STAND DYNAMICS FOLLOWING GAP-SCALE EXOGENOUS DISTURBANCE IN A SINGLE COHORT MIXED SPECIES STAND IN MORGAN COUNTY, TENNESSEE

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Abstract.—Differences in composition, structure, and growth under canopy gaps created by the mortality of a single stem were analyzed using analysis of variance under two scenarios, with stem removed or with stem left as a standing snag. There were no significant differences in composition and structure of large diameter residual stems within upper canopy strata. Some preexisting advance regeneration was recruited as a new cohort following the disturbance. On cut plots, the recruitment consisted of eastern white pine (*Pinus strobus*), yellow-poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*). On no cut plots, the advance regeneration recruited as a new cohort was comprised of red maple, American beech (*Fagus grandifolia*), and a few oaks (*Quercus* spp.). The removal of the gap maker provided a pathway to recruit suppressed stems into larger diameter and crown classes. Conversely, plots where the gap maker was left as a standing snag tended to result in larger radial increases by the closest major competitors.

INTRODUCTION

Forests of southern Appalachia are subject to both anthropogenic and nonanthropogenic disturbance. Disturbances affect the composition, structure, and future development of forests at varying scales and frequencies. Differences in disturbance types and characteristics can influence species composition, age, geographic location, time since previous disturbance, and developmental stage of the forest (Oliver and Larson 1996). The ability of trees to respond following a gap-scale disturbance depends on species characteristics, age, and the gap environment (Wilder et. al. 1999). Gap-scale disturbances are characterized by small openings within the canopy that occur due to the loss of one or a few trees. Gap-scale disturbances can affect species composition and stand structure by facilitating the establishment of new germinates, recruiting subcanopy trees to larger size classes, and lateral crown expansion of overstory stems (Hart and Grissino-Mayer 2009, Hart et. al. 2010, Wilder et. al. 1999).

Canopy gaps formed in secondary growth forests of the eastern United States are typically very small because of the smaller tree size and shorter distances between trees of forests in the precomplex stage of development (Hart and Grissino-Mayer 2009, Hart et. al. 2010, Wilder et. al. 1999). These small canopy gaps usually close by lateral crown expansion of adjacent overstory stems rather than height growth of understory trees. However, even small canopy gaps can alter stand composition and structure by establishing new sources of regeneration and recruiting understory stems into larger size classes (Hart and Grissino-Mayer 2009, Hart et. al. 2010, Runkle 1981). Successive gap-scale disturbances may allow understory trees to reach the canopy (Hart and Grissino-Mayer 2009, Hart et. al. 2010). Light availability on the forest floor can be two or more times greater under single tree canopy gaps compared to closed canopy conditions (Krasny and Whitmore 1992). Numerous studies

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have demonstrated that this light increase is sufficient enough to release only shade-tolerant species (Hart and Grissino-Mayer 2009, Hart and Kupfer 2011, Hart et. al. 2010, Hix and Helfrich 2003). However, some studies have suggested that species with intermediate shade tolerance will respond similarly to shade-tolerant species (Canham 1989, Naidu and DeLucia 1998).

In mixed species stands, disturbances caused by senescence, forest pests, and pathogens typically result in the mortality of single stems or single species dispersed throughout the stand (Hart and Kupfer 2011, Krasny and Whitmore 1992). These types of disturbances cause the gradual formation of canopy gaps over a period of years rather than suddenly (Krasny and Whitmore 1992). Researchers have hypothesized that forest response to gradual canopy gaps differs from sudden canopy gaps. Gradually formed canopy gaps that retain standing snags for a number of years are believed to differ from suddenly formed canopy gaps in the following manners: gaps with standing snags are smaller (Hart and Grissino-Mayer 2009, Hart and Kupfer 2011, Hart et. al. 2010, Krasny and Whitmore 1992); light and possibly belowground resources become available more gradually (Krasny and Whitmore 1992); gradual tree death is less destructive to advanced regeneration (Krasny and Whitmore 1992); and the bole and branches of standing dead trees may inhibit sunlight availability to the understory (Hart and Kupfer 2011, Krasny and Whitmore 1992). Despite numerous studies focusing on forest gap dynamics in mixed species stands, no research has 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.

JUSTIFICATION AND OBJECTIVES

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 upland mixed species forests of the Southeast. The goal of this study was to investigate stand dynamics following gap-scale exogenous disturbance. Specifically, the objectives were to determine differences in forest composition, structure, and growth response under canopy gaps created by the mortality of a single stem where the stem was either removed or left as a standing snag. We hypothesized that removing the stems responsible for the creation of canopy gaps would result in greater growth by intermediate and suppressed stems and increased variation of forest composition and structure.

STUDY SITE

The study was conducted in the Cumberland Forest field research unit of the University of Tennessee Forest Resources Research and Education Center located in Morgan County, Tennessee. This area is located within the Cumberland Mountain physiographic region, subregion two, land type association G, type 24 and 25, which is the Wartburg Basin and Jellico Mountains (Smalley 1984). Regionally, the topography is characterized by elevations of 1,200 to 3,000 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 1,200 to 1,500 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. They 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 °F (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 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. True mesophytic species dominate only 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 1989). Regionally, disturbance caused by detrimental logging practices (1800 to present), coal mining (1915 to present), wildfire, forest pests, and pathogens, have varied the community types located within the Wartburg Basin (Deselm et al. 1978).

The study area was heavily cut over in the years from 1915 to 1937 prior to being deeded to the University of Tennessee in 1937. 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. The southern pine beetle outbreak resulted in the mortality of nearly all overstory eastern white pine within the study area. In 2003, the management activities conducted on our site involved the salvage cutting of the easily accessible overstory eastern white pine stems that the southern pine beetles killed. The salvage cutting was limited to eastern white pine stems that were easily accessible, thereby minimizing the damage to residual vegetation. Due to the low basal area and relatively even distribution of eastern white pine on our site, many small canopy gaps were formed.

METHODS

Data Collection

Ten 0.2-acre research plots were established in 2010. Plots were restricted to canopy gaps created by the mortality of single stems, which, prior to the pine beetle outbreak, were in dominant or codominant positions. 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 0.2-acre plots were sampled for each treatment. For each 0.2-acre plot of a given treatment, a 0.2-acre plot of the opposite treatment was established on similar site conditions, e.g., aspect, landscape position, slope, and concavity (Table 1).

Table 1.—Description of site conditions for paired 0.2-acre plots

Site type	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

In each 0.2-acre plot, species, diameter at breast height (d.b.h.) and crown class were recorded for all stems with a d.b.h. ≥5 inches. Annual radial growth is directly proportional to annual height growth (Hart et. al. 2010, Kariuki 2002). To evaluate annual 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 eastern white pine, a tree other than the CMC within a dominant or codominant crown class, or a tree within the intermediate or suppressed crown class. 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 and was approximately 98 years of age. The "Silvics of North America" by Burns and Honkala (1990a, 1990b) describes five shade tolerance classes: very intolerant, intolerant, intermediate, tolerant, and very tolerant. This study used only three shade tolerance classes: intolerant, which includes very intolerant and intolerant species; intermediate, including only intermediate species; and tolerant, which is composed of very tolerant and tolerant species.

Within each plot, two 0.001-acre regeneration plots were established at a distance of 15 feet from plot center at azimuths of 0 degrees and 180 degrees. Density, cumulative height, and shade tolerance of advance regeneration were recorded for each species. Cumulative height was defined as the total height of all the trees of a certain species or species group per unit area.

Statistical Methods

Basal area, density, and species richness were determined for all trees with a d.b.h. ≥5 inches on the five 0.2-acre plots for each treatment. A randomized complete block design was used, blocking on site (Table 1). Analysis of variance was run, and means separation with the Tukey method of experimentwise error control was used to test for differences between treatments for all plots and by canopy class for each treatment. SAS Version 9.2 was used for all statistical analyses (SAS Institute Inc., Cary, NC).

Density and cumulative height were calculated for all sources of advanced regeneration on 20 of the 0.001-acre subplots. A randomized complete block design with sampling was used, blocking on site (Table 1). Analysis of variance was run and mean separation with the Tukey method of experimentwise error control was used to test for differences between treatments for all plots and by shade tolerance for each treatment.

Annual radial increase, as a measure of growth response, was measured on three tree cores (one for each competitor class) from five 0.2-acre plots for each treatment for 13 time periods between 1998 and 2010. A randomized complete block design with repeated measures was used, blocking on site (Table 1). Analysis of variance was run, and mean separation with the Tukey method of experimentwise error control was used to test for differences between treatments, time, and the interaction effect of treatment x time by each competitor class. 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 experimentwise 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 I error rate of 10 percent raised the power of these tests to an acceptable level of greater than 78 percent for all whole plot main effects. Power analysis was conducted using Proc power.

RESULTS

Significantly more trees occupied a dominant crown position on plots where the gap maker was left as a standing snag, but no significant differences were found between treatments for basal area, density, and species richness (Table 2). White oak (*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. White oak and red maple (*Acer rubrum*) were present in greatest densities on both treatment types. However, red maple made up a larger proportion of the basal area on the no cut treatment plots. Cut plots were mostly dominated by three species, white oak, northern red oak (*Quercus rubra*), and scarlet oak (*Quercus coccinea*), with oaks (*Quercus* spp.) constituting over 75 percent of the basal area. The basal area of the no cut treatment plots was more dispersed across species and included white oak, scarlet oak, red maple, yellow-poplar (*Liriodendron tulipifera*), northern red oak, and mockernut hickory (*Carya tomentosa*) (Table 3).

Table 2.—Means and standard errors for diversity, structural, and compositional measures on plots where the gap maker was salvage cut (Cut) and plots where the gap maker was left as a standing snag (No cut)

Parameter	Cut	No Cut
Basal area (ft^2/acre)	61.24 ± 5.89 a	70.18 ± 5.89 a
Density (trees/acre)	49.00 ± 3.24 a	55.00 ± 3.24 a
Richness (# of species)	5.20 ± 0.45 a	5.60 ± 0.45 a
Dominant (trees/acre)	10.00 ± 1.32 b	16.00 ± 1.32 a
Codominant (trees/acre)	19.00 ± 3.50 a	21.00 ± 3.50 a
Intermediate (trees/acre)	6.00 ± 2.69 a	11.00 ± 2.69 a
Suppressed (trees/acre)	14.00 ± 3.16 a	7.00 ± 3.16 a

Means within a row that are 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 (Cut) and plots where the gap maker was left as a standing snag (No Cut)

	Basal area (ft^2/acre)		Density (trees/acre)	
Species	Cut	No cut	Cut	No cut
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

Cut plots had a reverse J-shaped diameter distribution curve, which is representative of a single cohort stratified mixture (Fig. 1). No cut plots had a bi-modal diameter distribution, which is indicative of a stand recovering from disturbance (Fig. 1). Vertical structure differed in composition between treatment types in all crown classes except the dominant crown class which was dominated by oaks for both treatment types (Fig. 2). The codominant crown class of cut plots was almost entirely dominated by oaks while the same crown class of no cut plots, including both shade-intolerant and shade-tolerant species, was more heterogeneous (Fig. 2). The intermediate and suppressed crown classes of the no cut plots were dominated almost entirely by shade-tolerant species (Fig. 2).

Fourteen species of advance regeneration 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 red maple, mockernut hickory, white oak, northern red oak, black cherry (*Prunus serotina*), sourwood (*Oxydendrum arboretum*), eastern white pine, and yellow-poplar. Plots of the cut treatment supported a significantly higher cumulative height of advance regeneration (Table 4). Cumulative height of shade-tolerant species of advanced regeneration was significantly larger on cut plots (Table 5).

Analysis of variance revealed no significant differences in growth response between the main effects of treatment and time; these factors did not interact. However, a trend 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 (Fig. 3). Radial increase of the suppressed tree competitor class tended to be higher on plots that were salvage cut (Fig. 3).

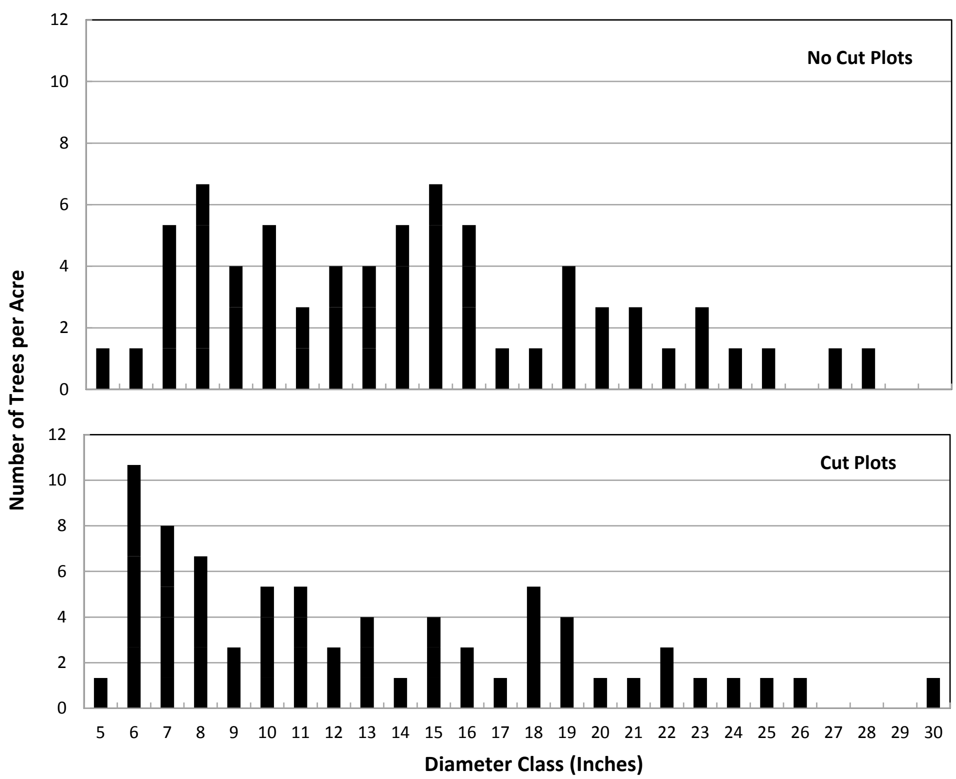

Figure 1.—Number of trees (with d.b.h. ≥5 inches) per acre by 1-inch diameter classes for all species on both cut and no cut plots.

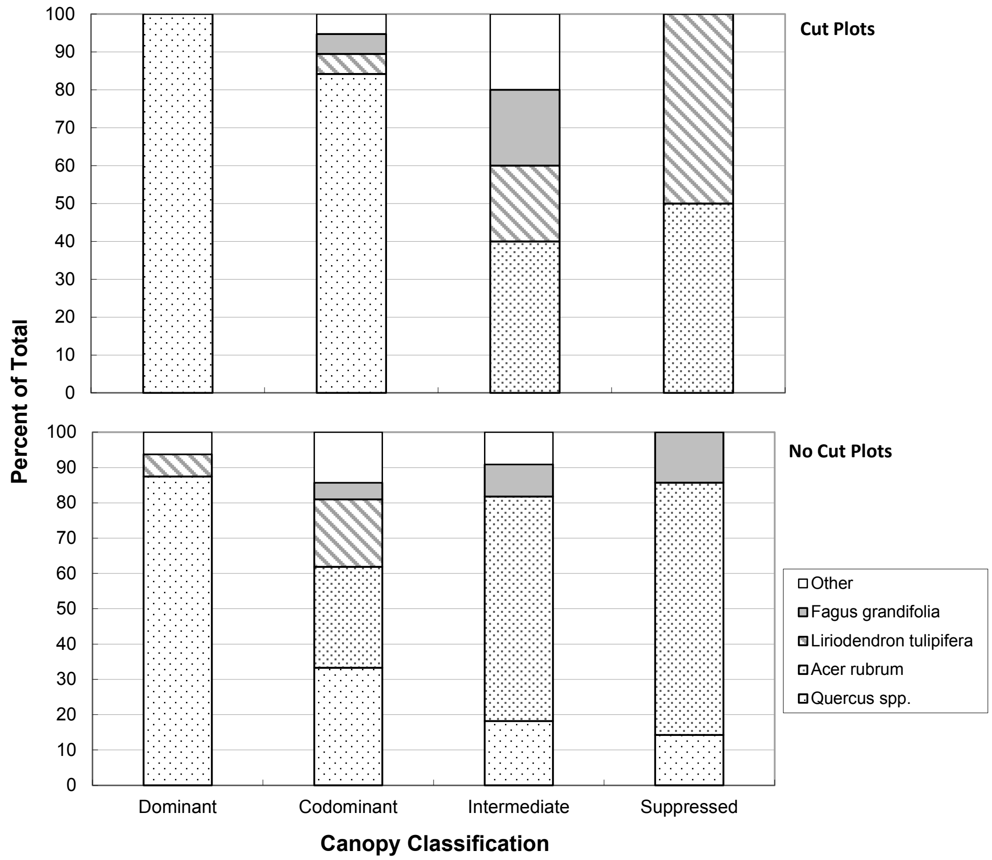

Figure 2.—Canopy class distributions for plots of each treatment. Categories are based on the amount and direction of intercepted light (Oliver and Larson 1996).

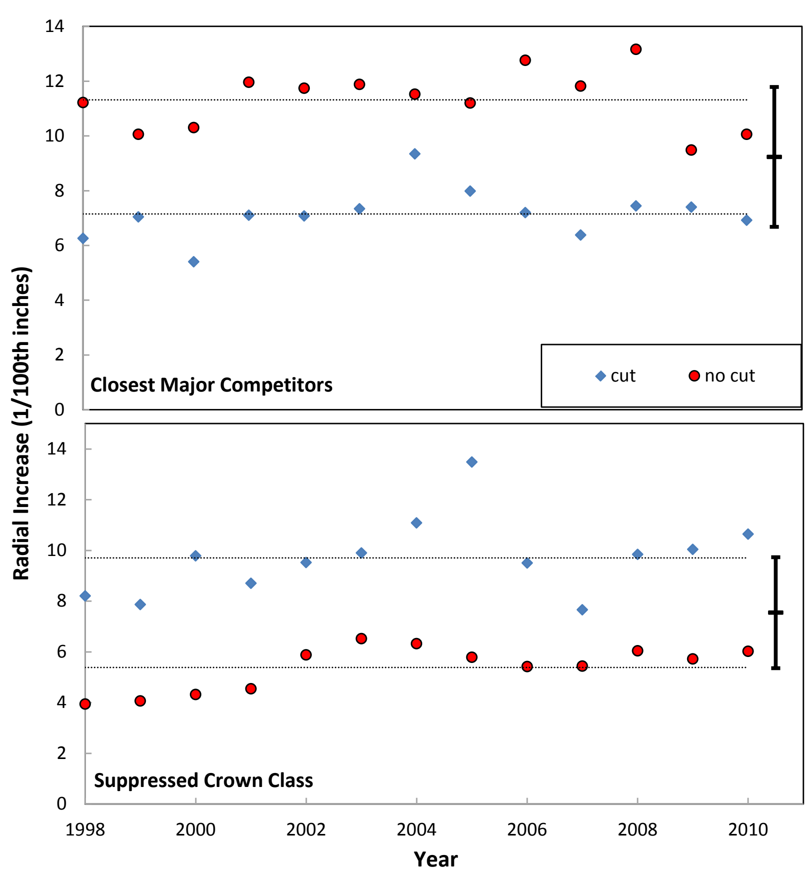

Figure 3.—Mean values of radial increase for each year of measure by treatment type (interaction effect). Dashed lines indicate mean radial increase for each treatment (main effect). Error bars represent Tukey mean separation values used to test for significant ($p < 0.05$) differences between treatments (main effect) for each competitor class.

Table 4.—Means and standard errors for measures of advanced regeneration on plots where the gap maker was salvage cut (Cut) and plots where the gap maker was left as a standing snag (No cut)

	Plots	
Parameter	Cut	No cut
Density (stems/acre)	24,600 ± 2505 a	18,700 ± 2505 a
Cumulative height (ft/acre)	52,700 ± 6,290 a	25,850 ± 6,290 b

Means within a row that are followed by the same letter are not significantly different ($p < 0.05$).

Table 5.—Means and standard errors for measures of advanced regeneration by shade tolerance on plots where the gap maker was salvage cut (Cut) and plots where the gap maker was left as a standing snag (No cut)

	Shade tolerant		Intermediate tolerance		Shade intolerant	
Parameter	Cut	No cut	Cut	No cut	Cut	No cut
Density (stems/acre)	10,200 ± 1,885 a	6300 ± 1885 a	8,500 ± 2,012 a	7,500 ± 2,012 a	5,900 ± 1,639 a	4,900 ± 1,639 a
Cumulative height (ft/acre)	16,900 ± 3,191 a	9450 ± 3191 b	19,050 ± 4,860 a	10,850 ± 4,860 a	16,750 ± 4,915 a	5,550 ± 4,915 a

Means within a row that are followed by the same letter are not significantly different ($p < 0.05$).

DISCUSSION

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), but stands with low pine densities can become infested if they are overstocked (Lorio 1980). The mortality of the 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. This result corroborates 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 Kupfer 2011, Hart et. al. 2010). The southern pine beetle disturbance transformed the stand from a fully to overstocked, single cohort, mixed species stand in the understory reinitiation stage of stand development into a moderately full to fully stocked, two cohort, mixed species stand in the understory reinitiation stage of development.

Despite changes in basal area and density resulting from the loss of the overstory pine, the southern pine beetle disturbance had no effect on the species composition of trees within the larger diameter classes and upper crown classes. However, small diameter, lower canopy stratum trees were released from competition. The changes caused by small canopy disturbances are often most prevalent in lower canopy stratum and the regeneration layer (Hart and Kupfer 2011). Response by stems of the lower canopy strata represent the pool of species that can be recruited to larger size classes and potentially the canopy (Hart and Kupfer 2011, Wilder et. al. 1999). Some preexisting advance regeneration was recruited as a new cohort following the disturbance. On cut plots, the recruitment consisted of eastern white pine, yellow-poplar, and red maple. On no cut plots, the advance regeneration recruited as a new cohort was comprised of red maple, American beech (*Fagus grandifolia*), and a few oaks. Unlike the results of Hart and Kupfer (2010), oak saplings were released under the same canopy gaps as red maple and American beech saplings. In their study, the gaps under which oaks were released existed on very dry sites where red maple and American beech are not competitive. None of the plots in our study were severely moisture deficient. We speculate that no oaks were released under gaps where the gap maker was removed because oaks were quickly outcompeted by the numerous shade-intolerant stems that responded to the cut treatment. For the most part, shade-intolerant species were recruited on cut plots. Canopy gaps created suddenly, as is the case with harvesting, are typically larger and transmit more light to the understory than gaps that retain a standing snag (Hart and Kupfer 2011, Krasny and Whitmore 1992). The density and growth response of shade-intolerant species under canopy gaps is proportional to the intensity of the disturbance (Canham 1989, Hart et. al. 2010, Hart and Kupfer 2011, Hix and Helfrich 2003). In contrast to the cut plots, mostly shade-tolerant species responded on plots where the gap maker was left as a standing snag. We speculate that prior to the disturbance, shade-tolerant saplings existed throughout the stand because of closed canopy conditions and were released under both treatments (Hart et. al. 2010, Hart and Kupfer 2011, Hix and Helfrich 2003).

Predictably, plots from the cut treatment supported greater densities and significantly larger cumulative height of regeneration. The differences in density and dominance can be attributed to the particular growth habits of each species. The significantly larger cumulative height and high density of shade-tolerant species of advance regeneration on cut plots indicate light increases to the forest floor that are favorable to the establishment of high numbers of relatively small shade-tolerant species. However, although not significantly different, the magnitude of difference in cumulative height between cut and uncut treatments for shade-intolerant and intermediate species exceeds that of shade-tolerant species. 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 regeneration. 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 disturbance, it is likely that these sources of regeneration will only persist as seedlings in the understory (Hart and Kupfer 2011).

Trends in radial increase indicated that smaller diameter trees within the intermediate or suppressed crown classes responded more vigorously than did other competitor classes when the gap maker was removed by salvage cutting. This response led to the recruitment of smaller diameter trees into successively greater diameter and crown classes. These results indicate that disturbances that do not leave a standing snag are more likely to foster crown closure as a result of vertical height growth than disturbances that do retain a standing snag. The removal of the gap maker may provide a pathway to recruit suppressed stems into the canopy; this is especially likely should future canopy disturbances occur (Hart and Kupfer 2011). Conversely, plots where the gap maker was left as a standing snag tended to result in larger radial increases by the closest major competitors. Standing snags in this study will eventually fall, likely as the result of a wind event (Hart and Kupfer 2011). How this delayed second disturbance event will affect future composition and structure is unknown.

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