

INFLUENCE OF GAP-SCALE DISTURBANCE ON DEVELOPMENT AND SUCCESSION IN A
CUMBERLAND PLATEAU *QUERCUS-PINUS* FOREST

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Abstract

Quercus-Pinus forests of the eastern US span > 13 million ha. It is important for managers to understand the methods used to sustain *Pinus* spp. in these mixtures or progress toward a more natural mixture of hardwoods. Understanding developmental and successional patterns in this forest type can help assess the need to actively manage natural processes, or to inform silvicultural prescriptions to achieve management goals. Little research has been conducted on localized disturbance processes in *Quercus-Pinus* forests. I examined 60 canopy gaps in a *Quercus-Pinus* forest on the Cumberland Plateau in Alabama to analyze their influence on development and succession. Most canopy gaps (53%) were single treefall events caused by snapped stems. The majority of gap maker trees (56%) were *Pinus* individuals while 44% were hardwoods. Most gaps (58%) closed by height growth of subcanopy trees. The majority of these gap filler taxa were hardwoods: *Quercus* (39%), *Carya* (14%), *Pinus* (14%), *Nyssa Sylvatica* (12%), and other (15%). Significant positive relationships existed between gap size and sapling diversity ($r^2 = 0.15$, $P = 0.002$), tree diversity ($r^2 = 0.21$, $P = 0.0002$), and total stem diversity ($r^2 = 0.29$, $P < 0.0001$). The number of *Pinus* gap makers and the number of gaps projected to fill by subcanopy recruitment of hardwoods indicated the forest was in the latter stages of a composition shift from *Pinus* to a much stronger *Quercus* component. To maintain a *Pinus* component, managers would likely need to create canopy gaps larger than those documented here and remove hardwood competition from the regeneration layer.

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1. INTRODUCTION

Forests are subject to disturbance events which shape developmental patterns and successional pathways. Disturbance extent and magnitude vary widely from catastrophic, stand-scale to highly localized, gap-scale events (Oliver and Larson, 1996). Localized, gap-scale events are the most common natural disturbances in eastern US forests (Runkle, 1985). These disturbances create structural changes associated with older forests by increasing large woody debris inputs, creating pit and mound topography, releasing understory trees from suppression, providing sites for new germinants, promoting multi-aged structure, and allowing for canopy expansion that leads to large canopy trees at wide spacings (Oliver and Larson, 1996; Frelich, 2002; Richards and Hart, 2011). Localized disturbances also shift species composition to shade-tolerant, late-seral species (Goebel and Hix, 1996; Goebel and Hix 1997; Franklin et al., 2002).

The influence of natural gap-scale disturbance processes on development and succession has been described for both secondary and old-growth hardwood stands of the temperate zone (e.g. Lorimer, 1980; Barden, 1981; Runkle, 1982; Cho and Boerner, 1991; Yamamoto, 1999, 2000; Runkle, 2000; Zeibig et al., 2005; Mountford et al., 2006; Hart and Grissino Mayer, 2009; Richards and Hart, 2011; Petritan et al., 2013). However, few studies have quantified natural canopy gap formation in hardwood stands with a strong *Pinus* component (Rantis and Johnson, 2002; Stambaugh, 2002; Stambaugh and Muzika, 2007); a forest type that spans over 13 million hectares of the eastern US (Smith and Darr, 2004). Thus, there is a paucity of quantitative information on natural canopy disturbances and their influence on developmental and successional processes in *Quercus-Pinus* systems.

Although development and succession in mixed hardwood and *Quercus-Pinus* stands may be influenced similarly by gap-scale disturbance processes, forest response to these discrete events may vary by forest type. For example, *Pinus* typically have more narrow crowns with stronger apical dominance compared to co-occurring hardwoods and *Pinus* stems are also able to extend 10–15 m above the main hardwood canopy (Rogers and Lindquist, 1992). Differences in crown and height characteristics of canopy trees may result in different gap characteristics, such as size and shape, which in turn influence gap closure mechanisms. Gap formation and closure are important controls on development and succession (Runkle, 1985; Rentch et al., 2003; Webster and Lorimer, 2005; Hart and Grissino-Mayer, 2008; Zeide, 2010).

The theoretical basis for successional pathways in *Quercus-Pinus* forests of the eastern US has been well established (e.g. Billings, 1938; Oosting, 1942; Braun, 1950; Quarterman and Keever, 1962; Halls and Homesley, 1966; Nicholson and Monk, 1975; Switzer et al., 1979; Peet and Christensen, 1980; Christensen and Peet, 1981, 1984; Christensen, 1989). At crown closure, shade-intolerant *Pinus* individuals typically dominate the canopy. *Pinus* stems are sparse to non-existent in the understory strata of these closed canopy stands and mortality of canopy *Pinus* provides the opportunity for the more shade-tolerant hardwoods to recruit to larger size classes and ascend to canopy positions. Eventually *Pinus* stems are phased out of these systems altogether via gap-phase succession. Although it is understood that gap-scale disturbance processes drive this successional trajectory, we lack a clear mechanistic understanding of the transition from *Pinus* to hardwood dominance in these systems. A mechanistic understanding of this process is required for managers interested in either

maintaining a *Pinus* component to successional stands, promoting more natural mixtures of hardwoods in managed *Pinus* systems, or accelerating succession to hardwood dominance.

Increasingly, forest managers wish to maintain a *Pinus* component in stands transitioning to hardwood dominance (Hart et al., 2012) for a variety of reasons such as biodiversity, fuels, drought tolerance, commodity production, and restoration of native forest conditions. *Pinus* trees contribute to the maintenance of diverse wildlife communities by providing habitat suitable for many early successional wildlife species (Dickson, 1982; Buckner, 1982; Owen, 1984). *Pinus* needles are highly flammable and encourage the spread of fire compared with some hardwood litter (Kane et al., 2008; Ellair and Platt, 2013). *Pinus* individuals also contribute large and resilient coarse woody debris, are more drought tolerant than hardwoods, and offer economic value in the form of wood products. *Pinus* stems provide a pathway for change within a forest system dominated by hardwood species because they increase the heterogeneity of the canopy, may have high live crown ratios, year-round foliage, and relatively acidic litter, wood, and bark (Harmon et al., 1986; Schulte et al., 2007; Fahey and Lorimer, 2013). Without active management or the absence of stand initiating or perhaps intermediate-scale disturbances, the *Pinus* component to many *Quercus-Pinus* systems in the eastern US will be lost or greatly diminished (Rantis and Johnson, 2002; Guyette et al., 2007; Stambaugh and Muzika, 2007; Hart et al., 2012). By quantifying the driving mechanisms of development and succession in *Quercus-Pinus* stands, I can provide the tools required to actively manage natural processes and to develop or refine silvicultural prescriptions intended to maintain a *Pinus* component in successional stands, progress toward a more natural mixture

of hardwoods in intensively managed *Pinus* systems, or to accelerate succession to hardwood dominance.

The overarching goal of this study is to examine gap-scale disturbance processes and the forest response to elucidate developmental and successional patterns in *Quercus-Pinus* stands. The specific objectives of my study were to: (1) document land fraction of forest within canopy gaps; (2) quantitatively describe gap characteristics and formation mechanisms; (3) characterize gap closure processes; and (4) examine the influence of gap-scale disturbances on development and succession in *Quercus-Pinus* systems.

2. STUDY AREA AND FIELD METHODS

2.1. Study area

The Sipsey Wilderness (Figure 1) is a 10,085 ha portion of the National Wilderness Preservation System maintained by the USDA Forest Service. It is situated within the William B. Bankhead National Forest in Lawrence and Winston Counties, Alabama. The reserve is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman, 1938). The underlying geology consists primarily of the Pennsylvanian Pottsville formation characterized by thick-bedded to pebbly quartzose sandstone and containing differing levels of interstratified shale, siltstone, and thin discontinuous coal (Szabo et al., 1988). Topography of the region is characterized by narrow ridges and valleys, extensive hills, and steep slopes (USDA, 1959; Smalley, 1979). Soils are acidic, well drained, and shallow (USDA, 1959). Study plots ranged in elevation from 740–918 m and slopes ranged from 5–41% with a mean of 16%.

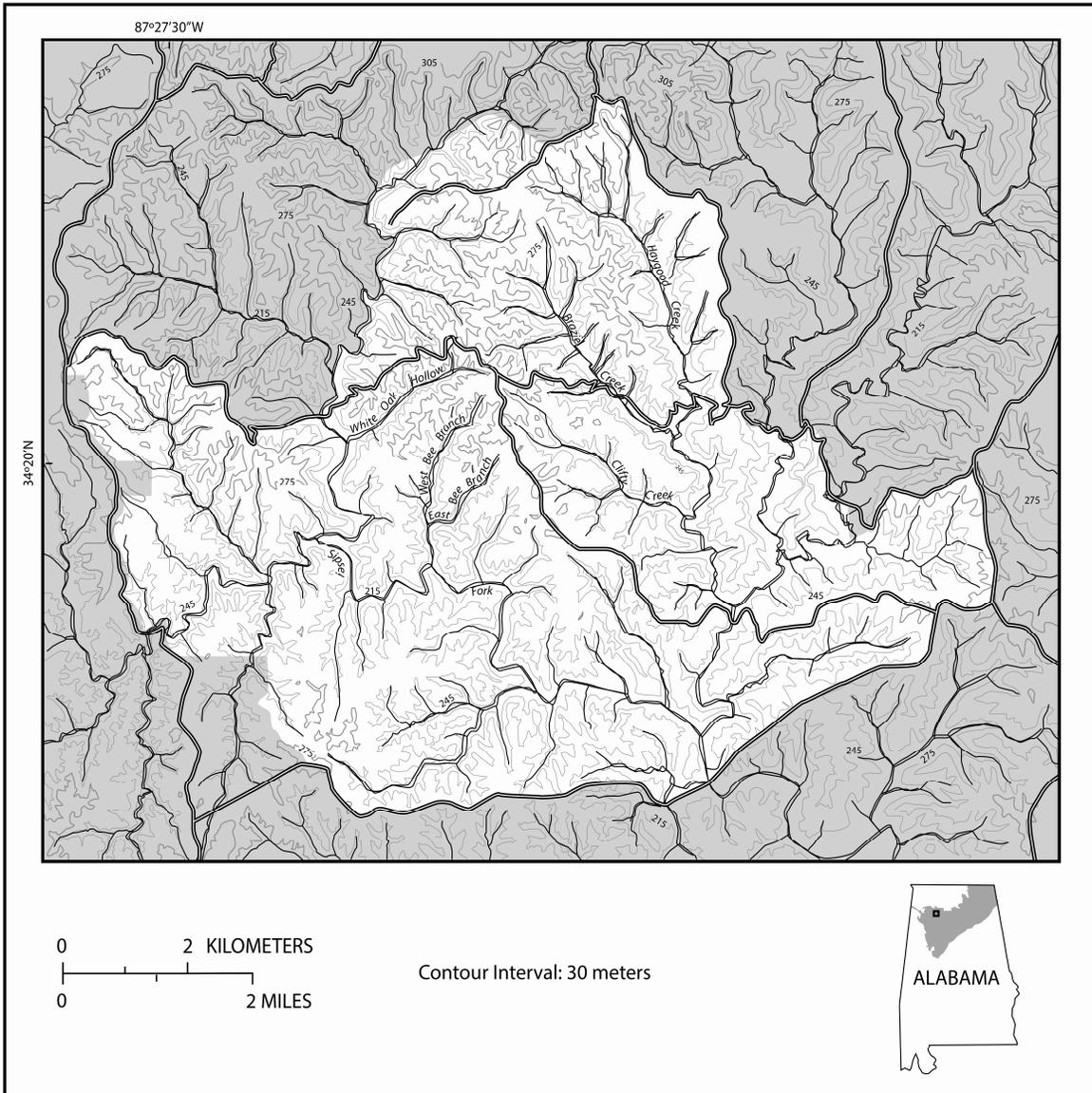


Fig. 1. Map of Sipsy Wilderness, Alabama. White area is the Sipsy Wilderness, thin lines are 30 m contour intervals, heavy lines are streams, and double lines are roads. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic section.

The climate of this region is classified as humid mesothermal with short, mild winters and long, hot summers (Thornwaite, 1948). The average frost free period is ca. 220 days and extends from late-March to early-November (Smalley, 1979). The mean annual temperature is 16 °C; the January average is 5 °C and the July average is 26 °C (Smalley, 1979). Precipitation remains stable throughout the year with no distinct dry season. Mean annual precipitation is 1463 mm with monthly means of 138 mm for January and 117 mm for July (PRISM Climate Group, 2013). Winter months are characterized by low intensity precipitation and are the result of frontal lifting whereas summer months are characterized by high intensity convection storms (Smalley, 1979).

Braun (1950) classified the area as a transitional region between the *Quercus-Pinus* Forest to the south and the Mixed Mesophytic Forest to the north. Species composition on the Cumberland Plateau is strongly influenced by topography and factors related to soil water availability (Hinkle, 1989; Clatterbuck et al. 2006). Cumberland Plateau forests are known for high species richness and gamma diversity with over 30 tree species that have canopy potential (Hinkle et al., 1993). In a gradient analysis study, Zhang et al. (1999) classified 14 ecological communities on the Sipsy Wilderness ranging from xeric sites dominated by *P. virginiana* to mesic sites dominated by *Fagus grandifolia* and *Acer saccharum* to sites with no overstory cover. Sampled stands were located on ridge tops dominated by *Quercus-Pinus* forest types and the *Pinus* contribution typically is reduced with increased distance downslope (Parker and Hart, 2014).

2.2. Field methods

To identify potential study stands, I used georeferenced field survey data provided by the USDA Forest Service, Bankhead Ranger District staff to locate *Quercus-Pinus* forest types (SAF forest cover types 13 and 16) in the Sipsey Wilderness. All suitable stands were then visited for reconnaissance and I selected for inclusion in the study only those that were not visibly damaged by broad-scale exogenous disturbances, such as insect or pathogen outbreaks, during development. All stands were located along ridgetop positions. Non-gap forest vegetation was quantified using a total of twenty 0.05 ha fixed-radius plots located randomly throughout the stands. In each plot I recorded species, diameter at breast height (dbh; ca. 1.4 m above the surface), and crown class for all stems ≥ 10 cm dbh. Crown class categories (overtopped, intermediate, codominant, and dominant) were based on the amount and direction of intercepted light (Oliver and Larson, 1996). To document stand age, increment core samples were taken from two trees per non-gap plot that I deemed would have been the oldest individuals. These data were used to establish composition and structural measures of the sampled stands and to examine the influence of gaps on these characteristics.

Canopy gaps ($n = 60$) were located along transects throughout the study stands using the line-intercept method (Runkle 1982, 1985; Veblen, 1985; Runkle, 1992). The fraction of land area in both the expanded and observed canopy gaps was calculated by dividing the transect distance in gaps by total transect length (Runkle 1985, 1992). Gaps were defined as locations with: (1) a noticeable void in the main forest canopy, (2) leaf height of the tallest gap stems less than three-fourths the height of the adjacent canopy, and (3) presence of a gapmaker (Taylor and Lorimer, 2003). No minimum or maximum gap size thresholds were used to ensure an

accurate representation of gaps was documented (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). When I encountered a gap that met my criteria it was sampled regardless of biophysical characteristics thus, the first 60 gaps that met these criteria were quantified.

I classified the area within each gap as being in either the observed or expanded gap. The observed gap was defined as the area directly beneath the void in the canopy and was determined by the use of a vertical densitometer and visual estimations (Richards and Hart, 2011). The expanded gap was defined as the total terrestrial area below the gaps extending to the bases of the canopy trees along the perimeter of the gap (Runkle, 1981). Gap area was determined for both the observed and expanded gaps by measuring the length of the greatest distance from gap edge to gap edge, and the width of the greatest distance from gap edge to gap edge perpendicular to the length. These measurements were fit to formula of an ellipse because gaps of the southern Appalachian highlands are usually elliptical in shape (Runkle, 1982, 1992; Clinton et al., 1993; Hart and Grissino-Mayer, 2009) and most gaps appeared elliptical.

Elevation, latitude, and longitude were recorded in the field using a handheld GPS device. Other physical site characteristics were recorded for each gap including percent slope, aspect, and average canopy height surrounding the gap. At each gap, the average of three canopy height measurements was taken using a digital hypsometer with a transponder. The quantity of perimeter canopy trees was recorded for each gap to analyze the number of individuals required to complete the canopy surrounding gaps and the number of canopy individuals with the potential to close the gaps through branch elongation (Runkle, 1982). Gap

age was determined using a variety of techniques. Increment core samples were taken from larger residual trees hypothesized to show increased radial growth rates coincident with gap formation (Hart et al., 2010; Rentch et al., 2010). Within gaps, individual stems and branches which appeared to have formed immediately following gap formation were cut at their base and transported to the laboratory to determine the establishment date (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). In the laboratory, all wood samples were processed and dated using standard dendrochronological techniques (Stokes and Smiley, 1996; Orvis and Grissino-Mayer, 2002). Tree-ring series on the increment core samples were visually analyzed for sudden and anomalous increases in radial growth (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). Furthermore, I visually examined saplings for increases in stem elongation by counting annual bud scars (Runkle, 1982). Results from these methods were compared by gap and all gap origin dates were then corroborated with gapmaker decay classes. All gapmakers were assigned to one of four decay classes following the criteria of Jones and Daniels (2008). Thus, multiple techniques were used in combination to assign gap formation years.

Canopy gaps can be created by several different mechanisms that cause overstory tree mortality. Different gap formation mechanisms may have different effects on biotic and abiotic forest conditions. For this reason, gap formation mechanisms were determined by observation of gapmaker and classified into one of three categories: snag (standing dead tree with crown intact), uprooted stem (root network uplifted), or snapped stem (bole broken below the crown; Putz, 1983; Clinton et al., 1993; Yamamoto, 2000). Gapmakers were taxonomically classified to quantify any species-specific overstory mortality patterns. The dbh of all gapmakers was

recorded to determine the amount of overstory basal area (m^2) lost during each event and provide information on the amount of basal area naturally removed through gap-scale processes.

I characterized gap vegetation by documenting species and crown class for all stems ≥ 5 cm dbh within expanded and observed gaps. Gap regeneration was characterized by tallying all saplings (woody stems < 5 cm dbh, ≥ 1 m in height) within the observed gap. To document forest response to canopy disturbance, I calculated relative density (contribution of each species to total stems), relative dominance (contribution of each species to total basal area), and relative importance (average of relative density and relative dominance) for all trees sampled in both the observed and expanded gap and all saplings within the observed gap. Intra-gap spacing of trees was calculated by dividing the expanded gap area by number of trees per gap (both the observed and expanded gap).

Likely closure mechanisms for each gap were determined to document successional and developmental changes within the forest. Gaps were projected to close through either lateral crown expansion of surrounding canopy individuals or height growth of subcanopy trees within each gap (Taylor and Lorimer, 2003; Cole and Lorimer, 2005; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). For gaps projected to close via subcanopy recruitment, species of the probable gap successor was recorded. Probable gap successors are individuals likely to fill the canopy void and can often be successfully identified in the field (Barden, 1979, 1980; White et al., 1985; Yamamoto and Nishimura, 1999; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). Documenting gap filling trees is important for projecting future stand composition and

analyzing the influence of gap-scale disturbances on developmental and successional patterns (Taylor and Lormimer, 2003).

To document gap shape patterns I calculated a ratio of length to width ($L:W$) for expanded and observed gaps (Hart and Grissino-Mayer, 2009; Rentch et al., 2010; Richards and Hart, 2011). I also calculated diameter to height ratios ($D:H$) using expanded gap width as diameter and average height of canopy trees surrounding each gap as height (Marquis, 1965; Dey, 2002). These data provided information on the micro-scale variations that occur within the individual gap types. Physical gap characteristics (e.g. gap size, average canopy height, intra-gap spacing of trees) were analyzed for relationships between gap formation mechanisms as well as projected gap closure mechanisms. All statistical tests were performed with SAS v. 9.3 after data were visually assessed and statistically analyzed for normality and variance.

3. RESULTS

3.1. Forest Composition and Structure

Mean establishment year of the 40 trees used to document stand age was 1899 ± 14.0 years (SD). The oldest stem was a *P. taeda* with a dbh of 58 cm that established in 1884, and the youngest tree was also a *P. taeda* with a dbh of 31 cm that established 1920. Sampled stands on the Sipse Wilderness were dominated by *Quercus alba*, *P. taeda*, and *Q. prinus* (Table 1), collectively representing 83% of the basal area. The next most dominant taxa were *O. arboreum*, *Carya* spp., *Q. rubra*, *L. tulipifera*, *P. virginiana*, *N. sylvatica* and *Q. falcata*, cumulatively comprising 20% of the basal area. Basal area of all stems ≥ 10 cm dbh was $36.14 \text{ m}^2 \text{ ha}^{-1}$. *Quercus alba* ($n = 112 \text{ ha}^{-1}$) and *Q. prinus* ($n = 81 \text{ ha}^{-1}$) were the most abundant species, representing 53% of all stems ≥ 10 cm dbh in the sampled forest. *Pinus taeda* ($n = 35 \text{ ha}^{-1}$) had the next highest density, representing 10% of all stems. Density of stems ≥ 10 cm dbh was 362 ha^{-1} .

Of the 12 trees ha^{-1} with dominant positions in the forest canopy, 10 were *P. taeda* individuals and the other two were a *L. tulipifera* and a *Q. rubra*. The largest tree documented

Table 1

Density, dominance, and relative importance (average of relative density and relative dominance) for stems ≥ 10 cm dbh in 20 non-gap plots in Sipsey Wilderness, Alabama.

Species	Density ha ⁻¹	Relative Density (%)	Dominance (m ² ha ⁻¹)	Relative Dominance (%)	Relative Importance
<i>Quercus prinus</i>	81	22.38	13.47	37.28	29.83
<i>Quercus alba</i>	112	30.94	8.51	23.55	27.25
<i>Pinus taeda</i>	35	9.67	7.86	21.74	15.70
<i>Oxydendrum arboreum</i>	33	9.12	0.56	1.56	5.34
<i>Carya</i> spp.	19	5.25	0.80	2.23	3.74
<i>Quercus Rubra</i>	12	3.31	1.46	4.04	3.68
<i>Liriodendron tulipifera</i>	11	3.04	1.19	3.29	3.16
<i>Pinus virginiana</i>	13	3.59	0.97	2.67	3.13
<i>Nyssa sylvatica</i>	19	5.25	0.25	0.68	2.97
<i>Quercus falcata</i>	6	1.66	0.46	1.28	1.47
<i>Magnolia macrophylla</i>	5	1.38	0.07	0.18	0.78
<i>Fagus gradifolia</i>	5	1.38	0.05	0.15	0.77
<i>Quercus velutina</i>	2	0.55	0.19	0.53	0.54
<i>Quercus stellata</i>	2	0.55	0.15	0.41	0.48
<i>Acer rubrum</i>	2	0.55	0.02	0.06	0.31
<i>Pinus echinata</i>	1	0.28	0.07	0.21	0.24
<i>Prunus serotina</i>	1	0.28	0.02	0.06	0.17
<i>Fraxinus americana</i>	1	0.28	0.01	0.04	0.16
<i>Sassafras albidum</i>	1	0.28	0.01	0.04	0.16
<i>Cornus florida</i>	1	0.28	0.01	0.02	0.15
TOTAL	362	100.00	36.14	100.00	100.00

on a non-gap plot was a *P. taeda* with a dbh of 76 cm. Average dbh for trees in a dominant canopy position was 60.7 cm \pm 8.6 (SD). The majority of stems (56%) occurred in the codominant crown class. The codominant canopy position was occupied by *Q. alba* (n = 86 ha⁻¹), *Q. prinus* (n = 49 ha⁻¹), *P. taeda* (n = 25 ha⁻¹), *P. virginiana* (n = 12 ha⁻¹), and *Q. rubra* (n = 11 ha⁻¹). Mean dbh for trees in the codominant canopy position was 34.8 cm \pm 10.3. *Quercus prinus* was the most abundant species in the intermediate canopy position (n = 33 ha⁻¹), followed by *O. arboreum* (n = 31 ha⁻¹), *Q. alba* (n = 26 ha⁻¹), *N. sylvatica* (n = 18 ha⁻¹) and *Carya*

spp. ($n = 11 \text{ ha}^{-1}$). Only one *Pinus* stem (a *P. virginiana*) was found in an intermediate position and the species was absent from the overtopped position.

3.2. Gap fraction, gap, and gapmaker characteristics

Total transect length was 3.0 km, with 28% of the total length in expanded and observed gaps, and 12% in observed gaps only. Standardized to the hectare level, $2,800 \text{ m}^2 \text{ ha}^{-1}$ were in expanded gaps and $1,150 \text{ m}^2 \text{ ha}^{-1}$ were in observed gaps. Gap ages ranged from 2 to 29 years with an average age of $11 \text{ years} \pm 6$ (Figure 2).

I documented 74 gapmakers that formed the 60 studied gaps. *Pinus* individuals represented 56% of gapmakers and the remaining 44% were hardwoods. Only two species of *Pinus* gapmakers were found, *P. taeda* ($n = 32$) and *P. virginiana* ($n = 9$). Out of the 33 hardwood gapmakers, 31 were *Quercus*. *Quercus prinus* ($n = 13$) and *Q. rubra* ($n=10$) accounted for the majority of *Quercus* gapmakers and *F. grandifolia* and *L. tulipifera* were the only two non-*Quercus* gapmaking hardwood species I documented. Taxonomic classification of gapmaker (*Pinus* v. hardwood) was not significantly related to the following variables:

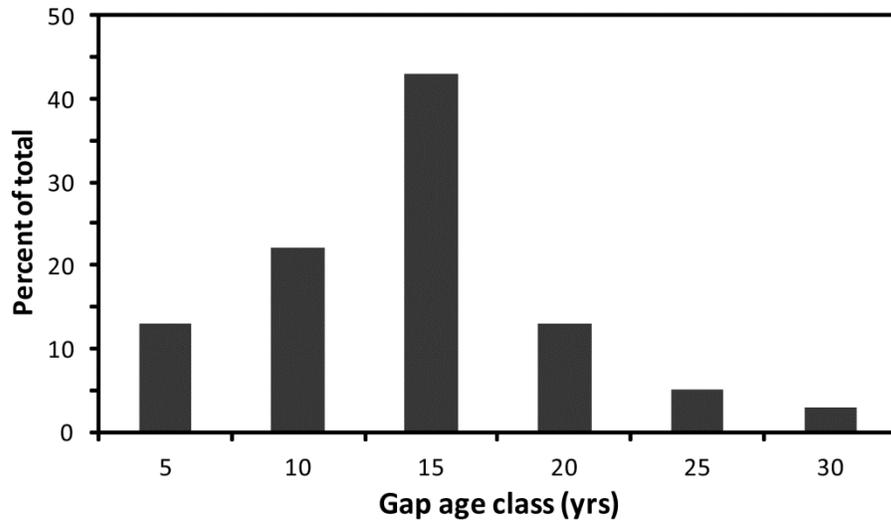


Fig. 2. Distribution of 60 canopy gaps by five-year age classes in Sipsey Wilderness, Alabama.

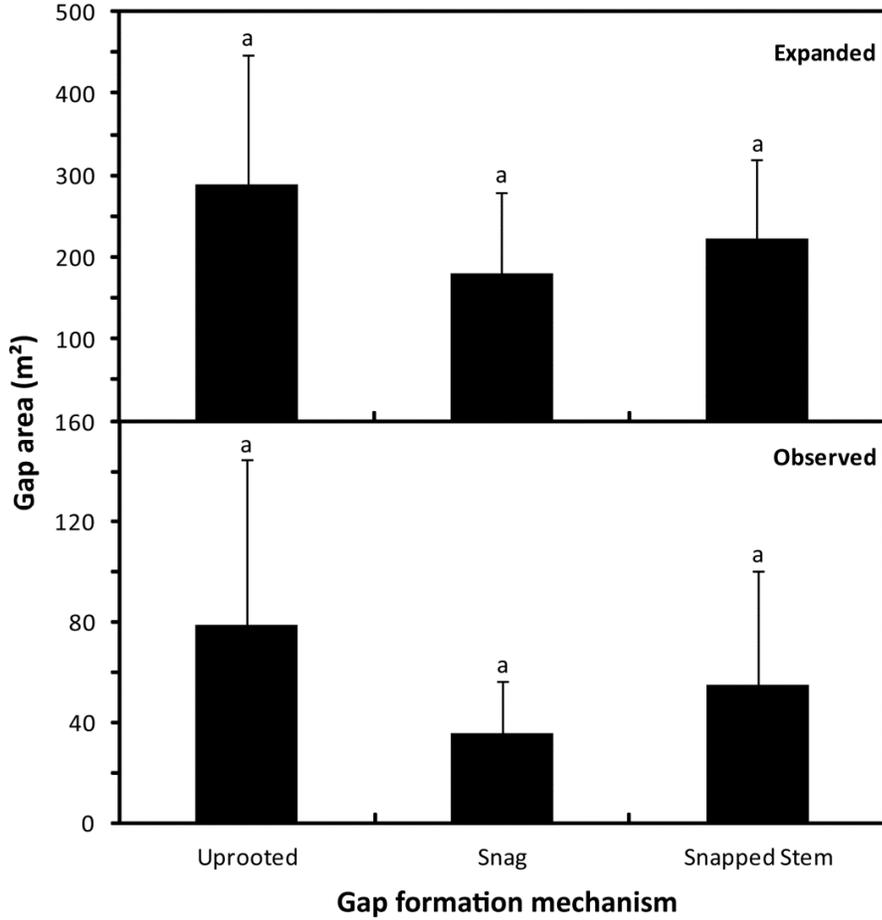


Fig. 3. Mean sizes (\pm SD) of observed and expanded gaps by gap formation mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant ($P < 0.05$) difference between gap origins as detected by ANOVA with Scheffe post hoc-testing.

expanded gap area, observed gap area, $L:W$ ratio of expanded gap, or $L:W$ ratio of observed gap. The mean size of expanded gaps was $226 \text{ m}^2 \pm 113$. The largest expanded gap was 488.8 m^2 and the smallest was 75.2 m^2 . The mean size of observed gaps was $55 \text{ m}^2 \pm 47$, with a maximum of 201.8 m^2 and a minimum of 4.0 m^2 . Mean $L:W$ ratios of expanded gaps and observed gaps were $1.44:1$ and $1.84:1$, respectively. The mean $D:H$ ratio for expanded gaps was $0.53:1$ and for observed gaps was $0.23:1$. The majority of canopy gaps were formed by snapped stems (53%) followed by snags (27%) and uprooted stems (20%). Expanded gap size, observed gap size, and $L:W$ ratios were not significantly different across gap formation mechanisms (Figure 3). However, $L:W$ ratios of observed gaps were significantly greater ($P = 0.005$) than $L:W$ ratios of expanded gaps.

All gaps were caused by the death of one or two trees. Single tree gaps represented 73% of all gaps and two-tree gaps accounted for 27%. Gaps created by a single tree fall had a mean expanded area of $199 \text{ m}^2 \pm 91$, with a maximum 488.84 m^2 and a minimum of 75.23 m^2 , and a mean observed area of $42 \text{ m}^2 \pm 31$ with a maximum of 175.91 m^2 and a minimum of 4.01 m^2 . Two-tree gaps had a mean expanded area of $298 \text{ m}^2 \pm 143$ with a maximum of 487.96 m^2 and a minimum of 80.18 m^2 , and a mean observed area of $86 \text{ m}^2 \pm 62$ with a maximum of 201.08 m^2 and a minimum of 10.13 m^2 . Mean basal area lost for single tree events compared to multi-tree events was $0.16 \text{ m}^2 \pm 0.08$ and $0.30 \text{ m}^2 \pm 0.15$, respectively. Significant positive relationships were found between basal area lost during a disturbance and both expanded gap ($r = 0.48$, $P = 0.0001$) and observed gap sizes ($r = 0.52$, $P = < 0.0001$). Significant positive relationships were also found between gapmaker dbh and expanded gap size ($r = 0.41$, $P = 0.006$) (Figure 4).

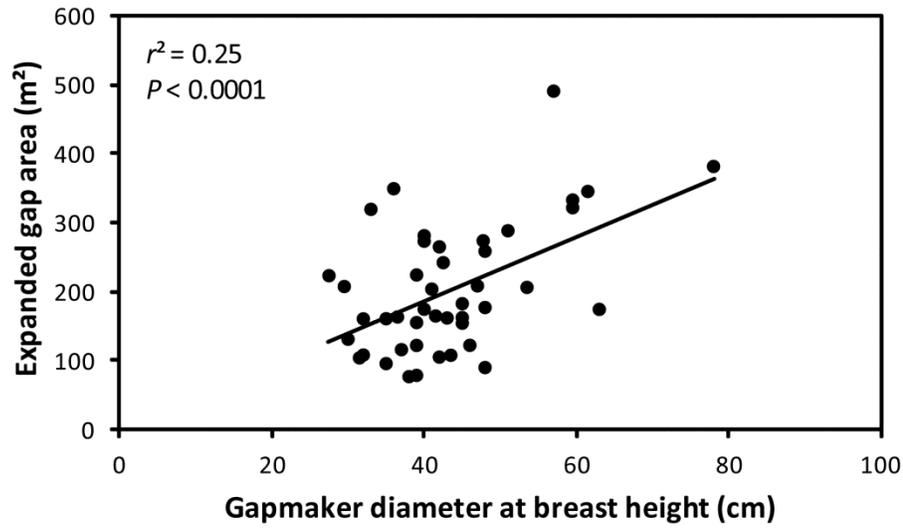


Fig. 4. Relationship between gapmaker diameter at breast height (cm) and expanded gap area (m²) in Sipsey Wilderness, Alabama.

Average dbh of *Pinus* and hardwood gapmakers was 43.1 ± 11.6 and 40.7 ± 8.2 , respectively, with an overall average dbh of $42.6 \text{ cm} \pm 11.4$.

3.3. Density and diversity within gaps

The mean number of canopy trees that bordered gaps was 6.3 ± 1.9 , ranging between three and eleven. Overall, larger gaps were surrounded by a higher number of trees than smaller gaps. The mean number of trees ≥ 5 cm dbh within expanded gaps was 6.3 ± 4.9 with a maximum of 23 and a minimum of zero. The mean number of trees ≥ 5 cm dbh in the observed gap was 5.9 ± 5.2 with a maximum of 25 and a minimum of zero. The mean number of trees ≥ 5 cm dbh in both the expanded and observed gap was 12.3 ± 9.1 . The mean intra-gap spacing of trees was $26.6 \text{ m}^2 \pm 19.9$ and ranged from 8.62 to 102.41 m^2 .

In the observed gap, species richness of trees ≥ 5 cm dbh was 26. *N. sylvatica* was the most abundant of all trees ≥ 5 cm dbh in observed gaps (13.9%) followed by *F. grandifolia* and *Q. alba*. The most dominant species were *Q. alba* and *Q. prinus* (Table 2). *P. virginiana* and *P. taeda* represented only 5.36% and 1.26% of observed gap trees, respectively. Average Shannon diversity (H') of all trees in both the expanded and observed gaps was 1.48 ± 0.58 with a maximum of 2.48 and a minimum of zero.

Observed gaps contained 39 different species in the sapling layer. *A. rubrum* had the highest relative density, representing 36.9% of all sapling stems. *Carya* spp. had the next highest relative density (8.6%). The average number of saplings in observed gaps was 34 ± 23 . Mean sapling diversity (H') was 1.68 ± 0.41 . Maximum sapling diversity was 2.52 and the

Table 2

Density, dominance, and relative importance (average of relative density and relative dominance) for all trees ≥ 5 cm dbh in 60 observed gaps in Sipsey Wilderness, Alabama.

Species	Density ha ⁻¹	Relative Density (%)	Dominance (m ² ha ⁻¹)	Relative Dominance (%)	Relative Importance
<i>Quercus alba</i>	111.42	11.67	3.02	23.04	17.35
<i>Nyssa sylvatica</i>	132.50	13.88	0.95	7.28	10.58
<i>Quercus prinus</i>	60.23	6.31	1.88	14.32	10.32
<i>Fagus gradifolia</i>	114.43	11.99	1.01	7.68	9.84
<i>Pinus virginiana</i>	51.19	5.36	1.25	9.57	7.47
<i>Carya spp.</i>	57.21	5.68	0.99	7.36	6.52
<i>Acer rubrum</i>	90.34	9.46	0.33	2.53	6.00
<i>Oxydendrum arboreum</i>	45.17	4.73	0.66	5.05	4.89
<i>Cornus florida</i>	63.24	6.62	0.30	2.28	4.45
<i>Magnolia macrophylla</i>	42.16	4.42	0.35	2.64	3.53
<i>Amelanchier arborea</i>	39.15	4.10	0.27	2.06	3.08
<i>Pinus taeda</i>	12.05	1.26	0.49	3.71	2.49
<i>Prunus serotina</i>	27.10	2.84	0.24	1.83	2.34
<i>Quercus Rubra</i>	15.06	1.58	0.20	1.50	1.54
<i>Fraxinus americana</i>	18.07	1.89	0.14	1.07	1.48
<i>Quercus velutina</i>	6.02	0.63	0.30	2.25	1.44
<i>Liriodendron tulipifera</i>	12.05	1.26	0.20	1.52	1.39
<i>Ostrya virginiana</i>	18.07	1.89	0.10	0.80	1.34
<i>Ilex opaca</i>	12.05	1.26	0.06	0.43	0.85
<i>Quercus falcata</i>	3.01	0.32	0.14	1.06	0.69
<i>Quercus stellata</i>	3.01	0.32	0.10	0.80	0.56
<i>Juniperus virginiana</i>	6.02	0.63	0.06	0.47	0.55
<i>Sassafras albidum</i>	6.02	0.63	0.04	0.28	0.45
<i>Ulmus alata</i>	3.01	0.32	0.03	0.20	0.26
<i>Vaccinium arboreum</i>	3.01	0.32	0.01	0.05	0.18
<i>Acer saccharum</i>	3.01	0.32	0.01	0.05	0.18
TOTAL	954.58	100.00	13.11	100.00	100.00

minimum was 0.41. Mean total diversity for all stems ≥ 1 m was 2.03 ± 0.30 with a maximum of 2.75 and a minimum of 1.39. Significant positive relationships were found between gap size and number of saplings ($r_s = 0.79$, $P < 0.0001$), trees ($r_s = 0.69$, $P < 0.0001$), and total stems ($r_s = 0.84$, $P < 0.0001$). Positive relationships also existed between gap size and sapling diversity ($r^2 = 0.15$, $P = 0.002$), tree diversity ($r^2 = 0.21$, $P = 0.0002$), and total stem diversity ($r^2 = 0.29$, $P < 0.0001$) (Figure 5). Shannon diversity (H') is a dimensionless index such that gap size would not bias the diversity measure.

3.4. Gap closure and recruitment

The majority (58%) of gaps were projected to close via subcanopy recruitment and 42% were projected to close via lateral crown expansion. The gaps projected to close by lateral crown expansion and subcanopy recruitment had average expanded areas of 162 m² and 242 m², respectively (Figure 6). The following variables were significantly greater for gaps projected to close via subcanopy recruitment: expanded gap area ($P < 0.001$), observed gap area ($P < 0.001$), number of perimeter trees surrounding each gap ($P = 0.006$), the number of perimeter trees that were *Pinus* surrounding each gap ($P = 0.006$), the $D:H$ ratio for expanded gaps ($P = 0.002$), and the $D:H$ ratio for observed gaps ($P = 0.0005$). Intra-gap spacing of trees was significantly greater ($P = 0.03$) for gaps projected to close via lateral crown expansion. Gap closure was not significantly related to average canopy height or $L:W$ ratio.

Of the 35 gaps projected to close via subcanopy height growth, *Quercus* was the most common gap filling genus, projected to capture 25% of these gaps. Other gap filling taxa were *Carya* spp. (14%), *N. sylvatica* (12%), *F. grandfolia* (10%), *P. virginiana* (8%), *P. taeda* (6%), *A.*

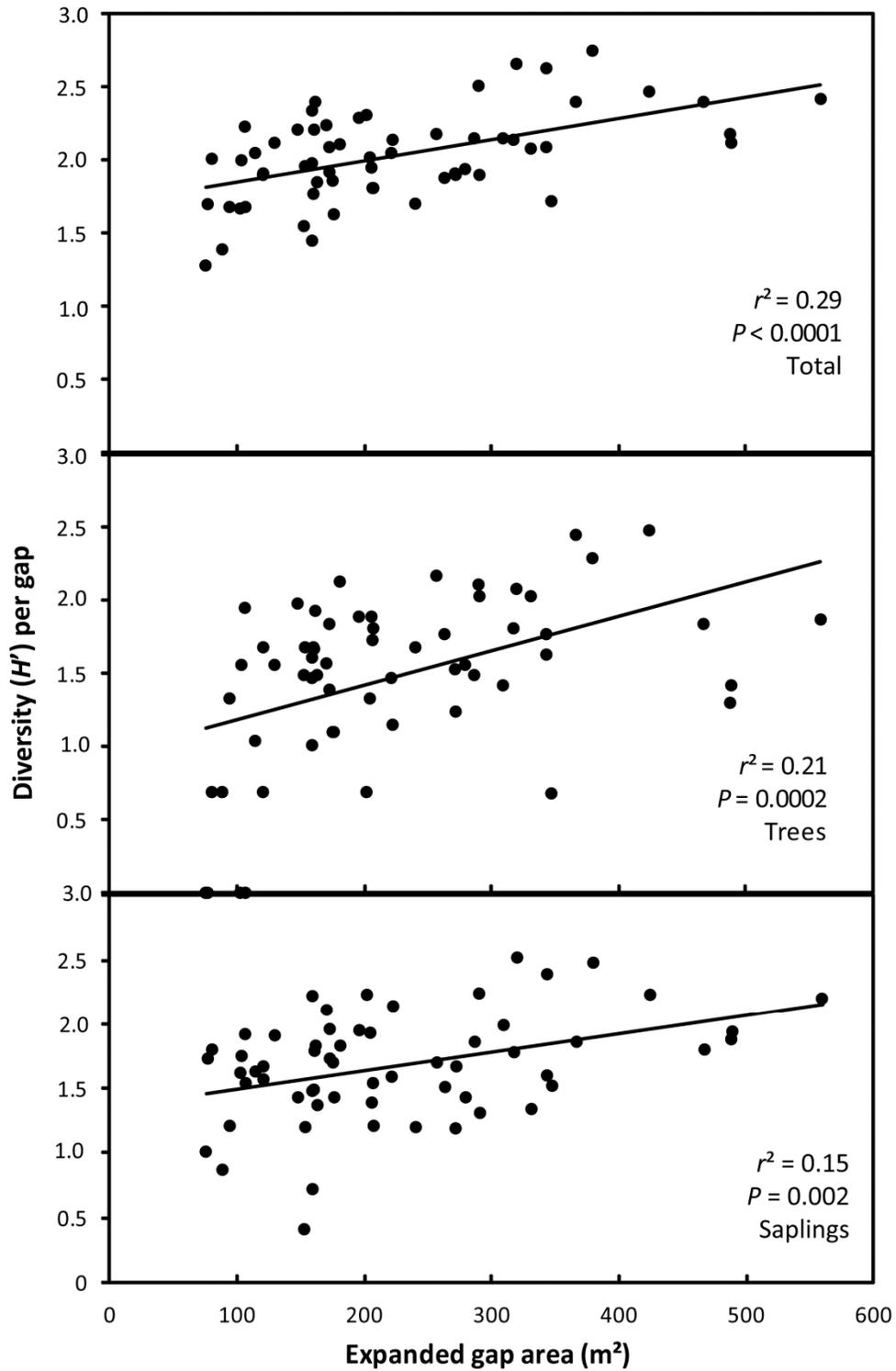


Fig. 5 Relationships between diversity values for saplings (≥ 1 m height, < 5 cm dbh), trees (≥ 5 cm dbh), and total stems (all stems ≥ 1 m height) and expanded gap area in Sipsey Wilderness, Alabama.

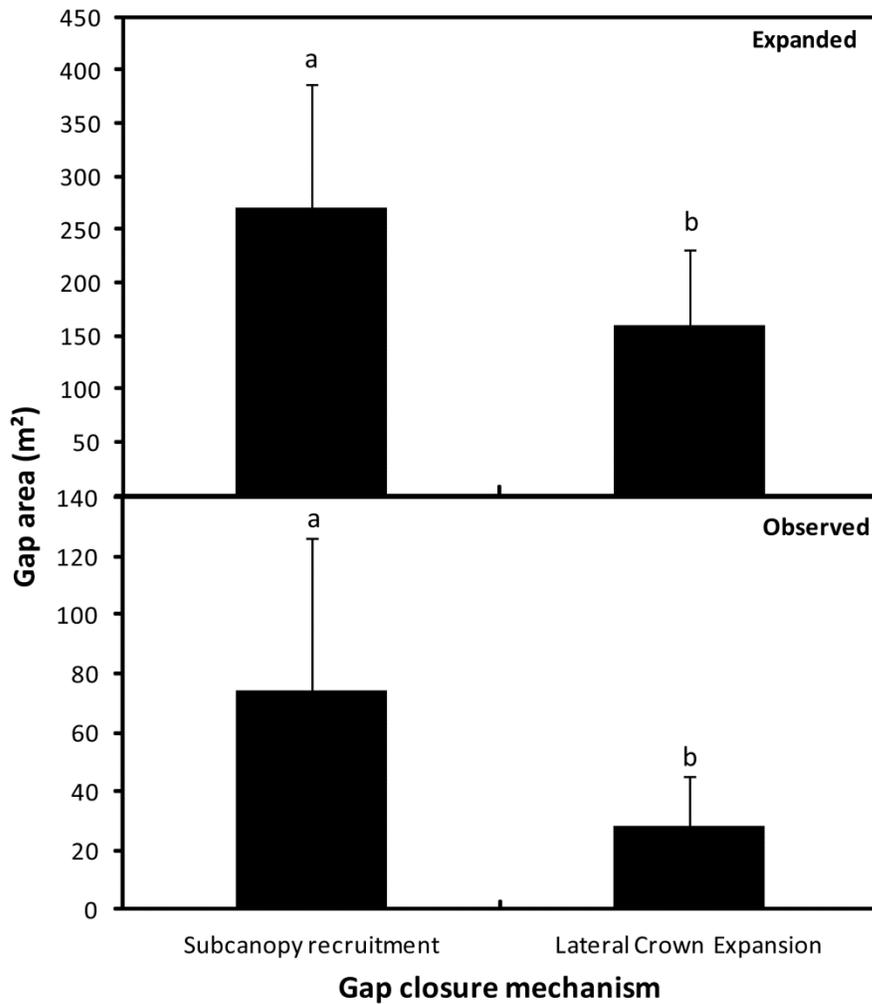


Fig. 6. Mean sizes (\pm SD) of observed and expanded gaps by gap closure mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant ($P < 0.0001$) difference between gap closure mechanisms as detected by two-tailed t-tests.

rubrum (4%), followed by *L. tulipifera*, *P. serotina*, *F. americana*, and *Q. stellata* (2% each). Gaps projected to close by a *Quercus* individual had an average expanded gap area of $276 \text{ m}^2 \pm 104$ and gaps projected to close by a *Pinus* stem had a mean expanded area of $273 \text{ m}^2 \pm 114$.

4. DISCUSSION

4.1. Gap fraction, gap, and gapmaker characteristics

Data regarding the fraction of land area within a gap environment in *Quercus-Pinus* systems is lacking. Bottero et al. (2011) found that stands with a strong *Picea* and *Abies* component in the canopy had a greater percentage of the stand in a gap environment compared to stands with a dominant hardwood canopy. They speculated that since *Picea* and *Abies* have less capacity for lateral crown growth, a higher gap fraction is expected for stands with a low hardwood component in the canopy layer. *Pinus* spp. also have less capacity to extend their crowns laterally, and my results show a high portion of sampled stands within a gap environment compared to what has been reported elsewhere in the temperate zone (e.g. Runkle, 1982; Hart Grissino-Mayer, 2009; Rentch et al., 2010). Although gap fraction was high, my results also show that gap sizes were similar to those found in other studies (e.g. Runkle, 1982; Hart and Grissino-Mayer, 2009; Rentch et al., 2010; Richards and Hart, 2011). Therefore the gap formation rate in the sampled stands, which were located on ridge tops, was high compared with other gap formation rates in the temperate zone (e.g. Runkle, 1982; Hart Grissino-Mayer, 2009; Rentch et al., 2010). Ridge tops have thin soils and experience high wind velocities compared to lower slopes; both of these factors would lead to a greater probability of windthrow and thus relatively high gap formation rates.

Gap age distribution lacks a reverse J-shape indicating the rate of gap formation is not in equilibrium. Gap formation rates peak 10–15 years ago, and this pulse co-occurs with the southern pine beetle outbreak of 1999–2001. However, other studies conducted in the Sipsey have noted a similar gap age distribution, and these studies did not have a *Pinus* component

(Richards and Hart, 2011). Therefore, the pulse of gap formation 10—15 years ago does not appear to be related to the southern pine beetle outbreak of 1999—2001.

No significant difference was found between gap size and shape based on gap origin. This may be explained by the high number of uprooted gaps involving a single tree in the studied stands; 9 out of 12 uprooted gaps were the result of a single treefall. The fall of uprooted stems has a greater potential to remove or damage neighboring canopy trees causing multi-tree gaps compared to snapped stems or snags (Yamamoto and Nishimura, 1999). However, if the uprooted gapmaker does not remove other canopy trees, the gap should not be significantly different in size or shape than gaps formed by other mechanisms (Bormann and Likens, 1979). Also, I anticipated that, compared to gaps caused by a falling hardwood, a canopy void caused by the death of a *Pinus* individual would have a greater $L:W$ ratio because of differences in crown architecture. I hypothesized that a falling *Pinus* stem would leave a narrower gap compared to a falling hardwood tree because of crown spread. Although *Pinus*-formed gaps had a greater mean $L:W$ ratio than hardwood formed gaps, $L:W$ ratios were not significantly different.

Snapped-stem formed gaps were the most frequent cause of gap formation, representing 53% of all gaps and, out of gaps formed from the death of a *Pinus* individual, snapped stems accounted for 67% of canopy gaps. Interestingly, Jones et al. (1981) reported that *Pinus* trees are more likely to become snags, however I found only 6% of *Pinus* gapmakers stood as snags. A possible reason could be gap age. Conner and Saenz (2005) observed a 90% loss of large *Pinus* snags with a dbh > 40 cm 10 years after tree death. In my study, the average dbh of *Pinus* gapmakers was 43.1 ± 11.6 and the average age for each gap formation

mechanism was: uprooted 9.7 ± 5.1 , snag 9.6 ± 6.1 , and snapped stem 12.4 ± 5.7 . Therefore, a large majority of snapped and uprooted stems in my study may have stood as snags before falling from a wind disturbance. This region experiences ca. 58 thunderstorms annually (Smalley, 1979) that have the power to uproot and snap living and dead trees.

4.2. Density and diversity within gaps

In my study, I found increasing density and diversity (H') of saplings and trees with increasing gap size. Unlike stem density, diversity (H') is scale independent (McCune et al., 2002); therefore, gap size should not have an influence on diversity. Instead, the relationship between gap size and diversity is largely determined by a combination of niche partitioning and chance (Brokaw and Busing, 2000) and varies depending on habitat type and site quality. Results from prior studies that examined gap size-diversity relationships have been contradictory as researchers have noted positive effects hypothesized to be attributed to an influx of shade-intolerant species (e.g. Runkle, 1982; Phillips and Shure, 1990; Busing and White, 1997) and no effects, which were attributed to the dominance of advanced shade-tolerant regeneration (e.g. Shields et al., 2007; Hart and Grissino-Mayer, 2009; Bolton and D'Amato, 2011; Kern et al., 2013). Niche partitioning is rarely observed on sites that contain shade-tolerant advanced regeneration present before gap formation (Brokaw and Busing, 2000). Gap composition is thus largely determined by existing vegetation prior to gap formation (Raich and Christensen, 1989; Midgley et al., 1995; Brown and Jennings, 1998), in other words by chance (Brokaw and Scheiner, 1989). However, on xeric ridge tops where shade-tolerant species are often not competitive, the lack of advanced shade-tolerant regeneration may

provide more niche space and thus, explain the positive relationship between gap size and diversity found in the sampled stands. Therefore, on relatively low quality sites such as ridge tops well suited for shade-intolerant species, increasing gap size may be used as a tool to increase diversity (H'). For example, group selection harvests, which create large gaps, have been specifically used to maintain a shade-intolerant species component (Leak and Filip, 1977; Leak, 1999; Kelty et al., 2003).

4.3. Gap closure, recruitment, and succession

Expanded and observed gap sizes varied significantly by gap closure mechanism. Gaps that were projected to close via lateral crown expansion were smaller than those projected to close through subcanopy recruitment. Gaps closed by the height growth of subcanopy individuals need to be sufficiently large to prevent closing through the lateral extension of neighboring canopy tree crowns, thus, allowing an understory tree time to ascend to the main forest canopy (Runkle, 1982). Gaps projected to close via subcanopy height growth had a mean gap size of 242 m², which is similar to the subcanopy recruitment threshold reported in Richards and Hart (2011). Compared to hardwoods, *Pinus* crowns are more narrow and conical, which allows more light to reach the understory and midstory layers. For example, on the North Carolina Piedmont, Swan and Lieth (1976) found *Quercus* stands had 59% lower incoming solar radiation than *Pinus* stands, but only 15% more basal area. In my study, the crowns of hardwood trees appeared to be taking advantage of this additional light penetration through the canopy. Gaps projected to close by lateral crown expansion as a result of a *Pinus* gapmaker had an area of 174 m². In contrast, the mean size of gaps projected to close via lateral crown

expansion as the result of a hardwood gapmaker had a mean expanded gap area of 150 m². This result indicates that hardwood crowns adjacent to *Pinus* canopy trees may extend further laterally than they would if they were adjacent to another canopy hardwood tree. Thus, being located adjacent to a dominant *Pinus* individual, allowed hardwoods to capture a wider gap through lateral crown expansion than they would have if they were adjacent to another hardwood tree. *Pinus* crowns allowed adjacent canopy hardwood crowns to stretch further, and thus when the *Pinus* died the hardwood crown was in a more advantageous position to fill the void via lateral crown expansion.

The *Quercus-Pinus* forest in this study was in the beginning of the complex stage of development based on the number of gaps projected to fill by subcanopy recruitment. At this stage, stands should exhibit structural characteristics, such as large canopy gaps, that are typically used to characterize old-growth conditions (Oliver and Larson, 1996). The development of gaps sufficiently large so that they close via subcanopy recruitment can be attributed to gap-scale processes that occur continuously throughout prior stages of development (Richards and Hart, 2011). The complex stage begins once the progression of increasing gap size requires subcanopy recruitment to be the primary mode of gap closure (Oliver and Larson, 1996).

Our results show that gap-scale events are the dominant disturbance mechanism within this forest. Forests dominated by localized gap-scale disturbances favor shade-tolerant species (Henry and Swan, 1974; Dahir and Lorimer, 1996; McClure et al., 2000; Taylor and Lorimer, 2003) and species composition within gaps is a good predictor of future forest composition (Runkle and Yetter, 1987). In my study, I found that 14 of the 35 gaps projected to close

through subcanopy recruitment were filled by *Quercus* individuals. *Quercus* was also the most dominant genus of trees ≥ 5 cm dbh in observed gaps, representing 37% of the basal area. *Acer rubrum* accounted for 37% of the stems in the sapling layer; *Quercus* individuals only represented 13%. I suggest that under the current gap-based disturbance regime, the existing *Q. alba*, *P. taeda*, and *Q. prinus* canopy will yield dominance to the present-day intermediate canopy class dominated by *Q. prinus* and *Q. alba*. Continuing along this successional pathway, the current sapling layer, comprised mostly of *A. rubrum*, will be the next cohort to grow into dominant canopy position.

Pinus spp. were not regenerating nor were they recruiting into canopy positions. Only 6% of trees within observed gaps were *Pinus* individuals; *P. virginiana* represented 5% and *P. taeda* accounted for 1% of the relative density of observed gap trees. Few *Pinus* saplings were present in the regeneration layer; only 12 *Pinus* saplings ha^{-1} were documented in observed gaps, which accounted for < 1% of the relative density. Of the 35 gaps projected to close via subcanopy height growth, only four gaps were projected to fill by recruitment of *Pinus* individuals.

Unlike more shade-tolerant species, regeneration and recruitment of shade-intolerant *Pinus* spp. typically requires large gaps (Palik and Peterson 1996; Brockway and Outcalt, 1997; McGuire et al., 2001; Gagnon et al., 2003; Stambaugh and Muzika, 2004; York et al., 2012). In a study examining relationships between canopy openness and *P. echinata* regeneration, Stambaugh and Muzika (2004) observed that the maximum number of *P. echinata* seedlings regenerating was eight times higher in larger gaps (1700 m^2) than smaller gaps (400 m^2). Larger gaps increase the potential for *Pinus* regeneration because gaps receive more insolation and

thus, higher temperatures at the forest floor that may accelerate litter decomposition (Liming 1945). Less leaf litter results in more bare mineral soil, a requirement for *Pinus* seedling establishment (Skeen 1976; Rantis and Johnson 2002; Duncan and Linhoss 2005; Coleman, 2008). Therefore, the presence of hardwood litter could hinder *Pinus* regeneration, although some studies have found *Pinus* spp. can germinate in thin layers of litter (Duncan, 2005). However, it should be noted that a forest with a well-developed understory and midstory will intercept insolation before it reaches the forest floor thus, negating the influence of large gaps on *Pinus* reproduction.

Research has shown that certain gap sizes can lead to successful regeneration and recruitment of certain *Pinus* spp. However, few studies have examined the relationships between gap-scale disturbances and regeneration and recruitment of the three *Pinus* spp. found in this study; *P. taeda*, *P. virginiana*, and *P. echinata*. Considerably more research has been conducted to document the effects of gap-scale disturbances on *P. palustris* regeneration and recruitment. While gap areas that promote *P. palustris* may not necessarily encourage *P. taeda*, *P. virginiana*, and *P. echinata* growth, the lack of data necessitates examination of the relationship between gap-scale disturbances and a *Pinus* spp that was not found in this study. *Pinus palustris* is slightly more shade intolerant than *P. taeda*, *P. virginiana*, and *P. echinata* (Wahlenberg, 1960; Fowells, 1965; Eyre, 1980) and grows slower early in life (Fowells, 1965). For example, Schmidting (1987) planted *P. taeda* and *P. palustris* adjacent to each other and found that, although *P. taeda* had a 2.5 m height advantage at age 10, by age 17 heights of the two species were not significantly different. *Pinus taeda*, *P. virginiana*, and *P. echinata*, all have similar levels of intolerance to shade tolerance (Wahlenberg, 1960; Fowells, 1965; Eyre, 1980).

Because *P. palustris* is even more shade intolerant and has a slower early growth rate than *P. taeda*, *P. virginiana*, and *P. echinata*, gap sizes which translate to successful regeneration and recruitment of *P. palustris* may also lead to successful regeneration and recruitment of *P. taeda*, *P. virginiana*, and *P. echinata*. McGuire et al. (2001) successfully regenerated *P. palustris* with artificially created expanded gaps > 1,100 m² and Brockway and Outcalt (1998) suggest canopy gaps be at least 40 m in diameter. For unobstructed growth of *P. palustris* regeneration Palik et al. (1997) recommend a minimum gap size of ca. 1,400 m². It should be emphasized that vegetation response to gap size may differ by species, forest type, and stage age, so gap sizes that promote *P. palustris* regeneration may not necessarily encourage *P. taeda*, *P. virginiana*, and *P. echinata* regeneration and recruitment.

Although large gaps enhance the ability of shade-intolerant *Pinus* species to ascend to the canopy, the four gaps projected to close by subcanopy growth of *Pinus* trees in my study had an average expanded gap size of only 273 m², with a maximum size of 424 m². Interestingly, two of these gaps were quite small, 162 m² and 163 m², and had little hardwood competition. In these two gaps, there were a combined 11 trees within the observed gap, and five of them were *Pinus* spp. Also, although there was only one *Pinus* individual per hectare found in an intermediate canopy position in non-gap plots, 21 intermediate *Pinus* stems (63 ha⁻¹) were found in observed gaps. Out of these 21 intermediate observed gap *Pinus* trees, 10 of them were found in these four gaps projected to be filled from subcanopy recruitment of a *Pinus* stem. Therefore, gaps projected to be closed by *Pinus* individuals had little competition from hardwoods. Thus, in addition to gap size, reduced hardwood competition is also a major factor in maintaining a *Pinus* component in *Quercus-Pinus* forests.

5. MANAGEMENT IMPLICATIONS

The size and shapes of gaps found in this study promoted hardwood regeneration and canopy recruitment of subcanopy hardwood stems. Although over half of the canopy gaps documented in this study were caused by the removal of a *Pinus* tree, hardwood species, specifically *Q. alba* and *Q. prinus*, were the most likely species to capture canopy gaps. Of the 60 gaps sampled, only four were projected to close through the subcanopy recruitment of *Pinus* individuals. *Pinus* stems represented only 6% of observed gap trees, only one *Pinus* stem was found in an intermediate canopy position in non-gap plots, and only 12 *Pinus* saplings ha⁻¹ were found in observed gaps. Therefore, this forest was in the latter stages of the transition from *Pinus* to hardwood dominance. In the absence of silvicultural treatments, I hypothesize the *Pinus* component of this system will continue to decrease under the current disturbance regime.

Maintaining a *Pinus* component alongside hardwoods is difficult because the most common disturbance in these forests, gap-scale events, favor the more shade-tolerant species. In sampled stands, the characteristics that are hypothesized to promote regeneration of shade-intolerant *Pinus* individuals, namely gap sizes >1,400 m², bare mineral soil, and a low density of hardwood competition, were largely absent. To maintain a *Pinus* component, managers would likely need to create canopy gaps larger than those documented here. Multi-tree gaps are part of the historical disturbance regime in *Quercus-Pinus* forests and these gaps can be large enough to regenerate and recruit *Pinus* spp. (Hart et al., 2012). Group selections and variable retention harvests may provide the conditions needed to regenerate and recruit shade-intolerant *Pinus* spp. while at the same time mimicking natural disturbance processes.

My results combined with field observations revealed that *Pinus* stems were clustered in these stands, giving credence to the idea that a gap based approach can be used to manage for *Pinus* in systems dominated by hardwoods. Thus, uniform silviculture treatments may not be required to maintain or recruit *Pinus* spp. Based on my results and those of other studies (e.g. Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Gagnon et al., 2003; York et al., 2012), expanded gap areas should be > 1,400 m² with a *D:H* ratio of at least 1.5:1. These treatments should be centered around existing *Pinus* cohorts. Residual *Pinus* stems should remain within each group selection as a seed source and hardwood stems < 1.5 m in height can remain to maintain the hardwood component, however, basal area of stems within the group selection should not exceed 17 m² (Cain, 1993; Murphy et al., 1993; Shelton and Murphy, 1994; Guo and Shelton, 1998; Shelton and Cain, 2000). Competition reduction methods, such as fire and herbicide application, should follow these group selections to inhibit hardwood reproduction. If there is no existing *Pinus* composition, or if a stronger *Pinus* component is desired, seedlings can be planted after the burn. Planting should be done at wide spacings, ranging between 3 m x 3 m to 4.5 m x 4.5 m (Phillips and Abercrombie, 1987; Waldrop, 1997). This would mean planting roughly 66–156 seedlings inside a 1,400 m² gap. Planted seedlings should be able to overtop residual hardwood stems that are < 1.5 m in height in ca. 4–7 years (Phillips and Abercrombie, 1987; Waldrop, 1997).

Group selections and variable retention harvest methods can also be used by managers that wish to promote mid-tolerant hardwood species, such as *Quercus* and *Carya*, in a stand comprised of a *Pinus* overstory and a hardwood understory. To promote mid-tolerant taxa, light levels should be increased, but excessive canopy removal should be avoided. Too much canopy

removal will favor recruitment of shade-intolerant *Pinus* spp. while too little canopy removal will favor more shade-tolerant species such as *Acer* (Dey, 2002). Based on my results I suggest gaps sizes greater than ca. 250 m² with a *D:H* ratio ≤ 1.0 be used for *Quercus* regeneration. Gaps of this size were large enough to promote subcanopy recruitment of understory trees into the canopy and similar sizes have been recommended for *Quercus* regeneration in other studies (Marquis, 1965; Dey, 2002; Richards and Hart, 2011). Competition reduction measures such as fire or herbicidal application should follow these harvests (Schweitzer and Dey, 2011). Understory burning should be repeated for 2–3 year intervals until *Quercus* advanced reproduction is competitive (van Lear, 2002). Although the initial fire may benefit *Pinus* germination, seedlings of most species of *Pinus* will be killed by subsequent fires (Baker and Langdon, 1990; Carter and Snow, 1990). Young *P. taeda* and *P. virginiana* are vulnerable to fire and need to reach at least 1.5 m tall and 10 cm dbh to survive a fire (Baker and Langdon, 1990; Carter and Snow, 1990). *Pinus echinata* has the ability to sprout, therefore herbicidal applications may be needed to promote *Quercus* in system dominated by *P. echinata* (Lawson, 1990).

Group selections or variable retention harvests would result in patches of even aged treatments applied within a stand rather than uniformly treating an entire stand and would result in multiple age classes across a single stand. This would cause an increase in intra-stand heterogeneity which challenges the notion of stands as the fundamental management unit of silviculture. However, stands should still be considered the fundamental management unit, but management needs to be adaptive and consider within stand treatments as well as uniform whole stand treatments (O'Hara and Nagel, 2013).

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