INFLUENCE OF INTERMEDIATE-SCALE WIND DISTURBANCE ON DEVELOPMENT AND SUCCESSION IN *QUERCUS* STANDS ON THE CUMBERLAND PLATEAU

by

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ABSTRACT

Natural disturbances play important roles in shaping the structure and composition of all forest ecosystems and can be used to guide silvicultural practices. Disturbance intensity is measured along a gradient ranging from highly localized, gap-scale events to stand-replacing events. High wind storms such as downbursts, derechos, and low intensity tornadoes typically fall in the center of this gradient and result in intermediate-scale disturbances, removing 30-60% of basal area. Despite their frequency and widespread occurrence, little is known about how intermediate-scale disturbances drive stand development. On 20 April 2011, the Sipsey Wilderness Area in Alabama was affected by an EF1 tornado with accompanying straight-line winds. Stands were sampled in a stratified subjective sampling design to evaluate the effects of intermediate-scale wind disturbance on the development of *Quercus* stands in regard to structure and recruitment. My specific objectives were to: 1) quantify damage severity in basal area reduction and percent canopy loss of this particular disturbance along a gradient of wind disturbance, 2) detect structural acceleration or retrogression of stand development caused by an intermediate-scale wind disturbance, and 3) elucidate compositional acceleration or retrogression for an intermediate-scale wind disturbance. I established 109 0.04 ha plots across a gradient of disturbance, classified as control (undamaged), light, and moderate to inventory the effect of wind damage on development and succession. Basal area was reduced from 25.5 $m^2 ha^{-1}$ to 24.0 $m^2 ha^{-1}$ and 15.5 $m^2 ha^{-1}$ ($p < 0.001$) for light and moderate damage, respectively. The percent of live and damaged trees for control, light, and moderate was 0.3%, 3.0%, and 10.7%, respectively. PAR was significantly increased within the moderately damaged areas ($p < 0.001$). Logistical regression showed an increasing probability of mortality during wind

disturbance with increasing diameter. Based on my findings, this intermediate-scale disturbance increased intra-stand heterogeneity and accelerated succession, favoring shade-tolerant taxa established in the understory.

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1. INTRODUCTION

Disturbances are strong influences in shaping the structure, composition, and function of all forest ecosystems and are often classified according to their spatial extent and magnitude ranging from fine (i.e. canopy gaps) to coarse spatial scales (i.e. catastrophic, stand-replacing) (White and Pickett 1985, Oliver and Larson 1996, White and Jentsch 2001). As stands age following a regeneration event, they mature structurally and develop complex conditions via gap-scale dynamics if not subsequently affected by stand-initiating exogenous disturbance (White and Pickett 1985, Oliver and Larson 1996). In recent years, researchers have called for forest management operations to emulate the effects of natural disturbances which may include managing for complex structural conditions (Seymour and Hunter 1999, O'Hara and Nagel 2013). Legacies of gap-scale disturbances are often short lived as gaps are commonly captured by neighboring canopy individuals rather than through subcanopy accession of understory stems, particularly in younger stands (Clebsch and Busing 1989, Hart and Grissino-Mayer 2009, Runkle 1985, Yamamoto and Nishimura 1999, White and Jentsch 2001). During stem exclusion, canopy trees are tightly spaced and have limited crown spreads resulting in small canopy voids when mortality occurs. Adjacent trees typically capture these small canopy gaps by expanding their crowns laterally (Hart and Grissino-Mayer 2009, Richards and Hart 2011). Canopy gap size typically increases as stands age as spacing between canopy trees and average canopy tree crown area increases (Yamamoto and Nishimura 1999). Larger gaps provide an opportunity for understory individuals to be recruited into canopy positions, as neighboring trees are incapable of capturing the entire gap through lateral crown expansion (Yamamoto 2000, Richards and Hart 2011). Runkle (1985) proposed that the species expected

to colonize gaps via subcanopy accession is a function of gap size, i.e. the larger the gap, the less shade-tolerant the individual must be to capture it.

Stand-replacing disturbances (large, infrequent disturbances) have longer return intervals, but longer-lasting and contrasting biological legacies when compared to gap-scale disturbances (Turner et al. 1998). Stand-replacing disturbances revert conditions to the stand-initiation phase of development and result in even-aged structures (Oliver and Larson 1996). Examples of large, infrequent disturbances include crown fires, hurricanes, strong tornadoes (EF4 and EF5 events) as well as anthropogenic activities such as forest clearing. In the southern Appalachian Highlands of the eastern US, stands affected by a stand-replacing disturbance are even-aged and often have a stronger component of shade-intolerant taxa such as *Pinus* spp. or *Liriodendron tulipifera* relative to pre-disturbance composition (Clebsch and Busing 1989).

A disturbance gradient exists between gap-scale and stand-initiating events, broadly classified as being of an intermediate scale. A disturbance may be classified as intermediate-scale (sometimes termed moderate severity) by either its spatial distribution or return interval (Pickett and White 1985). Within the context of forest science and management, a spatially classified intermediate-scale disturbance has been defined as causing 30–60% removal of the canopy within a stand (Hanson and Lorimer 2007; Fraver et al. 2009). However, a disturbance could be classified as intermediate-scale if it does not meet the criteria for gap-scale or stand-initiating allowing a broad spectrum to be called intermediate-scale. Intermediate-scale disturbances may accelerate stand development or regress structural maturity to a previous state, without reverting to the stand initiation phase (Oliver and Larson 1996). Acceleration would move a stand forward in development towards complex structural conditions (e.g.

conditions typical of older stands), while retrogression would move a stand backwards toward the stand-initiation stage (e.g. structures typical of young stands) (Hanson and Lorimer 2007). This trajectory may depend upon the timing, type, and intensity of disturbance and may be unique to specific stages of stand development. Recent research has shown intermediate-scale disturbances may play a more influential role on stand dynamics over time than large, infrequent disturbances (Frelich and Lorimer 1991, Stueve et al. 2011). Strong wind events associated with tornadoes, derechos, downbursts, and tropical storms are common forms of natural, intermediate-scale disturbances in many forested ecosystems (White and Pickett 1985). Wind damage can span from the removal of large branches from isolated canopy trees in a single stand to near complete overstory destruction across multiple stands. The damage resulting from windstorms is, however, highly variable and difficult to predict in a meaningful manner (Peterson and Pickett 1991, Everham and Brokaw 1996, Peterson 2000). Spatially erratic patterns of storm damage can be partly attributed to the nature of high intensity storms, changes in terrain, and specific stand vulnerability conditions such as structural maturity or species composition (Foster 1988, Evans et al. 2007).

In the eastern US, tornadoes and thunderstorm downbursts frequently disturb forest stands (Canham and Loucks 1984, Oliver and Larson 1996, Peterson 2000). The National Climate Data Center (2013) stated that from 1991–2010, the continental US received 1,215 tornadoes annually that were in the EF2, EF1, or EF0 categories, cumulatively accounting for 95% of all tornadoes. At the stand scale, tornadoes of these categories are not sufficiently powerful to revert conditions to the stand-initiation stage, but typically do remove more canopy trees than disturbance events classified as gap scale. Concannon et al. (2000) reported

that northwest Alabama experiences 30 days per century with at least one EF2 or greater for every 6,400 km^2. Additional forms of wind disturbance such as tropical storms, straightline winds, microbursts, and derechos may affect stands at various intervals and create low return intervals for an intermediate-scale wind disturbance at the stand scale.

It is largely unknown how intermediate-scale disturbances may alter the successional trajectory or structural development of a stand. As a moderately shade-tolerant genus, *Quercus* requires more light to reach individuals in the understory (20–50% of full sunlight) than is typical in second-growth *Quercus* stands throughout the eastern US (0–5% of full sunlight) (Lorimer 1989). An intermediate-scale canopy disturbance would theoretically allow taxa with moderate light requirements to increase in dominance (Runkle 1985). Thus, a moderate removal of the canopy might result in favorable conditions for the recruitment of moderately shade-tolerant genera such as *Quercus* and *Carya*.

A better understanding is needed of the structural and compositional alterations intermediate-scale disturbances create in upland *Quercus* systems. I evaluated the effects of intermediate-scale wind disturbance on the development of *Quercus* stands in regard to structure and recruitment. My specific objectives were to: 1) quantify damage severity in basal area reduction and percent canopy loss of this particular disturbance along a gradient of wind damage, 2) detect structural acceleration or retrogression of stand development, and 3) elucidate compositional acceleration or retrogression for an intermediate-scale wind disturbance. Based on my results, I provided silvicultural guidelines for management that were based upon natural disturbance processes. Although this study examined wind disturbance only, it served as a proxy for other top-down, incomplete stand-scale disturbances, such as ice

storms and the prior role of *Ectopistes migratorius* L. by using basal area reduction and percent canopy loss to quantify damage intensity for the purpose of better managing resilient *Quercus* stands.

2. METHODS

2.1 Study Area

This study was conducted on the Sipsey Wilderness within the William B. Bankhead National Forest in Alabama (34°20'N, 87°25'W; Figure 1). The Sipsey Wilderness is a 10,085 ha reserve within the National Wilderness Preservation System created in 1975 by the Eastern Wilderness Act of 1969. The Sipsey Wilderness occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). Topography is characterized by high relief with narrow ridges, steep slopes, and deep valleys (Smalley 1979). The geology of the region is Pennsylvanian quartzose sandstone interspersed with layers of shale, siltstone, and coal (Szabo 1988). Regionally, soils are strongly acidic, excessively drained, and somewhat shallow, ranging from 38 to 97 cm to bedrock (USDA SCS 1959). The climate is classified as humid mesothermal (Thronthwaite 1948) and is characterized by short, mild winters and long, hot summers. Mean annual precipitation is 149 cm with no distinct dry season (PRISM Climate Group, 2013). Mean temperatures for January and July are 5 °C and 26 °C, respectively. The average growing season is 220 days beginning in mid-March and ending in early-November.

Plant communities on the Cumberland Plateau are influenced largely by topography and factors associated with soil-water availability (Hinkle 1989, Clatterbuck et al. 2006). Cumberland Plateau forests are recognized for having high plant species richness and landscape-level diversity (Hinkle et al. 1993). Braun (1950) classified this region as a transition zone between the Mixed Mesophytic Forest to the north and the Quercus-Pinus Forest to the south. However, true mixed mesophytic communities occur only in shaded coves and riparian areas. Stands may contain taxa that typically dominate at both higher and lower latitudes, and

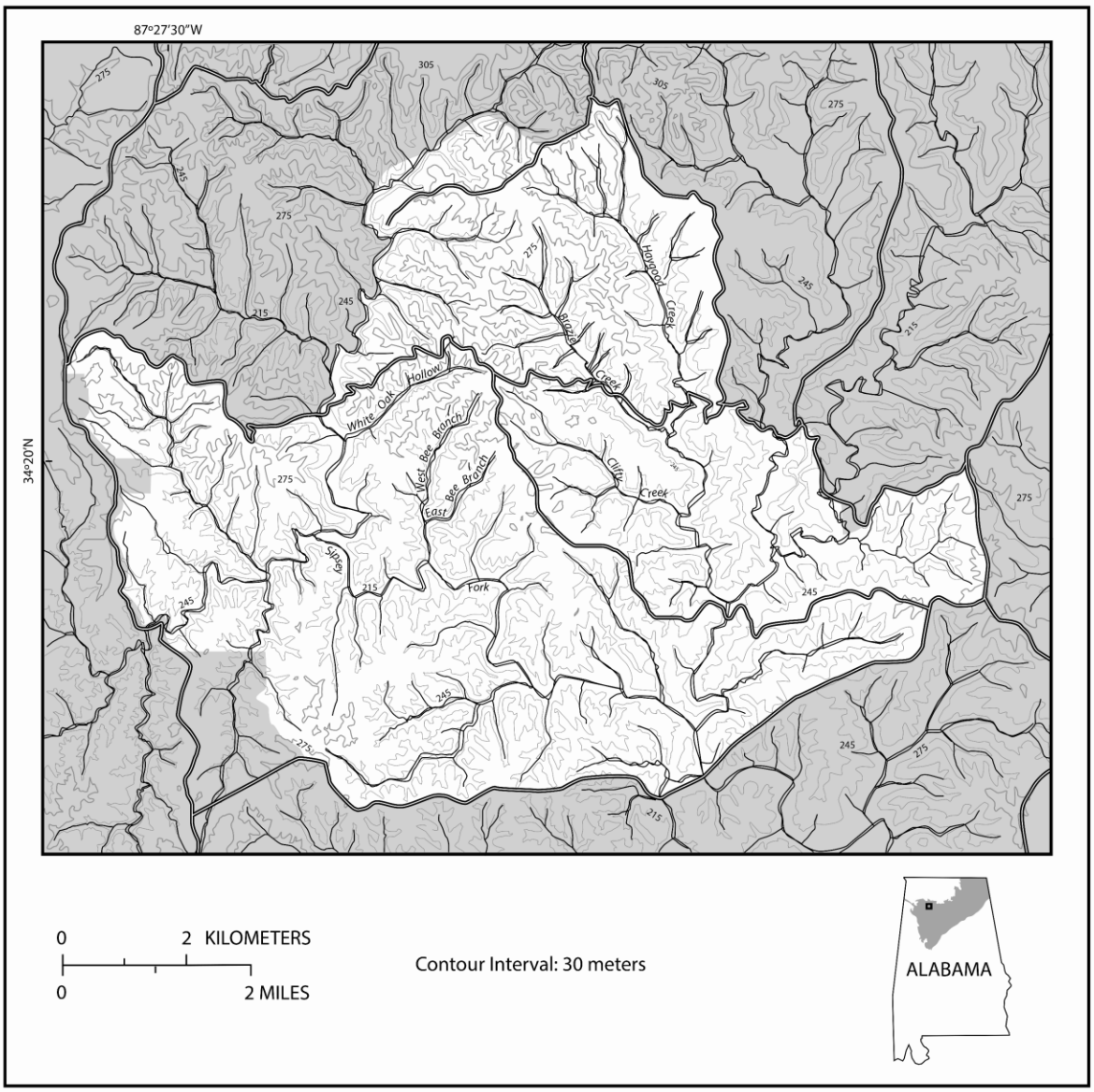


Figure 1. Map of the Sipsey Wilderness, Alabama. Shaded inset on map of Alabama is the Cumberland Plateau physiographic province.

environmental gradients are steep (Hardin and Lewis 1980, Richards and Hart 2011, Parker and Hart 2014). Zhang et al. (1999) developed a classification scheme that included 14 different ecological communities on the Sipsey Wilderness Area portion within BNF. These community types ranged from xeric sites dominated by *Pinus virginiana* Mill. to mesic sites dominated by *Fagus grandifolia* Ehrh. and *Acer saccharum* Marsh. to barren communities. *Quercus* was the most dominant genus in the Sipsey Wilderness Area and was a component of almost all community types (Hardin and Lewis 1980, Zhang et al. 1999).

On 20 April 2011, an EF1 tornado embedded in a bow echo system affected Bankhead National Forest, damaging a number of stands in the Sipsey Wilderness. The tornado produced a recorded maximum 3 second wind gust of 153 kph and was accompanied by other straight-line winds with bursts between 130–145 kph (NWS 2011). The most severe damage was concentrated in the path of the tornado and decreased in intensity with distance from the center of the storm. Within the Sipsey Wilderness, damage was sporadic and created a patchwork mosaic of blowdown areas.

2.2 Field Methods

Field sampling was conducted June–July 2013 during the third growing season following the disturbance. Sampling followed a stratified subjective scheme to adequately capture damaged areas within the Sipsey Wilderness. To select study stands I created a map in ArcMap v. 10.0 from geo-referenced data provided by the USDA Forest Service that included quantitative information on stands (species composition and establishment year), compartments, the tornado damage path, roads, and established trails. Geo-referenced aerial

photographs and USGS quadrangles were imported as basemaps and used to identify terrain features such as slope and aspect. Using this information and field reconnaissance, I subjectively selected stands that met the following criteria: 1) were *Quercus alba* dominated, 2) between 100–120 years of age, 3) fully contained within the Sipsey Wilderness, 4) directly affected by the 2011 tornado, 5) on generally west-facing slopes (which lent them to sustain the proper range of wind damage from this storm), and 6) without noticeable indications of a previous exogenous, anthropogenic or natural disturbance during stand development. Once study stands were identified, plot centerpoints were selected to ensure adequate spatial coverage and an even sampling distribution within stand boundaries using ArcMap. The waypoints were then entered into a handheld GPS receiver. In the field, I navigated to the pre-determined waypoints and assessed each plot for appropriate microsite characteristics. If plots captured a trail or stream, plot center was moved 15 m in the direction away from the intrusion. Each plot was labeled as belonging to one of three damage intensities based on visual assessment of the immediate area: undamaged (control; n = 20), light damage (n = 52), and moderate damage (n = 37). Moderately damaged plots were defined as 3 or more canopy trees downed within or running through the plot. Lightly damaged plots had one or two canopy trees in or running through the plot. Control plots had completely intact canopy and no damage within or adjacent to the plot. Control plots were assumed to be representative of pre-disturbance conditions. I used a space–for–time substitution because I did not have pre-storm data or other baseline conditions.

A fixed-radius 0.04 ha overstory plot was placed at each pre-determined point where all trees ≥ 5 cm diameter at breast height (dbh, 1.37 m high) were measured, recorded to species

(except for *Carya*), and labeled as belonging to one of four crown classes: dominant, codominant, intermediate, or overtopped. Crown class was based on the amount of intercepted light and height in relation to the adjacent canopy (Oliver and Larson 1996). The intermediate crown class was further subdivided for additional stand structural data: intermediate 1 (I1: < 50% the height of residual canopy trees), intermediate 2 (I2: 50–75% the height of residual canopy trees), or intermediate 3 (I3: ≥ 75% of residual canopy trees). A single 10 m^2 regeneration plot was nested within each overstory plot at plot center where all stems < 5 cm dbh were tallied, identified to the lowest taxonomic level, and classified as seedling (< 1 m tall) or sapling (≥ 1 m tall and > 5 cm dbh). Within the overstory plot, all dead stems (large woody debris) were measured for diameter at 1.37 m above the root collar (estimated standing dbh), identified to the lowest possible taxonomic level, and classified as one of the following: an uprooted stem (root network uplifted), a snapped stem (bole broken below the crown), or a snag (standing dead tree with crown largely intact) (Clinton et al. 1993, Yamamoto 2000, Richards and Hart 2011). Dead stems were placed in one of four decay classes: class 1 (sound wood, bark intact, small to medium sized branches present); class 2 (sound to partially rotten wood, branch stubs firmly attached with only larger stubs present, some bark slippage); class 3 (substantially rotten wood, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet); or class 4 (mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log is oval or flattened in shape) (adapted from Fraver et al. 2002). The lowest threshold considered large woody debris was when the log was broken down to duff level.

Interception of photosynthetically active radiation (PAR) was quantified on each plot

using two Decagon AccuPAR LP-80 ceptometers at breast height (µmol photon m^{-2} s^{-1}). One ceptometer was used to take 80 individual readings divided among the four cardinal directions within the overstory plot. These 80 readings were averaged to provide a single value for each plot. The other ceptometer was placed in open sky (i.e. without any canopy obstruction). The simultaneous ceptometer readings were used to calculate percent of total insolation for each overstory plot (percentage of full sunlight).

2.3 Laboratory Methods

Stems ≥ 5 cm dbh were analyzed for standard descriptors of density (stems ha^{-1}), relative density (contribution to total stems), dominance (m^2 ha^{-1}), relative dominance (contribution to total basal area), and relative importance (relative density + relative dominance). Seedlings and saplings were analyzed for density, relative density, frequency (number of plots on which the species occurred), and relative frequency (percent of plots the species occurred). Trees were categorized and tallied into 5 cm dbh classes (Nyland 2002) to evaluate the structural distribution of stems across damage classes. To display additional regeneration and recruitment patterns, species were clustered into one of four taxonomic groups based on functionality: *Acer–Fagus*, *Quercus* spp., *Liriodendron tulipifera*, and Others. Stands were evaluated for structural acceleration and regression. I defined structural acceleration as advancing the structural distribution of a stand to more closely resemble complex, "old-growth" conditions as defined by Oliver and Larson (1996). Structural regression was defined as moving the structural distribution of a stand back to a prior stage of development.

I defined living damaged trees (live trees with visible storm damage) as having at least 25% canopy removed or boles bent more than 30° vertically while maintaining vigorous foliage without sign of excessive stress to the remaining crown. Percent basal area loss was determined by taking the difference in disturbance basal area of decay class 1 large woody debris and control decay class 1 large woody debris (i.e. removing the background, gap–scale mortality) and dividing it by the same value with the addition of the live basal area of the class.

Statistical comparisons were performed in SAS v. 9.3. One way analysis of variance (ANOVA) was used to detect differences in means across damage classes for all analyses. A Scheffe post-hoc test was used to distinguish means when significance ($P < 0.05$) was found. The Scheffe post-hoc test is the most conservative to avoid a type 1 error, particularly when sample sizes are unequal. Data were tested for normality using a Kolmogorov–Smirnov test and through histograms. When distributions did not conform to normal distributions and homoscedasticity, data were log-, square root-, or rank-transformed to meet the assumptions for ANOVA. Logistic regression was performed for the fate of stems in both damage classes according to dbh.

3. RESULTS

3.1 Structural Analysis

Basal area for control, light, and moderate damage classes was 25.6, 24.0, and 15.3 m^2 ha^{-1}, respectively (Table 1). Moderate mean plot basal area was significantly lower than the other two classes ($P < 0.001$ for both comparisons), with no difference between control and moderate. Control class had the highest density of stems ≥ 5 cm dbh with 771 stems ha^{-1} followed by light and then moderate with 666 and 531 stems ha^{-1}, respectively.

Overall, size distribution resembled a reverse J shape in control, light and moderate classes with mean q–factors of 1.7, 1.5, and 1.7, respectively (Figure 2). The *Acer–Fagus* and Others groups exhibited the reverse J shape, indicating continuous regeneration and recruitment into larger diameter classes. *Quercus* spp. was the only group to display the uni-modal distribution that typifies a failure to regenerate.

Total basal area of large woody debris for control, light, and moderate was 3.9, 9.6, and 17.1 m^2 ha^{-1}, respectively (Table 2). Overall densities for large woody debris were 88.8, 142.3, and 250.3 stems ha^{-1} for control, light, and moderate classes, respectively. Decay class 1 basal area was 0.33, 6.44, and 14.08 m^2 ha^{-1} for control, light, and moderate classes, respectively. When classes were tested on a plot basis, ANOVA revealed that the mean basal area per plot was unique to each class (Table 3), thus confirming the field-assigned disturbance classes. Quadratic mean diameter for decay class 1 was 13.28, 32.46, and 30.14 m^2 ha^{-1} for control, light, and moderate treatments, respectively. An ANOVA test revealed significant differences in means per plot between all classes (Table 3). Trees from all size classes were removed by the storm in both disturbance categories, but a higher proportion of stems came from larger size

Table 1. Density, relative density, dominance, relative dominance, and relative importance (relative density + relative dominance) measures for all live stems ≥ 5 cm dbh across three disturbance intensities in a *Quercus alba* forest on the Sipsey Wilderness, Alabama.

	Density (stems/ha)			Relative Density (%)			Dominance (m^2/ha)			Relative Dominance (%)			Relative Importance (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer rubrum	9	15	12	1.1	2.3	2.3	0.1	0.1	0.1	0.3	0.4	0.4	1.4	2.7	2.7
Acer saccharum	95	43	46	12.3	6.5	8.7	2.0	1.0	0.8	7.8	4.1	5.0	20.1	10.6	13.6
Carpinus caroliniana	8	6	16	1.0	0.0	3.1	0.0	0.0	0.1	0.2	0.1	0.4	1.1	—	3.5
Carya spp.	65	51	41	8.4	7.7	7.6	3.7	2.5	2.2	14.3	10.7	14.4	22.8	18.4	22.1
Cercis canadensis	23	5	11	2.9	0.7	2.0	0.1	0.0	0.0	0.5	0.1	0.2	3.4	0.8	2.3
Cornus florida	31	34	18	4.1	5.1	3.3	0.1	0.2	0.1	0.6	0.7	0.5	4.6	5.7	3.8
Fagus grandifolia	44	65	38	5.7	9.7	7.1	0.6	1.8	0.8	2.3	7.4	5.1	8.0	17.2	12.2
Frangula caroliniana	11	0	1	1.5	0.1	0.3	0.0	0.0	0.0	0.2	0.0	0.0	1.6	0.1	0.3
Fraxinus americana	13	8	11	1.6	1.2	2.0	0.2	0.5	0.3	0.8	2.0	1.9	2.5	3.1	3.9
Juglans nigra	4	0	—	0.5	0.1	—	0.3	0.1	—	1.0	0.3	—	1.5	0.4	—
Juniperus virginiana	5	6	1	0.6	0.9	0.3	0.1	0.3	0.0	0.5	1.3	0.3	1.1	2.2	0.5
Liriodendron tulipifera	11	14	7	1.5	2.2	1.4	1.2	1.9	0.3	4.8	8.0	2.1	6.2	10.2	3.5
Magnolia acuminata	9	11	9	1.1	1.7	1.8	0.3	0.3	0.2	1.2	1.5	1.5	2.4	3.1	3.3
Magnolia macrophylla	18	61	49	2.3	9.2	9.3	0.1	0.5	0.4	0.4	2.0	2.5	2.6	11.2	11.8
Nyssa sylvatica	34	45	28	4.4	6.7	5.2	0.3	0.5	0.4	1.3	2.0	2.6	5.7	8.8	7.8
Ostrya virginiana	209	124	142	27.1	18.6	26.7	1.2	0.7	0.7	4.6	2.9	4.6	31.6	21.5	31.3
Others**	8	3	3	1.0	1.4	0.6	0.0	0.0	0.0	0.1	0.1	0.2	0.9	0.6	0.6
Oxydendrum arboreum	4	16	5	0.5	2.4	1.0	0.0	0.2	0.1	0.2	1.0	0.8	0.6	3.4	1.8
Pinus echinata	—	1	—	—	0.2	—	—	0.2	—	—	0.7	—	—	0.9	—
Pinus taeda	1	5	5	0.2	0.8	1.0	0.5	0.4	1.7	2.0	1.8	10.8	2.1	2.6	11.8
Pinus virginiana	—	1	—	—	0.2	—	—	0.1	—	—	0.4	—	—	0.6	—
Prunus serotina	4	8	2	0.5	1.2	0.4	0.0	0.1	0.0	0.2	0.3	0.3	0.6	1.5	0.7
Quercus alba	105	95	53	13.6	14.3	9.9	10.6	9.0	5.4	41.4	38.2	35.4	55.0	52.5	45.3
Quercus falcata	3	4	4	0.3	0.6	0.8	0.3	0.4	0.6	1.2	1.5	3.8	1.5	2.1	4.6
Quercus muehlenbergii	20	2	4	2.6	0.4	0.8	1.2	0.1	0.3	4.5	0.5	1.7	7.1	0.9	2.5
Quercus prinus	15	20	5	1.9	3.0	0.9	0.8	1.2	0.4	3.1	5.0	2.8	5.0	8.0	3.7
Quercus rubra	8	6	1	1.0	0.9	0.3	1.4	1.2	0.1	5.4	5.0	0.6	6.4	5.9	0.9
Quercus stellata	1	1	1	0.2	0.2	0.1	0.1	0.1	0.1	0.4	0.3	0.5	0.5	0.5	0.6
Sassafras albidum	—	3	1	—	0.4	0.3	—	0.1	0.0	—	0.2	0.0	—	0.7	0.3
Tilia americana	—	1	2	—	0.1	0.4	—	0.1	0.0	—	0.5	0.2	—	0.6	0.6
Ulmus alata	10	5	10	1.3	0.7	1.9	0.1	0.1	0.1	0.5	0.6	0.4	1.8	1.3	2.4
Ulmus americana	—	2	2	—	0.3	0.4	—	0.1	0.1	—	0.5	0.8	—	0.8	1.2
Ulmus rubra	8	1	1	1.0	0.2	0.3	0.1	0.0	0.0	0.5	0.0	0.1	1.5	0.2	0.4
Total	**771**	**666**	**531**	**100.0**	**100.0**	**100.0**	**25.7**	**23.7**	**15.3**	**100.0**	**100.0**	**100.0**	**200.0**	**200.0**	**200.0**

**Others category consists of species with all importance values less than 0.05% and includes *Rhamnus cathartica, Morus rubra, Ilex opaca, Aesculus pavia, Amelanchier arborea, Asimina triloba , Betula lenta,* and *Acer negundo*.

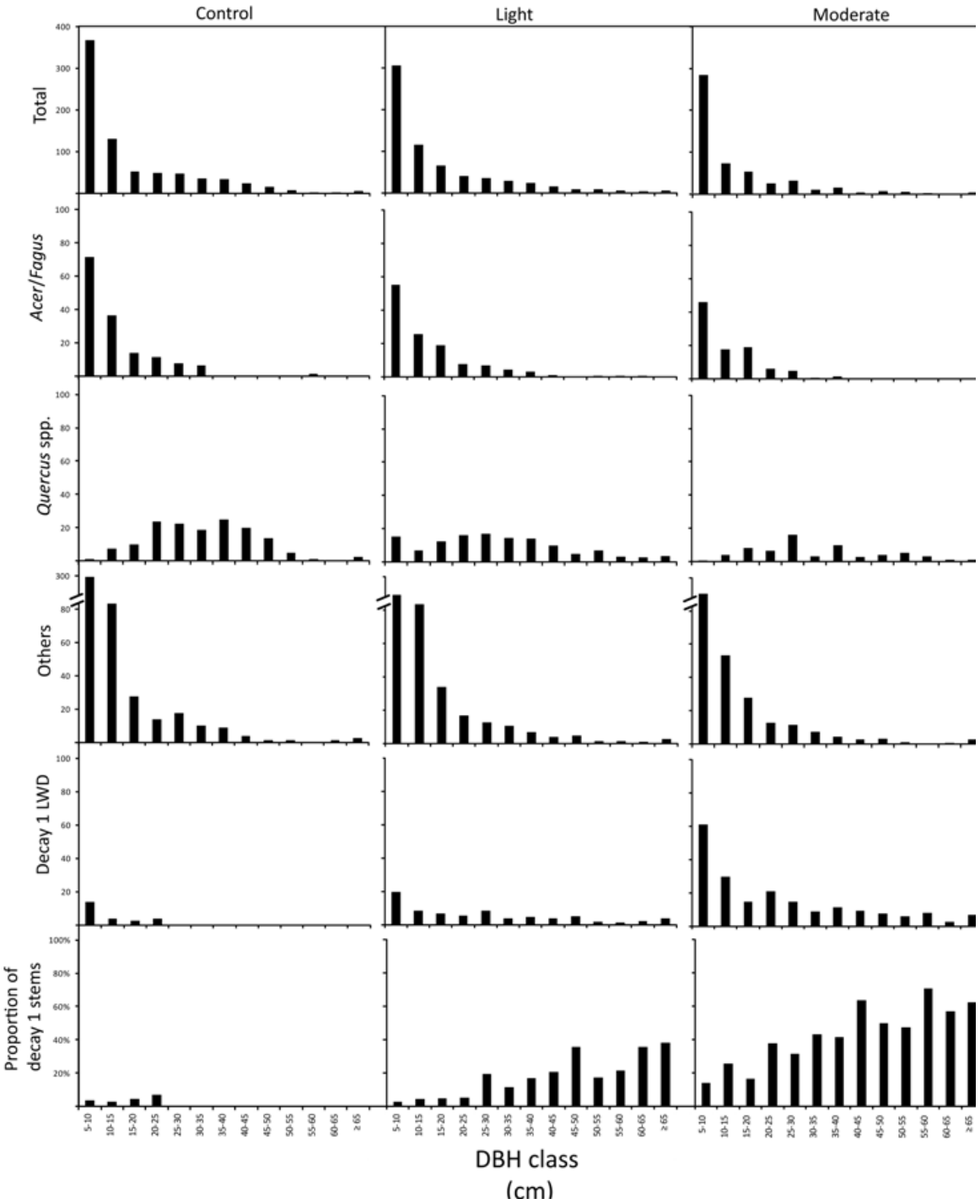


Figure 2. Density of stems ha^{-1} in 5 cm diameter classes across three disturbance intensities in a *Quercus alba* forest on the Sipsey Wilderness, Alabama. Proportion of decay class 1 stems was determined by comparing decay class 1 density to total density in each respective class.

Table 2. Density, relative density, dominance, and relative dominance for all large woody debris (> 5 cm estimated standing dbh) across three disturbance intensities in a *Quercus alba* forest on the Sipsey Wilderness, Alabama.

	Density (stems/ha)			Relative Density (%)			Dominance (m^2/ha)			Relative Dominance (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer rubrum	—	2.4	0.7	—	1.7	0.3	—	0.0	0.0	—	0.1	0.0
Acer saccharum	6.3	2.4	14.9	7.0	1.7	6.0	0.1	0.1	0.4	1.9	0.6	2.5
Amelanchier arborea	—	—	1.4	—	—	0.5	—	—	0.0	—	—	0.0
Betula lenta	—	—	0.7	—	—	0.3	—	—	0.0	—	—	0.0
Carpinus caroliniana	—	—	3.4	—	—	1.3	—	—	0.0	—	—	0.1
Carya spp.	5.0	17.3	36.0	5.6	12.2	14.4	0.3	1.3	2.9	8.1	13.4	16.7
Cercis canadensis	3.8	3.4	3.4	4.2	2.4	1.3	0.0	0.0	0.0	0.4	0.2	0.2
Cornus florida	1.3	7.2	5.4	1.4	5.1	2.2	0.0	0.0	0.0	0.1	0.4	0.2
Fagus grandifolia	1.3	3.8	5.4	1.4	2.7	2.2	0.0	0.8	0.6	0.1	8.3	3.7
Frangula caroliniana	1.3	—	—	1.4	—	—	0.0	—	—	0.1	—	—
Fraxinus americana	2.5	—	4.7	2.8	—	1.9	0.0	—	0.3	0.5	—	1.8
Juglans nigra	—	—	0.7	—	—	0.3	—	—	0.1	—	—	0.4
Juniperus virginiana	12.5	10.6	11.8	14.1	7.4	4.7	0.3	0.2	0.3	8.4	2.1	1.6
Liriodendron tulipifera	5.0	4.8	6.1	5.6	3.4	2.4	0.6	0.4	1.0	14.5	3.6	6.1
Magnolia acuminata	—	0.5	4.1	—	0.3	1.6	—	0.0	0.2	—	0.1	1.1
Magnolia macrophylla	5.0	3.8	16.9	5.6	2.7	6.7	0.1	0.0	0.2	2.5	0.3	1.0
Nyssa sylvatica	1.3	3.8	8.8	1.4	2.7	3.5	0.0	0.0	0.2	0.8	0.5	0.9
Ostrya virginiana	2.5	6.7	37.9	2.8	4.7	15.1	0.0	0.0	0.2	0.4	0.3	1.3
Oxydendrum arboreum	—	4.8	4.1	—	3.4	1.6	—	0.1	0.2	—	0.6	1.5
Pinus taeda	5.0	10.1	6.1	5.6	7.1	2.4	0.2	0.7	1.6	4.4	7.2	9.4
Pinus virginiana	1.3	11.5	0.7	1.4	8.1	0.3	0.0	0.8	0.1	0.5	8.5	0.5
Prunus serotina	1.3	2.9	1.4	1.4	2.0	0.5	0.0	0.0	0.1	0.5	0.5	0.3
Quercus alba	18.8	27.9	44.2	21.1	19.6	17.6	1.1	3.3	5.3	29.2	33.9	31.1
Quercus falcata	2.5	1.0	4.7	2.8	0.7	1.9	0.1	0.1	0.4	3.2	1.2	2.5
Quercus muehlenbergii	2.5	1.0	1.4	2.8	0.7	0.5	0.1	0.0	0.0	2.2	0.5	0.2
Quercus prinus	2.5	6.7	4.7	2.8	4.7	1.9	0.0	0.6	0.9	1.2	5.8	5.1
Quercus rubra	7.5	6.7	14.4	8.5	4.7	5.8	0.8	1.0	1.7	21.0	10.5	9.9
Quercus stellata	—	1.4	0.7	—	1.0	0.3	—	0.1	0.0	—	0.8	0.2
Quercus unidentified	—	1.0	2.0	—	0.7	0.8	—	0.0	0.2	—	0.4	1.0
Sassafras albidum	—	0.5	0.7	—	0.3	0.3	—	0.0	0.0	—	0.0	0.0
Tilia americana	—	—	0.7	—	—	0.3	—	—	0.0	—	—	0.1
Ulmus alata	—	—	2.0	—	—	0.8	—	—	0.1	—	—	0.3
Vaccinium arboreum	—	—	0.7	—	—	0.3	—	—	0.0	—	—	0.0
Total	**88.8**	**142.3**	**250.5**	**100.0**	**100.0**	**100.0**	**3.9**	**9.6**	**17.1**	**100.0**	**100.0**	**100.0**

Table 3. Basal area measures, quadratic mean diameter, and photosynthetically active radiation (PAR) percentages ± SE across three disturbance intensities in a *Quercus alba* forest on the Sipsey Wilderness, Alabama. Values with different letters indicate differences at $P < 0.05$.

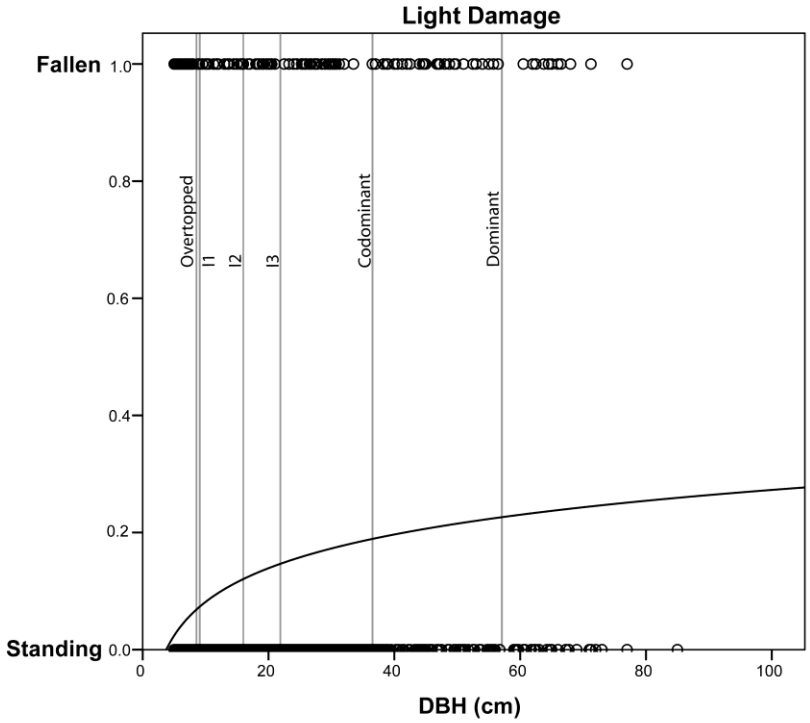
		Damage Treatment		
		Control	**Light**	**Moderate**
Live BA (m^2)	per plot	1.02 ± 0.06 a	0.96 ± 0.04 a	0.61 ± 0.06 b
	per ha	25.6	24.0	15.3
Decay class 1 BA (m^2)	per plot	0.01 ± 0.00 a	0.26 ± 0.02 b	0.56 ± 0.05 c
	per ha	0.33	6.44	14.08
% BA removed in decay class 1		1.49 ± 0.40 a	21.06 ± 1.90 b	48.07 ± 3.16 c
Quadratic mean diameter (cm)	Live trees	20.75 ± 0.76 ab	21.59 ± 0.61 a	18.77 ± 0.67 b
	Decay class 1	8.23 ± 1.67	33.37 ± 1.91	30.06 ± 1.34
PAR (% of full sunlight)		9.00 ± 2.92 a	11.55 ± 2.09 a	22.21 ± 3.59 b

classes (Figure 2). Logistic regression of fate revealed an increasing probability of mortality with diameter for both disturbance classes and results were significant ($P < 0.001$; Figure 3). In the light category, the storm reduced basal area from 30.4 to 24.0 m^2 ha^{-1} (a 21.1% reduction). Basal area was reduced from 29.4 to 15.3 m^2 ha^{-1} in the moderate category, a 48.1% reduction. Basal area loss was significantly different ($P < 0.05$) between all treatments (Table 3).

Most stems killed by the storm were snapped; the light and moderate category had 53% and 55% of decay class 1 stems snapped, respectively (Figure 4). Modes of death in decay class 1 in the control were 74% snag, 16% snapped, and 11% uprooted. The light damage class had 53% snapped, 23% snag, and 23% uprooted stems in decay class 1. The moderate damage class had 55% snapped, 35% uprooted, and 10% snag stems in decay class 1. The number of live trees damaged by the storm increased with disturbance severity. The percent of live and damaged trees for control, light, and moderate was 0.3%, 3.0%, and 10.7%, respectively.

3.2 Compositional Analysis

In all three damage classes, the most important taxa were *Quercus alba*, *Ostrya virginiana*, and *Carya* spp. *Ostrya virginiana* ranked first in relative density in all disturbance classes representing 27.1%, 18.6%, and 26.7% of all stems for control, light and moderate classes, respectively (Table 1). *Quercus alba* and *Carya* spp. were the first and second in relative dominance measures for all three disturbance classes. *Acer saccharum* decreased in importance in both wind damaged classes when compared to the control class. Total *Quercus* importance decreased with increasing storm damage: control, light, and moderate importance of *Quercus* was 75.6%, 69.8%, and 57.6%, respectively. *Fagus grandifolia* increased following



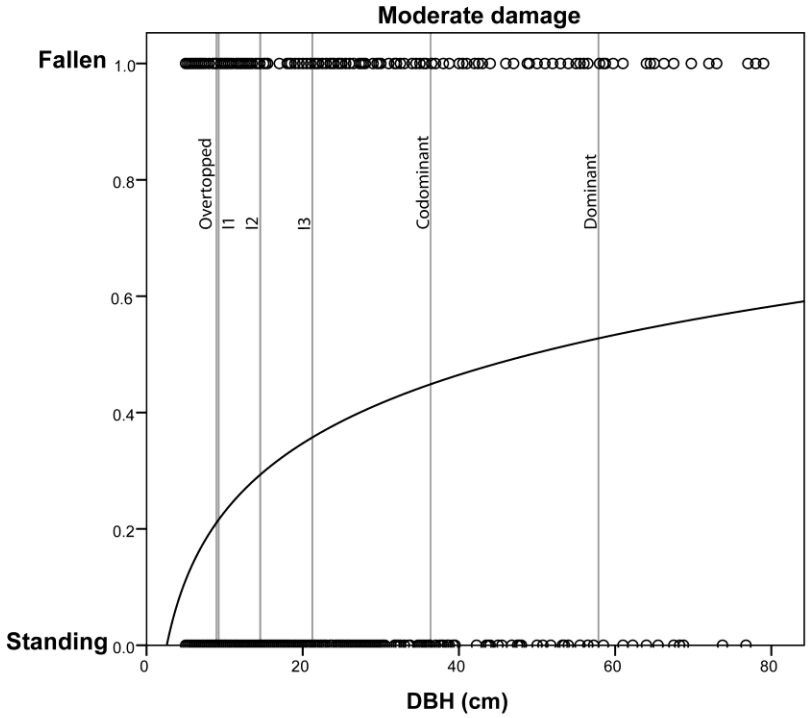


Figure 3. Linear regression of fate for decay class 1 large woody debris in light and moderate treatments of wind damaged areas on the Sipsey Wilderness, Alabama. Gray lines display the mean ($\bar{x}$) diameter of live trees in each canopy class.

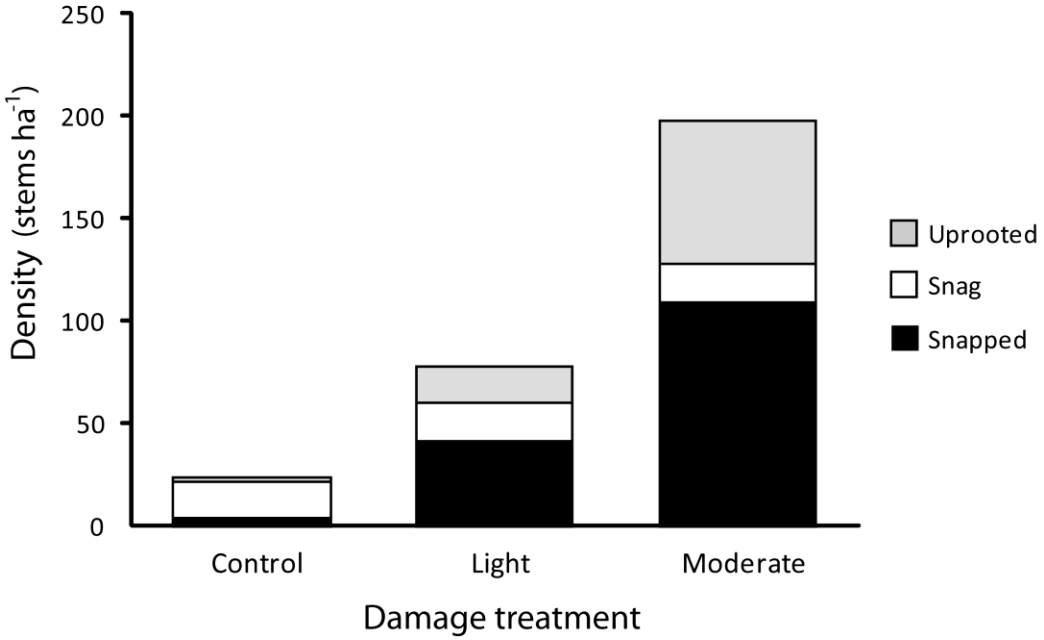


Figure 4. Mode of death and density of decay class 1 large woody debris in three treatments on the Sipsey Wilderness, Alabama.

light disturbance from 8.0% to 17.2%, but decreased slightly with moderate disturbance.

Quercus alba had the highest large woody debris relative density and relative dominance in all three damage classes. In control, the highest relative densities in large woody debris were *Q. alba, Juniperus virginiana,* and *Q. rubra*. The highest debris relative dominances in large woody debris were *Q. alba, Q. rubra,* and *L. tulipifera*. In the light damage class, *Q. alba, Carya* spp.*,* and *Pinus virginiana* were the highest relative densities in large woody debris. *Quercus alba, O. virginiana,* and *Carya* spp. were the highest relative densities for large woody debris in the moderate damage class. The light and moderate categories were similar in rankings for relative dominance: *Q. alba* ranked the highest, followed by *Carya* spp. and *Q. rubra*. No shade-tolerant species had a relative density or relative dominance over 7.0%, aside from *O. virginiana* in the moderate class (15.1%) and the relative dominance of *Fagus grandifolia* in the moderate category (8.3%).

In decay class 1, *Quercus* spp. comprised a larger proportion of stems in the light damage (34%) than in moderate damage (24%). Similarly, *L. tulipifera* percentages slightly declined with increasing disturbance with 4% and 3% for light and moderate classes, respectively. *Quercus* and *Carya* increased in overall density in decay class 1, but *Acer/Fagus* was not as well represented comparatively (Figure 5).

3.3 Regeneration and PAR

Seedling density was 18,250 ha^{-1} in control, 17,883 ha^{-1} in light, and 16,678 ha^{-1} in moderate damage classes (Table 4). In control treatment, the species with the highest relative density were *Acer saccharum* and *Fraxinus americana,* followed by *Quercus alba, A. rubrum,*

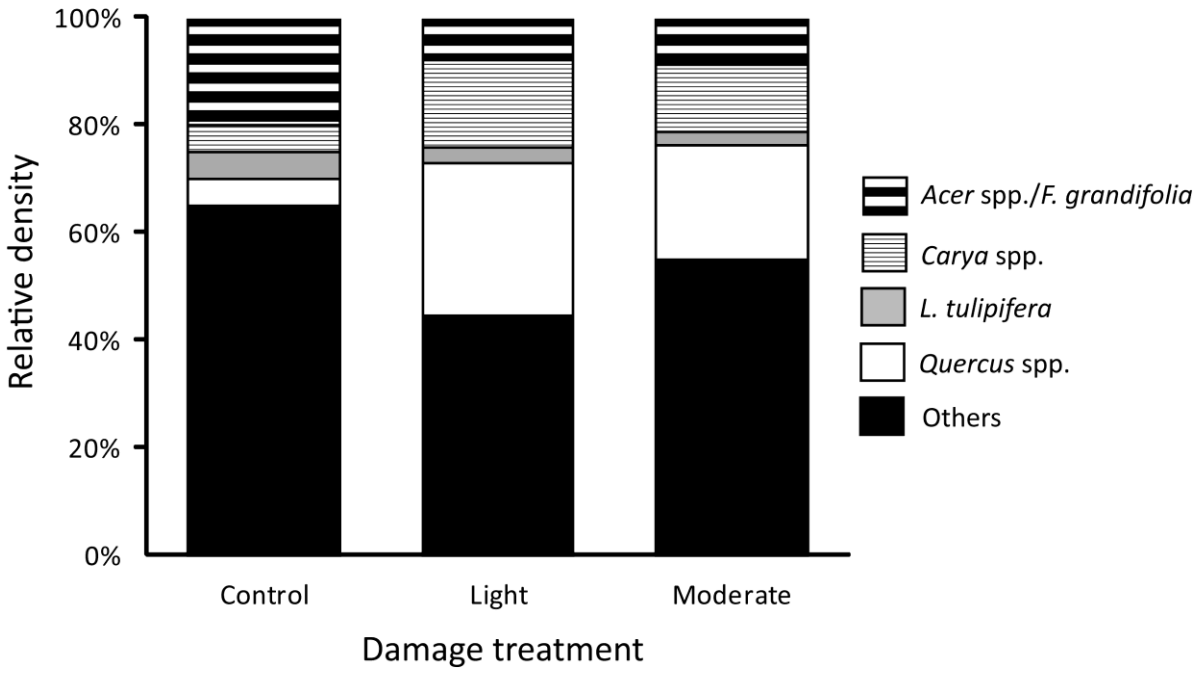


Figure 5. Relative density of decay class 1 large woody debris in three treatments on the Sipsey Wilderness, Alabama.

Table 4. Density, relative density, frequency, and relative frequency for all seedlings (< 1 m height, ≤ 5 cm dbh) in three treatments on the Sipsey Wilderness, Alabama. Frequency is the number of plots on which each species occurred by damage class, and relative frequency is the percent of plots on which each species occurred by damage class.

	Density (stems/ha)			Relative Density (%)			Frequency (# plots)			Relative Frequency (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer saccharum	2400	1942	1946	13.2	10.9	11.7	16	27	28	80.0	51.9	75.7
Fraxinus americana	2400	1038	892	13.2	5.8	5.3	8	17	17	40.0	32.7	45.9
Quercus alba	1950	2154	1162	10.7	12.0	7.0	12	30	17	60.0	57.7	45.9
Acer rubrum	1450	1885	919	7.9	10.5	5.5	12	38	19	60.0	73.1	51.4
Quercus rubra	1400	538	649	7.7	3.0	3.9	13	18	12	65.0	34.6	32.4
Viburnum acerifolium	1100	1615	2135	6.0	9.0	12.8	5	18	15	25.0	34.6	40.5
Ostrya virginiana	900	1192	892	4.9	6.7	5.3	10	31	18	50.0	59.6	48.6
Fagus grandifolia	750	462	270	4.1	2.6	1.6	3	12	7	15.0	23.1	18.9
Carya spp.	650	1250	892	3.6	7.0	5.3	7	29	18	35.0	55.8	48.6
Ulmus rubra	650	308	216	3.6	1.7	1.3	5	7	6	25.0	13.5	16.2
Ligustrum sinense	600	212	1351	3.3	1.2	8.1	7	6	5	35.0	11.5	13.5
Cercis canadensis	550	423	351	3.0	2.4	2.1	6	14	10	30.0	26.9	27.0
Prunus serotina	500	423	324	2.7	2.4	1.9	6	17	11	30.0	32.7	29.7
Frangula caroliniana	450	96	81	2.5	0.5	0.5	3	5	2	15.0	9.6	5.4
Ulmus alata	350	77	243	1.9	0.4	1.5	7	3	8	35.0	5.8	21.6
Aralia spinosa	250	38	81	1.4	0.2	0.5	2	2	2	10.0	3.8	5.4
Lindera benzoin	250	115	—	1.4	0.6	—	1	3	—	5.0	5.8	—
Nyssa sylvatica	200	404	703	1.1	2.3	4.2	4	16	15	20.0	30.8	40.5
Vaccinium arboreum	200	769	162	1.1	4.3	1.0	1	15	4	5.0	28.8	10.8
Amelanchier arborea	150	115	81	0.8	0.6	0.5	2	2	3	10.0	3.8	8.1
Asimina triloba	150	154	216	0.8	0.9	1.3	3	5	3	15.0	9.6	8.1
Carpinus caroliniana	150	115	135	0.8	0.6	0.8	2	5	4	10.0	9.6	10.8
Magnolia acuminata	150	77	81	0.8	0.4	0.5	3	4	3	15.0	7.7	8.1
Quercus muehlenbergii	150	77	—	0.8	0.4	—	3	1	—	15.0	1.9	—
Juniperus virginiana	100	115	54	0.5	0.6	0.3	2	6	2	10.0	11.5	5.4
Quercus prinus	100	250	135	0.5	1.4	0.8	1	7	3	5.0	13.5	8.1
Styrax grandifolius	100	38	81	0.5	0.2	0.5	1	2	2	5.0	3.8	5.4
Aesculus pavia	50	135	—	0.3	0.8	—	1	3	—	5.0	5.8	—
Celtis occidentalis	50	19	—	0.3	0.1	—	1	1	—	5.0	1.9	—
Cornus florida	50	538	460	0.3	3.0	2.8	1	14	11	5.0	26.9	29.7
Quercus falcata	50	38	27	0.3	0.2	0.2	1	2	1	5.0	3.8	2.7
Liriodendron tulipifera	—	481	243	—	2.7	1.5	—	3	5	—	5.8	13.5
Pinus taeda	—	192	432	—	1.1	2.6	—	5	7	—	9.6	18.9
Sassafras albidum	—	96	649	—	0.5	3.9	—	3	3	—	5.8	8.1
Oxydendrum arboreum	—	77	—	—	0.4	—	—	1	—	—	1.9	—
Quercus velutina	—	77	108	—	0.4	0.6	—	3	3	—	5.8	8.1
Rhododendron catawbiense	—	77	162	—	0.4	1.0	—	4	1	—	7.7	2.7
Magnolia macrophylla	—	58	243	—	0.3	1.5	—	3	8	—	5.8	21.6
Pinus virginiana	—	58	81	—	0.3	0.5	—	2	2	—	3.8	5.4
Crataegus phaenopyrum	—	38	—	—	0.2	—	—	2	—	—	3.8	—
Rhamnus cathartica	—	38	—	—	0.2	—	—	2	—	—	3.8	—
Betula lenta	—	19	—	—	0.1	—	—	1	—	—	1.9	—
Ilex opaca	—	19	—	—	0.1	—	—	1	—	—	1.9	—
Kalmia latifolia	—	19	—	—	0.1	—	—	1	—	—	1.9	—
Morus rubra	—	19	—	—	0.1	—	—	1	—	—	1.9	—
Pinus echinata	—	—	54	—	—	0.3	—	—	2	—	—	5.4
Ulmus americana	—	—	54	—	—	0.3	—	—	1	—	—	2.7
Diospyros virginiana	—	—	27	—	—	0.2	—	—	1	—	—	2.7
Juglans nigra	—	—	27	—	—	0.2	—	—	1	—	—	2.7
Quercus stellata	—	—	27	—	—	0.2	—	—	1	—	—	2.7
Tilia americana	—	—	27	—	—	0.2	—	—	1	—	—	2.7
Total	**18250**	**17883**	**16678**	**100.0**	**100.0**	**100.0**	—	—	—	—	—	—

and *Q. rubra.* In the light damage treatment, *Quercus alba* had the highest seedling density followed by *Acer saccharum* and *A. rubrum*. In moderate damage, *Viburnum acerfolium, A. saccharum,* and *Ligustrum sinense* were the highest seedling densities. The most frequently occurring seedling species on control plots was *A. saccharum*, on light damage plots was *A. rubrum*, and on moderate damage plots was *A. saccharum*. *Quercus alba* seedlings occurred on 60.0%, 57.7%, and 45.9% of plots in control, light, and moderate classes, respectively.

Total sapling density was 5,890, 6,922, 10,461 ha^{-1} for control, light, and moderate treatments, respectively (Table 5). Unlike seedlings, sapling densities increased with disturbance intensity. The highest relative densities in the control were *Acer rubrum* and *Ostrya virginiana,* followed by *Ligustrum sinense* and *Fagus grandifolius*. In the light damage class, *Ostrya virginia* had the highest relative density followed by *A. rubrum* and *A. saccharum*. In the moderate damage class, *O. virginiana* and *A. saccharum* tied for the highest relative density followed by *A. rubrum* and *Cornus florida*. Few *Quercus* individuals were present in the sapling size class for all treatments, as relative density for all *Quercus* spp. in control, light, and moderate treatments were 4.2%, 2.2%, and 3.1%, respectively. Relative frequency values for *Quercus* spp. were also low, as all *Quercus* spp. occurred on less than 6.0% of plots except for *Q. rubra* in the moderate damage class.

PAR levels for control, light, and moderate damage treatments were 9.00% ± 2.92 (SE), 11.55% ± 2.09, and 22.21% ± 3.59 of full sunlight, respectively. The percent of insolation for the moderate treatment was significantly higher than both control and light treatments; however, no significant ($P < 0.05$) difference was detected between the control and light damage classes.

Table 5. Density, relative density, frequency, and relative frequency for all saplings (> 1 m height, ≤ 5 cm dbh) in three treatments on the Sipsey Wilderness, Alabama. Frequency is the number of plots on which each species occurred by damage class, and relative frequency is the percent of plots on which each species occurred by damage class.

	Density (stems/ha)			Relative Density (%)			Frequency (# plots)			Relative Frequency (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer rubrum	900	1115	1135	15.3	16.1	10.9	9	23	16	45.0	44.2	43.2
Ostrya virginiana	900	1192	1324	15.3	17.2	12.7	8	28	22	40.0	53.8	59.5
Ligustrum sinense	850	192	649	14.4	2.8	6.2	5	5	4	25.0	9.6	10.8
Fagus grandifolia	500	462	189	8.5	6.7	1.8	4	11	4	20.0	21.2	10.8
Acer saccharum	400	692	1324	6.8	10.0	12.7	6	20	22	30.0	38.5	59.5
Fraxinus americana	400	346	432	6.8	5.0	4.1	7	9	12	35.0	17.3	32.4
Styrax grandifolius	200	—	108	3.4	—	1.0	1	—	2	5.0	—	5.4
Aesculus pavia	150	269	—	2.5	3.9	—	1	4	—	5.0	7.7	—
Carpinus caroliniana	150	192	540	2.5	2.8	5.2	3	5	8	15.0	9.6	21.6
Cercis canadensis	150	58	351	2.5	0.8	3.4	3	2	7	15.0	3.8	18.9
Quercus prinus	150	—	54	2.5	—	0.5	1	—	1	5.0	—	2.7
Viburnum acerifolium	150	404	297	2.5	5.8	2.8	2	10	4	10.0	19.2	10.8
Frangula caroliniana	100	19	135	1.7	0.3	1.3	2	1	3	10.0	1.9	8.1
Juniperus virginiana	100	38	54	1.7	0.6	0.5	2	2	2	10.0	3.8	5.4
Rhamnus cathartica	100	—	—	1.7	—	—	1	—	—	5.0	—	—
Tilia americana	100	—	—	1.7	—	—	1	—	—	5.0	—	—
Ulmus alata	100	38	108	1.7	0.6	1.0	2	2	4	10.0	3.8	10.8
Lindera benzoin	90	500	—	1.5	7.2	—	2	2	—	10.0	3.8	—
Cornus florida	50	289	676	0.8	4.2	6.5	1	10	14	5.0	19.2	37.8
Magnolia macrophylla	50	38	324	0.8	0.6	3.1	1	2	6	5.0	3.8	16.2
Nyssa sylvatica	50	135	540	0.8	1.9	5.2	1	6	9	5.0	11.5	24.3
Prunus serotina	50	58	135	0.8	0.8	1.3	1	3	5	5.0	5.8	13.5
Quercus alba	50	58	54	0.8	0.8	0.5	1	2	1	5.0	3.8	2.7
Quercus rubra	50	58	189	0.8	0.8	1.8	1	3	6	5.0	5.8	16.2
Ulmus rubra	50	38	81	0.8	0.6	0.8	1	1	3	5.0	1.9	8.1
Vaccinium arboreum	50	—	81	0.8	—	0.8	1	—	2	5.0	—	5.4
Carya spp.	—	192	216	—	2.8	2.1	—	10	4	—	19.2	10.8
Magnolia acuminata	—	96	135	—	1.4	1.3	—	4	4	—	7.7	10.8
Asimina triloba	—	77	189	—	1.1	1.8	—	4	2	—	7.7	5.4
Amelanchier arborea	—	58	—	—	0.8	—	—	—	—	—	—	—
Celtis occidentalis	—	38	—	—	0.6	—	—	2	—	—	3.8	—
Diospyros virginiana	—	38	81	—	0.6	0.8	—	2	3	—	3.8	8.1
Rhododendron catawbiense	—	38	—	—	0.6	—	—	1	—	—	1.9	—
Betula lenta	—	19	—	—	0.3	—	—	1	—	—	1.9	—
Castanea dentata	—	19	27	—	0.3	0.3	—	1	1	—	1.9	2.7
Liriodendron tulipifera	—	19	81	—	0.3	0.8	—	1	3	—	1.9	8.1
Morus rubra	—	19	—	—	0.3	—	—	1	—	—	1.9	—
Oxydendrum arboreum	—	19	27	—	0.3	0.3	—	1	1	—	1.9	2.7
Pinus taeda	—	19	81	—	0.3	0.8	—	1	1	—	1.9	2.7
Quercus falcata	—	19	—	—	0.3	—	—	1	—	—	1.9	—
Quercus velutina	—	19	—	—	0.3	—	—	1	—	—	1.9	—
Sassafras albidum	—	19	406	—	0.3	3.9	—	1	2	—	1.9	5.4
Ulmus americana	—	19	—	—	0.3	—	—	1	—	—	1.9	—
Arundinaria tecta	—	—	406	—	—	3.9	—	—	1	—	—	2.7
Quercus muehlenbergii	—	—	27	—	—	0.3	—	—	1	—	—	2.7
Total	**5890**	**6922**	**10461**	**100.0**	**100.0**	**100.0**	—	—	—	—	—	—

4. DISCUSSION

4.1 Structural Analysis

The relationship between size classes (q-factor) was not altered between control and moderate treatments. The q-factor was only slightly lower in the light damage class compared to the control category. Trees from all size classes were removed by the storm in both disturbance severity categories, but larger size classes exhibited higher rates of mortality compared to smaller size classes. This pattern was also noted following an intermediate-scale disturbance in the Northern Hardwood Forest (Hanson and Lorimer 2007). Although I documented significant relationships between tree diameter and mortality, the actual drivers of wind-induced removal were likely tree height and crown volume. Increased canopy height and crown volume resulted in increased wind drag, which can uproot or snap trees if a critical threshold is exceeded (Foster and Boose 1992, Peterson and Rebertus 1997, Peterson 2000, Rich et al. 2007). Thus, I hypothesized diameter was only related to mortality because of the autocorrelation between diameter and tree height and crown volume (Peterson 2000). The percentage of stems removed decreased by crown class; dominant trees were the most susceptible to wind damage, followed by codominant, I3, I2, I1, and finally overtopped classes. I speculated that wind damage will blow down trees in the canopy first then affect lower strata of the stand as overstory layers are removed and subcanopy trees are exposed to damaging winds. Indeed, logistic regression of fate compared to diameter exhibited a sharp increase in mortality until ca. 20 cm dbh. This value approximates the mean diameter of the I3 crown class. Thus, I noted that canopy trees were more likely to be damaged than intermediate stems and that the likelihood of mortality increased abruptly between intermediate and canopy

crown positions. QMD of moderate and light damage treatments differed significantly, but neither damage class was significantly different from the control. The larger QMD in the light damage class may indicate that larger trees are the most prone to blow down in low to moderate windstorms, but I speculated that such a small difference in diameter is not meaningful although statistically significant (ca. 2 cm difference).

The size distributions of all trees in each disturbance category resembled the reverse J shape, indicating continuous regeneration and recruitment of smaller size classes. When divided into taxonomic groups, the diameter distributions were quite different. In the control class, *Quercus* spp. exhibited a bell-shaped frequency distribution, therefore density of small stems was likely insufficient to maintain *Quercus* dominance. In contrast, the *Acer*/*Fagus* group was well represented in the small sizes and displayed the reverse J shape distribution. This pattern is typical of *Quercus* stands throughout the Central Hardwood Forest (McEwan et al. 2011, Hart et al. 2011). Indeed, *Quercus* stands across the eastern United States appear to be transitioning to dominance by more shade tolerant taxa, principally *Acer* spp. (i.e. the *Quercus*–to–*Acer* phenomenon; Lorimer 1984, Abrams 2005, Nowacki and Abrams 2008, Fei et al. 2011, McEwan et al. 2011, Hart et al. 2012).

Based upon q-factor and QMD, I cannot say with confidence this disturbance significantly altered stand structure to conclude structural regression or acceleration along an intermediate-scale disturbance gradient. However at the stand scale, the storm created a heterogeneous mosaic of blowdown areas with varying patch sizes and severities of disturbance. I observed highly variable patch dynamics; each stand affected by the storm contained an array of damage severities including patch blowdowns with no standing trees,

clusters of undamaged trees, single treefall gaps, and areas undamaged by the storm. New research is needed to analyze the spatial dynamics of damage resulting from windstorms that allows for intra-stand analyses so that variability can be captured at a sub-stand scale. The top-down disturbance documented made available new growing space for the recruitment of new individuals, so I acknowledge that the diameter distributions will change with time since disturbance. The extent to which wind disturbances drive development over time is not known, and new research is needed to quantify this recovery process. As the stands mature, they will be more structurally and spatially complex, having multiple age classes and neighborhoods of both larger and smaller stems of varying distributions. The storm event increased intra-stand structural heterogeneity; thus, I concluded that structural development was accelerated to more complex conditions at the stand scale.

4.2 Compositional Analysis

The storm did not allow for recruitment of moderately shade-tolerant species to larger size classes, but favored later-successional, shade-tolerant individuals already established in mid-story and understory positions. Following intermediate-scale wind disturbance, *Acer* increased in dominance and *Quercus* declined thus hastening the *Quercus*–to–*Acer* transition. No species-specific mortality trends were noted, although species-specific trends have been documented following some wind-disturbance events (Everham and Brokaw 1996, Canham et al. 2001). Probability of blowdown seems to be more dependent upon canopy position rather than species, as suggested in other studies (Peterson 2007, Rich et al. 2007). *Acer saccharum* large woody debris was not common despite its high live-stem importance value. I suggest this

may be a function of height, as *A. saccharum* was not found in a dominant canopy position in any control plot. Similarly, I did not find any shade-tolerant, mesophytic species to be more important in large woody debris than in the live trees except for *Cercis canadensis*. Following canopy disturbance, PAR levels increased in the mid- and understory, thus releasing individuals in those strata. The successional trajectory of a stand may be strongly influenced by its stage of development. During the understory reinitiation phase of development, the understory of *Quercus*-dominated stands often contain a high density of shade-tolerant mesophytic species and low densities of *Quercus* advanced reproduction. The intermediate-scale wind disturbance documented here, removed canopy individuals and released those in mid- and understory positions, therefore accelerating succession. These findings are consistent with the disturbance-mediated accelerated succession scenario proposed by Abrams and Scott (1989) that stated a disturbance event, whether natural or anthropogenic, occurring during understory reinitiation will favor a composition of shade-tolerant taxa in the future stand.

Successional acceleration following wind disturbance has been found in other studies: Arevalo et al. (2000) for *Pinus strobus* and *Quercus ellipsoidallis* stands in central Minnesota, Holzmueller et al. (2012) for mixed *Quercus* stands in southern Illinois, and Hanson and Lorimer (2007) evaluated *Tsuga canadensis*–northern hardwoods stands in northern Wisconsin. Disturbance during different stages of stand development may affect differently the successional trajectory of the stand. The stands sampled in this study were in the understory reinitiation phase of stand development, which is typical of most *Quercus* stands in the Central Hardwood Forest. This disturbance killed canopy individuals (mostly *Quercus*) while releasing understory and midstory individuals (mostly *Acer*). The wind disturbance affected the stand

based on its structural assemblage, not based on differential susceptibility to wind damage.

4.3 Regeneration and PAR

Widespread *Quercus* regeneration failure has been noted across the Central Hardwood Region (Abrams 2005, Fei et al. 2011, Lorimer 1984, Nowacki and Abrams 2008, Hart et al. 2012). *Quercus* saplings occurred in low density and frequency (Table 5), despite the high density and relative frequency of *Quercus* seedlings in all classes (Table 4). The failure of *Quercus* seedlings to recruit into the sapling size class has been widely documented and coined the "*Quercus* bottleneck." Abundant shade-tolerant seedlings and saplings such as *Acer* spp. and *O. virginiana* were documented in the stands studied here, likely resulting in low *Quercus* sapling density and inhibition of *Quercus* recruitment from seedling to sapling size classes. Thus, *Quercus* are not in competitive positions to take advantage of newly available growing space that resulted from canopy disturbance.

Low *Quercus* densities in small diameter classes are primarily attributed to competition from shade-tolerant seedlings and saplings (Lorimer 1994). Recruitment of subcanopy *Quercus* to canopy positions typically requires that the gap size be at least as large as the surrounding canopy trees are tall (Dey 2002). Gap-scale disturbances in secondary *Quercus* stands often do not meet this 1:1 ratio (Hart and Grissino-Mayer 2009, Richards and Hart 2011). In the third growing season following disturbance, understory PAR percentages were below the 20–50% thresholds required for *Quercus* (Dey 2002), despite basal area reductions being within these bounds for both light and moderate damage classes. I hypothesized the increased light was captured by a growth release of shade-tolerant individuals that were established in midstory

and understory positions following the canopy disturbance (Lorimer et al. 1994). Additionally, I attribute the lack of *Quercus* saplings to increased competition from established shade-tolerant individuals in the understory, preventing recruitment from seedlings to saplings. The successional trajectory of a stand may be significantly impacted by the stage of stand structural development in conjunction with the type of disturbance. In this study, primarily canopy individuals were killed by the storm, but advanced reproduction in subcanopy strata were able to respond to increased sunlight which precluded establishment of new seedlings. Thus, a top-down disturbance during the understory reinitiation phase might be only able to accelerate the *Quercus*–to–*Acer* transition in the Central Hardwood Forest. A disturbance prior to understory reinitiation (i.e. prior to the proliferation of *Acer* and other shade-tolerant mesophytes in the understory) might allow *Quercus* reproduction to become established in the understory.

5. MANAGEMENT IMPLICATIONS

Forest managers are increasingly interested in the use of silvicultural practices that emulate the extent and frequency of natural disturbances that occurred historically for given sites. Natural disturbance-based silviculture uses tools (e.g. timber harvesting and chemical herbicide) to simulate the ecological processes that historically occurred on a site with the ultimate goal of minimizing disparity between natural and managed systems while simultaneously satisfying other management objectives. The rationale is that forest communities will be less prone to suffer degradation if anthropogenic disturbances exhibit the characteristics of the disturbances to which species and communities are adapted. Emulating a wind disturbance should be considered by forest managers, as high wind is the most common and likely the most influential exogenous disturbance agent in the Central Hardwood Forest (Runkle 1985, 1996). Wind disturbance may be used as a template for silviculturists to achieve a wide range of objectives as wind damage can be highly variable in spatial extent and magnitude (e.g. can result in a range of patch blowdown sizes with different impacts on size and vertical structure).

The tornado documented in this study, which is characteristic of low intensity tornadic events, resulted in a thin, linear path of complete destruction with adjacent patch blowdown areas of varying sizes, although generally decreasing in size with increasing distance from the swath. I suggest that an access road for logging trucks and equipment be created in a relatively straight line to access timber without regard to stand delineations or boundaries to mirror the tornado path (i.e. the zone of castastrophic disturbance). Trails used by skidders or forwarders should run perpendicular to the access road for transporting trees and/or logs from the group

selections or small patch clearcuts to a central landing. To mimic the effects of low intensity tornadoes, silviculturists should prescribe group selections of variable sizes within a stand. Crop trees should be based on structural attributes such as canopy position and diameter. This system also allows for flexibility to select species of greater value. Within each patch, trees with canopy positions should be selected; however taller and larger diameter trees should be preferred to mimic the effects of wind disturbance. Only ca. 10% of overtopped trees should be removed, while ca. 30% of codominant trees and ca. 35% of dominant trees should be harvested. I recommend that between 30–40% of trees with dbh greater than 40 cm be harvested to mimic the effects of this type of windstorm. Overall, basal area should be reduced between 20–50% within patches of varying sizes, and severity of disturbance should increase with patch size (i.e. more timber harvesting in larger patches; Peterson et al. 2013). Size distribution relationships (q-factor) should remain static across patches, despite variable harvests within group selections.

The above recommendations may pose problems for landowners in the Central Hardwood Forest with coexisting goals of managing according to natural disturbances and maintaining *Quercus* dominance in perpetuity. Indeed, the wind disturbance addressed in this study accelerated succession and furthered the *Quercus*–to–*Acer* transition, therefore making a direct application of these results unadvisable. However, mimicking the effects of natural disturbances and favoring *Quercus* may not be mutually exclusive. Silviculture patterned after natural disturbance may need only slight modifications to be successful at achieving both objectives. An intermediate-scale, top-down disturbance can be coupled with a bottom-up disturbance such as fire, mechanical thinning, or chemical herbicide to reduce competition

from shade-tolerant taxa in the understory. Indeed, the primary obstacle for *Quercus* regeneration is competition from shade-tolerant individuals established in the understory (Lorimer et al. 1994). I found high densities and relative frequencies of *Quercus* seedlings but not of *Quercus* saplings. *Quercus* seedlings are well distributed throughout these stands and could potentially release to larger size classes if not for competition from shade-tolerant taxa. Therefore, a bottom-up disturbance prior to harvest may make available growing space for moderately shade-tolerant taxa such as *Quercus* to establish and release following canopy disturbance. Although the operations would not as closely emulate wind-disturbance with this modification, the end result may be more desirable to such landowners than the strict adherence to natural disturbance-based management.

The wind damage documented in this study did not affect any of the sampled stands uniformly, but rather increased intra-stand heterogeneity in regards to stem densities, vertical stratification of foliage, and species composition. The resulting stands will retain distinct neighborhoods in varying stages of succession including neighborhoods of both early and late succession species, large and small trees, and varying foliar strata. At the stand scale, this silvicultural system would create multi-aged structures through even-aged group selections. Mimicking this natural disturbance makes stand-level analyses difficult and challenges the basis of the stand as the fundamental management unit of silviculturists. However, we contend that even with these non-uniform approaches, the stand is still the basic unit for the silvicultural system (O'Hara and Nagel 2013).

This wind event also provided information on the importance of disturbance timing in relation to stage of stand development in *Quercus* stands. During the stem exclusion stage,

canopy individuals fully occupy all growing space and preclude the establishment of new stems (Oliver and Larson 1996). Intense competition among many individuals causes frequent mortality and an abundance of small canopy openings that are quickly captured by neighboring individuals (Oliver and Larson 1996, Zeide 2010). Eventually, overstory trees no longer aggressively capture available light in these small gaps, which allows other stems to exploit newly available growing space. When new stems develop a layer beneath the canopy, the stand enters the understory reinitiation phase of development (Oliver and Larson 1996). I suggest that a disturbance in *Quercus* stands may be more successful in reducing proliferation of shade-tolerant individuals with an entry during the stem exclusion stage of development. A non-commercial harvest in *Quercus* stands in this stage may provide the 20–50% light required for *Quercus* regeneration prior to the establishment of shade-tolerants in the understory. *Acer* has been shown to establish earlier during the understory reinitiation stage than *Quercus*, thus, precluding *Quercus* regeneration (Lorimer et al. 1994, Hart and Grissino-Mayer 2008). Hart and Grissino-Mayer (2008) found a distinct pulse of *Acer* establishment ca. 30 years after a stand-initiating disturbance in an upland Quercus stand on the Cumberland Plateau. A regenerating disturbance at this time may allow *Quercus* reproduction to establish, creating a two-aged stand, prior to development of a shade-tolerant understory (which will inhibit *Quercus* recruitment from seedling to sapling size classes).

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