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Stand Dynamics Following Gap Scale Exogenous Disturbance in a Single Cohort Mixed Species Stand in Morgan County, Tennessee

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To the Graduate Council:

I am submitting herewith a thesis written by Brian Hughett entitled "Stand Dynamics Following Gap Scale Exogenous Disturbance in a Single Cohort Mixed Species Stand in Morgan County, Tennessee." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Forestry.

Wayne Clatterbuck, Major Professor

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Abstract

Southeastern mixed species stands vary greatly in terms of composition, structure, and disturbance. Limited research has been conducted on the successional processes occurring after small scale exogenous disturbance within second growth mixed species forests of the southeast. During the years of 1998-2002, southern pine beetle (*Dendroctonus frontalis* Zimmerman) populations reached epidemic proportions, affecting forests throughout the southeastern United States. The southern pine beetle outbreak resulted in the mortality of nearly all overstory *Pinus strobus* on the study area. Due to the low basal area and relatively even distribution of eastern white pine on the study area, numerous single stem canopy gaps were formed. Management activities conducted in 2003 following this disturbance involved the salvage cutting of easily accessible overstory *Pinus strobus* stems.

The goal of this study is to investigate stand dynamics following gap scale exogenous disturbance within a secondary forest stand during the understory re-initiation stage of development. Differences in composition, structure, and growth under single stem canopy gaps were analyzed under two scenarios, using analysis of variance, where the stem was either removed or left as a standing snag. There were no significant differences in composition and structure of large diameter residual stems within upper canopy strata. Advance reproduction was recruited as a new cohort following the disturbance. Where the stem was removed, the recruitment consisted of eastern white pine (*Pinus strobus*), yellow-poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*). Where the stem was left as a

standing snag, the advance reproduction recruited as a new cohort was comprised of red maple, American beech (*Fagus grandifolia*), and oaks (*Quercus spp.*). The removal of the gap maker provides a pathway to recruit suppressed stems into larger diameter and crown classes. Salvage cutting fostered the growth of stems from intermediate or suppressed crown classes whereas leaving a standing snag favored the growth of adjacent stems within dominant or codominant crown classes.

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Chapter 1: Introduction

Forests of southern Appalachia are subject to both anthropogenic and non-anthropogenic disturbance. Disturbances affect the composition, structure, and future development of forests at varying scales and frequencies. Differences in disturbance types and characteristics can be attributed to species composition, age, geographic location, time since previous disturbance, and developmental stage of the forest (Oliver and Larson 1996). Gap scale disturbances are characterized by small openings within the canopy that occur due to the loss of one or a few trees. Small canopy gaps often close quickly as a result of lateral crown expansion, which limits the growth response of understory trees. The ability of trees to respond following gap scale disturbance depends on species characteristics, age, and the gap environment (Wilder and others 1999).

Between 1998 and 2002, southern pine beetle (*Dendroctonus frontalis Zimmerman)* populations reached epidemic proportions, affecting forests throughout the southeastern United States. Prior to the pine beetle epidemic, eastern white pine (*Pinus strobus*) accounted for an average of 18 percent of the total basal area of overstory trees on our sites. Previous research has shown that high basal area of hardwoods relative to that of pine species limits the spread of southern pine beetle (Schowalter and Turchin 1993). However, research has also demonstrated that stands with low pine densities can become infested if they are overstocked (Lorio 1994). The southern pine beetle outbreak resulted in the mortality of nearly all overstory *Pinus strobus* within the study area. Due to the low basal area and relatively even distribution of *Pinus strobus* on our sites, numerous canopy gaps formed. Management activities conducted on our sites following the outbreak involved the salvage cutting of the easily accessible overstory *Pinus strobus* stems killed by the southern pine beetles.

Limited research has been conducted on the successional processes occurring after small scale exogenous disturbance within second growth mixed species forests of the Southeast, especially *Pinus strobus*-hardwood mixtures. Despite numerous studies focusing on forest gap dynamics in mixed species stands, research has not directly compared the changes in species composition and growth response under canopy gaps formed by the mortality of a single stem where the stem was either cut or left as a standing snag (Runkle, 1981, 1985, 1990, 1991, 1998; Yamamoto, 2000; Webster and Lorimer, 2005; Hart and Grissino-Mayer, 2009; Cox et al., 2016). The goal of this study was to investigate stand dynamics following gap scale exogenous disturbance. Specifically, the objectives are to determine differences in forest composition, structure, and growth response under canopy gaps created by the mortality of a single stem in which the stem was either removed, or left as a standing snag.

Chapter 2: Literature Review

Forest Disturbance

All forests are subject to disturbance. Forest disturbances are defined as relatively discrete events that change stand structure, resource availability, or modify the abiotic conditions within a forest (Pickett and White, 1985). Forest disturbance is frequent in eastern forest systems and can modify stand structure, species composition, growth rates, and habitat. Disturbances can also be defined as the driver of forest succession by providing the growing space and resources necessary for regeneration (Runkle 1985; Oliver and Larson 1996). The change following a disturbance is dependent upon the magnitude of the disturbance event as well as the susceptibility of the stand to the disturbance type (Odum, 1971; White, 1979; Spurr and Barnes, 1980).

Disturbance Classification

Forest disturbances are often classified by severity, spatial distribution, frequency, and causal agent (Bazzaz 1983; White and Pickett, 1985). Typically, disturbances are grouped into three categories based on the amount of overstory removed: stand-replacing disturbances, intermediate-severity disturbances, and gap-scale disturbances (Oliver and Larson, 1996; Cowden et al., 2014). Stand-replacing disturbances kill or remove most existing trees. Examples of stand-replacing disturbances are: extreme wind events, glaciers, and severe fires. Following stand-replacing disturbances, the resulting cohort of regeneration competes only against itself and is free from existing overstory competition (Oliver and Larson, 1996).

Intermediate-severity disturbances kill only trees of a specific size or species resulting in a mosaic of mortality throughout a stand (Everham and Brokaw, 1996; Canham et al., 2001; Peterson, 2007; White et. al., 2015). Intermediate-severity disturbances often kill a patchwork of overstory stems throughout a stand without affecting the remainder of the overstory individuals (Frelich et al., 1998; Cox et al., 2016). Gap-scale disturbances occur when one or more overstory stems are either injured or killed (Watt, 1947; Runkle, 1981; Runkle, 1985; Yamamoto, 2000). These canopy gaps create only temporary increases in light and resource availability (Canham, 1988). The causes of gap-scale disturbances are commonly: senescence, insects, disease, wind-throw, lightning strikes, and partial harvesting (Runkle and Yetter, 1987).

Disturbance Frequency

Research suggests that disturbance intensity and disturbance frequency are inversely related (Frelich and Lorimer, 1991; Mitchell, 2013). Within the Central Hardwood Forest, the time between stand-replacing disturbances is far greater than the life-span of the overstory trees (Runkle, 1991). The average return interval of stand-replacing disturbances in parts of the eastern United States is about 1,000 years (Canham and Loucks, 1984; Lorimer and Freich, 1989). However, the return interval of intermediate-severity disturbances is only 30-50 years (Nowacki and Abrams, 1997; Ruffner and Abrams, 1998; Hart et al., 2012). Disturbance frequency is also dictated in part by stand age and various anthropogenic factors (Seymour and Hunter, 1999; Dahir and Lorimer, 1996). Both old growth remnant and secondary growth hardwood forests of the eastern United States are frequently disturbed by gap-scale disturbances (Cox et. al., 2016; Hart and Grissino-Mayer, 2008; Runkle 1985; Runkle, 1991).

Forest Gaps

Forest gaps are created by the injury or death of one or more overstory stems which create small, temporary canopy openings (Yamamoto, 2000). Forest gaps vary in size, shape, and gap formation mechanism. Runkle (1992) defined two types of gap formation: a treefall gap, where the stem has fallen or tipped over and a snag gap, where the stem remains standing. The differences between the two types of gaps are the amount or severity of soil exposure, light, and disturbance. Snag gaps alter the gap environment differently than sudden gaps (Franklin et al., 1987; Krasny and Whitmore 1992; Clinton et al., 1994). For example, the bole and branches snags may block additional sunlight increasing the likelihood of gap closure by perimeter trees (Hart and Grissino-Mayer, 2008).

Gap size and shape are often dependent on how the gap was formed, the number of overstory individuals involved, and the age of the overstory (Yamamoto, 2000). A gap resulting from the injury of a single stem would be smaller than a gap involving the loss of several stems. In older stands, the crowns of overstory stems are larger and the spacing between stems is greater. When canopy gaps are created within these older stands, the gaps are large (Runkle, 1998; Yamamoto, 2000). The shape of forest gaps are highly variable and can change over time. When trees are uprooted, they often impact surrounding individuals, further changing the shape and size of the gap.

Forest Gap Dynamics

Forest development after gap-scale disturbances is more complicated than development following a stand-replacing disturbance. Gap-scale disturbances alter stand structure, species composition, and the growth rates of residuals depending on how much of the existing forest is remaining, its species composition, and crown positions (Oliver and Larson, 1996). The focus of much of the research on gap dynamics involves determining the method of gap closure and the associated growth response of individuals based on their species specific growth characteristics and position within the vertical structure of the stand. The prevailing theory on gap closure is that when a small gap is formed, the surrounding overstory stems are able to capture the growing space through lateral crown expansion. In these small gaps, tree size and overstory structure is modified with only modest increases in understory species diversity and height growth (Hart and Grissino-Mayer, 2008). Conversely, when larger gaps are formed, the surrounding overstory stems aren't able to completely fill the gap and allow a new cohort to regenerate (Runkle, 1985; Webster and Lorimer, 2005).

Species-specific growth rates and successional strategies influence the ability of trees to respond to newly formed canopy gaps. To simplify these differences, tree species are often grouped into categories based on shade tolerance. Rapid establishment and fast growth are characteristic of shade intolerant stems such as *Liriodendron tulipifera* (Oliver and Larson, 1996). These characteristics are advantageous in larger gaps where they may be able to reach the canopy in a single disturbance event (Hart and Gissino-Mayer, 2008). On the other end of the spectrum are shade tolerant stems such as *Acer saccharum*. These shade tolerant species can survive for long periods in relatively low light conditions. However, most shade tolerant species still require canopy disturbance to become a future component of the overstory (Runkle, 1990; Oliver and Larson 1996).

The horizontal and vertical position of a given tree prior to the formation of a canopy gap is also critical in determining how a gap will close and by which stems (Tryon et al., 1992). In eastern forests, the most dominant successional pathway is the release of advance reproduction within canopy gaps (Clinton et al. 1994; Kimball et al. 1995). Taller seedlings and saplings existing as advance reproduction can limit the establishment of shade intolerant species within canopy gaps (Connell, 1989). Other regeneration mechanisms such as stump or root sprouting have been shown to be highly competitive within canopy gaps of all sizes (Philips and Shure, 1990).

Eastern White Pine

Pinus strobus is primarily a northern species. However, it is still fairly abundant in the Southeast where it exists primarily in mixtures with various hardwood species (United States Forest Service, 1983). In these mixed hardwood forests, *Pinus strobus* frequently occurs as scattered dominant and emergent stems at low densities (Hibbs, 1982). *Pinus strobus* is also present as advance reproduction in mature mixed hardwood forests where it can eventually reach the canopy following overstory disturbance. The shade tolerance and successional strategy of *Pinus strobus* is somewhat unique. *Pinus strobus* can act as both a pioneer species due to its ability to become established on exposed sites. In mature hardwood mixtures, *Pinus strobus* is an advance regeneration dependent species with intermediate to high shade tolerance and slow growth of young stems. *Pinus strobus* seedlings can tolerate as much as 80 percent full shade, but they become less shade tolerant with age (Shirley, 1945). Height and diameter growth is also slow initially, but between 10 and 20 years of age or following release from overstory competition, the growth of *Pinus strobus* eguals or exceeds that of hardwoods on most sites (Wendel and Smith, 1990).

Chapter 3: Objectives

1. To compare the basal area, density, and species richness of overstory stems between 1/5th acre plots where the gap maker was either salvage cut in 2003 or left as a standing snag (treatments).
2. To compare the density and species composition of overstory stems by crown position between treatments.
3. To examine the diameter distributions of 1/5th acre plots for each treatment.
4. To compare the density and cumulative height of regeneration between treatments.
5. To compare the density and cumulative height of regeneration by shade tolerance between treatments.
6. To compare overstory growth response between treatments, time, and the interaction effect of treatment and time.

Chapter 4: Methods

Study Site

The study was conducted in an 88.4 acre stand within the Cumberland Forest field research unit of the University of Tennessee Forest Resources Research and Education Center located in Morgan County, Tennessee (Figure 1). This area is located within the Cumberland Mountain Physiographic Region, subregion two, landtype association G, which is the Wartburg Basin and Jellico Mountains. Regionally, the topography is characterized by elevations of 1200 to 3000 feet above sea level, steep slopes of 20 to 60 percent, narrow crests and narrow, winding valleys (Smalley 1984). Within the study site, elevation ranged from 1200 to 1500 feet above sea level with slopes of 5 to 45 percent. Regional soils are deep sandy-silt loams derived from weathered colluvial sandstone and shale. Soils are described as acidic, well to excessively drained, and are of moderate to moderately low productivity (Smalley 1984). Soils within the study area were predominantly of the Gilpin-Petros complex or the Lonewood series, which reflects the regional description.

The climate is classified as humid mesothermal with long moderately hot summers and short moderately cold winters. The mean annual temperature is 55 degrees Fahrenheit (Thornthwaite 1948). The frost free period is typically 180 to 190 days with the first freeze in mid- to late October and the last freeze occurring in mid-April. The region receives an average annual precipitation of 49 inches, which is usually well distributed throughout the year. However, the region is prone to short periods of intense

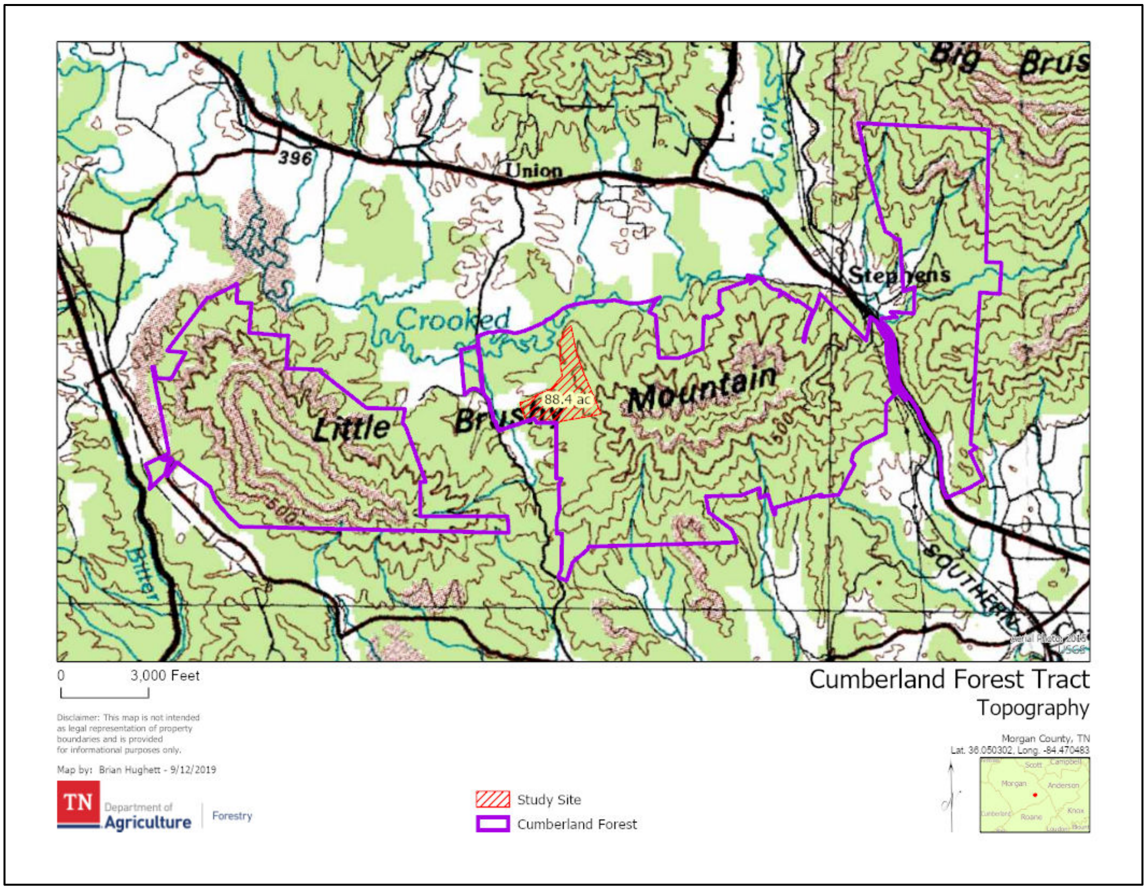

Figure 1. Location of study site and University of Tennessee Forest Resources Research and Education Center in south-central Morgan County, Tennessee

precipitation or drought (Smalley 1984). Braun (1950) included the Wartburg Basin as part of the Cumberland Mountain region and classified it as the "outlying area" of the Mixed Mesophytic Forest region. Local topography and soils are known to influence forest composition. True mesophytic species (*Tilia americana* and *Aesculus flava*) dominate only in protected lowland areas. Within the Wartburg Basin, upland pine and pine oak communities are prevalent (Braun 1950). Despite the patchy old-growth mixed mesophytic forest remaining today, much of the region's forest structure and composition has changed (Hinkle 1978). Regionally, disturbance caused by detrimental logging practices (1800-present), coal mining (1953-present), wildfire, forest pests, and pathogens has altered the community types located within the Wartburg Basin (Deselm et al. 1978).

Prior to 1950, the Cumberland Forest field research unit property was primarily an apple orchard that had diminished over time due to a lack of management. Much of the property contained areas of abandoned pasture and forested stands in various stages of stand development. Mixed stands containing *Pinus strobus,* likely developed in these abandoned areas. The property was purchased by the University of Tennessee in 1950. With university ownership, what remained of the apple orchards was cleared. No major disturbances occurred on the site while under university ownership until 2003.

Between 1998 and 2002, southern pine beetle (*Dendroctonus frontalis Zimmerman)* populations reached epidemic proportions, affecting forests throughout the southeastern United States. By the end of this epidemic, most of the southern yellow pines had been killed; causing the southern pine beetle to infest non-preferred hosts such as *Pinus strobus* and *Tsuga canadensis* (Cassidy, 2005). The southern pine beetle outbreak resulted in the mortality of nearly all overstory *Pinus strobus* within the study area by 2003. Due to the low basal area and relatively even distribution of *Pinus strobus* on our sites, numerous canopy gaps formed. Management activities conducted on our sites following the outbreak involved the salvage cutting of the easily accessible overstory *Pinus strobus* stems that the southern pine beetles killed.

At the time of data collection in 2010, the stand was approximately 98 years of age. The stand form is even aged with no overstory trees differing in age by more than 20 percent. There was no visible evidence of disturbance since stand initiation other than the loss of overstory *Pinus strobus* from southern pine beetle. The stand is understocked with an average basal area of 66 square feet per acre and an average density of 52 trees per acre. The quadratic mean diameter was 15.8 inches diameter at breast height (dbh). The stand has a mixed species composition with *Quercus spp*. dominating the overstory. By number of stems, the dominant crown class was 93% *Quercus spp*. The codominant crown class was 58 percent *Quercus spp*. but also contained *Acer rubrum, Pinus strobus*, and *Liriodendron tulipifera*. The intermediate and suppressed crown classes were dominated by *Acer rubrum* comprising 52 and 61 percent of the stems respectively. *Acer rubrum, Pinus strobus*, *Quercus spp.*, and *Liriodendron tulipifera* were also present in these crown classes.

The midstory was mostly dominated by *Pinus strobus*, *Acer rubrum*, and flat topped *Quercus spp*. Understory reproduction was abundant throughout the stand. Fourteen species of advance reproduction were found. The species with the highest densities were *Acer rubrum*, *Carya tomentosa*, *Quercus alba*, *Quercus rubra*, *Prunus serotina*, *Oxydendrum arboretum*, *Pinus strobus*, and *Liriodendron tulipifera*.

Prior to the pine beetle epidemic, *Pinus strobus* accounted for an average of 18 percent of the total basal area of overstory trees on our sites. The average dbh of the *Pinus strobus* stems killed by the southern pine beetle (gap makers) were 21 inches for all gaps measured in our study. There was little variation in dbh of the gap maker between treatments. The average dbh of the gap maker on plots where the gap maker was removed was 22 inches and on plots where the gap maker was left the average dbh was 20 inches. To describe the size of the gaps we determined the minimum expanded gap area (MEGA). MEGA is calculated by determining the area of a circle where the radius is the horizontal distance from the center of the gap maker's bole to the center of the nearest dominant or codominant overstory competitor's bole. The average MEGA of all measured gaps was 856 square feet. There was little variation in the size of the gaps between treatments. The average MEGA on salvage cut plots was 837 square feet and on no cut plots the MEGA averaged 876 square feet.

Data Collection

Ten 1/5th acre research plots were established in 2010. Plots were restricted to canopy gaps created by the mortality of a single *Pinus strobus* stem which, prior to the pine beetle outbreak, were in a dominant or codominant position. Plots were separated into two treatment categories according to whether the pine was harvested in 2003 (salvage cut) or left as a standing snag (not cut). Five 1/5th acre plots were sampled for each treatment. For each 1/5th acre plot of a given treatment, a 1/5th acre plot of the opposite treatment was established on similar site conditions, e.g., aspect, landscape position, slope, and concavity (Table 1).

In each plot, species, diameter at breast height and crown class were recorded for all stems greater than or equal to 5 inches dbh. To evaluate diameter growth from 1998 to 2010, three trees on each plot were cored at breast height with an increment borer. Thirteen measurements of annual radial increase, one for each year from 1998 to 2010, were taken on each tree core. Each cored tree fell into one of three competitor classes: the closest major competitor (CMC) to the dead or removed *Pinus strobus*, a tree other than the CMC within a dominant or codominant crown class, or a tree within the intermediate or suppressed crown class. On each plot, one tree from each competitor class was cored. To reduce bias in growth response, cored trees in each competitor class across all plots had a similar shade tolerance and age. For example, each CMC tree cored had an intermediate shade tolerance such as *Quercus alba* and was approximately 98 years of age. Burns and Honkala (1990) describe five shade tolerance classes: very intolerant, intolerant, intermediate, tolerant, and very tolerant. This study uses only three shade tolerance classes: intolerant, which includes very intolerant and intolerant species; intermediate, including only intermediate species; and tolerant, which is comprised of very tolerant and tolerant species.

Table 1. Description of site conditions for paired 1/5th acre plots

Site Number	Aspect	Landscape Position	Slope (%)	Concavity
1	west	mid-slope	22-26	convex
2	west	ridge	5-9	concave
3	southwest	ridge	12	convex
4	southwest	low-slope	18-20	concave
5	south	mid-slope	24-27	concave

Within each plot, two 1000th acre regeneration plots were established at a distance of 15 feet from plot center at an azimuth of 0 degrees and 180 degrees (Figure 2). Density, cumulative height, and shade tolerance of advance reproduction were recorded for each species. Cumulative height is defined as the total height of all the trees of a certain species or species group per unit area. Cumulative height is analogous to other forest measurements, such as basal area, that incorporate both size and density into a single value and is used to summarize seedling development following disturbance (Fei et al. 2005).

Statistical Methods

Basal area, density, and species richness were observed for all trees ≥ 5 inches dbh on five 5th acre plots for each treatment. Species richness is defined as number of species. A randomized block design was used, blocking on plots with similar aspect and landscape position. Analysis of variance (SAS 2009) was run; mean separation with the Tukey method of experiment-wise error control was used to test for differences between treatments for all plots and by canopy class for each treatment (Figure 3). The null hypothesis was that basal area, density, and species richness for all trees > 5 inches dbh on plots of each treatment are equal.

Density and cumulative height were observed for all sources of advanced reproduction on twenty 1000th acre subplots, 10 subplots for each treatment. A randomized block design with sampling was used, blocking on plots with similar aspect and landscape position. Analysis of variance (SAS

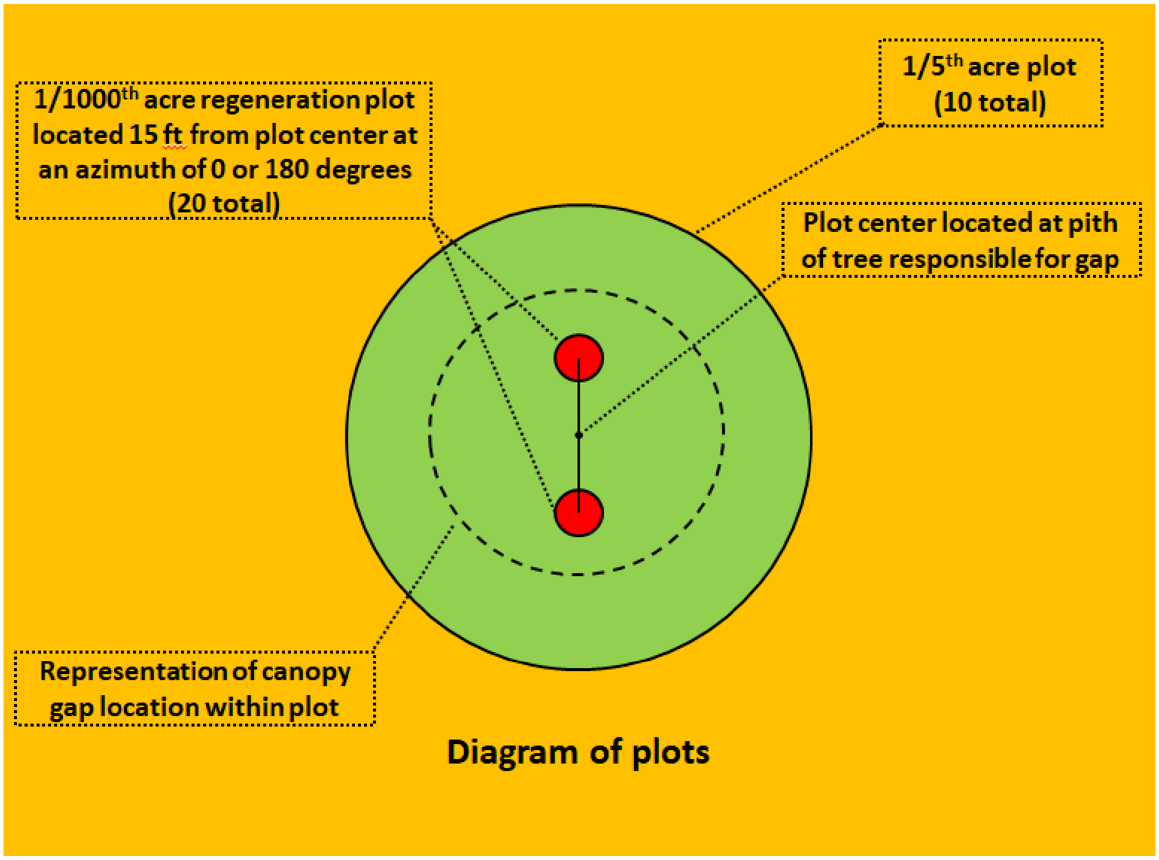

Figure 2. Diagram of 1/5th acre plot and nested regeneration plots

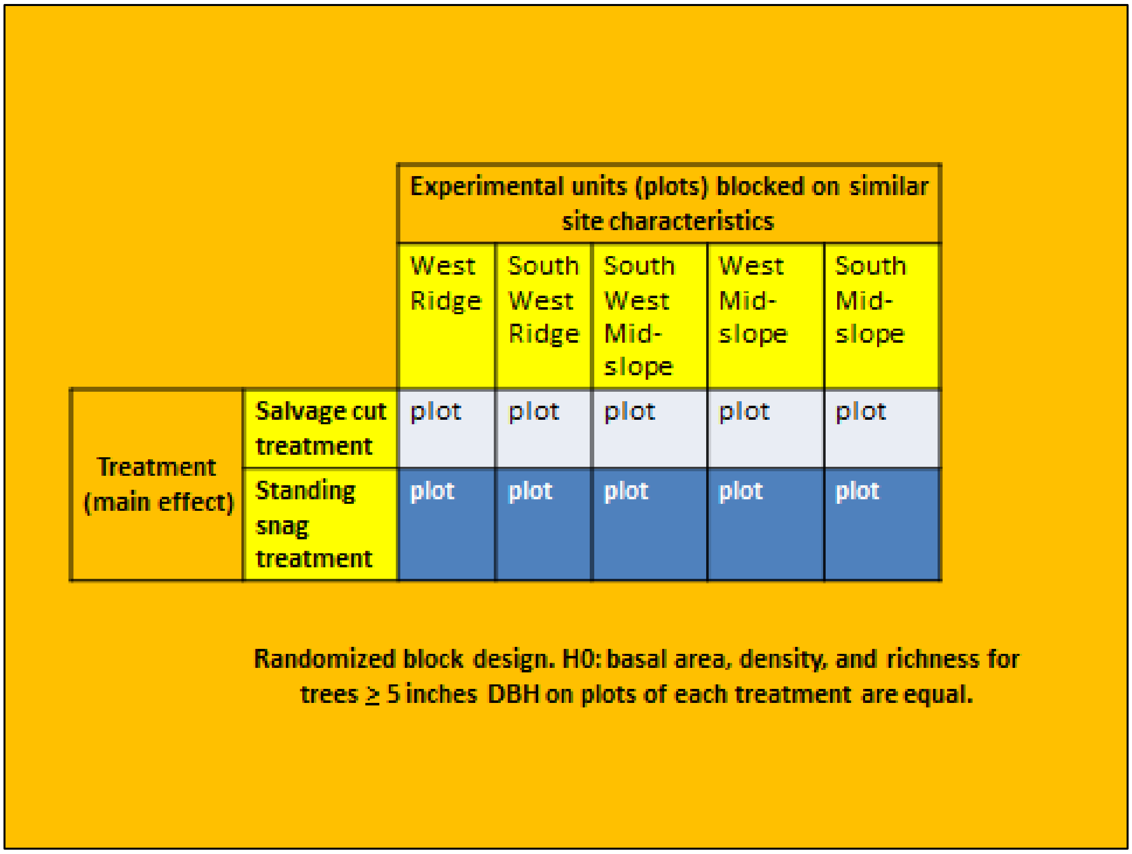

Figure 3. Conceptual diagram of experimental design used to compare the basal area, density, and species richness of overstory stems.

2009) was run; mean separation with the Tukey method of experiment-wise error control was used to test for differences between treatments for all plots and by shade tolerance for each treatment (Figure 4). The null hypothesis was that density and cumulative height of reproduction in plots of each treatment are equal.

Annual radial increase, as a measure of growth response, was measured on three tree cores (one for each competitor class) from five 1/5th acre plots for each treatment for 13 time periods between 1998 and 2010. A randomized block design with repeated measures was used, blocking on similar aspect and landscape positions. Analysis of variance (SAS 2009) was used; mean separation with the Tukey method of experiment-wise error control was used to test for differences between treatments by each competitor class (Figure 5). The null hypothesis was that radial increase by competitor class for plots of each treatment is equal. A conventional type one error rate of five percent was chosen for all tests of statistical difference. However, trends ($0.05 \leq P \geq 0.1$) were also reported for tests utilizing repeated measures treatment design. Trends were reported because the Tukey method of experiment-wise error control and repeated measures treatment design resulted in an unacceptable level of statistical power when testing at the 0.05 alpha level. Testing at a type one error rate of 10 percent raised the power of these tests to an acceptable level: greater than 78 percent for all whole plot main effects. Power analysis was conducted using proc power (SAS 2009).

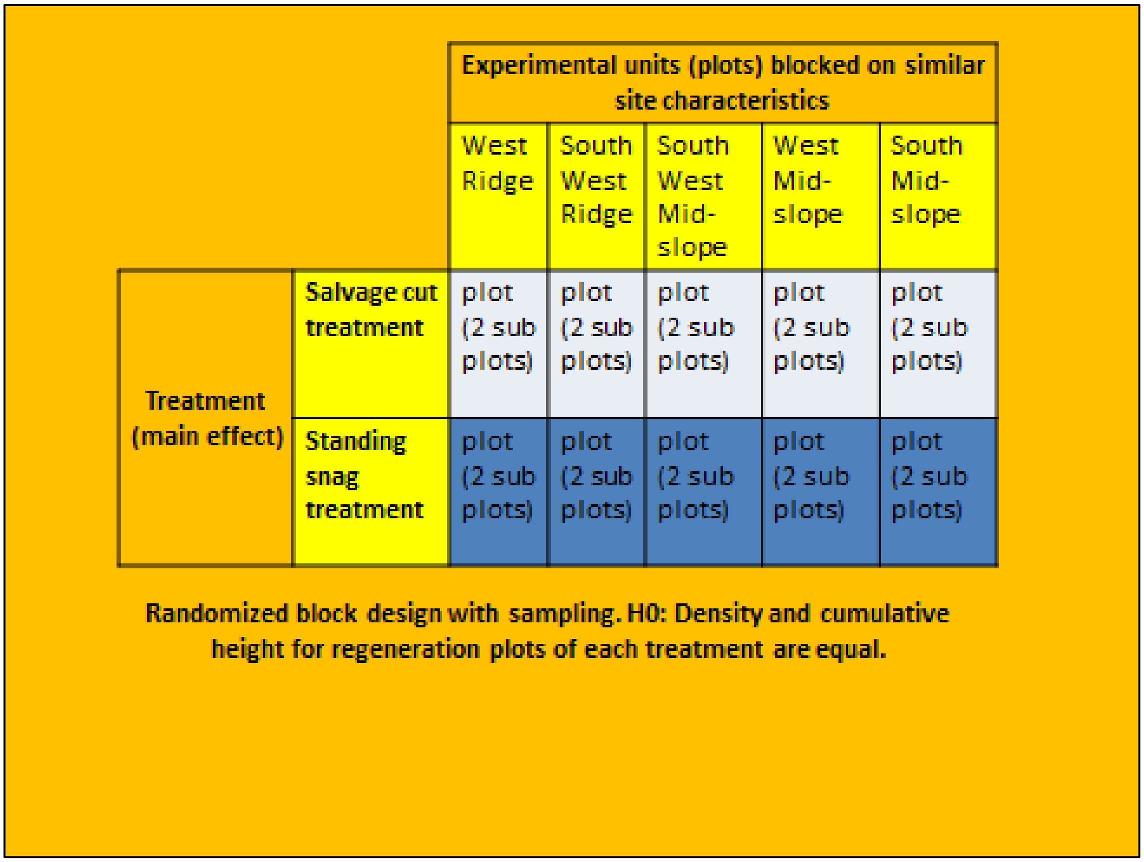

Figure 4. Conceptual diagram of experimental design used to compare the density and cumulative height of regeneration.

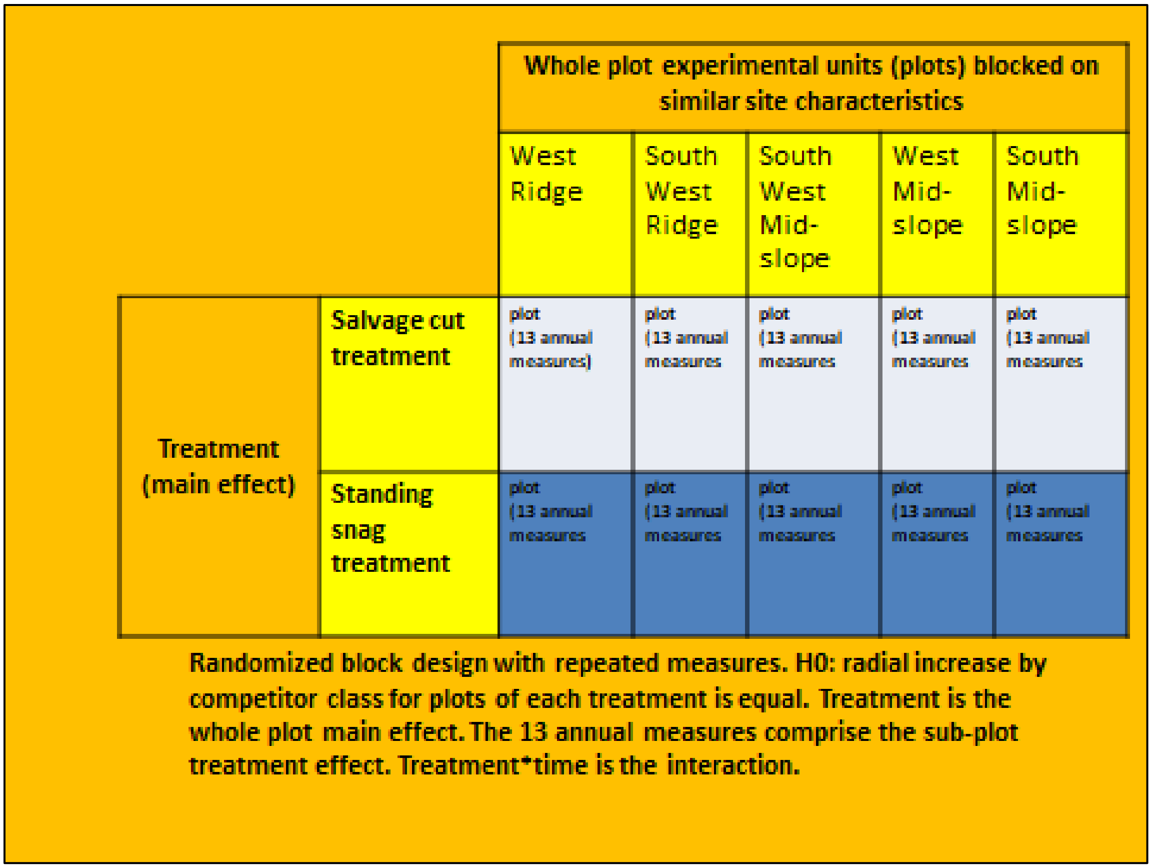

Figure 5. Conceptual diagram of experimental design used to compare the overstory growth response.

Chapter 5: Results

Significantly ($p<0.05$) more trees occupied a dominant crown position on plots where the gap maker was left as a standing snag (Table 2). No significant differences ($p>0.05$) were found between treatments for basal area, density, and species richness (Table 2). *Quercus alba,* composing 30 percent of the total basal area on each type, was the species of greatest dominance for both the cut and no cut treatment types (Table 3). *Quercus alba* and *Acer rubrum* were present in greatest densities on both treatment types. However, *Acer rubrum* made up a larger proportion of the basal area on the no cut treatment plots. Cut plots were mostly dominated by three species: *Quercus alba, Quercus rubra,* and *Quercus coccinea,* with *Quercus spp.* constituting over 75 percent of the basal area. The basal area of the no cut treatment plots was more dispersed across species which included *Quercus alba, Quercus coccinea, Acer rubrum, Liriodendron tulipifera, Quercus rubra, and Carya tomentosa* (Table 3).

Cut plots had a reverse J-shaped diameter distribution curve, which is representative of a single cohort stratified mixture (Figure 6). No cut plots had a bi-modal diameter distribution, which is indicative of a stand recovering from disturbance (Figure 6). Vertical structure differed in composition between treatment types in all crown classes except the dominant crown class, which was dominated by *Quercus spp.* for both treatment types (Figure 7). The codominant crown class of cut plots was almost entirely dominated by *Quercus spp.* while the same crown class of no cut plots, including both shade intolerant and shade tolerant species, was

Table 2. Means with standard errors of basal area, density and richness of plots where the gap maker was salvage cut (Cut) and plots where the gap maker was left as a standing snag (No Cut). Measures for density and the crown classifications are number of trees per acre.

Parameter	**Cut**	**NoCut**
Basal area	61.24 ± 5.89 a	70.18 ± 5.89 a
Density	49.00 ± 3.24 a	55.00 ± 3.24 a
Richness	5.20 ± 0.45 a	5.60 ± 0.45 a
Dominant	10.00 ± 1.32 b	16.00 ± 1.32 a
Codominant	19.00 ± 3.50 a	21.00 ± 3.50 a
Intermediate	6.00 ± 2.69 a	11.00 ± 2.69 a
Suppressed	14.00 ± 3.16 a	7.00 ± 3.16 a

Means within rows followed by the same letter are not significantly different ($p<0.05$)

Table 3. Average basal area and average density by species for plots where the gap maker was salvage cut (C) and plots where the gap maker was left as a standing snag (NC). Values shown are per acre. Basal area is expressed as ft^2/acre.

	Basal area		**Density**	
Species	C	NC	C	NC
Fagus grandifolia	.	1.8	.	4
Quercus prinus	2.1	5.5	1	3
Carya tomentosa	1.2	8.3	1	5
Quercus rubra	25.4	8.4	9	4
Acer rubrum	5.4	15.0	12	24
Quercus coccinea	8.5	17.0	3	9
Quercus falcata	3.3	.	1	.
Liquidambar styraciflua	.	1.6	.	1
Oxydendrum arboretum	0.5	.	1	.
Quercus alba	28.2	27.4	20	16
Liriodendron tulipifera	2.3	8.7	4	7
Pinus strobus	4.8	.	12	.
Sum	**81.7**	**93.6**	**65**	**73**

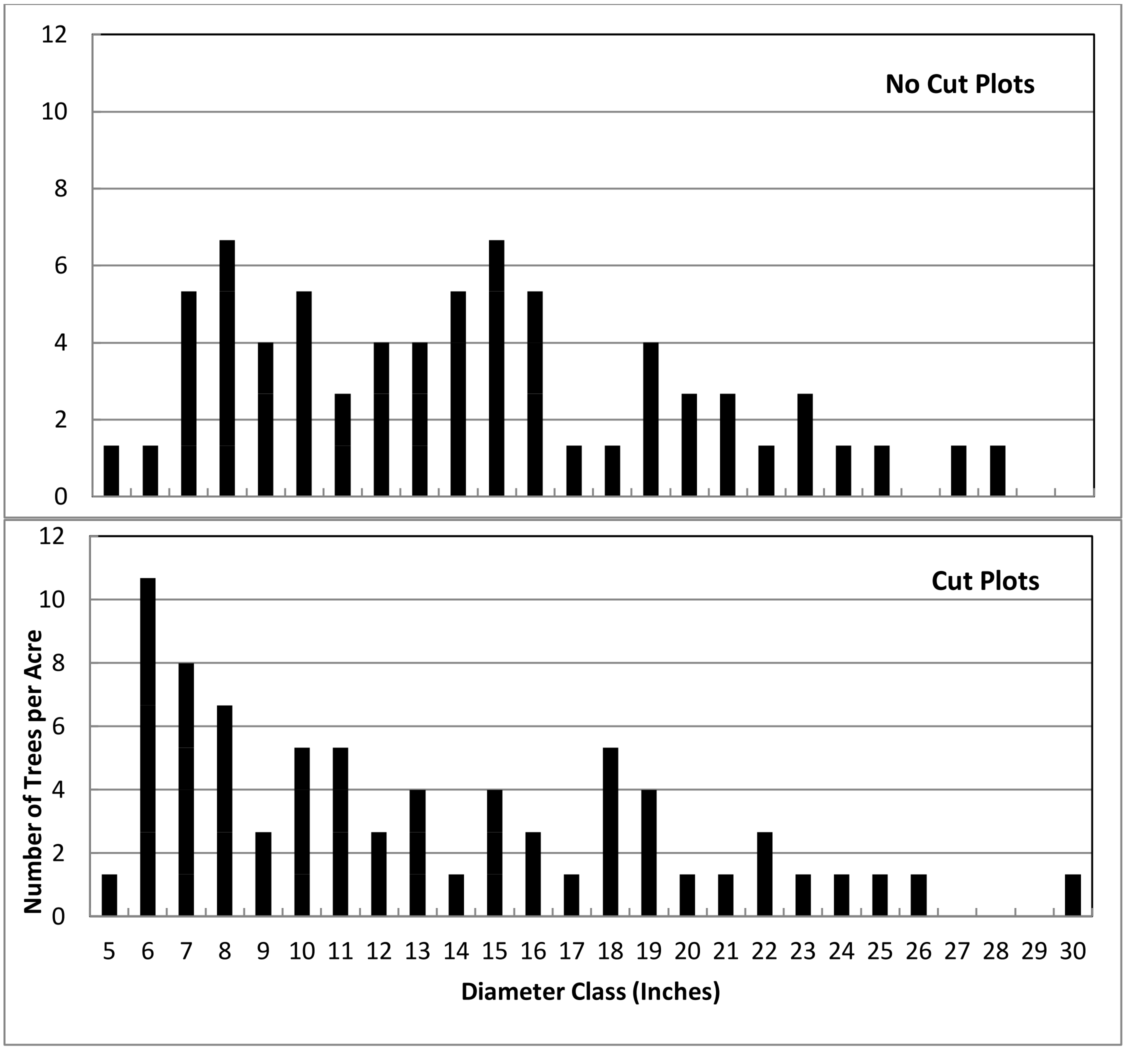

Figure 6. Number of trees per acre greater than or equal to 5 inches dbh per one inch diameter classes for all species on cut and no cut plots.

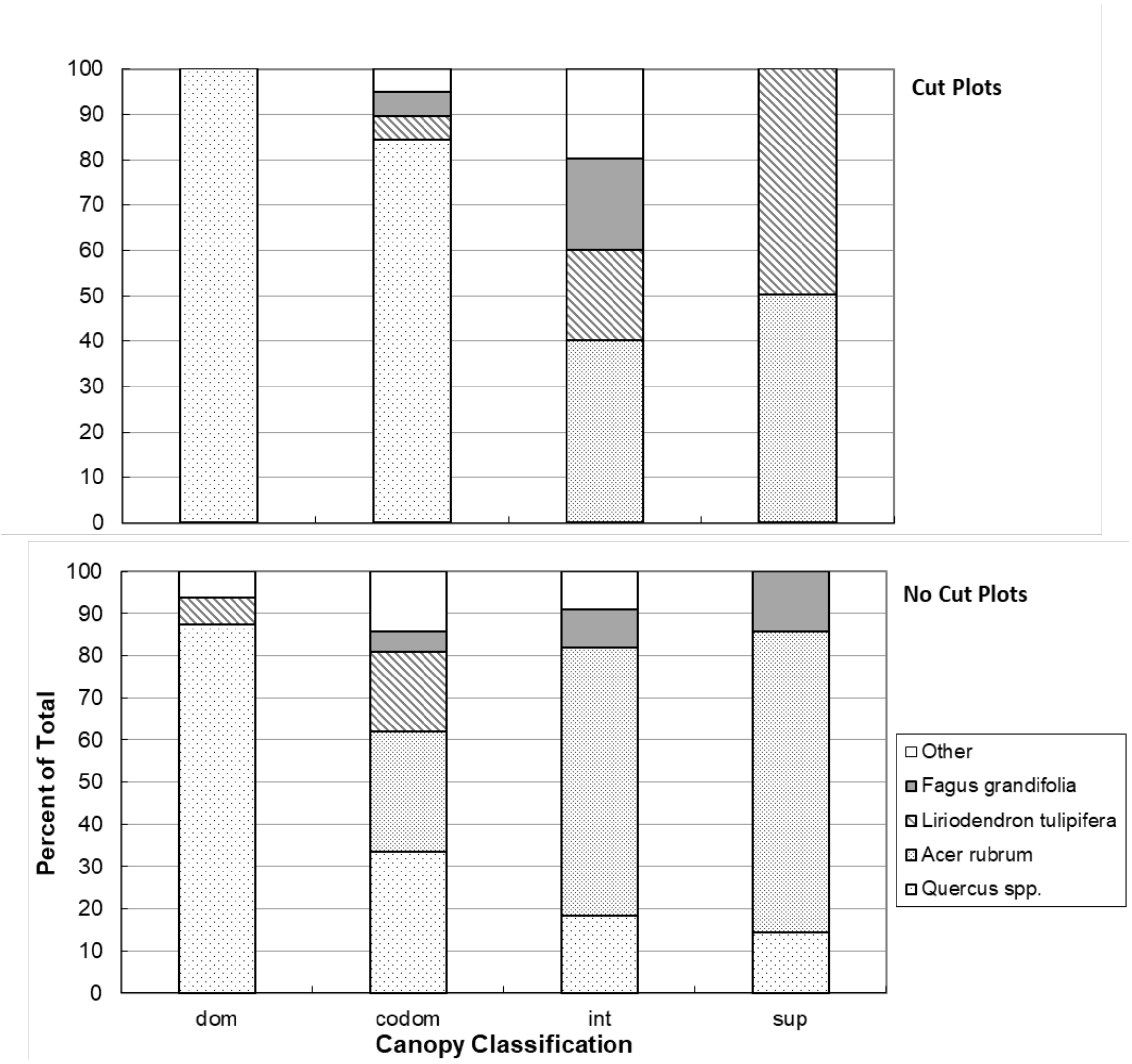

Figure 7. Canopy class distributions for plots of each treatment. Categories are based on the amount and direction of intercepted light (Oliver and Larson, 1996). sup (suppressed), int (intermediate), codom (codominant), dom (dominant)

more heterogeneous (Figure 7). The intermediate and suppressed crown classes of the no cut plots were dominated almost entirely by shade tolerant species (Figure 7).

Fourteen species of advance reproduction were found on the 20 subplots taken across the two treatment types. There were no significant differences in density between the two treatments (Table 4). The species with the highest densities on plots of each treatment type were *Acer rubrum, Carya tomentosa, Quercus alba, Quercus rubra, Prunus serotina, Oxydendrum arboretum, Pinus strobus,* and *Liriodendron tulipifera.* Plots of the cut treatment supported a significantly greater cumulative height of advance reproduction (Table 4). Cumulative height of shade tolerant species of advanced reproduction were significantly larger on cut plots (Table 5).

Analysis of variance revealed no significant differences ($p>0.05$) in growth response between the main effects of treatment and time; these factors did not interact ($p>0.05$). However, a trend ($0.05<p<0.01$) was evident for the main effect of treatment for both the CMC and suppressed tree competitor classes. Radial increase of the CMC competitor class tended to be higher on plots where the gap maker was left as a standing snag (Figure 8). Radial increase of the suppressed tree competitor class tended to be greater on plots that were salvage cut (Figure 8).

Table 4. Means with standard errors for measures of advanced reproduction on plots where the gap maker was salvage cut (C) and plots where the gap maker was left as a standing snag (NC). Values shown are per acre. Cumulative height is expressed as feet per acre.

	Plots	
Parameter	C	NC
Density	24600 ± 2505 a	18700 ± 2505 a
Cumulative height	52700 ± 6290 a	25850 ± 6290 b

Means with rows followed by the same letter are not significantly different ($p<0.05$)

Table 5. Means with standard errors for measures of advanced reproduction by shade tolerance on plots where the gap maker was salvage cut (C) and plots where the gap maker was left as a standing snag (NC). Values shown are per acre. Cumulative height is expressed as feet per acre.

	Shade tolerant		**Intermediate tolerance**		**Shade intolerant**	
Parameter	C	NC	C	NC	C	NC
Density	10200 ± 1885 a	6300 ± 1885 a	8500 ± 2012 a	7500 ± 2012 a	5900 ± 1639 a	4900 ± 1639 a
Cumulative height	16900 ± 3191 a	9450 ± 3191 b	19050 ± 4860 a	10850 ± 4860 a	16750 ± 4915 a	5550 ± 4915 a

Means with rows followed by the same letter are not significantly different ($p<0.05$)

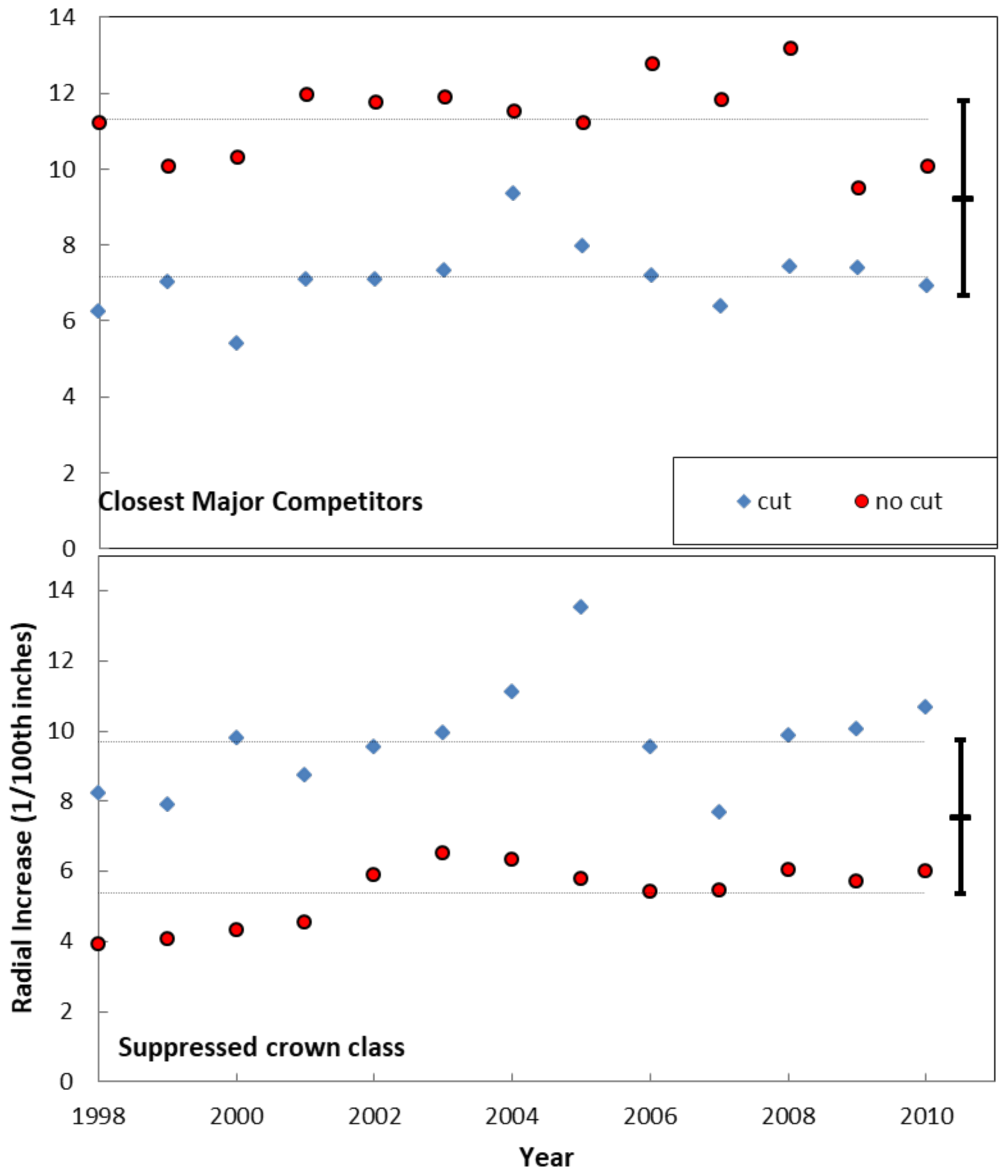

Figure 8. Mean values of radial increase for each year of measure by treatment type (interaction effect). Black dashed lines indicate mean radial increase for each treatment (main effect). Error bars represent Tukey mean separation values used to test for significant ($p<0.05$) differences between treatments (main effect) for each competitor class.

Chapter 6: Discussion

Overstory

The mortality of the emergent pine component, which comprised roughly 18 percent of the total basal area prior to the southern pine beetle disturbance, altered the stand structure and composition by transforming the stand from a fully stocked, single cohort, mixed species stand in the stem exclusion phase of stand development into a under stocked, two cohort, mixed species stand in the understory reinitiation stage of development. When comparing diameter distributions, these structural changes are most evident on plots where the gap maker was left as a standing snag (Figure 6). These results corroborate the findings of similar studies which demonstrated that small canopy gaps within secondary forests can influence stand structure and successional pathways (Hart and Grissino-Mayer 2009, Hart and others 2010, Hart and Kupfer 2011).

Despite changes in basal area and density resulting from the loss of the overstory pine, the southern pine beetle disturbance had little effect on the species composition of residual trees within the larger diameter classes and upper crown classes on all plots (Figure 7). However, significantly fewer trees occupied the dominant crown class on cut plots (Table 2) indicative of a stand with a higher level of biomass allocated within lower canopy stratum (Fei et al., 2005). The variability in species composition within the codominant crown class between treatments (Figure 7) can be attributed to inherent variability associated with natural, mixed species stands and their associated developmental processes.

Small diameter, lower canopy stratum trees were released when a gap maker died or was removed. As illustrated by other studies, the changes caused by small canopy disturbances are most prevalent in lower canopy stratum and the regeneration layer (Hart and Kupfer, 2011; Wilder et al., 1999). Some existing advance reproduction was recruited to the overstory as a new cohort following the disturbance. Response by stems of the lower canopy strata represent the pool of species likely to be recruited to larger size classes and potentially emerge to canopy positions (Hart and Kupfer, 2011). On cut plots, the recruitment consisted of *Pinus strobus, Liriodendron tulipifera, and Acer rubrum*; a mixture of both shade tolerant and shade intolerant species.

Only shade tolerant and intermediate species such as *Acer rubrum* and *Fagus grandifolia* and *Quercus spp*. were recruited on no cut plots where the gap maker was left as a standing snag. Prior to the disturbance, shade tolerant seedlings and saplings likely existed throughout the stand because of the closed canopy conditions. This advance reproduction was released under both treatments (Hix and Helfich, 2002; Hart et al., 2010; Hart and Kupfer, 2011). Furthermore, the ability of a standing snag to block additional light within the gap likely decreased the competitiveness of shade intolerant stems (Hart and Grissino-Mayer, 2009).

Reproduction

Plots from the cut treatment supported greater densities and significantly larger cumulative height of advance reproduction. Canopy gaps created suddenly, as was the case with our salvage cut plots, are typically larger and transmit more light to the understory than gaps that retain a standing snag (Kransy and Whitmore 1992; Hart and Kupfer, 2011). The differences in density and dominance can be attributed to the particular growth habits and light tolerances of each species. The significantly larger cumulative height and greater density of shade tolerant species of advance reproduction on cut plots indicate light increases to the forest floor that are favorable to the establishment of shade tolerant species (Tables 4 and 5). The regeneration of shade tolerant stems under small canopy gaps in second growth eastern hardwood forests is a common response to these types of disturbances (Hart and Grissino-Mayer, 2009; Hart et al., 2010; Hart and Kupfer, 2011).

However, although not significantly different, the difference in cumulative height between cut and uncut treatments for shade intolerant and intermediate species exceeds that of shade tolerant species (Table 5). This result, along with the relatively low densities, indicates that the light increase to the forest floor on cut plots is also favorable to the establishment of few relatively tall stems of shade intolerant and intermediately tolerant species of reproduction. The lack of statistical difference between cut and no cut plots can likely be attributed to the high level of variability between plots resulting in large standard errors for both shade intolerant and intermediate species. Without continued disturbances to increase or maintain the availability of light, more intermediate and shade intolerant stems are likely to persist as seedlings in the understory (Hart and Kupfer 2011).

Unlike the results of Hart and Kupfer (2011), *Quercus spp.* seedlings and saplings regenerated under the same canopy gaps as *Acer rubrum* and *Fagus grandifolia*. Specifically, the regeneration of *Quercus spp*. occurred within plots of both treatment types. However, fewer *Quercus spp*. stems were present in plots where the gap maker was removed. In the Hart and Kupfer (2011) study, the gaps under which *Quercus spp*. were regenerated existed only on very dry sites where *Acer rubrum* and *Fagus grandifolia* are not competitive. None of the plots in our study were severely moisture deficient. Fewer *Quercus spp*. were regenerated under gaps where the gap maker was removed because the site was quickly dominated by the vigorously growing and more numerous shade tolerant individuals.

Growth

Trends indicated that smaller diameter overstory trees within the intermediate or suppressed crown classes responded more vigorously than stems from other crown classes when the gap maker was removed by salvage cutting (Figure 8). This response led to the recruitment of smaller diameter trees into successively greater diameter and crown classes. These results suggest that disturbances that do not leave a standing snag are more likely to foster crown closure as a result of vertical height growth rather than lateral crown expansion by the surrounding dominant or codominant trees. The removal of the gap maker provides a pathway for suppressed overstory stems to grow and emerge into higher crown class positions. Conversely, plots where the gap maker was left as a standing snag tended to result in larger radial increases by the closest major competitors (Figure 8). Crown closure by lateral crown expansion would be more likely in gaps where the gap maker is left as a standing snag. Eventually, standing snags will fall, likely from a wind event (Hart and Kupfer, 2011). Repeated disturbance events have the potential to provide additional resources to the stems that did not reach the canopy in a single disturbance. This repetitive small scale disturbance regime is believed to foster the growth and canopy attainment by shade tolerant species (Hart and Grissino-Mayer, 2009).

Conclusions

The primary goal of this study was to investigate stand dynamics following gap scale exogenous disturbance within a secondary forest stand during the understory reinitiation stage of development. We hypothesized that removing the stems responsible for the creation of canopy gaps would reallocate more resources to competing stems, thus resulting in a greater growth response by intermediate and suppressed stems and increased variation within forest composition and structure. Our results revealed significant differences in composition and structure only in small diameter stems within lower canopy strata. Salvage cutting provided an abrupt change in the amount of sunlight whereas leaving the gap maker as a standing snag provided only a gradual increase of light with time. Both salvage cutting and leaving the gap maker as a standing snag resulted in the release of understory individuals. However, shade tolerant species alone were released in the no cut treatment. Differences in cumulative height of reproduction indicated low levels of light reaching the forest floor on cut plots, which favored the growth of shade tolerant species. Salvage cutting fostered the growth of stems from intermediate or suppressed crown classes allowing them to emerge to more dominant positions. Leaving a standing snag favored the growth of adjacent stems within dominant or codominant crown classes inhibiting the growth of subordinate individuals.

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