THE EFFECTS OF INTERMEDIATE-SCALE WIND DISTURBANCE ON FOREST COMPOSITION, STRUCTURE, AND SUCCESSION WITH IMPLICATIONS FOR MANAGEMENT

by

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ABSTRACT

Forest disturbances are discrete events in space and time that disrupt the biophysical environment and impart lasting legacies on forest composition, structure, and stand development. Intermediate-scale disturbances may promote stand heterogeneity, including uneven-aged structure, and their effects can range in size and distribution from small, patchy gaps to the removal of large portions of overstory vegetation. These events are often classified along gradients of intensity, which in this study were defined using post-tornado aerial photographs and visual assessments in the field. The specific objectives of this study, which took place two growing seasons after an EF1 tornado, were to quantify and compare canopy structure, understory light regimes, woody species composition, and species diversity along a gradient of canopy disturbance and to analyze the influence of intermediate-scale disturbance on the successional trajectory of an upland hardwood forest. We found no significant differences in tree layer Shannon diversity among the control (no storm damage), moderately, or severely disturbed plots. We found significant differences ($P < 0.01$) in percent of intercepted PAR between the control and severe classes and between moderate and severe classes. This disturbance acted primarily as a release mechanism for advanced regeneration and stems in the midstory. Our results can be used to refine silvicultural prescriptions that attempt to minimize the disparity between managed and unmanaged stands and to promote intra-stand heterogeneity.

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Chapter 1: Introduction

Forest disturbances are discrete events in space and time that disrupt the biophysical environment (White and Pickett 1985) and impart lasting legacies on forest composition, structure, and stand development patterns (Lorimer 1980, Foster et al. 1998, White and Jentsch 2001, Foster et al. 2002). Disturbances are often classified along a gradient of magnitude and spatial extent. This gradient spans from catastrophic, stand-replacing events to highly localized, gap-scale events (Oliver and Larson 1996). The range between endpoints of this disturbance classification gradient is vast and makes quantifying disturbances that are too broad to be considered gap-scale and those too localized to be considered catastrophic difficult. Within this framework, intermediate-scale disturbances can differ widely from each other yet have the same disturbance classification. Natural disturbance agents that often cause intermediate-scale damage include strong winds, ice storms, insect attacks, and pathogens (Oliver and Larson 1996). Although disturbances can be categorized by many different parameters (Sousa 1984, White and Pickett 1985, White and Jensch 2001), the standard convention at the stand scale is to classify disturbances according to the amount of basal area removed (Hanson and Lorimer 2007). In the Northern Hardwood Forest, it has been estimated that disturbances that remove 30–60% of the canopy occur once every 300–390 years (Frelich 1986, Frelich and Lorimer 1991a, 1991b, Hanson and Lorimer 2007). At a site in the Central Hardwood Forest, Hart et al. (2012) documented four stand-wide disturbance events that removed at least 30% of the canopy in approximately 300 years, and determined the average return interval for all stand-wide events was 50 years. The return interval of intermediate-scale events, which is more frequent than catastrophic events and can occur at least once within the lifespan of the dominant taxa, indicates these types of disturbances likely play a significant role in influencing successional and developmental pathways and stand structure (Stueve et al. 2011, Buchanan and Hart 2012). The effects of intermediate-scale disturbances range from the removal of significant portions of overstory vegetation, which initiates secondary succession and alters the availability of understory light, which is the most limiting factor in closed canopy forests of the eastern US significantly increases the quantity, quality, and spatial distribution of light in the understory (Canham and Loucks 1984, Hanson and Lorimer 2007, Grayson et al. 2012), to the death of single canopy trees, which modifies fine-scale environmental conditions only (White 1979, Christenson and Peet 1981, Oliver 1981). Finally, intermediate disturbances may increase stand heterogeneity and promote uneven-aged structure (Hanson and Lorimer 2007).

Approximately 1,250 tornadoes occur in the United States annually, and 95% of these are classified as EF0, EF1, or EF2 events (NCDC 2013). Tornadoes of this magnitude typically result in intermediate-scale disturbances. These storms are characterized by a central track associated with catastrophic damage, and damage severity typically decreases with increased distance from the main storm path. Consequently, forest damage from low intensity tornadoes varies spatially from zones of catastrophic damage, to zones with progressively less damage, and eventually to undamaged areas. At the stand scale these events would be considered an intermediate disturbance. In the eastern United States, the return interval for intermediate-scale disturbance is shorter than the life span of most canopy individuals, and much shorter than the return interval of catastrophic disturbances (Frelich and Lorimer 1991, Lorimer 1989, Stueve et al. 2011, Lorimer 2001). Despite the high frequency of these intermediate-scale disturbances, there is a paucity of data available on the effects of these events on forest composition, biodiversity, and sub-canopy light regimes, especially when compared with gap-scale and catastrophic disturbances (Fujita 1978, Foster and Boose 1992, Trickel 2002, Stueve et al. 2011).

In recent decades, there has been a fundamental philosophical change in the management of forest resources. Increasingly, managers are utilizing approaches that emulate natural ecological processes including natural disturbance regimes (Franklin and Johnson 2012, Hanson et al. 2012, Franklin and Johnson 2013). In most forest types, this management approach allows for considerable flexibility when designing silvicultural prescriptions because managers can theoretically mimic any disturbance event within the historical range of variability for a site. As this ecologically-based model is not restricted to any one silvicultural practice, managers can implement a range of treatments across even, two-aged, and uneven-aged approaches, while attempting to minimize the disparities between anthropogenic and natural systems (Kaufman et al. 1994, Franklin et al. 2007, Kuuluvainen and Grenfell 2012). Intermediate-scale disturbances promote intra-stand heterogeneity as disturbed areas within a single stand can range from stand-initiating to gap-scale events (Hanson and Lorimer 2007). Thus, silviculture to emulate such disturbances, with an ultimate goal of reducing disparities between managed and unmanaged stands, may utilize a variety of treatments. Ultimately, emulating intermediate-scale disturbance should increase intra-stand heterogeneity possibly beyond that which would occur between individual stands (O'Hara and Nagel 2013).

The overarching goal of this study was to elucidate the effects of intermediate-scale wind disturbances on forest composition, structure, and succession. The specific objectives were to quantify and compare canopy structure, understory light regimes, woody species composition, and species diversity along a gradient of canopy disturbance and to analyze the influence of intermediate-scale disturbance on the successional trajectory of an upland hardwood forest. The results of this study were interpreted in the context of silvicultural practices and specific, quantitative recommendations for managers that wish to emulate intermediate-scale disturbance were provided.

Chapter 2: Methods

2.1 Study Area

This study was conducted in the Sipsey Wilderness Area on the William B. Bankhead National Forest (BNF) in Lawrence and Winston counties of north Alabama (Fig. 1). The Sipsey Wilderness is a 10,085 ha portion of the National Wilderness Preservation System and occurs on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938) and within the Southwestern Appalachian (level III) ecoregion (Griffith et al. 2001). The topography in this region consists of narrow ridges and valleys, steep slopes, and is so strongly dissected that it does not resemble a true plateau (Smalley 1979). The geology is mainly composed of the Pennsylvania Pottsville formation, which consists of a gray conglomerate, fine to coarse grained sandstone, and is known to contain limestone, siltstone, and shale, as well as anthracite and bituminous coal (Szabo 1988). The geology favors the weathering of the sandstone foundation, and the Cumberland Plateau is most weathered on the Alabama portion. The region contains soils that are acidic, shallow, and poorly drained (USDA SCS 1959). The regional climate is humid mesothermal characterized by short, mild winters and long, hot summers (Thornthwaite 1948). Mean annual temperature is 16 °C (January mean: 5 °C, July mean: 26 °C). The frost-free period is approximately 220 days in duration from late-March to early-November (Smalley 1979). Mean annual precipitation is 1390 mm with monthly means of 135 and 113 mm for January and July, respectively (PRISM Climate Group 2013). During winter, most precipitation events are of low intensity and are a result of

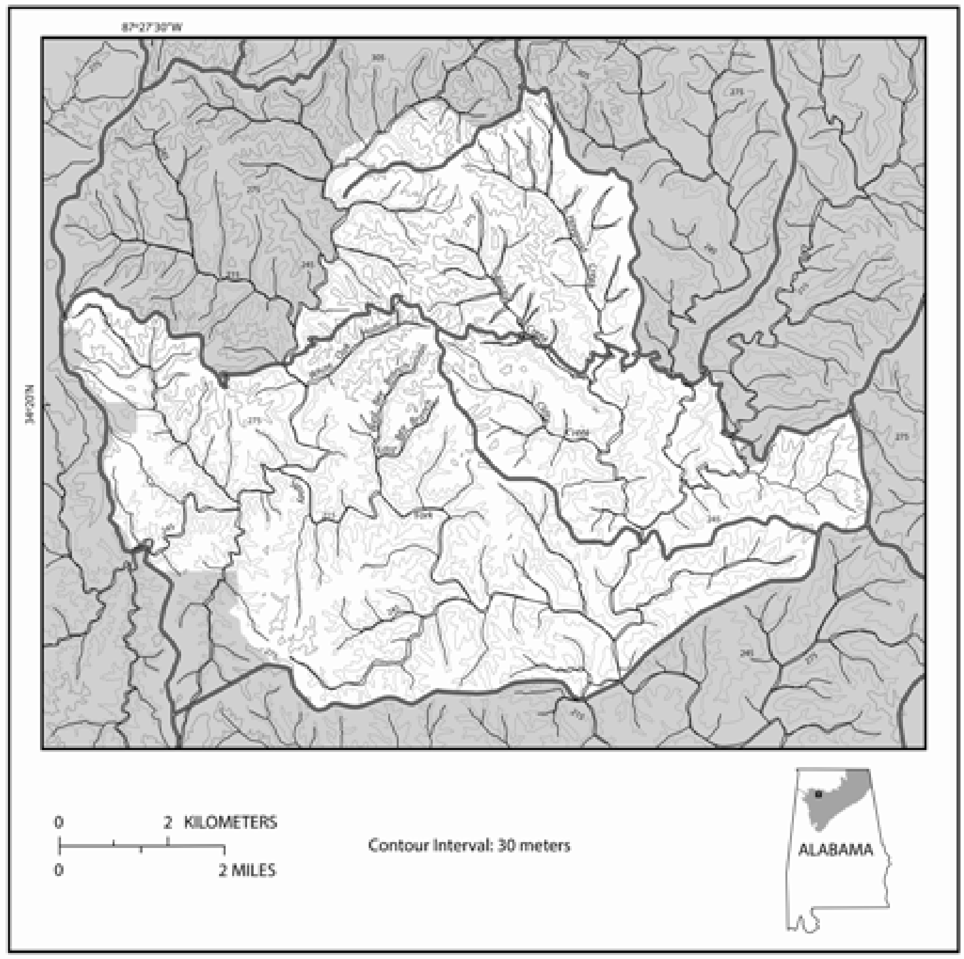

Fig. 1. Sipsey Wilderness on the Bankhead National Forest in Alabama, USA. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic section.

frontal lifting, whereas summer precipitation is frequently the result of convective storms producing more intense rainfall and occasionally lightning and hail (Smalley 1979).

This area of the Cumberland Plateau is classified as a transitional region between the *Quercus-Pinus* Forest Region to the south and the Mixed Mesophytic Forest Region to the north (Braun 1950). Species composition in this region varies locally based on topography (Zhang et al. 1999) and soil-water availability (Hinkle 1989). Ridge-top sites in this region are classified as *Quercus-Pinus*, while mid-slope sites are classified as *Quercus,* and mixed mesophytic communities occur in protected areas such as shaded coves and riparian zones. (Zhang et al. 1999). Hinkle et al. (1993) identified over 30 species on the Cumberland Plateau with the potential to reach the canopy, exemplifying the high species richness that is characteristic of this region. Zhang et al. (1999) classified 14 ecological communities on the Sipsey Wilderness and found *Quercus* was the most abundant genus and occurred in the majority of the delineated community types. 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 a stronger component 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 1992, Zhang et al. 1999, Richards and Hart 2011, Parker and Hart 2014).

On 20 April 2011 a long-lived, quasi-linear convective system developed in north-central Mississippi and tracked eastward through north Alabama (NCDC 2012). 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 were recorded with the wake low system. These types of wind disturbances are representative of damage that occurs throughout the Eastern Deciduous Forest Formation, thus my findings are applicable to sites throughout much of the eastern USA.

2.2 Field Methods

Stands were surveyed during the third growing season post-disturbance. All stands selected were within the same biophysical setting according to Smalley's (1979) land classification system to ensure analogousness of results. The majority of *Q. alba* L. stands within the Sipsey Wilderness established between 1890 and 1905 following anthropogenic clearing, and are at least 9 ha in size. The Sipsey Wilderness is divided into compartments and subdivided into stands, as is required by the US Forest Service, and stand boundaries were consistent with those established by management personnel on the BNF. For this study, I conducted a comprehensive inventory of post-disturbance biophysical conditions across a gradient of disturbance, in each stand. Undamaged neighborhoods within stands were considered the controls in this study, and it is assumed that they were representative of pre-disturbance conditions using a space-for-time substitution.

I overlaid shapefiles of stand boundaries, topography, and the tornado track using ArcGIS v. 10 in combination with aerial photographs and field reconnaissance to determine stands that would be included in the study. In each stand selected to ensure adequate spatial coverage, I subjectively established sample points (plot locations) using GIS software. These locations were inputted as waypoints into a handheld GPS device. In the field, I used a GPS device to navigate to the pre-determined waypoints. Plots that occurred in streams or on hiking trails were moved 15 m in one direction and the new coordinate pair for the plot was recorded. Plots were visually assigned to one of three damage classes based on the number of downed trees within or crossing through a plot and the proximity to the main storm tract. Plots with three or more downed trees of ≥ 20 cm dbh were classified as moderate damage (n = 37), and all other plots with visible wind damage (i.e. individuals were considered windthrown by the storm if they had been either uprooted so that the stem was less than 45° from the ground or if the trunk had been broken below the crown, sensu Canham et al. 2001) were deemed to be light damage plots (n = 52). Control plots (n = 20) exhibited no visible evidence of damage from the storm. At each sample point, I established a 0.04 ha fixed-radius overstory vegetation plot in which I recorded the species, crown class, and diameter at breast height (dbh) of every woody stem, live or dead, > 5 cm dbh. *Carya* spp. stems were only identified to the genus level. All live stems were classified as either undamaged or damaged (e.g. primary branch removed). Crown classification (dominant, co-dominant, intermediate, or overtopped) was based on the amount and direction of intercepted light (Oliver and Larson 1996). Additionally, to provide more information on the structural diversity of the canopy and canopy damage, the intermediate class was divided into intermediate I (I1: 0–50% of total canopy height), intermediate II (I2: 50–75% of total canopy height), and intermediate III (I3: ≥ 75% of total canopy height). Within each overstory plot, seedlings (stems < 1 m height) and saplings (stems

≥ 1 m height, < 5 cm dbh) were tallied by species within a 10 m^2 nested fixed-radius plot to quantify regeneration patterns.

All dead stems ≥ 5 cm dbh within each overstory plot, were classified to the lowest taxonomic level possible and placed into one of four decay classes to examine species-specific mortality trends and overstory composition changes (Fraver et al. 2002). The four classes were defined as follows: decay class I (sound wood, bark intact, small to medium sized branches present); decay class II (sound to partially rotten wood, branch stubs firmly attached with only larger stubs present, some bark slippage); decay class III (substantially rotten wood, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet); or decay class IV (mostly rotten wood, branch stubs rotted down to log surface, bark no longer attached or absent, log is oval or flattened in shape). All dead stems ≥ 5 cm dbh were classified as either: snag (standing dead tree with crown intact), snapped stem (bole broken below the crown), or uprooted stem (root network uplifted; Clinton et al. 1993, Yamamoto 2000, Hart and Grissino-Mayer 2009, Richards and Hart 2011). Each dead tree was determined to have been killed by the wind event or already dead at the time of the intermediate stand-scale disturbance by assessing the level of decay. Based on time since the disturbance, I assumed that trees killed by the April 2011 storm event were in the decay class I category. 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 Sipsey Wilderness. To account for dead trees in decay class I that were not killed by the storm, 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 wind damaged plot to estimate the basal area removed by the intermediate disturbance event.

For each overstory plot, one hemispherical photograph was taken at plot center and a second photograph was taken 50 m away from plot center, and when possible, was taken in the same damage class as the plot center photograph. All photographs were taken at breast height using a Panasonic Lumix (DMC-LX5) camera with a fish-eye lens attached to a self-leveling tripod using a Mid-OMount 10MP (Regent Instruments 2011). The aperture and shutter speed of the system used were set by the canopy analysis system distributor (Regent Instruments 2011). I attempted to collect all images in morning or afternoon hours or during overcast conditions to reduce glare from direct sunlight, which can cause errors with image interpretation (Robison and McCarthy 1999, Jonckheere et al. 2005). In the event that glare was unavoidable, I used a sun blocker device provided by the manufacturer to prevent direct sunlight from reaching the lens. The top of all images was oriented to true north. Finally, canopy interception of photosynthetically active radiation (PAR) ($\mu mol/m^2/s$) was quantified using two synchronized ceptometers (AccuPAR LP-80, Decagon Devices, USA). One ceptometer was placed in full sunlight, while the second recorded PAR within each plot. Twenty recordings were taken in each cardinal direction from the center of each plot (80 total readings per plot). These readings were averaged together to determine one value per plot. These data were used to establish relationships between the percent of full sunlight and the level of canopy disturbance on a per plot basis.

2.3 Laboratory Methods

All hemispherical photographs were analyzed using the WinSCANOPY program v. 2010a (Regent Instruments 2011). WinSCANOPY is a forest canopy analysis software that uses fish-eye photographs to describe canopy structure, map and quantify radiation microclimate beneath canopies, and estimate radiation indices (Breda 2003, Macfarlane et al. 2007, Regent Instruments 2011). The software was used to analyze changes in canopy openness at breast height and disturbance effects on sub-canopy solar radiation. All photos were analyzed by one individual, eliminating user bias and ensuring all images could be directly compared (Canham et al. 1990). Each image underwent 'pixel classification', or the process of classifying image pixels into two groups, canopy or sky, based on their grey levels (Regent Instruments, 2011). In photographs where I used the sun blocker device, a 'mask' defined within the software was delineated that excluded that portion from analysis. WinSCANOPY was used to calculate gap fraction, a measure of canopy openness, and leaf area index (LAI) (Wulder 1998, Regent Instruments 2011). Percent of full sunlight was calculated from ceptometer readings as the ratio between the PAR readings in each plot and the corresponding readings in open sunlight during the same time of day. This allowed me to neutralize slight changes in cloud cover or incidental differences in PAR.

All statistical analyses were performed in SAS v. 9.3. All plot-level data used to compare means between the three damage classes were statistically analyzed and visually checked for normality and homogeneity of variance, and variables that did not meet the test assumptions were log-, square root- or rank-transformed. To compare means among the three damage types, one-way analysis of variance (ANOVA) was performed for species richness, abundance, evenness, gap fraction, canopy openness at breast height, percent of full sunlight, LAI, basal area (total, live, DI), and Shannon diversity (*H'*). If a statistically significant difference was found among the three damage classes ($P \leq 0.05$), a Scheffe post-hoc test was conducted to identify which groups were different. A Pearson correlation test was used to assess the relationships between percent of full sunlight and the number of seedlings and saplings in each damage class. To test for differences in the likelihood of a decay class 1 stem to be uprooted, snapped, or remain standing as a snag, I used Pearson chi square with a significance threshold of $p = 0.05$ to detect trends.

Chapter 3: Results

3.1 Effects on composition and biodiversity

Mean basal area of the tree layer was 25.6, 23.7, and 15.3 m^2 ha^{-1} for control, light, and moderate damage classes, respectively, and values were significantly different between control and moderate classes and between light and moderate classes. Density of stems > 5 cm dbh for control, light, and moderate classes was 771.3, 665.9, and 531.1 m^2 ha^{-1}. The quadratic mean diameter (QMD) for each damage class was 20.6 for control, 21.3 for light, and 19.2 cm dbh for moderate. QMD was statistically different between light and moderate treatments. Species richness of the tree layer (stems ≥ 5 cm dbh) was 32, 37, and 33 for control, light and moderate damage classes, respectively, and was 40 for all treatments combined. Sapling richness was statistically different between control and moderate classes, and between light and moderate classes. Species richness was not significantly different between any other documented layers. Abundance was not statistically significant except between all three classes of the tree layer (stems ≥ 5 cm dbh), and within the sapling layer between the control and moderate damage classes and between the light and moderate classes. I documented no statistically significant differences in species evenness between damage classes. Mean Shannon diversity for the tree layer of control plots was 1.80 ± 0.06 (SE), for light damage plots was 1.85 ± 0.04, and moderate damage plots was, 1.70 ± 0.07.

Mean percent basal area lost in each damage class was 1.5%, 21.1%, and 48.1%, for control, light, and moderate classes, respectively, and these values were significantly different ($P < 0.05$). On average, basal area per plot was 1.0 ± 0.06, 0.96 ± 0.04, and 0.61 ± 0.06 for control, light, and moderate class, respectively, and these were not significantly different. Average basal area lost per plot was 0.56, 0.26, and 0.01 m^2. The mean dbh for all trees in the decay 1 class was 24.1 cm. The mean dbh of *Q. alba* individuals damaged during the storm was 38.1 cm, and the mean dbh of all *Quercus* individuals damaged was 38.2 cm. The mean dbh of *Carya* individuals was 29.3 cm, and the mean branch size documented was 22.54 cm dbh. Of stems within the decay class 1 category, 17% were snags, 53% were snapped stems, and 30% were uprooted stems. Stems were more likely to be snapped than either to be uprooted or to remain standing as snags ($P < 0.001$).

For the control plot trees > 5 cm dbh, *O. virginiana* (27%), *Q. alba* (14%), *A. saccharum* (12%)*, and Carya* spp. (8%) occurred in the highest densities. The species with the highest densities on light damage class plots were *O. virginiana* (19%), *Q. alba* (14%), *F. grandifolia* (10%)*,* and *M. macrphylla* (9%). *Ostrya virginiana* (27%), *Q. alba* (10%), *M. macrophylla* (9%), and *A. saccharum* (8%) were present in the highest densities on moderate damage class plots (Table 1). The four most dominant taxa based on basal area contribution within the control class were *Q. alba*, *Carya* spp., *A. saccharum*, and *L. tulipifera*. The five most dominant taxa on light damage plots were *Q. alba*, *Carya* spp., *L. tulipifera*, and *Q. prinus* and *Q. rubra*. Similarly, the taxa with the highest relative dominance on moderate plots were *Q. alba*, *Carya* spp., *P. taeda*, and *F. grandifolia* (Table 1). The most common species damaged within the control plots, which represents expected background mortality, based on relative densities were *A. saccharum*, *Q. alba*, *C. canadensis*, and *M. macrophylla* (Table 2). Within the light plots, *Q. alba*, *Carya* spp., *O. virginiana*, and *Q. prinus* were damaged in the highest densities. Taxa with the

Table 1. Density and dominance measures for all live stems ≥ 5 cm dbh in the Sipsey Wilderness, Alabama. Species are ranked according to relative dominance.

	Density (stems ≥ 5cm dbh/ha)			Relative Density (%)			Dominance (m^2/ha)			Relative Dominance (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Quercus alba	105.00	95.19	52.70	13.6	14.3	9.9	10.62	9.04	5.42	41.4	38.2	35.4
Carya spp.	65.00	51.44	40.54	8.4	7.7	7.6	3.68	2.52	2.21	14.3	10.7	14.4
Acer saccharum	95.00	43.27	45.95	12.3	6.5	8.7	2.00	0.96	0.76	7.8	4.1	5.0
Quercus rubra	7.50	5.77	1.35	1.0	0.9	0.3	1.40	1.19	0.10	5.4	5.0	0.6
Liriodendron tulipifera	11.25	14.42	7.43	1.5	2.2	1.4	1.22	1.91	0.31	4.8	8.0	2.1
Ostrya virginiana	208.75	124.04	141.89	27.1	18.6	26.7	1.17	0.69	0.70	4.6	2.9	4.6
Quercus muehlenbergii	20.00	2.40	4.05	2.6	0.4	0.8	1.16	0.13	0.26	4.5	0.5	1.7
Quercus prinus	15.00	20.19	4.73	1.9	3.0	0.9	0.79	1.17	0.43	3.1	5.0	2.8
Fagus grandifolia	43.75	64.90	37.84	5.7	9.7	7.1	0.60	1.76	0.77	2.3	7.4	5.1
Pinus taeda	1.25	5.29	5.41	0.2	0.8	1.0	0.50	0.42	1.66	2.0	1.8	10.8
Nyssa sylvatica	33.75	44.71	27.70	4.4	6.7	5.2	0.34	0.48	0.40	1.3	2.0	2.6
Magnolia acuminata	8.75	11.06	9.46	1.1	1.7	1.8	0.32	0.35	0.24	1.2	1.5	1.5
Quercus falcata	2.50	3.85	4.05	0.3	0.6	0.8	0.31	0.36	0.59	1.2	1.5	3.8
Juglans nigra	3.75	0.48	—	0.5	0.1	—	0.27	0.07	—	1.0	0.3	—
Fraxinus americana	12.50	7.69	10.81	1.6	1.2	2.0	0.22	0.47	0.29	0.8	2.0	1.9
Cornus florida	31.25	33.65	17.57	4.1	5.1	3.3	0.15	0.16	0.08	0.6	0.7	0.5
Ulmus rubra	7.50	1.44	1.35	1.0	0.2	0.3	0.14	0.01	0.02	0.5	0.0	0.1
Juniperus virginiana	5.00	6.25	1.35	0.6	0.9	0.3	0.13	0.31	0.04	0.5	1.3	0.3
Ulmus alata	10.00	4.81	10.14	1.3	0.7	1.9	0.12	0.14	0.07	0.5	0.6	0.4
Cercis canadensis	22.50	4.81	10.81	2.9	0.7	2.0	0.12	0.02	0.04	0.5	0.1	0.2
Quercus stellata	1.25	1.44	0.68	0.2	0.2	0.1	0.10	0.06	0.07	0.4	0.3	0.5
Magnolia macrophylla	17.50	61.06	49.32	2.3	9.2	9.3	0.09	0.48	0.39	0.4	2.0	2.5
Acer rubrum	8.75	15.38	12.16	1.1	2.3	2.3	0.07	0.10	0.06	0.3	0.4	0.4
Frangula caroliniana	11.25	0.48	1.35	1.5	0.1	0.3	0.04	0.00	0.00	0.2	0.0	0.0
Oxydendrum arboreum	3.75	15.87	5.41	0.5	2.4	1.0	0.04	0.24	0.12	0.2	1.0	0.8
Carpinus caroliniana	7.50	5.77	16.22	1.0	—	3.1	0.04	0.03	0.06	0.2	0.1	0.4
Prunus serotina	3.75	8.17	2.03	0.5	1.2	0.4	0.04	0.06	0.05	0.2	0.3	0.3
Rhamnus cathartica	2.50	0.48	1.35	0.3	0.1	0.3	0.01	0.00	0.00	0.0	0.0	0.0
Acer negundo	1.25	—	—	0.2	—	—	0.00	—	—	0.0	—	—
Amelanchier arborea	1.25	0.96	—	0.2	0.1	—	0.00	0.00	—	0.0	0.0	—
Aesculus pavia	1.25	0.48	—	0.0	0.1	0.1	0.00	0.00	—	0.0	0.0	—
Asimina triloba	1.25	—	—	0.2	0.9	—	0.00	—	—	0.0	—	—
Morus rubra	—	0.48	0.68	—	0.1	0.1	—	0.00	0.01	0.0	0.0	0.0
Pinus echinata	—	1.44	—	—	0.2	—	—	0.17	—	—	0.7	—
Tilia americana	—	0.96	2.03	—	0.1	0.4	—	0.12	0.03	—	0.5	0.2
Ulmus americana	—	1.92	2.03	—	0.3	0.4	—	0.11	0.13	—	0.5	0.8
Pinus viriginiana	—	1.44	—	—	0.2	—	—	0.10	—	—	0.4	—
Sassafras albidum	—	2.88	1.35	—	0.4	0.3	—	0.05	0.00	—	0.2	0.0
Ilex opaca	—	0.96	0.68	—	0.1	0.1	—	0.01	0.00	—	0.0	0.0
Betula lenta	—	—	0.68	0.2	—	—	—	—	0.01	—	—	0.1
Total	**771.25**	**665.87**	**531.08**	**100.0**	**100.0**	**100.0**	**25.68**	**23.67**	**15.32**	**100.0**	**100.0**	**100.0**

Table 2. Density and dominance measures for all decay class 1 stems ≥ 5 cm dbh in the Sipsey Wilderness, Alabama. Species are ranked according to relative dominance.

	Density (stems/ha)			Relative Density (%)			Dominance (m^2/ha)			Relative Dominance (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Quercus alba	3.75	15.87	29.73	15.8	20.4	14.6	0.10	2.34	4.27	31.0	36.2	30.1
Acer sacharum	5.00	2.40	14.19	21.1	3.1	7.0	0.05	0.06	0.42	16.3	0.9	3.0
Magnolia macrophylla	2.50	2.88	16.22	10.5	3.7	8.0	0.05	0.02	0.17	14.5	0.4	1.2
Quercus muehlenbergii	1.25	0.96	1.35	5.3	1.2	0.7	0.04	0.05	0.04	13.1	0.7	0.3
Carya spp.	1.25	14.90	30.41	5.3	19.1	15.0	0.03	1.15	2.63	9.6	17.7	18.5
Fraxinus americana	1.25	—	4.73	5.3	—	2.3	0.02	—	0.31	4.6	—	2.2
Ostrya virginiana	1.25	6.25	36.49	5.3	8.0	17.9	0.01	0.03	0.21	2.7	0.4	1.5
Cercis canadensis	2.50	0.96	3.38	10.5	1.2	1.7	0.01	0.01	0.03	2.5	0.1	0.2
Liriodendron tulipifera	1.25	2.88	5.41	5.3	3.7	2.7	0.01	0.32	1.03	1.9	4.9	7.2
Frangula caroliniana	1.25	—	—	5.3	—	—	0.00	—	—	1.3	—	—
Fagus grandifolia	1.25	2.88	5.41	5.3	3.7	2.7	0.00	0.65	0.63	1.1	10.1	4.4
Cornus florida	1.25	3.37	5.41	5.3	4.3	2.7	0.00	0.02	0.03	1.0	0.2	0.2
Juniperus virginiana	0.00	2.88	2.70	0.0	3.7	1.3	0.00	0.06	0.08	0.0	1.0	0.6
Nyssa sylvatica	0.00	3.37	8.11	0.0	4.3	4.0	0.00	0.04	0.14	0.0	0.6	1.0
Pinus taeda	0.00	0.00	3.38	0.0	0.0	1.7	0.00	0.00	0.95	0.0	0.0	6.7
Pinus virginiana	0.00	3.37	0.68	0.0	4.3	0.3	0.00	0.44	0.08	0.0	6.8	0.6
Prunus serotina	0.00	1.92	0.68	0.0	2.5	0.3	0.00	0.01	0.03	0.0	0.1	0.2
Quercus falcata	0.00	0.96	4.73	0.0	1.2	2.3	0.00	0.12	0.42	0.0	1.8	3.0
Quercus prinus	0.00	4.81	4.73	0.0	6.2	2.3	0.00	0.47	0.87	0.0	7.2	6.1
Quercus rubra	0.00	2.88	8.11	0.0	3.7	4.0	0.00	0.62	1.27	0.0	9.6	8.9
Sassafrass albidum	—	0.48	0.00	—	0.6	0.0	—	0.00	0.00	—	0.0	0.0
Magnolia acuminata	—	0.48	4.05	0.0	0.6	2.0	—	0.01	0.18	—	0.1	1.3
Acer rubrum	—	1.92	0.68	—	2.5	0.3	—	0.01	0.00	—	0.1	0.0
Oxydendron arboreum	—	0.96	3.38	0.0	1.2	1.7	—	0.02	0.21	—	0.3	1.5
Quercus stellata	—	0.48	0.68	—	0.6	0.3	—	0.04	0.03	—	0.7	0.2
Juglans nigra	—	—	0.68	—	—	0.3		—	0.08	—	—	0.5
Ulmus alata	—	—	2.03	—	—	1.0	—	—	0.06	—	—	0.4
Tilia americana	—	—	0.68	—	—	0.3	—	—	0.02	—	—	0.1
Carpinus caroliniana	—	—	3.38	—	—	1.7	—	—	0.01	—	—	0.1
Betula lenta	—	—	0.68	—	—	0.3	—	—	0.01	—	—	0.1
Amelanchier arborea	—	—	1.35	0.0	0.0	0.7	—	—	0.00	—	—	0.0
Vaccinium arboreum	—	—	0.00	—	—	0.0	—	—	0.00	—	—	0.0
Total	**23.75**	**77.88**	**203.38**	**100.0**	**100.0**	**100.0**	**0.33**	**6.47**	**14.22**	**100.0**	**100.0**	**100.0**

highest rates (based on density) of mortality on moderate damaged plots were *O. virginiana*, *Carya* spp., *Q. alba*, and *M. macrophylla*.

3.2 Effects on sub-canopy light regimes

Percent of full sunlight for control class plots was 9.0% ± 2.9, for light damage class plots was 11.6% ± 2.09, and for moderate damage class plots was 22.2% ± 3.6 (Figure 2). Percent of full sunlight was significantly different between control and moderate damage classes and between light and moderate damage classes. Three growing seasons post-disturbance, percent light reduction in the understory (measured at 1.4 m above the surface) for control, light, and moderate damage classes was 91.0%, 88.5%, and 77.8%, respectively (Table 3). Percent canopy cover for the control damage class was 95%, for light was 94%, and for the moderate class was 92%. Gap fraction, or the proportion of unobscured sky commonly used to describe canopy structure because of its influence on solar radiation in the sub-canopy, increased with increasing storm damage, but these differences were not significantly different (Figure 3). The mean gap fraction values for control, light, and moderate damage classes were 5.04% + 0.26, 6.05% + 0.25, and 8.36% + 0.57, respectively (Figure 3). Analysis of hemispherical photographs allowed me to calculate percent openness above breast height (i.e. the fraction of open sky in a specified region of the real canopy above the lens), which was 5.15% ± 0.27, 6.31% ± 0.26, and 8.81% ± 0.59 for control, light, and moderate damage classes, respectively (Figure 3). Leaf area index was 3.24 ± 0.07, 3.21 ± 0.07, 3.04 ± 0.12 for control, light, and moderate damage class plots, respectively (Figure 3).

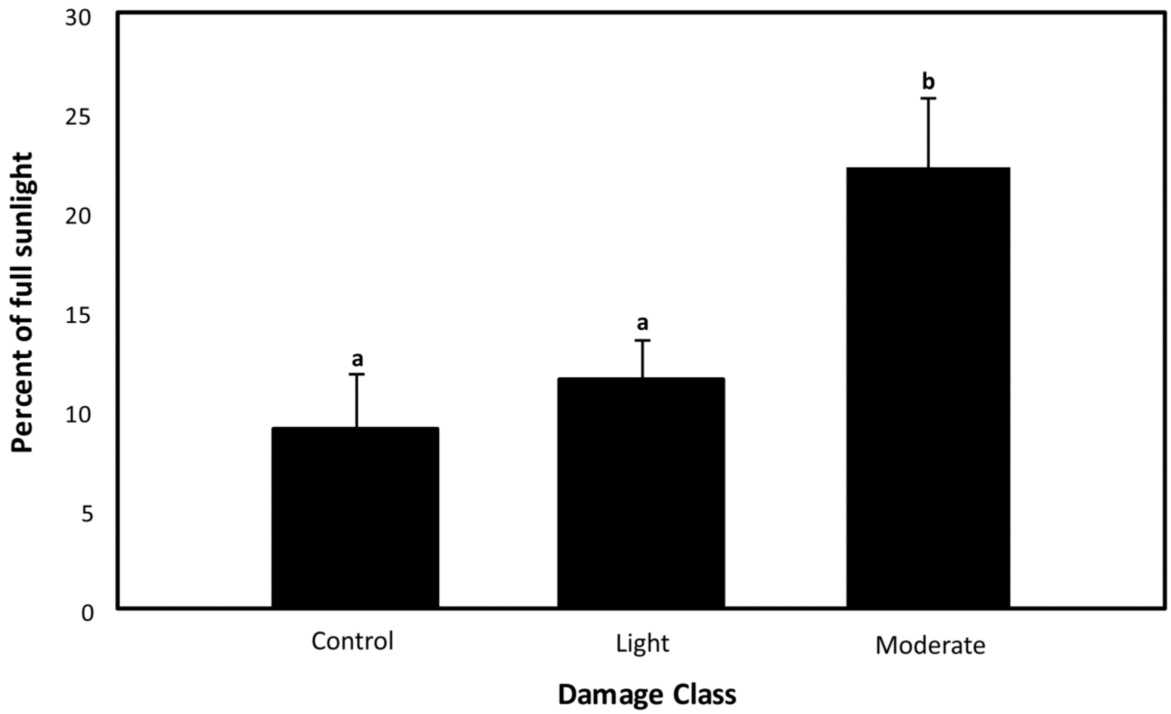

Figure 2. Mean (with standard error) percent of full sunlight values for control, light, and moderate damage classes. Bars with different letters are significantly different at the 0.05 level.

Table 3. Comparisons of diversity and structural measures of managed (50% retention (moderate) and 75% retention (light) shelterwoods) versus naturally disturbed stands on the Cumberland Plateau, Alabama.

	Jackson Co., Alabama[1]			Lawrence Co., Alabama		
	Control	Light	Moderate	Control	Light	Moderate
Diversity (H')	2.2	2.1	2.1	1.8	1.9	1.7
Basal area retention (m^2/ha)	23.1	26.3	10.1	25.6	25.4	15.3
Percent canopy cover	98.8	96.2	71.9	95.0	94.0	91.6
Percent light reduction	97.0	93.7	73.3	91.0	88.5	77.8

[1] Data from Schweitzer and Dey (2011).

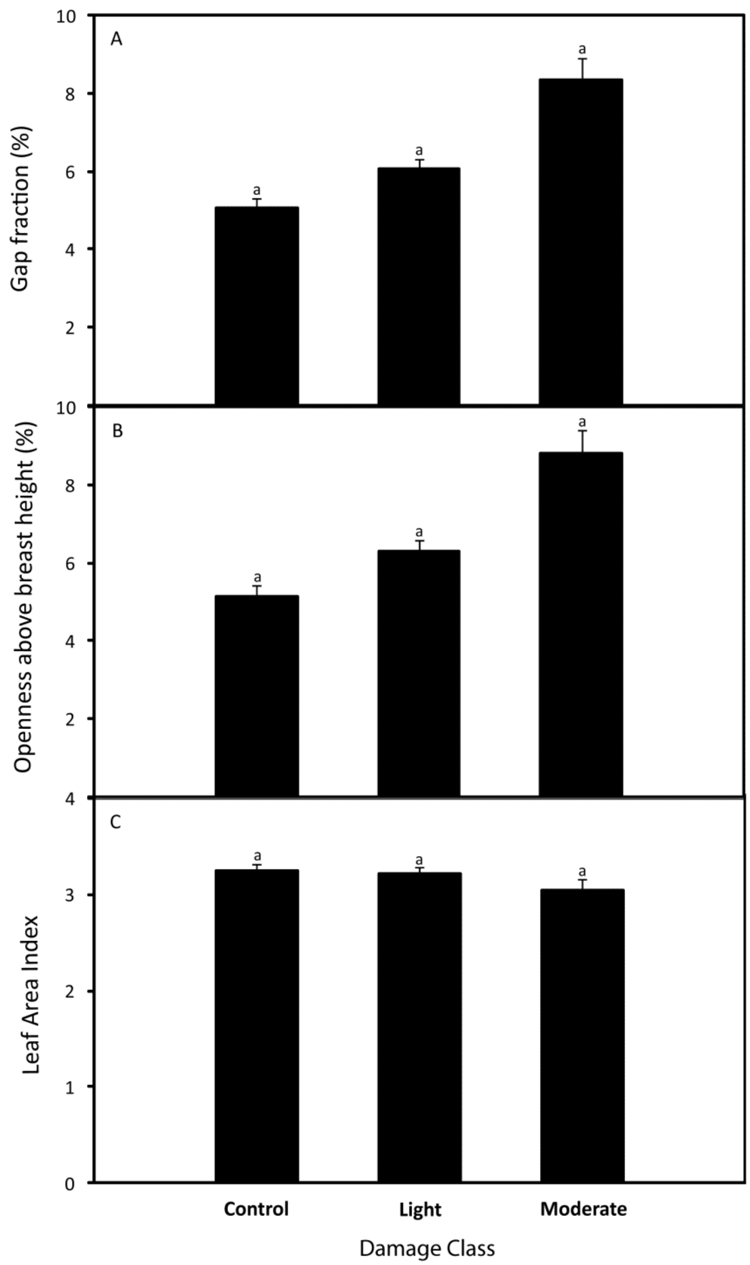

Figure 3. Mean (with standard errors) values for gap fraction, canopy openness above breast height, and leaf area index for control, light, and moderate damage classes. No values were significantly different (*P* < 0.05).

3.3 Effects on the regeneration layer

I documented 53 unique species throughout the seedling (stems < 1m) layer of the three damage classes (Table 4). Within the control plots, *A. rubrum*, *F. americana*, *Q. alba*, and *A. rubrum* had the highest relative densities. Species with the highest relative densities on light damage class plots were *Q. alba*, *A. sacharrum*, *A. rubrum*, and *V. acerifolium*. *Viburnum acerifolium*, *A. saccharum*, *L. sinense*, and *Q. alba* exhibited the highest relative densities in the seedling layer on moderate damage class plots. *Acer saccharum*, *Q. rubra*, *A. rubrum*, and *Q. alba* were each present on at least 10% of control plots. *Acer rubrum*, *O. virginiana*, *Q. alba*, and *Carya* spp. occurred on at least 20% of light damage class plots. Species that were recorded on at least 15% of moderate damage class plots were *A. saccharum*, *Carya* spp., *O. virginiana*, *F. americana*, and *Q. alba*. Only three *Quercus* species had relative densities above 1%, *Q. alba*, *Q. rubra*, and *Q. prinus*. However, the only *Q. prinus* density over 1% was in the light damage class with a value of 1.4%. I documented two alien species in the seedling layer, *L. sinense* and *R. cathartica*. *Ligustrum sinense* represented 3.3%, 1.2%, and 8.1% of total seedling layer stems in the control, light, and moderate classes, respectively.

Within the sapling layer (stems > 1 m, < 5 cm dbh), which included 45 unique species, the species with the highest relative densities were *A. rubrum*, *O. virginiana*, *L. sinense*, and *F. grandifolia* across the control plots (Table 5). Within the light damage class, the four most abundant species were *O. virginiana*, *A. rubrum*, *A. saccharum*, and *L. benzoin.* The species with the highest relative densities in the moderate damage class were *A. saccharum*, O. *virginiana*, *A. rubrum*, and *C. florida*. Species that were present on greater than 5% of control plots were *A. rubrum*, *O. virginiana*, *F. americana*, and *A. saccharum*. *Ostrya virginiana*, *A.*

Table 4. Density and frequency (number of plots on which each species occurred by damage class) measures for all seedlings (< 1 m height, ≤ 5 cm dbh) in the Sipsey Wilderness, Alabama. Species were ranked based on relative density.

	Density (stems/ha)			Relative Density (%)			Frequency (# plots)			Relative Frequency (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer saccharum	60.0	48.6	48.7	13.2	10.9	11.7	16.0	27.0	28.0	80.0	51.9	75.7
Fraxinus americana	60.0	26.0	22.3	13.2	5.8	5.3	8.0	17.0	17.0	40.0	32.7	45.9
Quercus alba	48.8	53.9	29.1	10.7	12.0	7.0	12.0	30.0	17.0	60.0	57.7	45.9
Acer rubrum	36.3	47.1	23.0	7.9	10.5	5.5	12.0	38.0	19.0	60.0	73.1	51.4
Quercus rubra	35.0	13.5	16.2	7.7	3.0	3.9	13.0	18.0	12.0	65.0	34.6	32.4
Viburnum acerifolium	27.5	40.4	53.4	6.0	9.0	12.8	5.0	18.0	15.0	25.0	34.6	40.5
Ostrya virginiana	22.5	29.8	22.3	4.9	6.7	5.3	10.0	31.0	18.0	50.0	59.6	48.6
Fagus grandifolia	18.8	11.5	6.8	4.1	2.6	1.6	3.0	12.0	7.0	15.0	23.1	18.9
Carya spp.	16.3	31.3	22.3	3.6	7.0	5.3	7.0	29.0	18.0	35.0	55.8	48.6
Ulmus rubra	16.3	7.7	5.4	3.6	1.7	1.3	5.0	7.0	6.0	25.0	13.5	16.2
Ligustrum sinense	15.0	5.3	33.8	3.3	1.2	8.1	7.0	6.0	5.0	35.0	11.5	13.5
Cercis canadensis	13.8	10.6	8.8	3.0	2.4	2.1	6.0	14.0	10.0	30.0	26.9	27.0
Prunus serotina	12.5	10.6	8.1	2.7	2.4	1.9	6.0	17.0	11.0	30.0	32.7	29.7
Frangula caroliniana	11.3	2.4	2.0	2.5	0.5	0.5	3.0	5.0	2.0	15.0	9.6	5.4
Ulmus alata	8.8	1.9	6.1	1.9	0.4	1.5	7.0	3.0	8.0	35.0	5.8	21.6
Aralia spinosa	6.3	1.0	2.0	1.4	0.2	0.5	2.0	2.0	2.0	10.0	3.8	5.4
Lindera benzoin	6.3	2.9	—	1.4	0.6	—	1.0	3.0	—	5.0	5.8	—
Nyssa sylvatica	5.0	10.1	17.6	1.1	2.3	4.2	4.0	16.0	15.0	20.0	30.8	40.5
Vaccinium arboreum	5.0	19.2	4.1	1.1	4.3	1.0	1.0	15.0	4.0	5.0	28.8	10.8
Amelanchier arborea	3.8	2.9	2.0	0.8	0.6	0.5	2.0	2.0	3.0	10.0	3.8	8.1
Asimina triloba	3.8	3.9	5.4	0.8	0.9	1.3	3.0	5.0	3.0	15.0	9.6	8.1
Carpinus caroliniana	3.8	2.9	3.4	0.8	0.6	0.8	2.0	5.0	4.0	10.0	9.6	10.8
Magnolia acuminata	3.8	1.9	2.0	0.8	0.4	0.5	3.0	4.0	3.0	15.0	7.7	8.1
Quercus muehlenbergii	3.8	1.9	—	0.8	0.4	—	3.0	1.0		15.0	1.9	0.0
Juniperus virginiana	2.5	2.9	1.4	0.5	0.6	0.3	2.0	6.0	2.0	10.0	11.5	5.4
Quercus prinus	2.5	6.3	3.4	0.5	1.4	0.8	1.0	7.0	3.0	5.0	13.5	8.1
Styrax grandifolius	2.5	1.0	2.0	0.5	0.2	0.5	1.0	2.0	2.0	5.0	3.8	5.4
Aesculus pavia	1.3	3.4	—	0.3	0.8	—	1.0	3.0	—	5.0	5.8	—
Celtis occidentalis	1.3	0.5	—	0.3	0.1	—	1.0	1.0	—	5.0	1.9	—
Cornus florida	1.3	13.5	11.5	0.3	3.0	2.8	1.0	14.0	11.0	5.0	26.9	29.7
Quercus falcata	1.3	1.0	0.7	0.3	0.2	0.2	1.0	2.0	1.0	5.0	3.8	2.7
Liriodendron tulipifera	—	12.0	6.1	—	2.7	1.5		3.0	5.0	0.0	5.8	13.5
Pinus taeda	—	4.8	10.8	—	1.1	2.6	—	5.0	7.0	—	9.6	18.9
Sassafras albidum	—	2.4	16.2	—	0.5	3.9	—	3.0	3.0	—	5.8	8.1
Oxydendrum arboreum	—	1.9	—	—	0.4	—	—	1.0	—	—	1.9	—
Quercus velutina	—	1.9	2.7	—	0.4	0.6	—	3.0	3.0	—	5.8	8.1
Rhododendron catawbiense	—	1.9	4.1	—	0.4	1.0	—	4.0	1.0	—	7.7	2.7
Magnolia macrophylla		1.4	6.1	—	0.3	1.5	—	3.0	8.0	—	5.8	21.6
Pinus virginiana	—	1.4	2.0	—	0.3	0.5	—	2.0	2.0	—	3.8	5.4
Crataegus phaenopyrum	—	1.0	—	—	0.2	—	—	2.0	—	—	3.8	—
Rhamnus cathartica	—	1.0	—	—	0.2	—	—	2.0	—	—	3.8	—
Betula lenta	—	0.5	—	—	0.1	—	—	1.0	—	—	1.9	—
Ilex opaca	—	0.5	—	—	0.1	—	—	1.0	—	—	1.9	—
Kalmia latifolia	—	0.5	—	—	0.1	—	—	1.0	—	—	1.9	—
Morus rubra	—	0.5	—	—	0.1	—	—	1.0	—	—	1.9	—
Pinus echinata	—	—	1.4	—	—	0.3	—	—	2.0	—	—	5.4
Ulmus americana	—	—	1.4	—	—	0.3			1.0	0.0	0.0	2.7
Diospyros virginiana	—	—	0.7	—	—	0.2	—	—	1.0	—	—	2.7
Juglans nigra	—	—	0.7	—	—	0.2	—	—	1.0	—	—	2.7
Quercus stellata	—	—	0.7	—	—	0.2	—	—	1.0	—	—	2.7
Tilia americana	—	—	0.7	—	—	0.2	—	—	1.0	—	—	2.7
Total	**456.3**	**447.1**	**416.9**	**100.0**	**100.0**	**100.0**	—	—	—	—	—	—

Table 5. Density and frequency (number of plots on which each species occurred by damage class) measures for all saplings (≥ 1 m height, ≤ 5 cm dbh) in the Sipsey Wilderness, Alabama. Species were ranked based on relative density.

	Density (stems/ha)			Relative Density (%)			Frequency (# plots)			Relative Frequency (%)		
Species	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**	**Control**	**Light**	**Moderate**
Acer rubrum	22.5	27.9	28.4	15.3	16.1	10.9	9.0	23.0	16.0	45.0	44.2	43.2
Ostrya virginiana	22.5	29.8	33.1	15.3	17.2	12.7	8.0	28.0	22.0	40.0	53.8	59.5
Ligustrum sinense	21.3	4.8	16.2	14.4	2.8	6.2	5.0	5.0	4.0	25.0	9.6	10.8
Fagus grandifolia	12.5	11.5	4.7	8.5	6.7	1.8	4.0	11.0	4.0	20.0	21.2	10.8
Acer saccharum	10.0	17.3	33.1	6.8	10.0	12.7	6.0	20.0	22.0	30.0	38.5	59.5
Fraxinus americana	10.0	8.7	10.8	6.8	5.0	4.1	7.0	9.0	12.0	35.0	17.3	32.4
Styrax grandifolius	5.0	—	2.7	3.4	—	1.0	1.0	—	2.0	5.0	—	5.4
Aesculus pavia	3.8	6.7	—	2.5	3.9	—	1.0	4.0	—	5.0	7.7	—
Carpinus caroliniana	3.8	4.8	13.5	2.5	2.8	5.2	3.0	5.0	8.0	15.0	9.6	21.6
Cercis canadensis	3.8	1.4	8.8	2.5	0.8	3.4	3.0	2.0	7.0	15.0	3.8	18.9
Quercus prinus	3.8	—	1.4	2.5	—	0.5	1.0	—	1.0	5.0	—	2.7
Viburnum acerifolium	3.8	10.1	7.4	2.5	5.8	2.8	2.0	10.0	4.0	10.0	19.2	10.8
Frangula caroliniana	2.5	0.5	3.4	1.7	0.3	1.3	2.0	1.0	3.0	10.0	1.9	8.1
Juniperus virginiana	2.5	1.0	1.4	1.7	0.6	0.5	2.0	2.0	2.0	10.0	3.8	5.4
Rhamnus cathartica	2.5	—	—	1.7	—	—	1.0	—	—	5.0	—	—
Tilia americana	2.5	—	—	1.7	—	—	1.0	—	—	5.0	—	—
Ulmus alata	2.5	1.0	2.7	1.7	0.6	1.0	2.0	2.0	4.0	10.0	3.8	10.8
Lindera benzoin	2.3	12.5	—	1.5	7.2	—	2.0	2.0	—	10.0	3.8	—
Cornus florida	1.3	7.2	16.9	0.8	4.2	6.5	1.0	10.0	14.0	5.0	19.2	37.8
Magnolia macrophylla	1.3	1.0	8.1	0.8	0.6	3.1	1.0	2.0	6.0	5.0	3.8	16.2
Nyssa sylvatica	1.3	3.4	13.5	0.8	1.9	5.2	1.0	6.0	9.0	5.0	11.5	24.3
Prunus serotina	1.3	1.4	3.4	0.8	0.8	1.3	1.0	3.0	5.0	5.0	5.8	13.5
Quercus alba	1.3	1.4	1.4	0.8	0.8	0.5	1.0	2.0	1.0	5.0	3.8	2.7
Quercus rubra	1.3	1.4	4.7	0.8	0.8	1.8	1.0	3.0	6.0	5.0	5.8	16.2
Ulmus rubra	1.3	1.0	2.0	0.8	0.6	0.8	1.0	1.0	3.0	5.0	1.9	8.1
Vaccinium arboreum	1.3	—	2.0	0.8	—	0.8	1.0	—	2.0	5.0	—	5.4
Carya spp.	—	4.8	5.4	—	2.8	2.1	—	10.0	4.0	—	19.2	10.8
Magnolia acuminata	—	2.4	3.4	—	1.4	1.3	—	4.0	4.0	—	7.7	10.8
Asimina triloba	—	1.9	4.7	—	1.1	1.8	—	4.0	2.0	—	7.7	5.4
Amelanchier arborea	—	1.4	—	—	0.8	—	—	—	—	—	—	—
Celtis occidentalis	—	1.0	—	—	0.6	—	—	2.0	—	—	3.8	—
Diospyros virginiana	—	1.0	2.0	—	0.6	0.8	—	2.0	3.0	—	3.8	8.1
Rhododendron catawbiense	—	1.0	—	—	0.6	—	—	1.0	—	—	1.9	—
Betula lenta	—	0.5	—	—	0.3	—	—	1.0	—	—	1.9	—
Castanea dentata	—	0.5	0.7	—	0.3	0.3	—	1.0	1.0	—	1.9	2.7
Liriodendron tulipifera	—	0.5	2.0	—	0.3	0.8	—	1.0	3.0	—	1.9	8.1
Morus rubra	—	0.5	—	—	0.3	—	—	1.0	—	—	1.9	—
Oxydendrum arboreum	—	0.5	0.7	—	0.3	0.3	—	1.0	1.0	—	1.9	2.7
Pinus taeda	—	0.5	2.0	—	0.3	0.8	—	1.0	1.0	—	1.9	2.7
Quercus falcata	—	0.5	—	—	0.3	—	—	1.0	—	—	1.9	—
Quercus velutina	—	0.5	—	—	0.3	—	—	1.0	—	—	1.9	—
Sassafras albidum	—	0.5	10.1	—	0.3	3.9	—	1.0	2.0	—	1.9	5.4
Ulmus americana	—	0.5	—	—	0.3	—	—	1.0	—	—	1.9	—
Arundinaria tecta	—	—	10.1	—	—	3.9	—	—	1.0	—	—	2.7
Quercus muehlenbergii	—	—	0.7	—	—	0.3	—	—	1.0	—	—	2.7
Total	**147.3**	**173.1**	**261.5**	**100.0**	**100.0**	**100.0**	—	—	—	—	—	—

rubrum, *A. saccharum*, and *F. grandifolia* each occurred on greater than 10% of light damage class plots. On moderate damage plots, *A. saccharum*, *O. virginiana*, *A. rubrum*, *C. florida*, and *F. americana* were the five species that were found on greater than 10% of plots. Notably, *Q. rubra* was the only *Quercus* sapling species that occurred on more than five plots, the majority of which were present in the moderate damage class. *Quercus alba*, which occurred in relatively high densities in the seedling layer, was only present on one control plot, two light plots, and one moderate plot. The two alien species that occurred in the seedling layer also occurred in the sapling layer. Notably, *L. sinense* represented 14.4%, 2.8%, and 6.2% of total sapling layer stems on control, light, and moderate plots, respectively. Only two *Quercus* species, *Q. prinus* and *Q. rubra*, had relative densities above 1% in any of the three sapling damages classes (Table 5). I found no significant statistical differences in Shannon diversity except in the sapling layer between light and moderate damage classes, for which mean values were 1.02 ± 0.07 and 1.32 ± 0.08 (P = 0.0122).

Chapter 4: Discussion

4.1 Light Regimes

The majority of variables I tested to elucidate the characteristics of understory light regimes following intermediate-scale disturbance had returned to pre-disturbance conditions after three growing seasons. However, between control and moderate damage plots and between light and moderate damage plots there was a significant difference in percent of full sunlight; possibly accounting for the differences in diffuse light at breast height that were not apparent in the data from hemispherical photographs. The different between percent of full sunlight on control v. light damage plots was not discernible, which does not necessarily mean canopy gaps have completely filled, but rather that well-developed individuals in the midstory increased sufficiently in height to negate the increases in light from canopy gaps. Although the canopy was still open, midstory stems restricted light to the seedling and sapling layers. Consequently, even though the mean percent of full sunlight in the moderate plots fell within the 20–40% range required to regenerate *Quercus* (Dey 2002), light levels below breast height were not sufficient. Percent of full sunlight on control and light damage plots, which best represent actual understory light levels at breast height, were comparable to those from the region (Canham et al. 1990, Schweitzer and Dey 2011). Schweitzer and Dey (2011) quantified forest response to different levels of regeneration harvests on a forest in north Alabama and noted levels of canopy openness and gap fraction were comparable to those found in this study after three growing seasons. The stage of stand development is particularly important when evaluating the effects of intermediate-scale disturbances on understory light levels. The majority of stems disturbed in wind events are canopy trees, and during the understory reinitiation stage, the midstory is well-developed. As such, rather than creating new opportunities for the establishment of new stems, the disturbance serves only as a mechanism that releases stems already present in the midstory. Consequently, the resultant changes in the light regime are ephemeral and last only a few growing seasons.

4.2 Effects on composition and biodiversity

Fewer compositional differences were found between the three damage classes than was originally hypothesized. Trees with larger diameters were disproportionately killed by the storm event. This is consistent with the results from other studies on wind disturbance (Foster and Boose 1992, Peterson and Rebertus 1997, Canham et al. 2001). I did not document species-specific mortality patterns among canopy trees and thus, canopy tree diversity was not significantly different across the three damage classes. In all overstory damage classes, *Q. alba* was a major component of the canopy and consequently, it was the species most consistently killed across both damage classes. *Quercus alba* represented 30% of the 1,617 stems within the intermediate 3 (I3) crown class. This is the crown class that I hypothesized would have the greatest potential to recruit to the canopy in the future (i.e. fill canopy space that is available after current dominant and co-dominant trees are removed), as these are the tallest and most developed stems within the intermediate crown class. Likewise, the genus *Quercus* and the group *Quercus-Carya* represented 43% and 65% of total I3 stems, respectively. Additionally, it is important to note that not only will I3 stems rapidly capture canopy positions after disturbances, but that they are also less susceptible to wind damage because of their size. If these stems are able to fill canopy positions created by the mortality of current dominant and co-dominant trees, this forest could remain dominated by *Quercus-Carya* (Xi and Peet 2011) until the point when *Acer* species begin to fill the majority of canopy openings. *Acer* saplings accounted for 48% of all sapling layer stems. Based on the preponderance of the *Acer* genus in the well-developed understory and midstory and according to canopy gap dynamics, I hypothesize that these species will succeed a majority of canopy trees as this forest moves toward the complex stage of development and the canopy is subsequently disturbed (Barden 1979, 1980, White et al. 1985, Yamamoto and Nishimura 1999).

In developing secondary stands that have not reached the complex stage of development, gaps created by the death of canopy trees are relatively small and typically close by lateral crown expansion rather than by height growth of sub-canopy stems (Hart and Grissino-Mayer 2009, Hart et al. 2011, Richards and Hart 2011). In contrast, as stands age the spacing between canopy trees increases and each canopy tree crown represents a larger portion of the main forest canopy. When one of these large canopy trees is removed, it creates a relatively large gap. These large gaps are typically filled by the height growth of sub-canopy individuals (Clebsch and Busing 1989, Busing 1995). The majority of forest stands in the eastern US are second growth (i.e. not primeval), less than 100 years old, and established after being anthropogenically cleared (Cowell 1998, Rebertus and Meier 2001). Prior to European settlement of the eastern US, it is estimated that a larger percentage of the landscape supported stands in the complex stage of development (Whitney 1994, Lorimer 2001). A change in stand structure from pre-European settlement to current, may have influenced canopy disturbance regimes, notably canopy gap size. Contemporary forests with relatively small canopy gaps that more often fill by lateral crown expansion, may have had significant impacts on regeneration of *Quercus*. In the forest studied here, which is in the understory reinitiation stage of development, canopy disturbances act as a top-down control on competition and serve only to release advanced regeneration, which is largely comprised of *Acer* spp. individuals. Intermediate-scale disturbances during this stage of development, without competition control measures, provide the proper amount of sunlight to regenerate *Quercus* spp., but do not provide the mechanism for these species to outcompete shade-tolerant mesophytes that are already present in the sapling layer.

I found no significant differences between Shannon diversity in the tree layer. The only statistical differences in Shannon diversity were between the light and moderate damage classes in the sapling layer, but neither damage class was significantly different from the control class. I attribute this finding, especially in the regeneration layer where the greatest disparity would be expected, to the amount of time since the disturbance. Any significant differences in biodiversity caused by the opening of canopy gaps from the storm have disappeared (Lorimer et al. 1994, Royo and Carson 2006, Beaudet et al. 2007, Hart and Grissino-Mayer 2009). In fact, diversity of all woody stems was lowest in the moderate damage class after three growing seasons. This finding contradicts the intermediate disturbance hypothesis proposed by Connell (1978), which posits that intermediate levels of disturbance, both in spatial and temporal extent, maintain the highest levels of biodiversity. This hypothesis has been intensely criticized (e.g. Wilkinson 1999, Bongers et al. 2009, Fox 2012, Fox 2013). Indeed, Fox (2012) called for the model to be abandoned and asserted that the hypothesis was too simplistic to incorporate the biological complexities of ecosystem response to disturbance. I hypothesized that Shannon diversity would increase with increasing disturbance because in highly disturbed plots both residual stems and new germinants that colonized the disturbed areas would be present. Furthermore, I hypothesized new germinants in disturbed neighborhoods would include shade intolerant species that were not present in the understory prior to the canopy disturbance event. I documented few shade-intolerant species that might have been expected to occur after this level of disturbance. The canopy disturbance event documented here served to release stems in the well-developed midstory that was comprised primarily of shade-tolerant mesophytes rather than create new niche space for the colonization of early seral species. I agree with Sheil and Burslem (2003, 2012) which state the hypothesis should be more narrowly defined as the theory does not hold for stands during the understory reinitiation stage when composition of the canopy and regeneration layer are different (i.e. in successional stands).

4.3 Effects on regeneration and biodiversity

Although I hypothesized that there would be discernible differences in regeneration layer Shannon diversity between control, light, and moderate damage classes, it may be these types of disturbances have an ephemeral effect on the regeneration layer. Instead, it is much more likely that wind storms of this intensity would cause indirect damage to seedlings and saplings through fallen canopy trees crushing patches of seedlings and saplings. Consequently, the effects of intermediate-scale wind disturbance act as a top-down control on regeneration by releasing midstory stems or developed regeneration when forests are in the understory reinitiation stage of development. In this specific case, the canopy gaps caused by the tornado released *Acer* stems and further widened the disparity between the presence of *Acer* and *Quercus* advanced regeneration. Hart and Grissino-Mayer (2009) found that in *Quercus* individuals, the increase in resources from a canopy opening would generally not be sustained in canopy trees for more than four years, which may also be true for the regeneration layer. This finding would corroborate our results from canopy openness above breast height and gap fraction above breast height, which after three growing seasons returned to pre-disturbance levels. Notably, I documented minimal amounts of shade-intolerant *L. tulipifera* in the understory, despite that they should be present when significant gaps are opened in the canopy (Boring et al. 1981, Phillips and Shure 1990, Busing 1995). This may illustrate the complexity of understory conditions that are present in the understory reinitiation phase of stand development and further emphasize why *Quercus* individuals are not able to outcompete shade-tolerant mesophytes in the sapling layer.

I documented relatively high densities of the alien invasive *L. sinense* on control and moderate regeneration plots in our study. *Ligustrum sinense* is a semi-evergreen to evergreen shrub, and a prolific seed producer whose fruit are distributed by berry-eating birds and other animals (Zhao et al. 2013). Its low light saturation point makes it adaptable to many sites, allowing this species to invade closed-canopy forests (Wilcox and Beck 2007, Hart and Holmes 2013). It is likely that the presence of this species, which has become a growing concern throughout the eastern US because of its ability to out-compete most vegetation and form dense monocultures, indicates the beginning of the invasion of *L. sinense* into this area (Langland and Craddock-Burks 1998, Wilcox and Beck 2007, Hart and Holmes 2012). Within the Sipsey Wildneress, governmental agencies are not allowed to use herbicide (the most common control measure of *L. sinsense*) and are typically restricted within Wilderness Areas to remove alien invasive plants, making it potentially difficult to control an invasion (U.S. Senate, 1964). I located all plots that contained privet (n = 13), and 4 were control, 4 were light damage, and 5 were moderate. One such plot contained 38 seedlings and 9 saplings, and was located on a plot classified as moderately damaged. The evenness of this species' presence across damage classes is somewhat contrary to literature that suggests that either intact forests have increased resistance to alien invasion or that alien invasives are almost exclusively disturbance obligate (Crawley 1987, Rejmánek 1989, Von Holle et al. 2003, Martin et al 2009). Additionally, Zhao et al. (2013) found no specific direction or primary front of invasion by *L. vulgare* into a forest in northeast Ohio. Rather, they posited that the invasion occurred as a general expansion from specific points rather than from a single patch or edge of the forest. Other studies determined that the particularly detrimental effect of *Ligustrum* is the genus' ability to form monospecific stands that in turn decrease species richness and abundance in invaded stands (Merriam and Feil 2002, Wilcox and Beck 2007). Notably, Hart and Holmes (2013) found that *L. sinense* was able to invade a small forest with an intact canopy in Alabama, and made up 97% of all woody stems surveyed. I did not find a relationship between damage class and the presence of *L. sinense*, indicating that this species is beginning to invade the Sipsey Wilderness, and that its establishment is not disturbance obligate.

Chapter 6: Management Implications

When implementing a natural disturbance-based approach to forest management, emphasis is placed on creating structures and community assemblages through silviculture that are similar to those that were historically produced by natural disturbance processes (Seymour and Hunter 1999). Wind is the most common and arguably the most influential canopy disturbance agent in hardwood forests of the eastern US (Runkle 1985). The goal of natural disturbance-based management is not to mimic the actual disturbance event (i.e. trees are not typically felled by winching to emulate the effects of strong winds), but rather to use the effects of such events (e.g. the altered light regime) as models for individual and cumulative silvicultural treatments with the penultimate goal of minimizing the structural, compositional, and functional disparities between managed and unmanaged stands. The success of this management approach requires clear and tangible guidelines that are based on quantitative data from stands that are situated in similar biophysical settings and are therefore appropriate analogues (Seymour et al. 2002, Franklin et al. 2007).

Based on the quantitative data collected and analyzed here, I recommend managers that wish to mimic the effects of intermediate-scale wind disturbances aim to create canopy gaps that provide light levels of ca. 20% of full sunlight in the understory. Additionally, while canopy openness and gap fraction values were influenced by individuals in the midstory, to create conditions similar to those found at breast height a value of approximately 8–10% of full sunlight would be appropriate. The average percent basal area removed was 48%, so I would recommend basal area retention be maintained between 35–50%. Mortality rates were highest for the genus *Quercus*, but this genus was the most abundant in the canopy and therefore, managers should remove trees based on size and markets more than attempting to bias against certain taxa. This trend should allow managers to marry ecological goals with economic constraints based on market fluctuations more easily. Lastly, as intermediate-scale wind disturbances do not affect stands uniformly, managers should not distribute treatments throughout a stand in a regular pattern, but rather implement various even-aged treatments in patches thereby creating two or more age classes within a stand. To emulate spatial patterns of natural wind disturbance, managers should apply treatments in patches that exhibit different gradients of damage which will increase intra-stand heterogeneity. Group selections, which serve as release and regeneration treatments and may include temporary or permanent leave trees, should be implemented in linear fashions. Such an approach may take advantage of existing road networks (Seymour 2005). Finally, management based on intermediate-scale wind disturbance should not be considered to affect woody plant biodiversity in positive or negative ways.

Regeneration failure of *Quercus* has been widely reported across all but the most xeric site types throughout the Central Hardwood Forest of the eastern US (Abrams 1992, Lorimer 1993, Nowacki and Abrams 2008, McEwan et al. 2011) and thus, managers that follow a natural disturbance-based management approach, but that also wish to maintain *Quercus*, must be careful. Although variability exists at the species-level, *Quercus* are generally considered only moderately tolerant of shade and canopy disturbance events that increase insolation in the understory are required for regeneration (Dey 2002). These canopy disturbances must be sufficiently large to provide adequate light levels, but not so large that they allow for the establishment of shade-intolerant species that can outcompete *Quercus* in high light environments (Runkle 1985, Grayson et al. 2012). A disturbance regime typified by localized, gap-scale events typically results in dominance by shade-tolerant species, while a disturbance regime of catastrophic events typically maintains shade-intolerant, early seral species. Canopy disturbances at the intermediate scale may be therefore be appropriate for regenerating *Quercus* and other moderately-shade tolerant taxa such as *Carya*. However, the intermediate-scale canopy disturbance event documented in this study was not sufficient to regenerate *Quercus* and other taxa moderately tolerant of shade. Similarly in Schweitzer and Dey (2011), various intensities of thinning treatments only ephemerally increased light levels in the understory for three years before the canopy and midstory layers were able to compensate and pre-disturbance light levels returned. I hypothesize this is a function of the high density of shade-tolerant individuals in understory and midstory strata. Thus, in stands with a significant component of shade-tolerant mesophytes in the understory and where the management objective is to regenerate *Quercus*, regeneration harvests should be implemented in conjunction with competition reduction measures such as fire or herbicide application (Loftis 1990, Schweitzer and Dey 2011, Hutchinson et al. 2012, Brose et al. 2013). Although competition removal may fall outside the historical range of variation (i.e. is not an element of a natural disturbance process), these actions may be essential to maintain mid-successional taxa such as *Quercus* and *Carya*.

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