i>	7.5	1.0	0.4	2.0	3.1
<i>Quercus falcata</i>	3.0	0.4	0.4	2.1	2.5
<i>Liriodendron tulipifera</i>	3.0	0.4	0.4	2.1	2.5
<i>Ulmus rubra</i>	8.0	1.1	0.2	1.1	2.2
<i>Pinus taeda</i>	2.0	0.3	0.4	2.0	2.2
<i>Magnolia acuminata</i>	10.0	1.4	0.1	0.7	2.1
<i>Acer rubrum</i>	9.0	1.2	0.1	0.3	1.5
<i>Quercus prinus</i>	3.5	0.5	0.2	1.0	1.5
<i>Viburnum rufidulum</i>	8.5	1.2	0.0	0.1	1.3
<i>Quercus muehlenbergii</i>	3.5	0.5	0.2	0.8	1.3
<i>Cercis canadensis</i>	7.5	1.0	0.0	0.1	1.2
<i>Carpinus caroliniana</i>	7.0	1.0	0.0	0.2	1.1
<i>Juniperus virginiana</i>	4.5	0.6	0.1	0.4	1.0
<i>Magnolia macrophylla</i>	5.0	0.7	0.0	0.2	0.8
<i>Tilia americana</i>	4.5	0.6	0.0	0.2	0.8
<i>Fraxinus pennsylvanica</i>	3.0	0.4	0.1	0.3	0.7
<i>Oxydendrum arboreum</i>	2.0	0.3	0.0	0.1	0.4
<i>Quercus rubra</i>	1.5	0.2	0.0	0.2	0.4
<i>Prunus serotina</i>	2.0	0.3	0.0	0.1	0.3
<i>Ilex opaca</i>	1.5	0.2	0.0	0.1	0.3
<i>Frangula caroliniana</i>	1.0	0.1	0.0	0.0	0.2
<i>Asimina triloba</i>	1.0	0.1	0.0	0.0	0.1
<i>Quercus stellata</i>	0.5	0.1	0.0	0.0	0.1
<i>Celtis laevigata</i>	0.5	0.1	0.0	0.0	0.1
<i>Ligustrum sinense</i>	0.5	0.1	0.0	0.0	0.1
Total	721	100.0	20.6	100.0	

Table 2. Heights (mean \pm SD) of all *Quercus* stems (0.5–5.5 m in height), the nearest competing stem (0.5–5.5 m in height), and the distance (mean \pm SD) between *Quercus* stems and their nearest competitor in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama

Species	n	<i>Quercus</i> stem height (m)	Competitor stem height (m)	Distance between stems (m)
<i>Q. rubra</i>	231	1.38 \pm 0.83	1.78 \pm 1.00	0.36 \pm 0.23
<i>Q. muhlenbergii</i>	190	1.47 \pm 0.72	1.77 \pm 0.90	0.28 \pm 0.27
<i>Q. alba</i>	111	1.11 \pm 0.83	1.53 \pm 1.05	0.29 \pm 0.22
<i>Q. prinus</i>	13	0.78 \pm 0.33	1.19 \pm 0.69	0.46 \pm 0.37
<i>Q. facalta</i>	8	0.64 \pm 0.20	1.07 \pm 0.63	0.43 \pm 0.24
Total	553	1.33 \pm 0.80	1.70 \pm 0.98	0.33 \pm 0.25

Quercus neighbors) was significantly different ($p < 0.01$). Correlation between competitor height and *Quercus* stem height revealed a significant positive relationship ($p < 0.01$; $r = 0.39$). The mean distance from a small-sized *Quercus* stem and its competing stem in the same size range was 0.32 ± 0.25 m (SD). Correlation between competitor height and distance between the two competing stems revealed a significant positive relationships ($p < 0.01$; $r = 0.26$).

Although the most common individual competitors were within the genus *Quercus* (i.e. intraspecific competition), 65% of overall competition was from interspecific competition. The majority of interspecific (i.e. non-*Quercus*) competitors were *A. saccharum* (14%), *O. virginiana* (12%), *Fraxinus Americana* L. (5%), and *Carpinus caroliniana* Walt. (4%). The average height of small-sized *Quercus* stems was 1.36 ± 0.83 (SD) when the average height of the intraspecific competitor was 1.44 ± 0.88 m (SD). The average height of small-sized *Quercus* stems was 1.32 ± 0.78 m (SD) when the average height of the interspecific competitor was 1.84 ± 1.00 m (SD). When interspecific competitors (69%) were taller than the neighboring *Quercus* stems, the average difference in height was 0.97 ± 0.95 m (SD). In instance when *Quercus* stems were taller than their interspecific competitors, the average difference in height was 0.45 ± 0.54 m (SD). The distance between *Quercus* stems and interspecific competitors averaged 0.39 ± 0.24 m (SD), whereas *Quercus* stems and intraspecific competitors had closer distances that averaged 0.20 ± 0.22 m (SD). Average distances between the two species groups (i.e. *Quercus* and non-*Quercus*) were significantly different ($p < 0.01$).

Heights and distances between small-sized *Quercus* stems and their competing stems varied between the different disturbance class neighborhoods and the forms of competition (i.e. intraspecific and interspecific; Table 3). For intraspecific competition, average height of small-sized *Quercus* stems, average height of competing *Quercus* stems, as well as distance between

the two competing stems in the three disturbances class neighborhoods were significantly different ($p < 0.05$) from the averages in the control neighborhood. For interspecific competition, average small-sized *Quercus* stem heights were significantly different ($p < 0.05$) between the control neighborhood and moderate disturbance class neighborhood. Average heights of the interspecific competitors were significantly different ($p < 0.05$) between the control neighborhood and light disturbance class neighborhood and the control neighborhood and the moderate disturbance class neighborhood. Only 9% of small-sized *Quercus* stems were taller than their interspecific competing stems in the control neighborhood. In the light disturbance class neighborhood 22% of *Quercus* stems were taller, in the moderate disturbance class neighborhood 39% of *Quercus* stems were taller, and in the severe disturbance class neighborhoods 18% of *Quercus* stems were taller than their competing interspecific stems. Average distances between small-sized *Quercus* stems and interspecific competitors were significantly different ($p < 0.05$) between the control neighborhood and moderate disturbance class neighborhood.

Average *Quercus* heights for the control neighborhood and the light, moderate, and severe disturbance class neighborhoods were 0.87 ± 0.55 m (SD), 1.27 ± 0.70 m (SD), 1.40 ± 0.85 m (SD), and 1.41 ± 0.74 m (SD) respectively. I noted a significant difference ($p < 0.05$) between average heights of small-sized *Quercus* stems in the control neighborhood and light disturbance class neighborhood, the control neighborhood and moderate disturbance class neighborhood, as well as the control neighborhood and severe disturbance class neighborhood. Average competitor heights for the control neighborhood, and the light, moderate, and severe disturbance class neighborhoods were 1.16 ± 0.60 m (SD), 1.73 ± 0.98 m (SD), 1.71 ± 0.98 m (SD), and 1.90 ± 1.03 m (SD), respectively. Similarly, I noted significant difference ($p < 0.01$)

Table 3. Intraspecific competition versus interspecific competition along the disturbance gradient (control, light, moderate, and severe). Heights (mean \pm SD) of all *Quercus* stems (0.5–5.5 m in height), heights of their nearest competing stem (0.5–5.5 m in height), height (mean \pm SD) difference between *Quercus* stems and their nearest competitor and the distance (mean \pm SD) between *Quercus* stems and their nearest competitor in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama.

Intraspecific Competiton	Control	Light	Moderate	Severe
<i>Quercus</i> stem height (m)	0.89 \pm 0.40	1.27 \pm 0.61	1.40 \pm 0.93	1.68 \pm 0.88
Competitor stem height (m)	0.92 \pm 0.42	1.41 \pm 0.81	1.50 \pm 0.92	1.54 \pm 0.92
Height difference between stems (m)	0.03 \pm 0.33	0.14 \pm 0.65	0.10 \pm 0.54	0.14 \pm 0.22
Distance between stems (m)	0.10 \pm 0.06	0.24 \pm 0.22	0.19 \pm 0.23	0.14 \pm 0.21
Interspecific Competiton				
<i>Quercus</i> stem height (m)	0.86 \pm 0.63	1.26 \pm 0.75	1.39 \pm 0.81	1.29 \pm 0.64
Competitor stem height (m)	1.3 \pm 0.65	1.92 \pm 1.02	1.82 \pm 1.00	2.10 \pm 1.06
Height difference between stems (m)	0.44 \pm 0.42	0.66 \pm 0.98	0.43 \pm 0.83	0.81 \pm 1.00
Distance between stems (m)	0.50 \pm 0.29	0.40 \pm 0.26	0.36 \pm 0.23	0.43 \pm 0.24

between average competitor heights in the control neighborhood and light disturbance class neighborhood, the control neighborhood and moderate disturbance class neighborhood, as well as the control neighborhood and severe disturbance class neighborhood. Average competitor heights in the light, moderate, and severe disturbance class neighborhoods were not significantly different ($p > 0.05$) from one another.

Competitive ability of small-sized *Quercus* stem nearest neighbors did not significantly ($p > 0.05$) change between disturbance classes. Competitive ability was significantly different ($p < 0.05$) amongst the functional groups; except *O. virginiana* and the ‘other’ group exhibited similar competitive ability. Our results did not reveal significant interactions ($p < 0.05$) between the four disturbance class and the four functional groups (Figure 2).

3.3 Effects of Insolation on Small-Sized *Quercus* Stems

The wind disturbance event removed 22% of the total basal area within the 2 ha plot. Percent full sunlight and basal area removed were significantly correlated ($p < 0.01$; $r = 0.53$) at 20 x 20 m resolution (i.e. the scale in which disturbance severity was classified). All disturbance neighborhoods had varying levels of damage, which caused an array of light levels ranging from 0.4–91.0% full sunlight (Figure 3). Average percent full sunlight was $4.8\% \pm 2.2$ (SD), $8.4\% \pm 2.7$ (SD), $10.8\% \pm 2.9$ (SD), $14.4\% \pm 3.6$ (SD) for the control neighborhood and the light, moderate, and severe disturbances class neighborhoods, respectively. Percent full sunlight was significantly different ($p < 0.05$) between the control neighborhood and light disturbance class neighborhood, the control neighborhood and moderate disturbance class neighborhood, the control neighborhood and severe disturbance class neighborhood, as well as the light disturbance

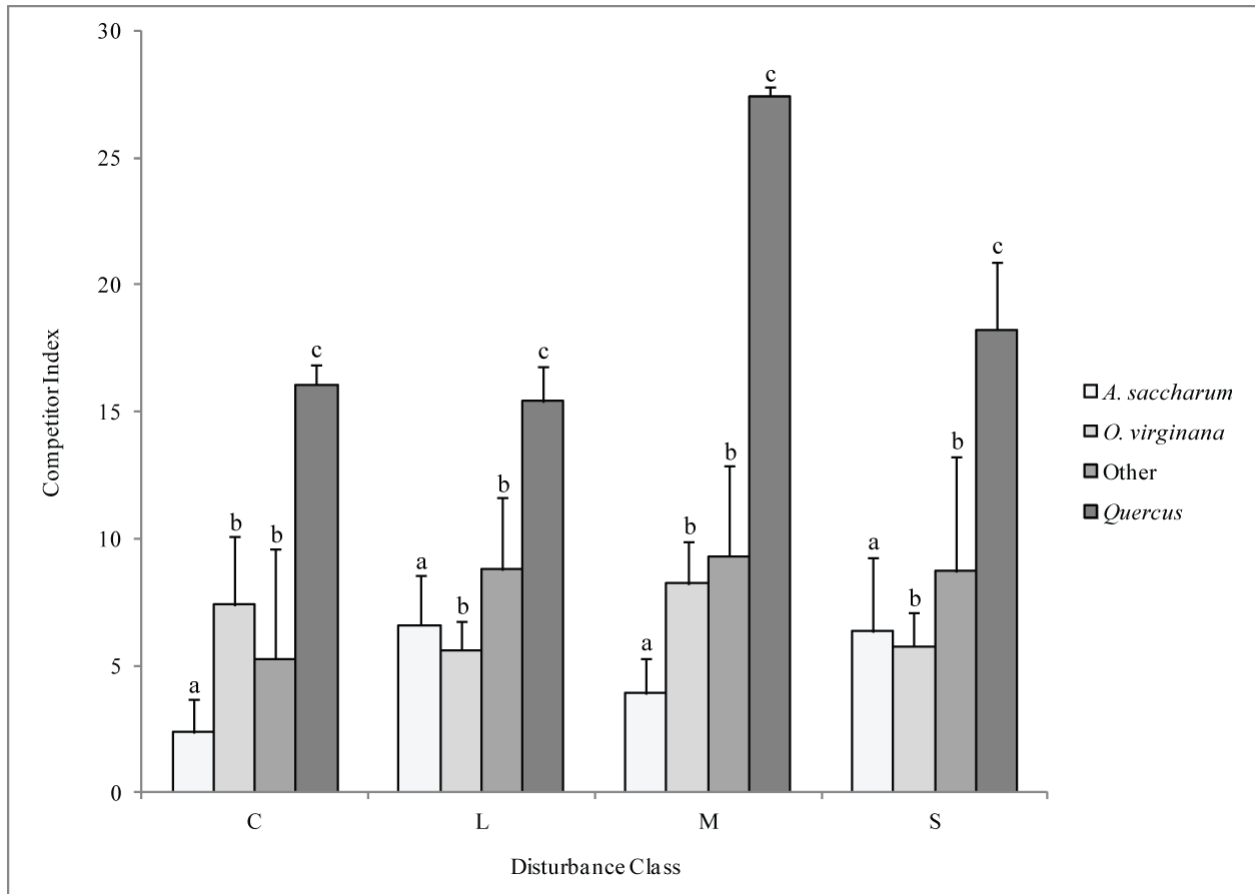


Figure 2. Average competitor indices with standard errors for competitor species (0.5-5.5 m ht) by functional group in the control neighborhood (C), and light (L), moderate (M) and severe (S) disturbance class neighborhoods. Bars with different lowercase letters within functional groups represent significant differences ($p < 0.01$) among species competitive ability.

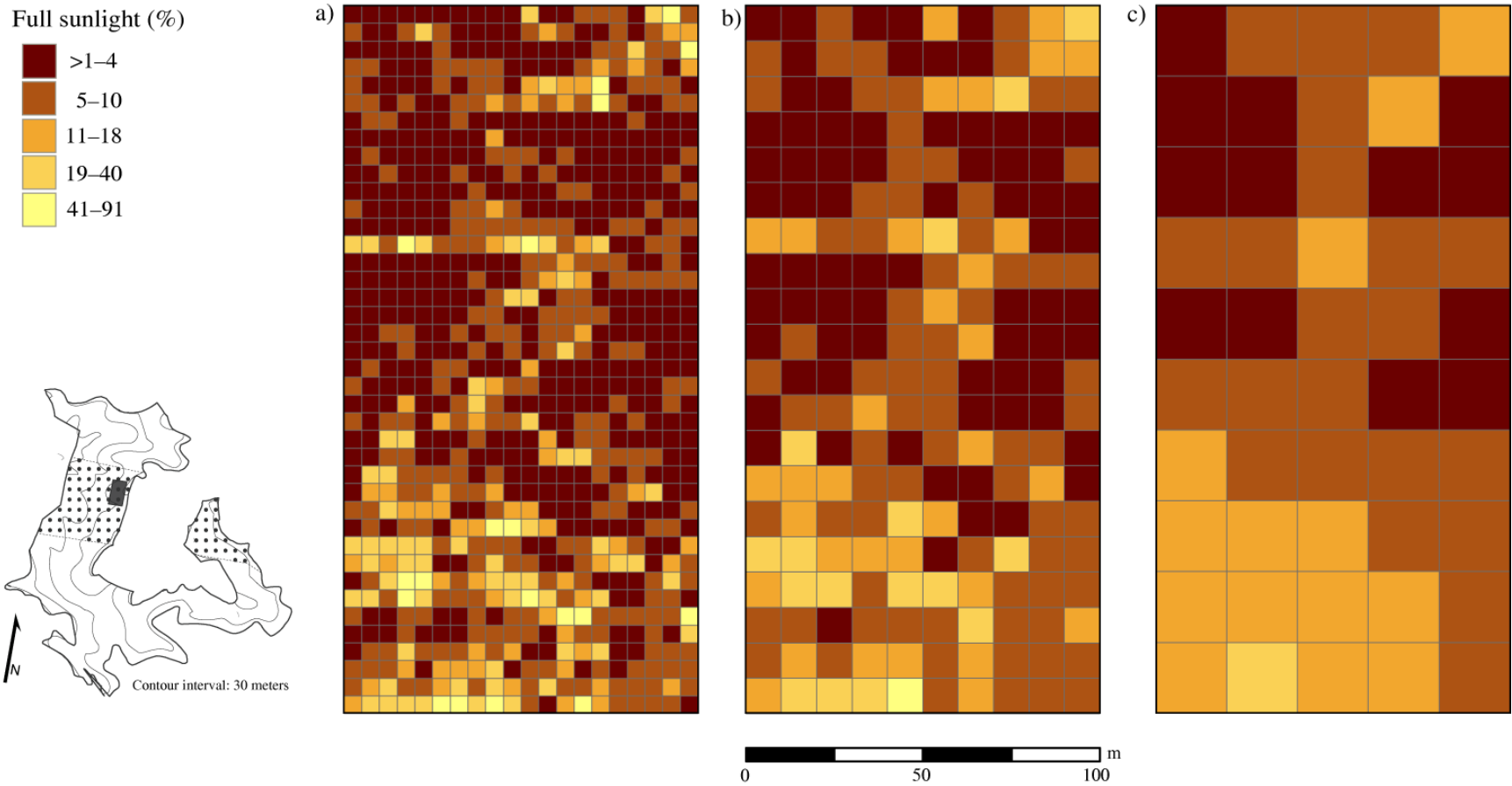


Figure 3. Spatial distribution of percent full sunlight taken at 1.4 m above ground across the 2 ha plot four years after the disturbance in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama. Insert map shows the *Quercus* stand boundary, tornado swath (dotted pattern), plot location, and topography. a) 5 x 5 m; b) 10 x 10 m; c) 20 x 20 m

not detected ($p > 0.05$) for the average percent full sunlight in the severe disturbance class. This could attribute to the small sample size ($n = 16$) of percent full sunlight values in the severe disturbance class neighborhood as opposed to the much larger sample sizes ($n = 224$; $n = 256$) in the light and moderate disturbance class neighborhoods.

Analysis at 5 x 5 m resolution revealed a significant positive relationship ($p < 0.01$) between percent full sunlight and density of small-sized *Quercus* stems, but correlation strength was low ($r = 0.26$). Competitor indices did not have a significant relationship ($p > 0.01$; $r = 0.003$) with the percent full sunlight values within the 5 x 5 m quadrat in which the *Quercus* stem and competitor were located. When scaled to 10 x 10 m and 20 x 20 m resolutions, percent full sunlight and density of small-sized *Quercus* stems had a stronger significant relationships ($r = 0.39$; $r = 0.60$, respectively). At 10 x 10 m and 20 x 20 m resolutions, density of small-sized *Quercus* stems and basal area removed were significantly correlated ($p < 0.01$; $r = 0.24$, $r = 0.52$, respectively).

Significant clusters of light levels (i.e. high values of percent full sunlight that were surrounded by similarly high values) occurred at all spatial scales tested: 5 x 5 m, 10 x 10 m, 20 x 20 m, ($p < 0.05$; $z = 14.21$). Small-sized *Quercus* stem clusters overlapped and were in close proximity (i.e. 5 m² radius from edge of *Quercus* clusters) with high values of percent full sunlight in multiple areas of moderate and severe disturbance (Figure 4). *Acer rubrum* only had one cluster (25 m²) that corresponded with high light levels. For the primary competitors, *A. saccharum* and *O. virginiana*, only two quadrats (50 m²) of high clustering for each species corresponded with high clustering of light levels. The spatial variability of primary competitors was lost at scales of 10 x 10 m and 20 x 20 m. Thus, clusters of competitors that were detected at coarser resolutions did not correspond to clusters of high light levels.

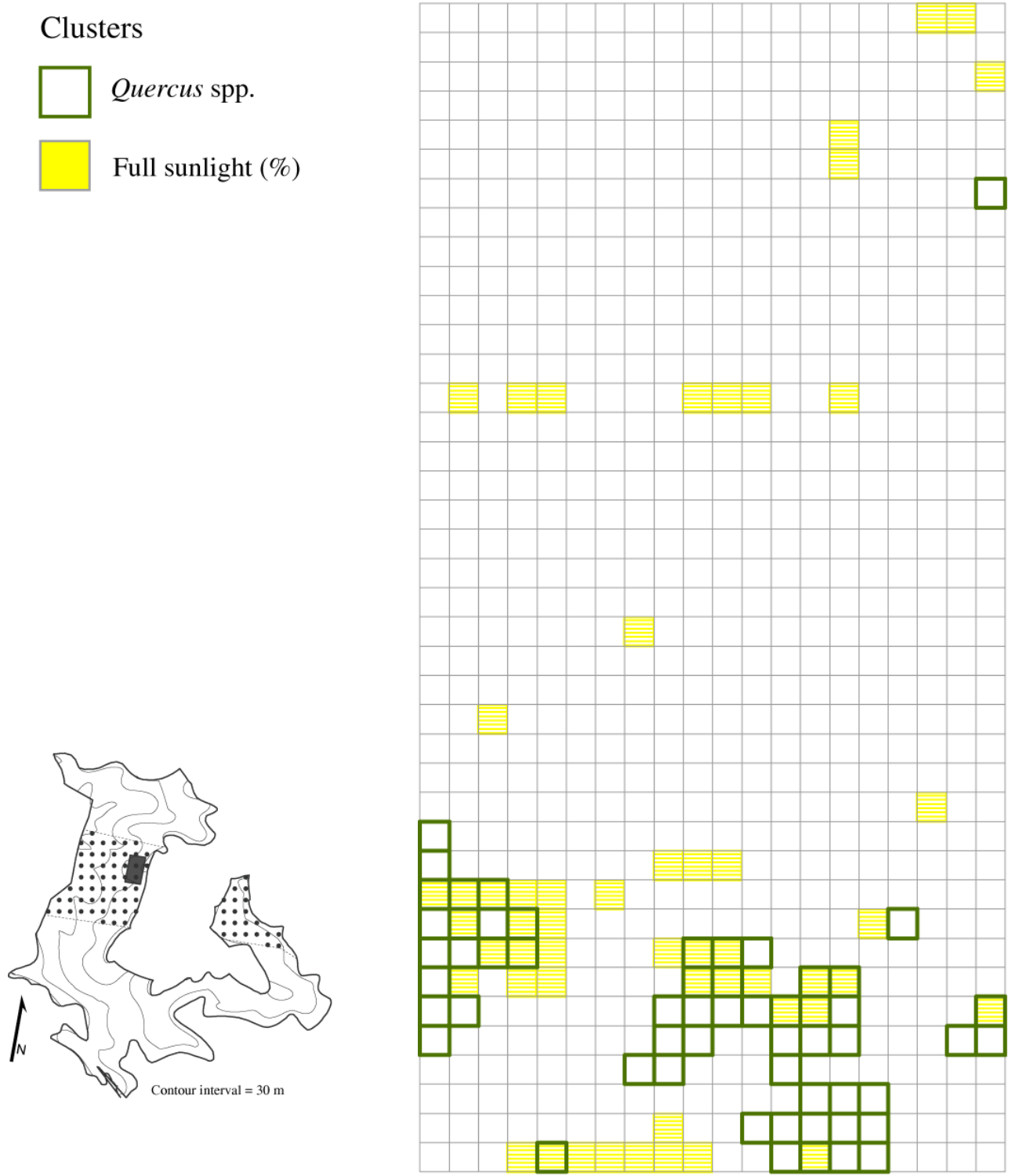


Figure 4. Distributions of *Quercus* spp. cluster compared to percent full sunlight clusters across the 2 ha plot (5 x 5 m resolution) four years after the disturbance in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama. Insert map shows the *Quercus* stand boundary, tornado swath (dotted pattern), plot location, and topography.

3.4 Spatial Patterns of *Quercus* and Competition

Density of small-sized *Quercus* stems varied amongst all disturbance classes, and densities were highest in the moderate and severe disturbance class neighborhoods. At the 5 x 5 m scale, the density of small-sized *Quercus* stems in control neighborhood and light, moderate, and severe disturbance class neighborhoods was 0.11 stems per quadrat ($>0.01 \text{ m}^{-2}$), 0.64 stems per quadrat (0.03 m^{-2}), 1.23 stems per quadrat (0.05 m^{-2}), and 3.68 stems per quadrat (0.15 m^{-2}) respectively. The density of small-sized *Quercus* stems in the control neighborhood and moderate disturbance neighborhood was significantly different ($p < 0.05$) than the density of small-sized *Quercus* stems in the severe disturbance neighborhoods. The density of *O. virginiana* stems (0.5 m in height to $> 5 \text{ cm DBH}$) in the control neighborhood and light, moderate, and severe disturbance class neighborhoods was 3.80 stems per quadrat (0.15 m^{-2}), 4.30 stems per quadrat (0.17 m^{-2}), 4.26 stems per quadrat (0.17 m^{-2}), and 5.25 stems per quadrat (0.21 m^{-2}) respectively. The densities of *O. virginiana* were not significantly different ($p > 0.05$) between each neighborhood. The density of *A. saccharum* stems (0.5 m in height to $> 5 \text{ cm DBH}$) in control neighborhood and light, moderate, and severe disturbance class neighborhoods was 1.30 stems per quadrat (0.05 m^{-2}), 1.67 stems per quadrat (0.07 m^{-2}), 3.41 stems per quadrat (0.14 m^{-2}), and 2.19 stems per quadrat (0.09 m^{-2}) respectively. The density of *A. saccharum* in the moderate disturbance class neighborhood was significantly different ($p > 0.05$) between each the control neighborhood and the light disturbance class neighborhood.

At the 5 x 5 m spatial resolution, densities of small-sized *Quercus* stems ($n = 338$ stems) exhibited clustered distribution with significant ($p < 0.05$; $z = 20.7$) clustering (i.e. where quadrats with high stem density were surrounded by other quadrats with high stem density;

cluster size: 1,425 m²) in the moderate and severe disturbance neighborhoods (Figure 5). Competitor species *O. virginiana* and *A. saccharum* had clustered distributions as well (i.e. clusters spanned 1,350 m² and 1,400 m², respectively). Throughout the plot, *O. virginiana* clusters were found in every disturbance class and the largest clusters (375–550 m²) occurred in the light and moderate disturbance classes. *Acer saccharum* clusters were found in the control neighborhood and the light and moderate disturbance class neighborhoods and the largest clusters (350–375 m²) were located where damage was classed as light or moderate disturbance class neighborhoods. The one large *A. rubrum* cluster (1,075 m²) was juxtaposed with the largest clusters of *Quercus* spp. (425–850 m²), *O. virginiana*, and *A. saccharum*. Interestingly, within moderate and severe disturbance class neighborhoods, there was little overlap of *Quercus* clusters and *A. saccharum* and *O. virginiana* clusters (Figure 6). The largest *Quercus* clusters occurred adjacent to and between the four major clusters of *A. saccharum* and *O. virginiana*. Correlations between the number of *Quercus* stems compared to *O. virginiana* and *A. saccharum* stems across the plot were negligible ($r = 0.013$; $r = 0.18$).

At the 10 x 10 m resolution, all species analyzed exhibited a clustered distribution throughout the 2 ha plot. Significant clusters ($p < 0.05$; $z < 1.96$) were still present, but at lower resolutions, some clusters were no longer detectable. For *Quercus* spp., three clusters (25 m²) were lost when scaling up. Although the addition of incorporated areas in the larger clusters at the 10 x 10 m scale added stems to the sample size ($n = 345$ stems). Clusters of *O. virginiana* were only detected in the control neighborhood and the light and moderate disturbance class neighborhoods. *Acer saccharum* and *A. rubrum* clusters were still detectable in the control neighborhood and the light and moderate disturbance classes as they had been at the 5 x 5 m scale. Correlations between the number of *Quercus* stems compared to *A. saccharum* stems

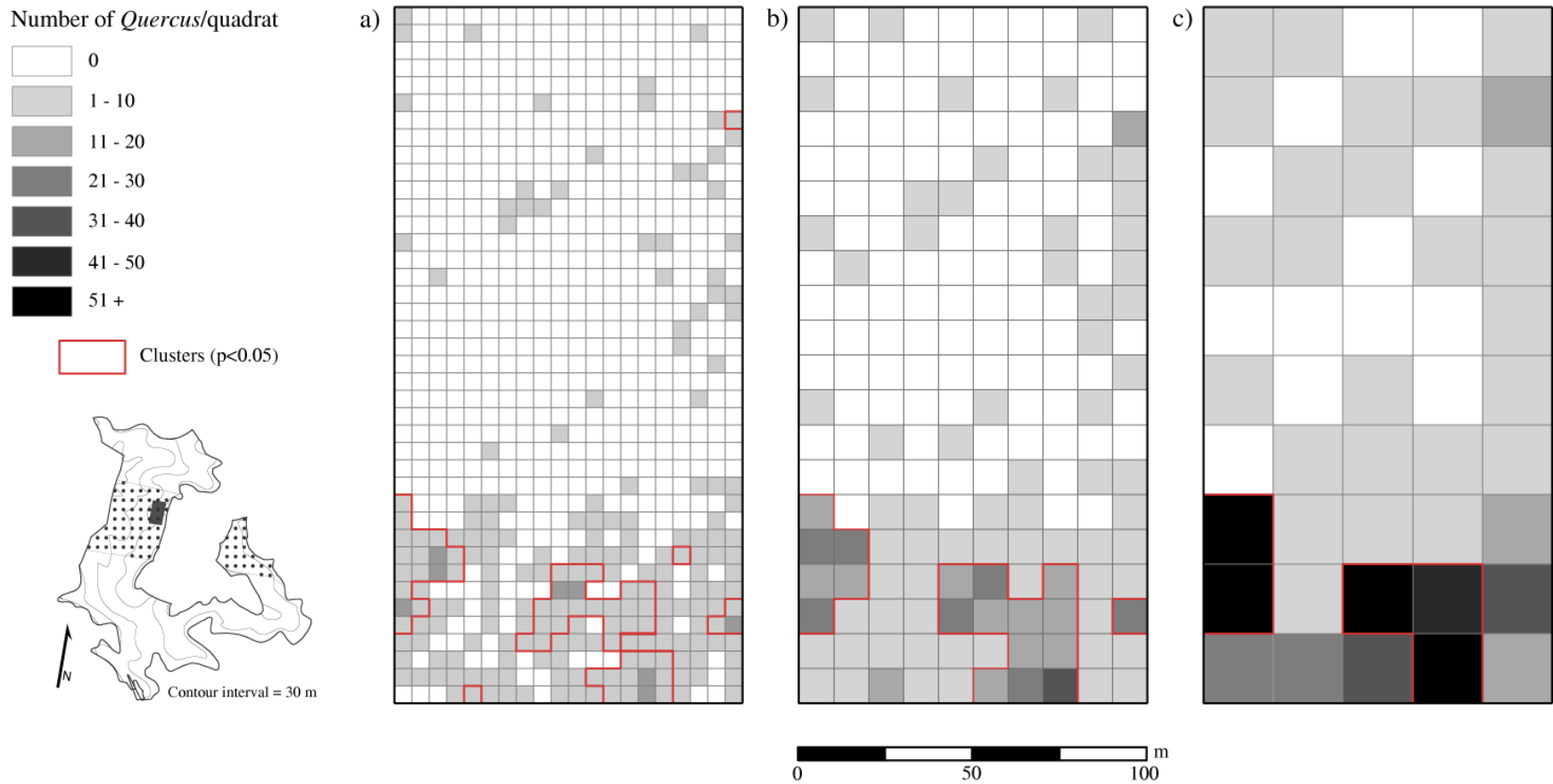


Figure 5. Distribution of small-sized *Quercus* stems across the 2 ha plot four years after the disturbance in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama. The red outlines represent the significant clustering ($p < 0.05$) of small-sized *Quercus* stems. Insert map shows the *Quercus* stand boundary, tornado swath (dotted pattern), plot location, and topography. a) 5 x 5 m; b) 10 x 10 m; c) 20 x 20 m

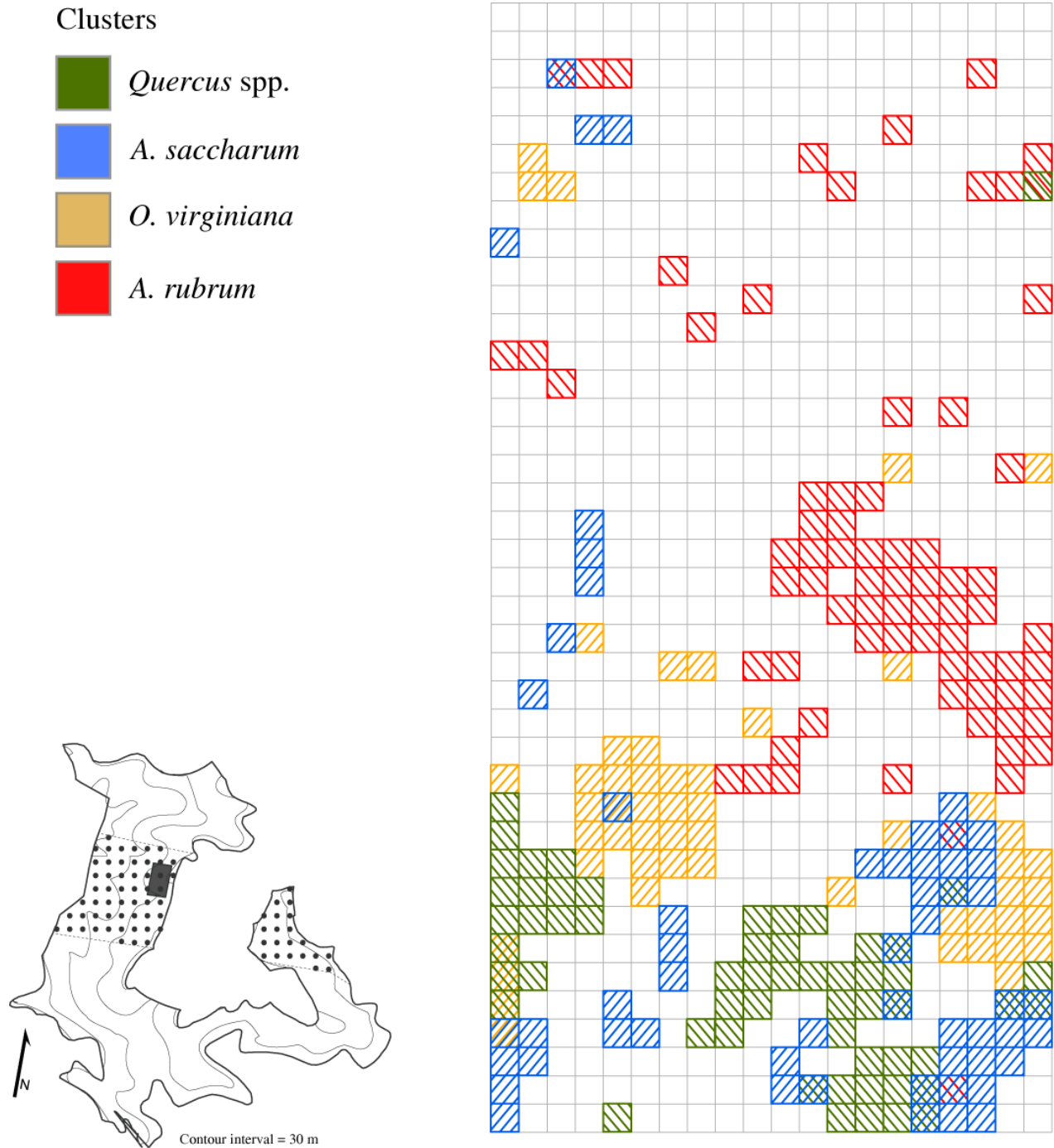


Figure 6. Distributions of *Quercus* spp., *A. saccharum*, *O. virginiana*, and *A. rubrum* clusters across the 2 ha plot (5 x 5 m resolution) four years after the disturbance in a *Quercus* dominated stand within the Sipsey Wilderness, Alabama.

across the plot became significantly positive ($p < 0.01$; $r = 0.24$) at this spatial scale.

At the 20 x 20 m resolution, clustered distributions were still significant ($p < 0.05$; $z < 1.96$). One *Quercus* spp. cluster (100 m²; 23 stems) was lost at this broad scale, causing the sample size ($n = 321$ stems) of small-sized *Quercus* stems to lessen at the 20 x 20 m scale. Multiple *A. saccharum* and *A. rubrum* clusters were lost at coarser resolutions. *Acer saccharum* clusters were only detected in neighborhoods of light and moderate disturbance and *A. rubrum* was detected in the control neighborhood and light disturbance class neighborhood. Correlations between the number of small-sized *Quercus* stems compared to *A. saccharum* stems had the strongest positive relationship ($p < 0.01$; $r = 0.35$) at the 20 x 20 m scale.

4.0: DISCUSSION

4.1 Effects of Competition on Small-sized *Quercus* Stems

The underrepresentation of understory *Quercus* stems and the ‘*Quercus*-to-*Acer*’ transition was observed in this *Quercus* stand. At an early stage of stem development, intense competition from either intraspecific or interspecific competition can impede *Quercus*’ ability to recruit into higher levels of vertical forest stratum regardless of stable biotic and abiotic site conditions for understory *Quercus* (e.g. the *Quercus* bottleneck). Out of the five *Quercus* species observed in this study, *Q. alba*, *Q. rubra*, *Q. muhlenbergii* and *Q. prinus* are known to have slow juvenile growth rates relative to associated competition and *Q. falcata* tends to have competitive growth rates (i.e. rates similar to competition; Smith, 1993). In the control neighborhood, only 9% of small-sized *Quercus* stems were taller than their interspecific competitors. Without canopy disturbance, a majority (91%) of *Quercus* stems remained subordinate to their competitors, thus inhibiting the recruitment of those *Quercus* stems to larger size classes. Since the heights of small-sized *Quercus* stems were significantly taller than those in the three disturbance class neighborhoods, I posit the removal of the canopy caused by the wind disturbance created favorable environmental conditions for small-sized *Quercus*. However, the canopy disturbance event also promoted the growth of non-*Quercus* stems in the understory. For *Quercus* to regenerate, the slow initial growth of *Quercus* reproduction must be balanced by sufficient levels of insolation favorable for seedling growth but low enough to hinder the

advancement of competitors (Johnson et al. 2009). Although the disturbance provided some small-sized *Quercus* stems with the opportunity for shoot growth, most stems stayed subordinate to competing stems because the regeneration window of *Quercus* reproduction is narrow in mesic sites (Hodges and Gardiner, 1993). This is not to say that *Quercus* spp. cannot outcompete initially faster growing stems as they age. Early dominance over competitors is not necessarily required for ascension of *Quercus* into higher vertical strata. Numerous studies have demonstrated the ability of *Q. rubra* to surpass their initially overtopping competitors and ascend into the canopy (Oliver and Stephens, 1977; Oliver, 1980; Hibbs, 1983; Arthur et al., 1997). Zenner et al. (2012) observed *Quercus* stems having a height deficiency of 1–1.5 m compared to their neighboring stems in their first decade of life, and still achieved a dominant crown position later in life (i.e. latent dominance). In this study, *Q. rubra* stems were the most abundant in the small-sized stem size class, but only 33% of the *Q. rubra* stems were taller than their neighboring competitor. At this early stage of stem development it is difficult to eliminate the potential for the 67% of shorter *Quercus* stems to surpass the heights of their competitors at a later stage. Although latent dominance (sensu O’Hara, 1986) in *Quercus* spp. is possible, this mechanism cannot compensate for the region-wide decline in the importance of *Quercus* spp. (Fei et al., 2011; Zenner et al., 2012).

Distance between competing stems plays a major role in the survival outcome of species. The closer the neighboring stems are to each other, the more likely for the stems with a competitive advantage to overtop the adjacent stem. Lockhart et al. (2006) provided results on the spacing of *Quercus pagoda* Raf. and interspecific competition, reporting that distances less than 1.8 m between stems could result in overtopping by the interspecific stem. The most distant stems were 1.45 m apart, so based on Lockhart et al. (2006) results I concluded that all small-

sized *Quercus* stems were exposed to some form of competition (i.e. interspecific or intraspecific). In each disturbance class neighborhood, intraspecific competing stems were found closer together than interspecific competing stems. The average distance between competing stems in the moderate disturbance class neighborhood were significantly closer than the average distance between competing stems in the control neighborhood (i.e. pre-disturbance conditions). Small-sized *Quercus* stems that were taller than competitors were nearer to each other than interspecific competitor stems that were taller than the *Quercus* stems.

A stem's competitive influence can be described as the ability to avoid or endure suppression and is accounted for by the proximity of a focal tree to competitors and the relative size of the stems. The formulation of Heygi's (1974) competition index provides the understanding that large stems closer to the focal tree are assumed to exert more competitive influence than smaller stems that are farther away. The species of the competing stem was an important factor in differences in competitive ability. Other small-sized *Quercus* stems (i.e. intraspecific competition) were the most competitive against the focal *Quercus* stems. The competition between intraspecific stems is often the greatest because individuals in one species have similar resource requirements (Tilman, 1982), growth rates, and root/crown habits. The 'other' functional group and *O. virginiana* were the second most competitive and had similar competitive ability. *Ostrya virginiana* lacks the potential to ascend into upper canopy levels, and have formed a "recalcitrant understory layer" (Royo and Carson, 2006; Cowden et al., 2014) and its abundance in the understory (Cowden et al., 2014; White et al., 2015) is likely inhibiting *Quercus* recruitment. *Acer saccharum* stems were the least competitive against small-sized *Quercus* stems. Despite the abundance of *A. saccharum* stems throughout the plot, they were not directly inhibiting small-sized *Quercus* stems relative to the other stems in the understory and

midstory. Instead, the *A. saccharum* stems were utilizing more of the growing space that *Quercus* stems could potentially occupy. I speculate this is because *A. saccharum* advanced regeneration need a canopy release to effectively compete with species like *Quercus*. However, the regeneration window for *Quercus* spp. is narrower in mesic sites compared to that of *Acer* spp., thus allowing for high abundances of *A. saccharum* advanced regeneration to respond more rapidly to the canopy release. Although competitive ability significantly differed ($p > 0.05$) between species, it did not vary between disturbance class neighborhoods. Therefore, conditions in one disturbance class neighborhood did not enable nearest neighboring stems to compete more effectively as compared to any other disturbance class neighborhood. Although there were no significant differences ($p > 0.05$) between disturbance class neighborhoods, the moderate disturbance class neighborhood had the tallest small-sized *Quercus* and 39 % of the stems were on average 0.44 ± 0.51 m (SD) taller than their nearest neighboring stem. Therefore, the severity of canopy disturbance in the moderate disturbance class neighborhood created conditions that provided small-sized *Quercus* stems to have greater competitive ability than the small-sized *Quercus* stems in the light and severe disturbance class neighborhoods.

4.2 Effects of Insolation on Small-sized *Quercus* Stems

The overstory trees that were removed by the wind disturbance event altered insolation levels (1.4 meters above the forest floor) throughout the study site. Moderate-severity wind events rarely disturb the forest understory except for areas impacted by fallen tree crowns, thus the canopy disturbance served as a mechanism to release stems already present in the understory and midstory. After four growing seasons post-disturbance, there were still prominent canopy gaps that contributed to the spatial patterns of increased insolation. The light regimes in the three

disturbed neighborhoods were comparable, but have not returned to pre-disturbance conditions. However, within the disturbed neighborhoods, smaller extents have high densities of advanced regeneration and midstory stems that are overtopping one another at 1.4 m above the forest floor, thus causing light regimes at that height to be similar to pre-disturbance conditions and causing overall light levels in the lower strata within each neighborhood to be low. Changes in environmental conditions after a disturbance are ephemeral, but the rapid increase in growth of *Quercus* in response to increased light levels may have important management implications given the critical necessity for *Quercus* regeneration to advance past the understory (Lhotka and Stringer, 2013).

Although *Quercus* at the genus level are considered moderately tolerant of shade, most are ultimately dependent on canopy disturbance to recruit into higher canopy strata (Carvell and Tryon 1961, Dey and Guyette 2000). The canopy openings (basal area removal) created by the disturbance were positively correlated with percent full sunlight; therefore the increased light levels followed the spatial pattern of the disturbance gradient. The gaps resulted in increasing light levels that were adequate (i.e. 20–50% full sunlight) for *Quercus* advanced regeneration to recruit to larger size classes, but rapid growth of the shoot can only occur if the stem's root system is well developed (Sander, 1972; Dey, 2002). Small-sized *Quercus* stem density was positively correlated with canopy openings and average percent full sunlight, which indicated the post-disturbance conditions were favorable to understory and midstory *Quercus* stems. The density of small-sized *Quercus* stems increased as disturbance severity and average percent full sunlight increased within neighborhoods. The severe disturbance neighborhood (i.e. greatest basal area removal) created the most growing space and increased percent full sunlight post

disturbance allowing for high densities (3.68 stems per 5 x 5 m quadrat) of well-developed individuals to recruit into higher forest strata.

4.3 Spatial Patterns of *Quercus* and Competition

Spatial dependence is often caused by underlying spatial processes that result in strong localized association among variables, and subsequently, cause clustering of similar values amongst these variables (Zhang et al., 2009). The moderate-severity storm disturbed 22% of the 2 ha plot and created a fine-grained mosaic pattern of varying damage in a matrix of an undisturbed stand. Openings in the canopy offered contrasting levels of light, temperature, and available soil moisture ultimately increased the abundance and diversity of stems in the understory (Dodson et al., 2008). Tree species in the understory differ in their ability to capture the newly available growing space created by the canopy gaps. *Quercus* spp. have a conservative regeneration technique that is usually disadvantageous when competing with species who have a more exploitive regeneration technique (Johnson et al. 2009). Thus, the small-sized *Quercus* stems that recruited to taller size classes likely did so in locations where the potential for competitive ability was greater. The clustered spatial patterns of these species are specific to this ecosystem and are empirically linked to desired ecological function (Puettmann et al., 2009). The ability to target clusters within my site, allowed for the examination of classical questions pertaining to plant communities (e.g. how can *Quercus* composition change post-disturbance?; Plotkin et al., 2002). Inferences can be drawn based on these observations about what processes are operating from observable patterns (Watt, 1947). The advanced regeneration found in the increased growing space released by the wind event may eventually dominate the site (Oliver and Larson, 1996).

I observed the presence of 39 understory species all of which were potentially competing with *Quercus* spp. for the increased resources available after the removal of overstory trees post-disturbance. Species examined for spatial patterns occurred in all disturbance class neighborhoods (except for the absence of *A. rubrum* in the severe disturbance class) and had neighborhoods of significant clustering which was expected because the exogenous disturbance was highly variable and resulted in increased intra-stand heterogeneity.

Relative stem density and average heights of *Quercus* stems increased with increasing canopy disturbance severity (i.e. from the control neighborhood to the severe disturbance neighborhood), indicating the variation of available resources (e.g. differing amounts of increased insolation in each disturbance class neighborhood) post-disturbance had a positive influence on *Quercus* recruitment, but a positive influence on other stems as well. The density of primary competitor did not increase linearly with increasing canopy disturbance severity, but *A. saccharum* had the highest density in the moderate disturbance class neighborhood and *O. virginiana* had the highest density in the severe disturbance neighborhood. *Acer saccharum*, *F. grandifolia* and species that typically lack the potential to ascend into upper levels of the canopy such as *O. virginiana* effectively formed a “recalcitrant understory layer” that altered succession after canopy disturbance (Royo and Carson, 2006; Cowden et al., 2014). High densities of *O. virginiana* have been reported in other studies conducted in the Sipsey Wilderness (Cowden et al., 2014; White et al., 2015) and although the species lacks the ability to be a true canopy dominant, its abundance in the regeneration layer was likely inhibiting *Quercus* recruitment. Interestingly, *A. rubrum* was not a primary competitor although it is abundant on the Bankhead National Forest (Zhang et al., 1999).

The largest patches of small-sized *Quercus* stems in the moderate and severe disturbance neighborhoods indicated environmental conditions were favorable for *Quercus* spp. post-disturbance. Broadening the scale (i.e. 5 x 5 m to 10 x 10 m or 10 x 10 m to 20 x 20 m) caused spatial variability to be lost amongst small-sized *Quercus* stems. As spatial scale broadened, clusters covered a larger area but small-sized *Quercus* stem densities stayed similar to those found at finer resolutions (e.g. fine-scale analysis revealed a 425 m² cluster with 108 stems and broad-scale analysis revealed an 800 m² cluster with 116 stems). At the 20 x 20 m scale, areas that did not contain small-sized *Quercus* stems were incorporated into the clusters. Therefore, the 5 x 5 scale was the best to identify *Quercus* clusters because analysis of individual stems of advanced regeneration in gaps is a fine-scale process. At a fine-scale (i.e. 5 x 5 m²) resolution, I was able to encompass the cumulative structural imprint that showed both the effects of the regeneration layer post-disturbance as well as a projection of future structure and composition (Zenner et al. 2015).

Clusters of competitor species were much larger than those of small-sized *Quercus* stems, which indicated the competitors were able to effectively compete over larger areas than *Quercus* spp. The highest densities of competitor species occurred in the moderate and severe disturbance class neighborhoods, but were found throughout the entire study site. For *A. saccharum* and *O. virginiana*, environmental gradients were probably the primary influence of the distribution of the species, despite their constitutive presence through the whole plot. Although these competitors have lower compensation points relative to *Quercus* spp., they benefited from varying amounts of opened overstory and allocated the newly available resources to enhance their competitive ability. Spatial patterns of *A. rubrum* were of interest based on its connection to the '*Quercus*-to-*Acer*' transition that has occurred across forests of the eastern United States.

Acer rubrum is a generalist species, therefore it has minimal affinity for specific site conditions, but there was an adequate seed source throughout the large cluster of *A. rubrum* advanced regeneration.

I predicted that the scale and magnitude of the wind event would create spatial variability across the plot and therefore result in patchiness and heterogeneity (e.g. species and resources) at the intra-stand level. The number of *Quercus* stems per quadrat was positively correlated with basal area removal. Thus, I speculate that a majority of small-sized *Quercus*' stems responded by the release of canopy trees, subsequently causing the advanced regeneration to follow the same pattern as the mosaic of disturbance. Analysis of spatial variability based on distribution of clusters was lost at coarser scales. Smaller clusters found in the control and light disturbance neighborhoods became negligible. Therefore, using the incorrect spatial resolution can make it difficult to isolate the actual dynamics and spatial patterns within a system, thus revealing artifacts of scale (Wiens, 1989). At certain spatial resolutions, individuals and patches of *Quercus* regeneration might be undetectable, which could lead to improper management for promotion of *Quercus* spp.

5.0: MANAGEMENT IMPLICATIONS

My study provided information on both the impacts of a wind disturbance as well as the exploration of the regeneration process that occurred post-disturbance. The results revealed that varying damage severities produced by the wind disturbance increased overall intra-stand heterogeneity but more notably promoted clusters of small-sized *Quercus* stems. The wind event magnified existing patchiness of distinct neighborhoods of *Quercus* advanced reproduction stems that varied by basal area removal, percent of full sunlight, and distribution of primary competitors. The moderate disturbance class neighborhood (30–60% BA removal) promoted the largest patches of *Quercus* regeneration and these *Quercus* stems competed best in this neighborhood. Overstory removal of this quantity is ideal for promotion of *Quercus* stems, but stems must be accumulated and well established in the understory before overstory removal can occur (Johnson et al., 2009). The regeneration potential of *Quercus* spp. is determinant on the number, size, and spatial distribution of the stems throughout a stand (Sander et al, 1984). Patches of small-sized *Quercus* stems serve as *Quercus* strongholds that have the potential to maintain the highest densities of *Quercus* stems as they progress to larger size classes. Although they are their own greatest competitor, *Quercus* reproduction has short life cycles of birth, growth, and death, and their sustainability lies in the ability for propagules to perpetuate. Silvicultural methods that assess spatial variability may need to focus on patches rather than a uniform treatment, because this results in a more intuitive and concrete way to promote the recruitment of small-sized *Quercus* stems and overall intra-stand heterogeneity. In addition to

targeting patches, competing stems in the understory must be removed prior to overstory removal. Every competing stem within a stand cannot be removed, but removal of shade-tolerant species at certain height and distance thresholds will be most effective because of their high competitive ability.

Innovative management prescriptions are needed to maintain *Quercus* in many stands throughout the eastern United States. Without active management and under the current disturbance regime, *Quercus* dominance will be restricted to less productive sites while more productive sites transition to dominance by late-successional taxa such as *Acer* and *Fagus grandifolia* (Nowacki and Abrams, 2008; Fei et al., 2011; McEwan et al., 2011). Sustaining the *Quercus* resource requires the regeneration and recruitment of *Quercus* into the overstory as mature trees. These two fundamental processes are often disassociated in *Quercus* management preventing the desired outcomes for *Quercus* sustainability (Dey, 2014). The high densities of shade-tolerant stems in the understory are causing a bottleneck in *Quercus* recruitment during the understory reinitiation stage of development.

Size and density of *Quercus* stems, size and density of competing stems, percent full sunlight, and basal area removal differed at each spatial scale. Scale should be considered when performing initial inventory of a stand and should match the spatial scale of the feature of interest. Fine-scale analyses will reveal greater detail about the underlying patterns that drive different biological mechanisms, whereas broad scale analyses are more likely to render generalizations (Wiens, 1989). Since clusters of *Quercus* stems are variable in size and are often intermittent within a stand, the use of coarse spatial scales can make it difficult to isolate these patches. O'Hara and Nagel (2013) stated the stand should remain the fundamental unit in silviculture, however prescriptions may and perhaps should be focused on neighborhoods (i.e. at

the intra-stand scale) and the new designated ‘stands’ need not be treated evenly. Re-conceptualizing the traditional stand requires a shift in the use of mensuration tools, traditional operational methods, and contractual processes, all of which can be time consuming and complex (Knapp et al., 2012; North and Sherlock, 2012; Churchill et al., 2013).

6.0: REFERENCES

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