

GAP DYNAMICS IN MATURE, *MESIC QUERCUS*
STANDS ON THE CUMBERLAND
PLATEAU, ALABAMA

by

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A THESIS

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ABSTRACT

Gap scale disturbances are important processes in forest stand development in the southern Appalachian Highlands. Canopy gaps within secondary forest throughout the southern Appalachian Highlands have been documented as critical mechanisms in canopy tree replacement and stand regeneration. I quantified gap characteristics, gap formation and closure mechanisms, and intra-gap tree and sapling distribution patterns for 60 canopy gaps in secondary mesic, *Quercus* stands on the Cumberland Plateau in north Alabama. Snag-formed gaps were the most common. I documented the influence gap formation mechanisms had on gap size, which ultimately contributed to gap closure. The projected closure mechanism was significantly related to the area of the gap whereby smaller gaps usually closed via lateral crown expansion and larger gaps typically closed by subcanopy recruitment. Based on the results, I hypothesized that gaps exceeding 200 m² had higher probabilities of closing via subcanopy recruitment rather than lateral crown expansion. Several gaps projected to close by subcanopy recruitment were doing so through *Quercus* capture. However, *Quercus* capture of gaps was restricted to upper slope position with low understory competition from shade tolerant species and adequate light levels based on the ratio of gap diameter to peripheral canopy height. *Liriodendron tulipifera* was projected to capture seven gaps, all of which were smaller than the hypothesized minimum gap area for capture by the species. The majority of gaps were projected to close via lateral crown expansion. Based on the composition of saplings and trees in gap environments, I project the forest to transition from a *Quercus* dominated system to one with much stronger *Fagus grandifolia* and *Acer saccharum* components. My study fills a void in the literature on the role of canopy gaps in

secondary, mesic *Quercus* stands that established just prior to 1900 for the southern Appalachian Highlands region.

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1. Introduction

Forest composition and structure are influenced by natural disturbance events of varying spatial and temporal scales. Disturbances are often classified according to the spatial extent and magnitude of the event and exist along a continuum spanning from broad scale, stand replacing events where most of the overstory is removed, to fine scale events resulting from the removal of single canopy individuals or small clusters of trees. For many forest types in the southern Appalachian Highlands, gap scale events are dominant disturbance mechanisms in forest stand development (Runkle 1981; Clinton et al. 1993; Clinton et al. 1994; Clebsch and Busing 1989; Yamamoto and Nishimura 1999; Hart and Grissino-Mayer 2009; Hart et al. 2010). A majority of the gap scale disturbance research in the southern Appalachian Highlands has focused primarily on old growth remnants (e.g. Runkle 1982; Runkle 2000; Rentch et al. 2003^a; Rentch et al. 2003^b), while recent studies have explored gap scale disturbances in developing secondary stands (e.g. Clebsch and Busing 1989; Clinton et al. 1993; Clinton et al. 1994; Hart and Grissino-Mayer 2008; Hart and Grissino-Mayer 2009; Hart et al. 2010). Secondary stands are representative of most of the forested land in the Eastern Deciduous Forest Region (Cowell 1998), and are defined here as non-primeval forests existing prior to a complex stage of development.

Anthropogenic impacts significantly decreased throughout much of the eastern U.S. at roughly the same time (ca. 1920–1940) creating the large expanses of even aged secondary stands (Abrams 1992; Abrams 2003; Foster et al. 1998; Foster et al. 2002).

The disturbance regimes of secondary and old growth remnants are distinct and feature documented differences of disturbance frequency, magnitude, and extent based on biomass arrangements, species compositions, and tree age distributions (Hart and Grissino-Mayer 2009).

Younger secondary stands feature high densities of relatively small individuals usually of a similar age (Oliver and Larson 1990). Intense competition for resources and self-thinning generally cause a high frequency of canopy disturbance events in developing secondary stands. When one individual dies, surrounding trees are able to quickly close the canopy gap by lateral crown expansion. Although these gaps are relatively small in size, they still act as a mechanism for stand structural change by modifying biomass arrangements and increasing species richness, as well as heterogeneity of tree ages and size distributions (Hart and Grissino-Mayer 2008; Hart and Grissino-Mayer 2009).

Conversely, old growth remnants have reduced competition and mortality rates leading to a lower frequency of canopy disturbance events (Zeide 2005). Canopy individuals in old growth remnants have relatively large crowns and when one of these individuals is removed from the canopy, a relatively large void is created and surrounding trees are often incapable of closing the gap via lateral crown expansion. These relatively larger gaps require a longer period to close because of their size, which increases the probability of a new individual recruiting into the main canopy through subcanopy ascension (Runkle 1982; Hart and Grissino-Mayer 2009; Zeide 2010). This gap replacement process facilitates the complex structures typical of old growth remnants, featuring differing age and size classes along with patchwork canopy composition (Lorimer 1980; Runkle 1982; Yetter and Runkle 1986; Runkle and Yetter 1987; Hart and Grissino-Mayer 2009).

Canopy gap research aiming to explain patterns and processes of current secondary forest conditions in the southern Appalachian Highlands is vital, yet, equally valuable is information regarding future stand development. My study is unique in that it seeks to document the role of canopy gap disturbance in forest development within mature, mesic *Quercus alba* L. stands in the southern Appalachian Highlands. I conducted my research in portions of the Sipsey Wilderness Area (SWA), in northwest Alabama because it is one of the few areas in the southern Appalachian Highlands that contains secondary, mesic *Quercus* stands that established pre-1900. Many stands in the region

initiated twenty to forty years later than the stands analyzed here. Thus, the mature *Quercus alba* stands on the SWA may provide a structural model for future management within secondary stands throughout the southern Appalachian Highlands.

My study was driven by two overarching goals: first, to document the specific patterns and processes of canopy gap disturbances in mature, mesic *Q. alba* secondary stands that established pre-1900 in the southern Appalachian Highlands. Second, to investigate the existence of a theoretical tipping point regarding stand age in which the primary gap closure mechanism shifts from lateral crown expansion to subcanopy ascension. Documenting this information is critical for better understanding how gap scale disturbances drive forest stand development and the role canopy gaps have in maintaining *Quercus* dominance in younger secondary stands throughout the southern Appalachian Highlands. To achieve these goals I established five primary questions:

- (1) What are the current patterns of canopy gap disturbance including canopy gap age, area, direction, and shape within mature secondary forest stands?
- (2) Which disturbance mechanism(s) initiates canopy gap formation (e.g. snapped stem, snag, or windthrown)?
- (3) Which mechanism is closing canopy gaps, lateral crown expansion or subcanopy ascension?
- (4) What is the current and projected species composition within canopy gaps?
- (5) What is the influence of gaps on structural development?

2. Study area and field methods

2.1. Study area

The SWA is a 10,085 ha portion of the National Wilderness Preservation System maintained by the National Forests in Alabama, a division of the USDA Forest Service (Fig. 1). SWA is situated within the Bankhead National Forest (BNF) in Lawrence and Winston Counties of northwestern Alabama. BNF is located on the Cumberland Plateau section of the Appalachian Plateaus physiographic province (Fenneman 1938). The geology of this region is composed primarily of the Pennsylvanian Pottsville formation characterized by light-gray thick-bedded to pebbly quartzose sandstone and containing differing levels of interstratified dark-gray shale, siltstone, and thin discontinuous coal (Szabo 1988). Topography of this region is strongly dissected to the point that it no longer resembles a plateau, and consists of narrow ridges and valleys, extensive hills, and steep slopes (USDA 1959; Smalley 1979). Soils are acidic, excessively drained, and shallow originating from the Muskingum and Pottsville series (USGS 1959). Bedrock depth varies from 0.3–1.2m. Study plots ranged in elevation from 656 to 955 m amsl and slopes ranged from 15 –70%.

Thornthwaite (1948) classified the climate of this region as humid mesothermal characterized by short, mild winters and long, hot summers. The mean annual temperature is 16°C (January mean 6°C; July mean 27°C) with a frost-free period ranging from late March to early November and a growing season of ca. 220 days (USDA 1959; Smalley 1979). Precipitation is distributed evenly throughout the year with no distinct dry season. Annual precipitation averages 123 cm with monthly means of 12 and 11 cm for January and July, respectively (USDA 1959; Smalley 1979). During winter, most precipitation events are of relatively low intensity and are a result of low pressure frontal boundaries, whereas

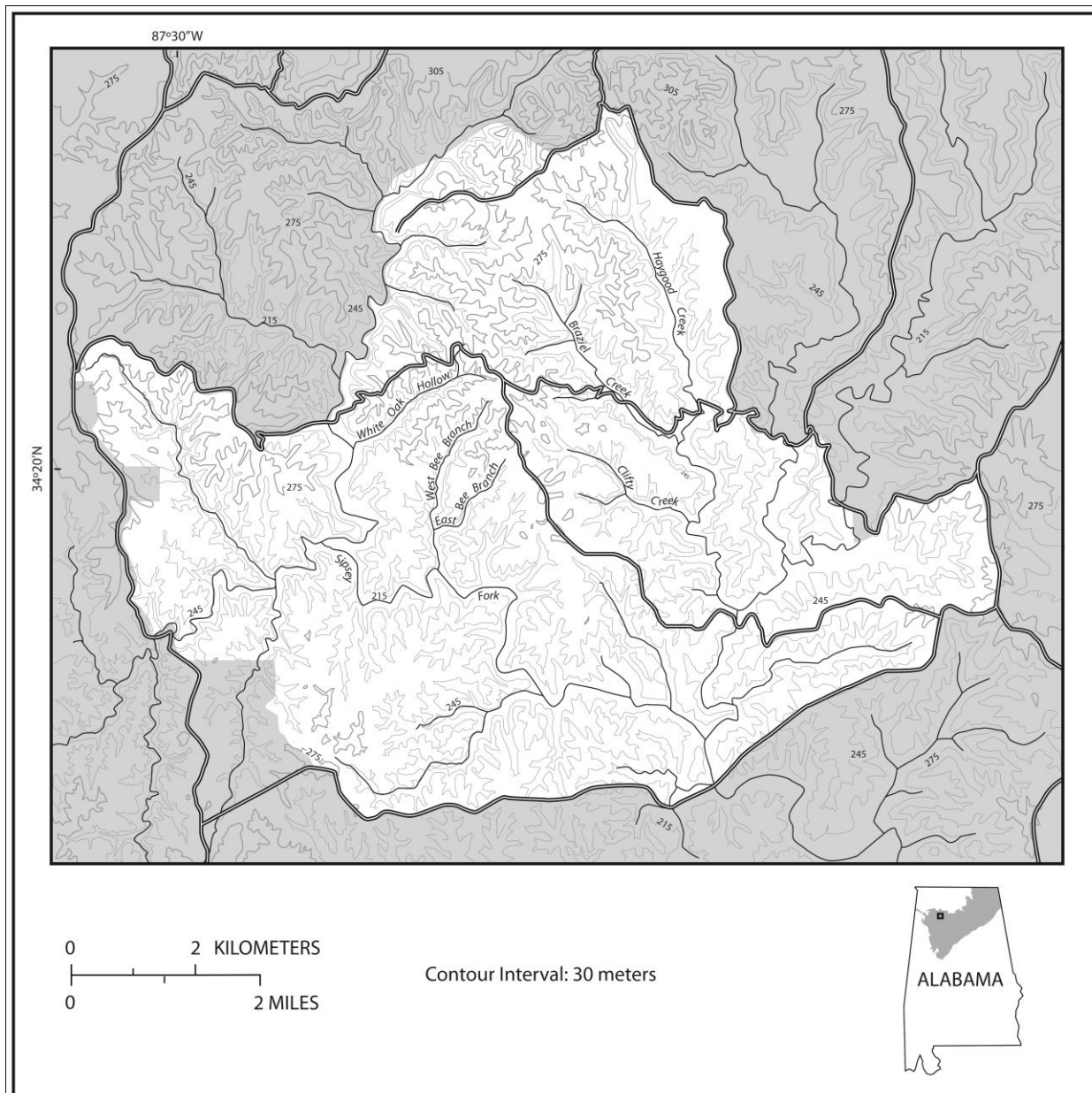


Fig. 1 Map of the Sipsey Wilderness Area, Alabama

summer precipitation events are mostly convective thunderstorms producing more intense rainfall (USDA 1959).

Braun (1950) classified the SWA as a transitional region between the *Quercus-Pinus* forest region to the south and the mixed mesophytic forest region to the north. Species composition varies based on local topography. Zhang et al. (1999) established fourteen ecological communities on the SWA. *Quercus alba* is a major component of the majority of communities, and is the second most dominant species on the site, based on basal area. Areas with shallow dry soils are dominated by *Pinus taeda*, *Pinus virginiana*, *Juniperus virginiana*, and *Carya* communities (Zhang et al.1999). *Acer rubrum* and *Acer saccharum* are dominant components in more mesic regions, and major components of *Tsuga canadensis*, and *Carya* communities. *Liriodendron tulipifera* was only a dominant component in *Quercus alba/Quercus rubra/Liriodendron tulipifera* communities.

2.2. Field methods

I used a map created in ArcGIS 9 to locate canopy gaps (n= 60) within the SWA that were dominated by *Q. alba* and established prior to 1900. The map was created from USDA field survey data containing information regarding stand ages and species compositions. I entered the coordinates of *Q. alba* dominant stands which established pre-1900 into a handheld GPS to ensure all gaps were sampled only on these sites. Gaps were defined by three criteria: (1) a noticeable void in the main forest canopy, (2) terminal leaders of the tallest stems less than three-fourths the height of the adjacent canopy, and (3) presence of a gapmaker (Taylor and Lorimer 2003). I did not establish minimum or maximum gap size thresholds to ensure that an accurate representation of gaps could be documented within the forest (Runkle 1982; Hart and Grissino-Mayer 2009). When I encountered a gap that met these criteria it was documented regardless of biophysical characteristics to capture an accurate representation of gaps in SWA. Thus the first sixty gaps that met my criteria were sampled.

I classed the area within each gap as being in either the observed or expanded gap. The observed gap was defined as the area of the forest floor directly beneath the void in the canopy and was determined via the use of a densiometer and visual estimations (Lorimer 1980). The expanded gap was defined as the total terrestrial area below the gap extending to the bases of the canopy trees that comprised the perimeter of the canopy void (Runkle 1981). Gap area was determined for both the expanded and observed 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 the formula of an ellipse (Runkle 1985; Runkle 1992; Hart and Grissino-Mayer 2009). Gaps of the southern Appalachian Highlands are commonly elliptical in shape (Runkle 1982; Runkle 1992; Clinton et al. 1993; Hart and Grissino-Mayer 2009), and most gaps in the SWA exhibited elliptical shapes. Fitting the length and width measurements to the formula of an ellipse was therefore appropriate in this study.

All gaps were sampled along mid-slope positions because this is where the pre-1900 mesic *Q. alba* stands are most common within the SWA. Elevation, latitude, and longitude were recorded using a handheld GPS unit. Other physical site characteristics were recorded for each gap including, percent slope, aspect, and average canopy height surrounding the gap (taken from three canopy height measurements). Physical characteristics of the gapmaker were noted, including identification to the lowest taxonomic level, diameter at breast height (dbh), relative fall direction to slope (parallel, perpendicular, or diagonal), and decay class. The formation mechanism that created each gap was determined via observation of the gapmaker and classified into one of three categories: windthrow, snag, or snapped stem. This information is important in understanding micro-site conditions that are unique based on formation mechanism. Basal area (m^2) was calculated for all gapmakers and totaled by gap in order to determine the amount of basal area lost for each gap formation mechanism. These data aid in understanding the way individual species are creating gaps. I characterized gap vegetation by

noting the species, and diameter of all trees ≥ 5 cm dbh. Additionally, I noted the crown class, which was visually characterized as overtopped, intermediate, co-dominant, or dominant depending on the quantity of light intercepted by the canopy (Oliver and Larson 1996).

All individuals were classified as being either perimeter trees (all individuals within the expanded gap) or interior trees (all individuals within the observed gap; Runkle 1982; Hart and Grissino-Mayer 2009). These data were used to analyze the number of perimeter individuals required to complete the surrounding canopy as well as the number of canopy individuals with the potential to close the gap through lateral expansion (Hart and Grissino-Mayer 2009). Gap regeneration was characterized by tallying all saplings (woody stems ≥ 1 m height, < 5 cm dbh) within the observed gap.

In order to document changes in forest structure, I recorded the likely canopy gap closure mechanisms, either lateral crown expansion of surrounding canopy individuals or the recruitment of a new individual from the subcanopy (Taylor and Lorimer 2003; Cole and Lorimer 2005). Probable gap successors are individuals likely to fill the canopy void and can often be identified in the field (Barden 1979; Barden 1980; White et al. 1985; Yamamoto and Nishimura 1999; Hart and Grissino-Mayer 2009). Documenting replacement trees is important for understanding future stand composition and analyzing the influence of canopy gaps on forest succession and stand development.

Recruitment was quantified based on the crown class distribution of all individuals within the observed gap in order to determine the individuals with greatest canopy recruitment potential (Hart and Grissino-Mayer 2009). Gap age was determined using several techniques. First, individual stems and branches were identified within and surrounding the gap which appeared to have originated immediately following gap formation (Runkle 1982; Hart and Grissino-Mayer 2009; Rentch et al. 2010). For larger individuals, increment-core samples were collected, processed using standard dendrochronological techniques (Stokes and Smiley 1996; Orvis and Grissino-Mayer 2002), dated, and visually analyzed for release events (sudden asynchronous increase in width of annual rings) with dates

that were compatible with the decay class of the gapmaker (Runkle 1982; Hart and Grissino-Mayer 2009; Hart et al. 2010). I further examined saplings for increases in height or branch growth by counting annual bud scars. Multiple techniques were used in combination to assign a formation year to most gaps.

Physical gap characteristics (e.g. gap size, average canopy height, intra-gap spacing of trees) were statistically evaluated in SAS 9.1 for relationships between gap formation mechanisms as well as projected gap closure mechanisms. I calculated a ratio of length to width (L:W) to document shape characteristics of gaps. I also calculated a diameter to height ratio (D:H) using diameter (width of the gap) and average canopy height. This information aids in understanding the micro-scale variations that occur within the individual gap types. For all trees sampled in the total gap area (i.e. sum of expanded and observed areas per gap) and within the observed gap area I calculated: relative frequency (percent of gaps in which each species occurred), 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 saplings in the observed gap area, I used relative frequency, relative density, and relative dominance values to quantify the regeneration layer.

3. Results

3.1. Gap characteristics

The total expanded gap area documented from all 60 gaps was 11,970.46 m² and the total area within the observed gaps was 1,820.60 m². The mean area of expanded gaps was 199.51 m² ± 97.88 (SD), with a maximum expanded gap area of 428.52 m² and a minimum of 39.64 m². Mean area of observed gaps was 30.34 m² ± 23.56 (SD). The maximum observed gap area was 123.43 m² and the minimum area was 3.28 m² (Fig. 2). The mean L:W ratio for expanded gaps was 1.48:1 with a minimum of 1.02:1 and maximum of 2.68:1. For observed gaps, the L:W average was 2.07:1 with a minimum of 0.42:1 and maximum of 5.62:1. Mean D:H ratio was 0.52 and 0.19 for expanded and observed gaps, respectively. The minimum D:H ratio in expanded gaps was 0.23 with a maximum of 1.07. In observed gaps, the minimum D:H ratio was 0.05 and the maximum was 0.56.

3.2. Gap formation and gapmaker

Snag-formed gaps were most common and accounted for 24 (40%) total gaps. Windthrow and snapped-stem gaps accounted for 19 (32%) and 17 (28%) gaps respectively. No statistically significant relationship was found between the L:W ratio for expanded or observed gaps and gap formation. Mean gap areas of neither observed nor expanded gap area exhibited a significant relationship with gap formation (Fig. 3). Mean observed gap area for snag-formed gaps was 34.72 m² ± 29.14 (SD), and the mean expanded area was 212.89 m² ± 115.69 (SD). Windthrown gaps exhibited the largest relative area in observed gaps (88.11 m² ± 14.66 (SD)), and expanded gaps (477.51 m² ± 66.32 (SD)). Gaps that were a result of snapped stems had an average observed area of 24.71 m² ± 18.17 (SD) with an expanded area

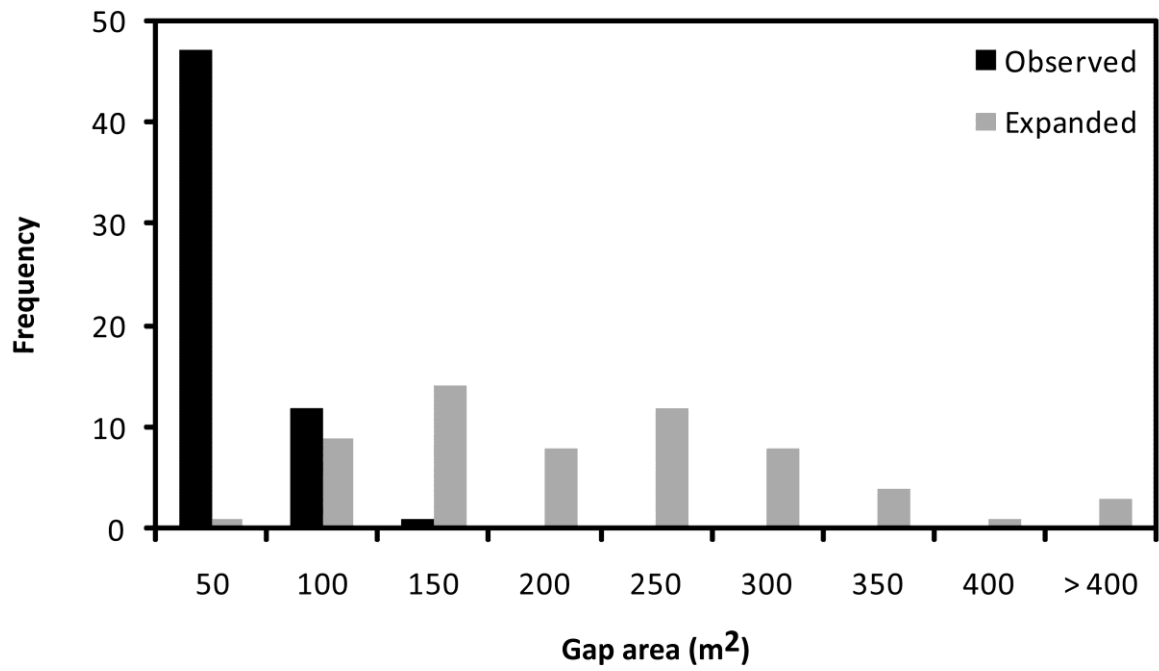


Figure 2 Frequency of observed and expanded canopy gaps in Sipsey Wilderness Area, Alabama

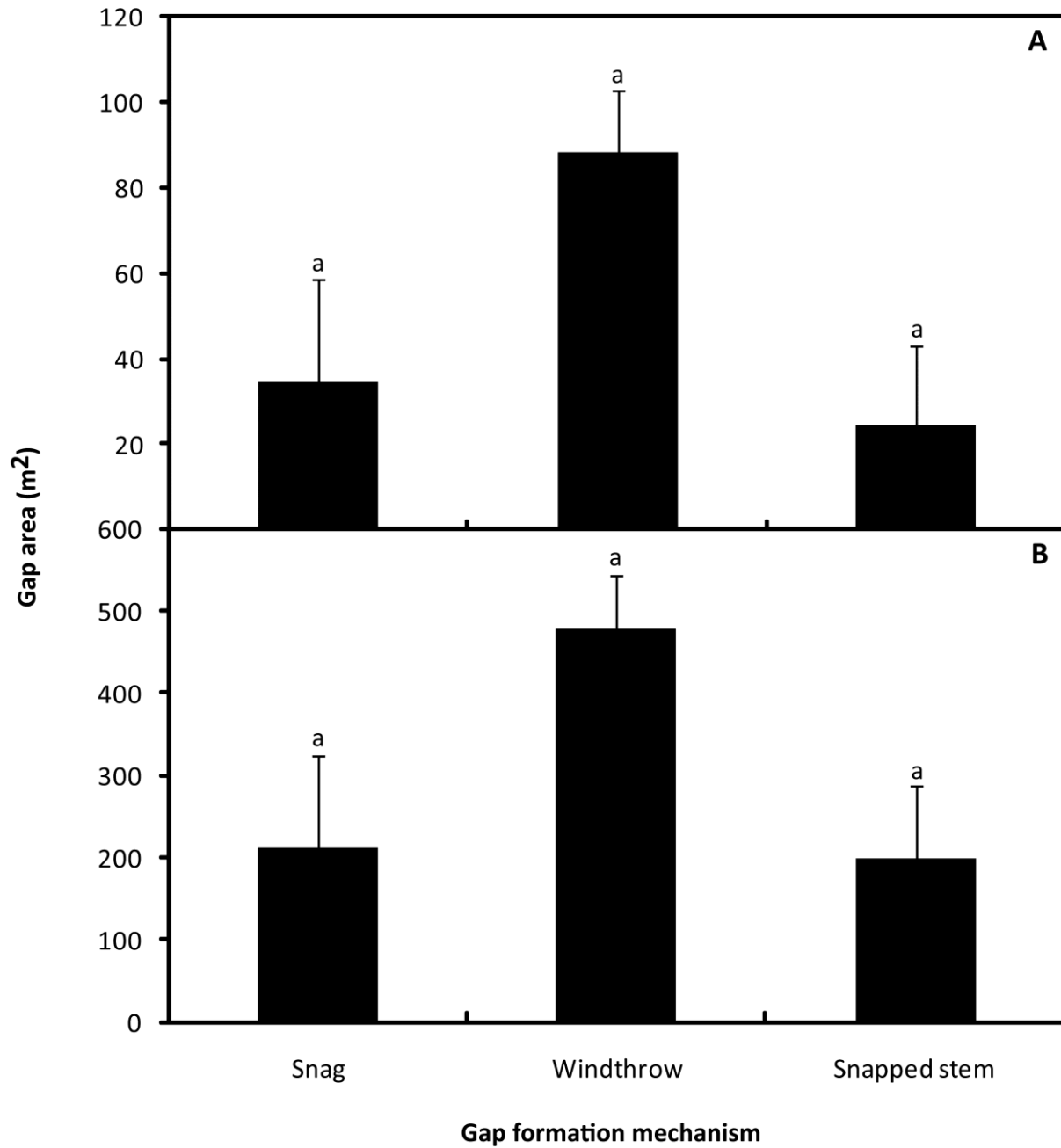


Figure 3 Relationship between gap formation mechanism and the observed (a) and expanded (b) area

of $198.03 \text{ m}^2 \pm 89.63$ (SD). The majority of canopy gaps were created by a single canopy individual ($n = 54$; 90%). Six gaps (10%) were formed from multiple individuals; of these six, four were the result of windthrow and two were formed by multiple snags. Single-tree gap events had a mean expanded gap area of $196.33 \text{ m}^2 \pm 97.80$ (SD), with a minimum area of 39.64 m^2 and a maximum area of 428.52 m^2 . Multi-tree gaps had a mean expanded area of $228.13 \text{ m}^2 \pm 84.94$ (SD) with a minimum area of 98.34 m^2 and a maximum of 345.96 m^2 . I found no statistically significant relationship between single and multi-tree gap events when compared to expanded gap area, observed gap area, and gapmaker basal area.

Gap ages ranged from 3 to 28 years with an average age of 16.53 years (Fig. 4). Multiple gaps formed in 11 distinct years. The years with the highest frequency of gap formation were 1991 ($n = 7$), 1989 ($n = 6$), 1992 ($n = 6$), 1998 ($n = 5$), and 1984 ($n = 4$).

I identified 67 gapmaker trees in the 60 gaps. Of these 67 gapmakers, 54 (81%) individuals were identified to the species level, three just to the genus level (4%), and 10 (15%) individuals were too decayed to be taxonomically classified. The 54 gapmakers identified to the species level represented a total of 11 species. *Carya tomentosa* was the most frequent gapmaker species accounting for 13 gaps. However, at the genus level, *Quercus* represented the largest number of gapmaker individuals ($n = 29$; 44%). Gapmakers ranged in size from 13–72 cm dbh, and had a mean dbh of $37 \text{ cm} \pm 14$ (SD). The mean gapmaker basal area lost was $0.14 \text{ m}^2 \pm 0.11$ (SD). The minimum basal area removed was 0.02 m^2 and the maximum was 0.41 m^2 . Gaps created by a single gapmaker lost a mean basal area of $0.13 \text{ m}^2 \pm 0.10$ (SD), a minimum of 0.02 m^2 , and a maximum of 0.41 m^2 . Gaps created by multi-gapmakers lost a mean basal area of $0.25 \text{ m}^2 \pm 0.11$ (SD), a minimum of 0.04 m^2 , and a maximum of 0.35 m^2 . I found a significant correlation between the dbh of gapmakers and the expanded gap area ($r = 0.36$, $P = 0.0026$).

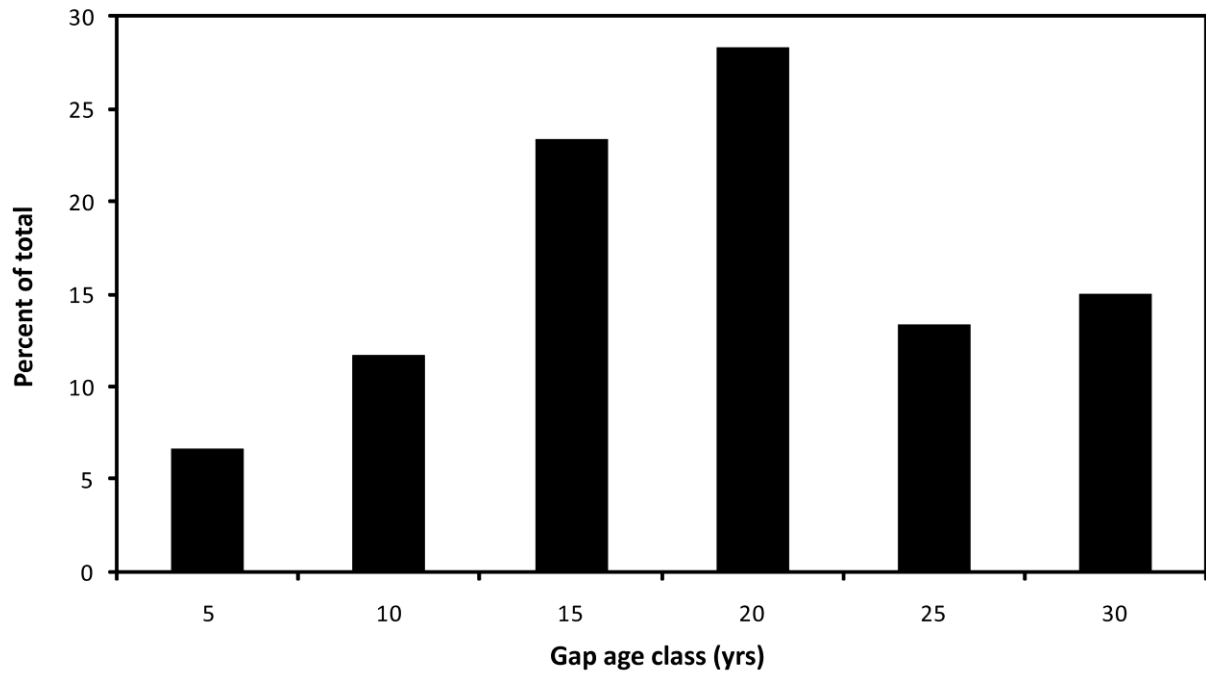


Figure 4 Distribution of 60 gap ages in five-year age classes in Sipsey Wilderness Area, Alabama

3.3. Gap closure, capture, and succession

Of the 60 total gaps, 39 (65%) were projected to close via lateral expansion while the remaining 21 (35%) were projected to close through subcanopy recruitment. I found a significant difference in the mean gap area of the expanded gap and the projected closure of the gap ($P < 0.01$; Fig. 5). Observed gap area and projected gap closure were also found to have a significant relationship ($P < 0.001$; Fig. 5). Additionally, the total number of perimeter canopy trees exhibited a significant relationship with projected gap closure ($P < 0.001$). I did not find a significant relationship between projected gap-closure and L:W ratio of either the expanded or observed gap area. Projected gap closure was also not significantly related to any of the following variables: average canopy height, intra-gap spacing of trees, or average dbh of canopy trees in the expanded gap area.

The mean number of trees within the expanded gap area was 11.22 ± 4.74 (SD) with a minimum of 4 and a maximum of 31. The average number of individuals within the observed gap was 3.64 ± 2.22 (SD) with a minimum of 0 individuals and a maximum of 10. Ten gaps contained no interior trees and seven of these 10 gaps were a result of snags. The mean intra-gap spacing between trees was $14.36 \text{ m}^2 \pm 5.03$ (SD) and ranged from 5.66 m^2 to 27.33 m^2 . I found statistically significant positive relationships between the basal area lost in each gap and both the expanded gap area ($r^2 = 0.14$, $P < 0.01$) and observed gap area ($r^2 = 0.14$, $P < 0.01$; Fig. 6).

Of the 21 gaps projected to close through subcanopy recruitment, a total of 10 species were documented as projected gap-capturers. The two most frequent gap-capturing species were *L. tulipifera* ($n = 7$; 31%) and *Q. alba* ($n = 6$; 27%). The other gap-capturing species were *M. macrophylla* ($n = 2$), *F. grandifolia* ($n = 1$), *C. cordiformis* ($n = 1$), *C. tomentosa* ($n = 1$), *L. styraciflua* ($n = 1$), *Q. prinus* ($n = 1$), *Q. rubrum* ($n = 1$), and *U. rubra* ($n = 1$). I found no significant relationship between the mean gap area of gap projected to close by *Quercus* ($n = 8$) and *L. tulipifera* ($n = 7$) for both the expanded and observed gap areas.

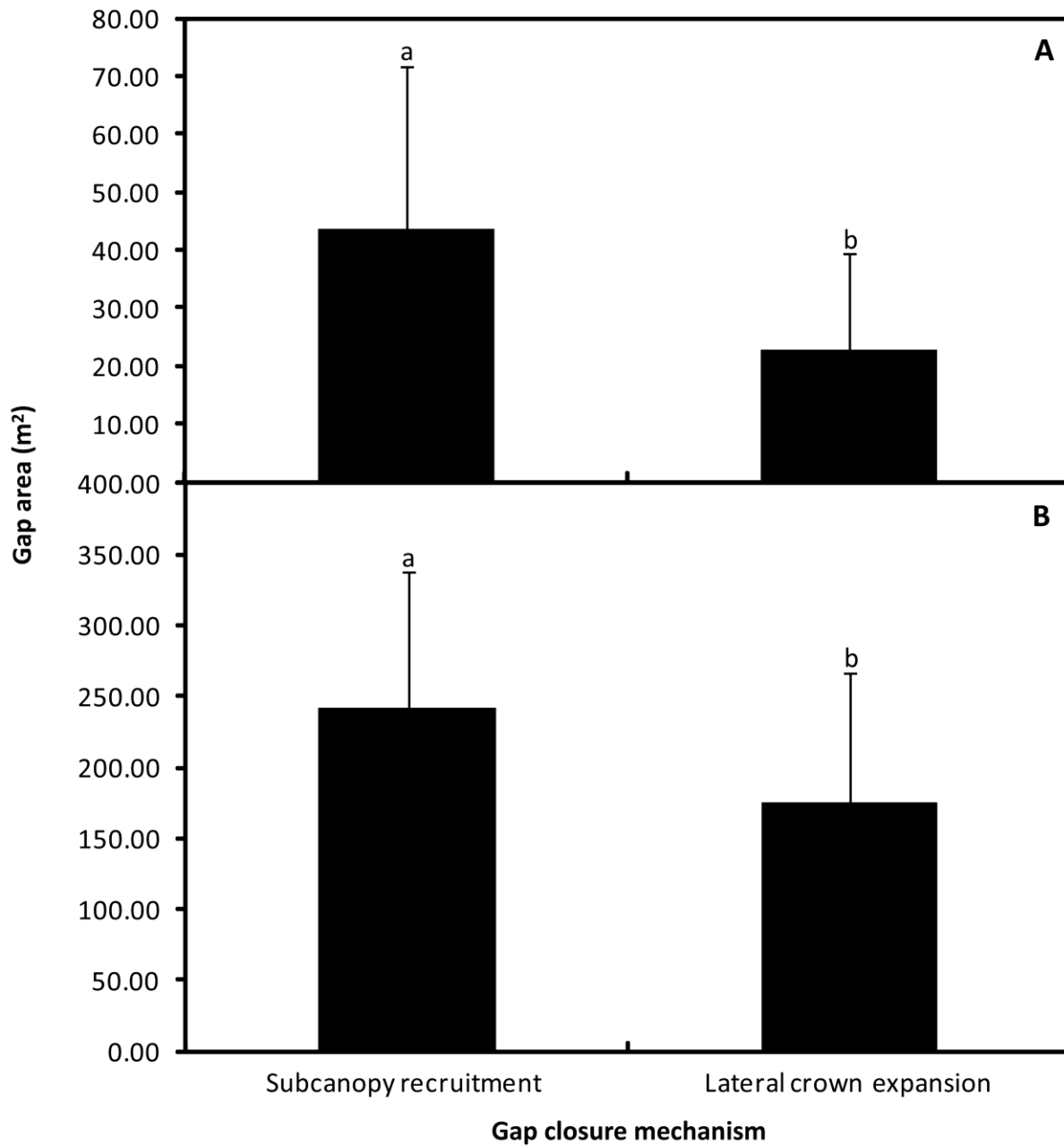


Figure 5 Relationship between the projected closure of gaps; (a) observed and (b) expanded area (m²)

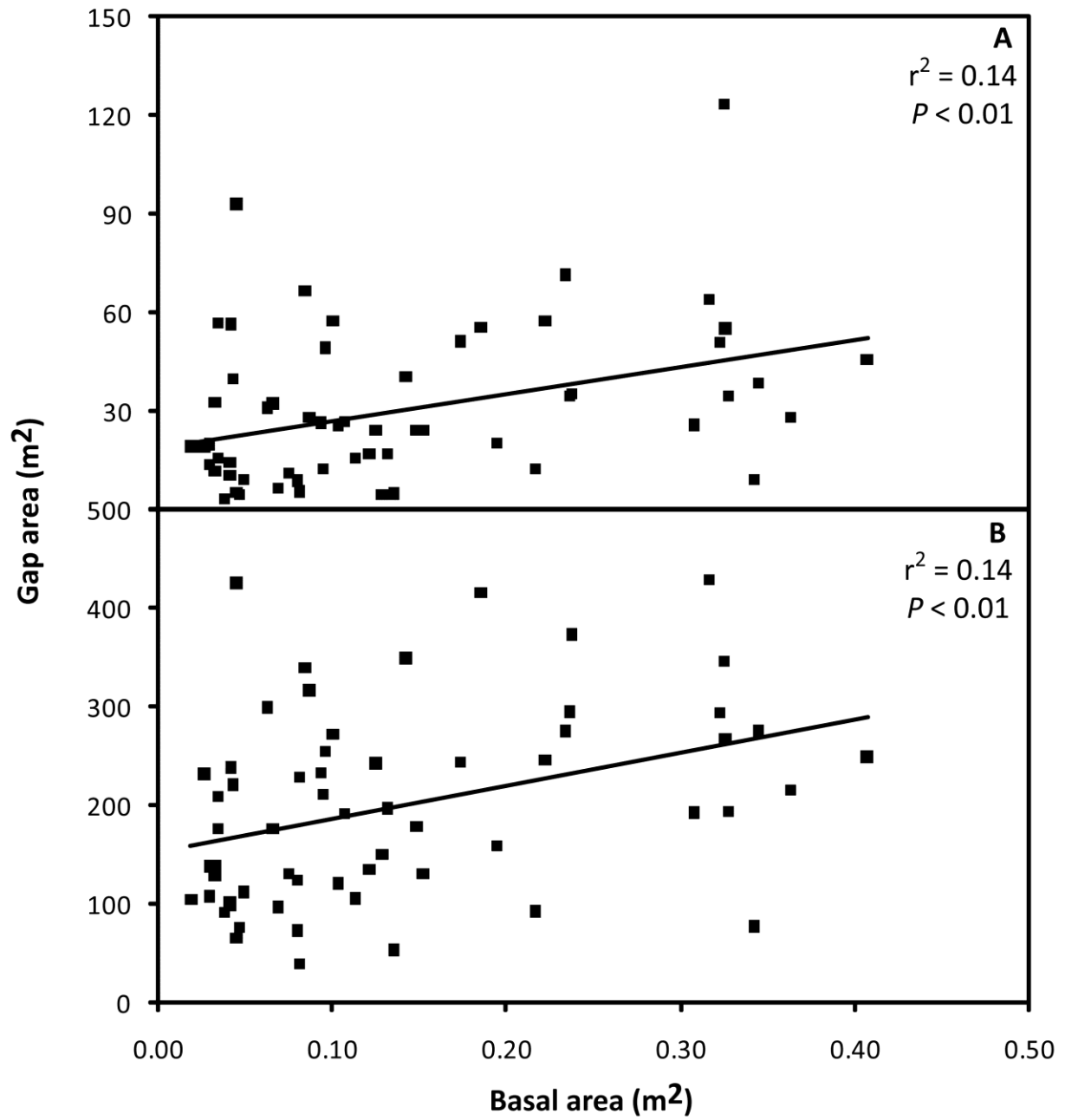


Figure 6 Relationship between gapmaker basal area and the (a) observed and (b) expanded area (m²)

The species richness value for all trees was 25. Three species represented as interior or perimeter trees were not represented in the sapling layer (*C. ovata*, *P. echinata*, *P. occidentalis*), while 15 sapling species were not represented as trees. *Fagus grandifolia* exhibited the highest relative frequency, relative density, and relative importance values when analyzed across the entire gap area (Table 1) and of all observed gap areas (Table 2). *Liriodendron tulipifera* had the highest relative dominance for both observed and expanded gaps. Among all individuals sampled, *F. grandifolia* was followed in both relative frequency and importance by *A. saccharum* and *L. tulipifera*. *Quercus alba* and *A. saccharum* had the second and third highest relative density and relative dominance values, respectively. Within the observed gaps, *F. grandifolia* was followed by *M. macrophylla* and *A. saccharum* in relative frequency, relative density, and relative importance values. Combined, these three species represented 42% of the total trees sampled in observed gaps. The species richness value among saplings was 37. In the sapling layer, *F. grandifolia* and *A. saccharum* had the highest relative frequency and relative importance followed by *Nyssa sylvatica* (Table 3). *Fagus grandifolia*, *N. sylvatica*, and *A. rubrum* exhibited the highest relative density among all saplings.

Table 1 Relative frequency, density, dominance, and importance for all trees

Relative frequency (percent of gaps species occurred), relative density (percent of total stems), relative dominance (percent of total basal area), and relative importance (IV; average of relative density and relative dominance) for all trees (≥ 5 cm dbh) in 60 gaps, Sipsey Wilderness Area, Alabama

Species	Relative Frequency	Relative Density	Relative Dominance	Relative IV
<i>Fagusgrandifolia</i> Ehrh.	76.67%	21.78%	14.46%	87.56%
<i>Acer saccharum</i> Marsh.	53.33%	7.96%	3.48%	57.31%
<i>Liriodendron tulipifera</i> L.	53.33%	7.38%	14.69%	57.02%
<i>Quercus alba</i> L.	51.67%	8.78%	0.74%	56.06%
<i>Caryatomentosa</i> (Poiret) Nutt.	46.67%	6.09%	8.09%	49.71%
<i>Magnolia macrophylla</i> Michx.	40.00%	7.38%	3.47%	43.69%
<i>Nyssa sylvatica</i> Marsh.	35.00%	4.10%	0.81%	37.05%
<i>Caryaglabra</i> (Mill.) Sweet	35.00%	3.98%	4.05%	36.99%
<i>Acer rubrum</i> L.	33.33%	3.40%	1.06%	35.03%
<i>Quercusprinus</i> L.	30.00%	3.86%	6.34%	31.93%
<i>Liquidambar styraciflua</i> L.	30.00%	3.51%	3.31%	31.76%
<i>Ostryavirginiana</i> (Mill.) K. Koch	23.33%	4.33%	0.41%	25.50%
<i>Quercusvelutina</i> Lam.	23.33%	2.58%	0.47%	24.62%
<i>Cornusfloridial</i> .	21.67%	2.69%	0.21%	23.01%
<i>Quercusrubra</i> L.	21.67%	1.64%	5.52%	22.49%
<i>Caryacordiformis</i> (Wangenh.) K. Koch	20.00%	2.22%	2.76%	21.11%
<i>Oxydendrum arboretum</i> (L.) DC	15.00%	1.41%	0.55%	15.70%
<i>Ulnusrubra</i> Muhl.	13.33%	2.11%	1.01%	14.39%
<i>Caryacaroliniana</i> Walt.	10.00%	1.76%	0.20%	10.88%
<i>Caryaovata</i> (Mill.) K. Koch	10.00%	1.52%	3.28%	10.76%
<i>Sassafras albidum</i> (Nutt.) Nees	5.00%	0.59%	0.03%	5.29%
<i>Quercusmuehlenbergii</i> Engelm.	5.00%	0.35%	5.19%	5.18%
<i>Juniperusvirginiana</i> L.	3.33%	0.35%	0.02%	3.51%
<i>Platanusoccidentalis</i> L.	1.67%	0.12%	19.79%	1.73%
<i>Pinusechinata</i> Mill.	1.67%	0.12%	0.05%	1.73%

Table 2 Relative frequency, density, dominance, and importance in observed gaps

Relative frequency (percent of gaps species occurred), relative density (percent of total stems), relative dominance (percent of total basal area), and relative importance(IV; average of relative density and relative dominance) for all trees (≥ 5 cm dbh) in 60 observed gaps, Sipsey Wilderness Area, Alabama

Species	Relative Frequency	Relative Density	Relative Dominance	Relative IV
<i>Fagusgrandifolia</i>	36.67%	23.89%	20.83%	22.36%
<i>Liriodendrontulipifera</i>	20.00%	7.78%	21.16%	14.47%
<i>Magnoliamacrophylla</i>	20.00%	9.44%	4.99%	7.22%
<i>Acersaccharum</i>	16.67%	8.89%	5.01%	6.95%
<i>Caryaovata</i>	6.67%	2.22%	11.66%	6.94%
<i>Quercusprinus</i>	6.67%	2.22%	9.13%	5.67%
<i>Caryaflorida</i>	11.67%	3.89%	5.84%	4.86%
<i>Oxydendrum arboretum</i>	18.33%	8.33%	0.59%	4.46%
<i>Nyssasylvatica</i>	18.33%	6.11%	1.17%	3.64%
<i>Acerrubrum</i>	15.00%	5.56%	1.53%	3.54%
<i>Liquidambarstyraciflua</i>	5.00%	2.22%	4.77%	3.50%
<i>Quercus alba</i>	11.67%	4.44%	1.06%	2.75%
<i>Ulmusrubra</i>	10.00%	3.89%	1.46%	2.67%
<i>Caryatomentosa</i>	10.00%	5.00%	0.30%	2.65%
<i>Caryaglabra</i>	1.67%	0.56%	4.72%	2.64%
<i>Caryacordiformis</i>	1.67%	0.56%	3.97%	2.26%
<i>Caryacaroliniana</i>	6.67%	2.22%	0.29%	1.26%
<i>Ostryavirginiana</i>	3.33%	1.11%	0.80%	0.95%
<i>Quercusvelutina</i>	1.67%	0.56%	0.67%	0.61%
<i>Juniperusvirginiana</i> L.	1.67%	1.11%	0.03%	0.57%

Table 3 Relative frequency, density, and importance of all saplings in observed gaps

Relative frequency (percent of gaps species occurred), relative density (percent of total stems), and relative importance(IV; average of relative frequency and relative density) for all saplings (≥ 1 m height, < 5 cm dbh) in 60 observed canopy gaps in Sipsey Wilderness Area, Alabama

Species	Relative Frequency	Relative Density	Relative IV
<i>Fagusgrandifolia</i>	53.33%	20.76%	37.05%
<i>Acersaccharum</i>	51.67%	9.38%	30.52%
<i>Nyssasylvatica</i>	45.00%	13.07%	29.03%
<i>Acerrubrum</i>	41.67%	12.86%	27.26%
<i>Magnoliamacrophylla</i>	30.00%	5.06%	17.53%
<i>Ulmusrubra</i>	23.33%	2.85%	13.09%
<i>Ostryavirginiana</i>	21.67%	4.32%	12.99%
<i>Quercus alba</i>	20.00%	4.74%	12.37%
<i>Tiliaheterophylla</i> Vent.	20.00%	4.53%	12.27%
<i>Caryatomentosa</i>	18.33%	3.48%	10.91%
<i>Caryacaroliniana</i>	13.33%	2.95%	8.14%
<i>Quercusprinus</i>	13.33%	1.48%	7.40%
<i>Asiminatriloba</i> (L.) Dunal	11.67%	1.79%	6.73%
<i>Caryaglabra</i>	8.33%	2.95%	5.64%
<i>Cornusflorida</i>	10.00%	1.05%	5.53%
<i>Aesculuspavia</i> L.	6.67%	2.11%	4.39%
<i>Liquidambarstyraciflua</i>	6.67%	0.74%	3.70%
<i>Quercusvelutina</i>	6.67%	0.74%	3.70%
<i>Caryacordiformis</i>	6.67%	0.53%	3.60%
<i>Sassafrasalbidum</i>	5.00%	0.84%	2.92%
<i>Callicarpadichotoma</i> (Lour.) K.Koch	5.00%	0.42%	2.71%
<i>Magnolia acuminata</i> (L.) L.	3.33%	0.32%	1.82%
<i>Fraxinusamericana</i> L.	1.67%	1.16%	1.41%
<i>Celtisoccidentalis</i> L.	1.67%	0.32%	0.99%
<i>Juniperusvirginiana</i>	1.67%	0.32%	0.99%
<i>Ulnusalata</i> Michx.	1.67%	0.21%	0.94%
<i>Betulanigra</i> L.	1.67%	0.11%	0.89%
<i>Cladrastislutea</i> (Michx. f.) K. Koch	1.67%	0.11%	0.89%
<i>Hamamelisvirginiana</i> L.	1.67%	0.11%	0.89%
<i>Ilex opaca</i> Aiton	1.67%	0.11%	0.89%
<i>Liriodendrontulipifera</i>	1.67%	0.11%	0.89%
<i>Oxydendrum arboretum</i>	1.67%	0.11%	0.89%
<i>Prunusserotina</i> Ehrh.	1.67%	0.11%	0.89%
<i>Quercusmuehlenbergii</i>	1.67%	0.11%	0.89%
<i>Quercusrubra</i>	1.67%	0.11%	0.89%
<i>Linderabenzoin</i> (L.) Blume	1.67%	0.11%	0.89%

4. Discussion

4.1. Gap characteristics

Mean L:W ratios revealed similar patterns for observed and expanded gaps. Gap shape is largely determined by gap formation mechanism (Hart and Grissino-Mayer 2009; Rentch et al. 2010). Snag-formed gaps have a higher probability of creating circular canopy voids since crowns are usually circular in shape and remain standing in the canopy for a period (Hart and Grissino-Mayer 2009). Snag gaps are typically smaller than gaps formed by windthrow and snapped stems. As snags decay and drop limbs, they gradually relinquish growing space (Clinton et al. 1993). However, as snags decay they are also more likely to snap during mild or severe wind events and therefore further disrupt the canopy having possibly a higher magnitude than the initial event. In contrast, windthrown trees create relatively large, linear gaps and disrupt a greater portion of the understory through the uplifted root network and the fall of the tree crown (Clinton et al. 1993; Clinton et al. 1994). Although gapmaker characteristics of snags and snapped stems can be similar, they each create different microsite conditions such as light levels, available growing space, and forest floor conditions (Clinton et al. 1993; Clinton et al. 1994; Hart and Grissino-Mayer 2009; Rentch et al. 2010).

The percentage of single gapmaker events (90% of gaps sampled) was higher than in many studies of old growth and secondary stands in the eastern US (Clinton et al. 1993; Clinton et al. 1994; Runkle 1982; Runkle 1990; Hart and Grissino-Mayer 2009). This disparity is likely a result of the higher proportion of snag-formed gaps documented in my study. Windthrow and snapped stems are more likely to remove multiple canopy trees because of their greater potential to modify site conditions from

the uprooting and falling crown (Hart and Grissino-Mayer 2009; Rentch et al. 2010; Hart and Kupfer in press).

The average dbh of gapmakers was 37.00 cm \pm 14.33 (SD) and the average dbh of canopy trees in the expanded gap was 38.15 cm \pm 6.83 (SD). The minimal diameter range between the dbh of gapmakers and the surrounding canopy trees indicate that any individual in the canopy exhibits an equal probability of being removed. Similar results were documented in other secondary stands in the southern Appalachian Highlands (Hart and Grissino-Mayer 2009).

4.2. Gap formation and gapmaker

Snag-formed gaps were the most frequent cause of gap formation (40% of all gaps). Other studies in the southern Appalachian Highlands region have found windthrow and snapped stems to be the most common gap origin (Barden 1979; Barden 1981; Romme and Martin 1982; Runkle 1982; Runkle 1985; Hart and Grissino-Mayer 2009). However, some secondary *Quercus* stands (as documented by Clinton et al. (1993) and Clinton et al. (1994) and *Picea rubens* Sarg. stands (as documented by Rentch et al. (2010) in the region have also found snags to be a common catalyst in gap formation.

The high percentage of snags documented in this study lead me to speculate that drought is an important disturbance mechanism on the site. Clinton et al. (1993, 1994) hypothesized that a severe drought in 1986 caused a regional mortality within mid-elevation mixed *Quercus* forests in the southern Blue Ridge. Of the 24 snags documented in my study, a total of 12 were formed by *Quercus* and six of those gaps formed between 1986 and 1991. Noticeably, after 1991 no *Quercus* snags were documented until 1999 when five occurred over a three-year period. From 1986–1993 and 1999–2002 the yearly mean PDSI values had Alabama classified in drought conditions (NCDC 2011). I used Palmer Drought Severity Index (PDSI) as a metric of drought conditions based on the supply and demand of available moisture in the soil (Palmer 1965). During drought years, communities can experience stressed

conditions as a result of a decrease in available soil moisture. In the SWA, snag-formed gaps created by *Quercus* appear to exhibit a pulse in frequency during drought periods. SWA experiences ca. 58 days of thunderstorms, periodic hailstorms, and tornado events throughout the year (USDA 1959). Each of these events would produce strong winds with the potential to uproot trees and snap boles (Hart and Grissino-Mayer 2009). The removal of 60% of all gaps from windthrown or snapped stems, I hypothesis strong wind events are also an important disturbance mechanism in the area.

4.3. Gap closure, capture, and succession

Statistically significant differences were documented between the projected closure of each gap and the observed and expanded gap area. Gaps with relatively smaller areas allow perimeter canopy trees to fill the canopy void through lateral crown expansion. In contrast, gaps projected to close through subcanopy recruitment need to be sufficiently large to allow new individuals to recruit into the canopy before the surrounding crowns fill the void.

Gap formation mechanism creates variable gap shapes (i.e. linear or circular) which are critical in projecting gap closure. Snag-formed gaps and windthrown gaps may both result in similar gap areas yet the physical gap shapes will not necessarily be similar. Canopy voids developed from snags feature relatively low L:W ratios and are circular in shape. Therefore, all perimeter trees have a relatively equal probability of filling the gap via lateral crown expansion. Conversely, gaps formed by windthrown individuals exhibit greater L:W ratios and are elliptical in shape. Therefore, the perimeter trees surrounding windthrown gaps do not exhibit equal probabilities of closing the gap via lateral expansion. Rather, individuals bordering the length of the gap have a greater likelihood of filling the gap as the lateral expansion must only span the width of the gap, not the length.

One goal of this project was to explore if a threshold existed between the sizes of gaps and the projected closure mechanism. The gaps projected to close by lateral crown expansion had an average

expanded gap area of $174.80 \text{ m}^2 \pm 91.73$ (SD). Projected subcanopy recruitment closures had a larger gap area of $242.18 \text{ m}^2 \pm 95.30$ (SD). I therefore hypothesize that forests in the southern Appalachians have an expanded gap area threshold of ca. 200 m^2 whereby the probability of the projected closure mechanism shifts from lateral crown expansion to subcanopy recruitment.

Light levels and soil moisture have been documented to increase at the center of a gap as the D:H ratio increases until leveling off at a value of ca. 2.0 (Runkle 1982; Dey 2002). The mean D:H: ratio in this study was 0.52 for expanded gap area and 0.19 for observed gap area. These values are comparable to other studies in the region although our maximum value for expanded gap area was 1.07 (Runkle 1982). The ideal ratio for advanced *Quercus* regeneration is 1.0 (Marquis 1965; Dey 2002). The maximum D:H ratio (1.07) was the result of a *Q. alba* snag and the gap was projected to close via subcanopy recruitment of another *Q. alba*. This result strengthens the effectiveness of using the D:H ratio to evaluate *Quercus* dominance and regeneration throughout its range in the eastern US.

Gap environments are heterogeneous both spatially and temporally as canopy height, slope position, aspect, and other physical characteristics differentially distribute resources both vertically and horizontally (Runkle 1982). These differing levels of resource availability throughout the gap facilitate the recruitment of varying species throughout the gap as it closes (Runkle 1982; Dey 2002). As gaps are captured, the resources available to recruits on the forest floor diminish; thus the potential for the establishment of new recruits is limited. As the individuals begin to compete with one another, self-thinning begins to occur within the gap and the establishment of new recruits is limited further.

Of the 21 gaps projected to close through subcanopy recruitment, eight (38%) were projected to be captured by a *Quercus* individual. The gaps projected to fill by *Quercus* individuals ranged in expanded gap area from 120.89 m^2 to 428.52 m^2 . Rather than gap area, the characteristics of the gapmaker seemingly exhibited greater influence on the gaps projected to close from *Quercus* individuals. Five of the eight gaps being closed by a *Quercus* individual were formed by a *Quercus*

individual with a mean dbh of 56.7 cm. This mean dbh is nearly 20 cm greater than the average of all other gapmakers sampled. Interestingly, snag-formed gaps accounted for five of the eight gaps being closed by a *Quercus* individual. Although the diameters of these five gapmakers were greater than the rest of the stand, the high frequency of snags resulted in a relatively large range of gap sizes.

Additionally, all eight gaps projected to close by a *Quercus* individual were documented at some of the upper most slope positions sampled with southern facing aspects. Relatively steep slopes positions and southern aspects allow for *Quercus* dominance due to decreased understory competition and increased insolation. These sites are also exposed to a greater amount of natural disturbance mechanisms allowing for relatively consistent canopy replacement. The gaps with a D:H ratio approaching those needed for *Quercus* regeneration (ca. 1.0) was in fact projected to close via *Quercus* individuals. The average D:H ratio for gaps projected to close by *Quercus* was 0.62, a slightly higher average than other gaps sampled. Field notes and physical observations provided evidence that these gaps exhibited relatively low competition in the understory, especially reduced competition from *F. grandifolia* and *A. saccharum*. The absence of these shade tolerant species allows for light to penetrate to the forest floor instead of being intercepted in the understory. Therefore, I speculate that certain micro-sites within the SWA are successfully maintaining *Quercus* dominance. Sites suitable for *Quercus* regeneration feature relatively constant disturbance events, an adequate supply of understory light, and minimal competition from shade tolerant species (Runkle 1982; Busing 1994; Busing 1995).

Studies in the southern Appalachian Highlands have found that *L. tulipifera* requires ca. 400 m² of gap area to close the void through subcanopy recruitment (Runkle 1982; Busing 1994; Busing 1995). In contrast, the gaps closing by *L. tulipifera* in this study had an average area of only 249.04 m² and the maximum gap area being filled by *L. tulipifera* was only 316.95 m². Four of the six gaps projected to close by *L. tulipifera* were gaps with southeastern facing slopes and a percent slope greater than 35%. In the SWA, a southern facing slope that is greater than or equal to 12% will experience direct insolation at

least some point during the year. I speculate that the topography of these sites allowed for *L. tulipifera* to reach a point in the understory where it was receiving enough light to continue growing to a canopy dominant position. Therefore, the aspect and steep slopes of these gaps seemingly provide the species with a disproportionate amount of insolation as compared to sites on flat terrain. The *L. tulipifera* individuals are therefore able to increase primary growth and obtain the resources necessary to continue height growth into the canopy.

Magnolia macrophylla presence on the landscape appeared to be site specific. Two gaps were projected to close by *M. macrophylla*. Both gaps exhibited steep slopes and had a high presence of *M. macrophylla* individuals in the intermediate level surround the gap area. The large area of *M. macrophylla* leaves reduces understory inter-species competition by not allowing sunlight to reach the forest floor. This was observed at both sites where grasses were dominant on the forest floor and saplings were sparse. When the gaps formed they were the only individuals in a position to capture the available growing space. While *M. macrophylla* is not considered a major canopy tree and does not typically reach the height of the main canopy, the steep topography resulted in a complex vertical stratification of tree crowns. With decreased competition and increased light resources, *M. macrophylla* appears to be able to reach a canopy position.

Throughout the 60 gaps, *F. grandifolia* exhibited high relative frequency, relative density, relative dominance, and relative importance values among the sapling layer, the trees sampled within the observed gaps, and the total species sampled across all gaps. *Fagus grandifolia*, *M. macrophylla*, and *A. saccharum* represented 42% of the total trees sampled within observed gaps. The high presence of *F. grandifolia* and *A. saccharum* are likely due to site conditions exhibiting a relatively higher species richness and sapling frequency within the gap. A dense understory was noted at most gaps documented, which would directly restrict light from reaching the forest floor, and ultimately favor shade-tolerant species such as *F. grandifolia* and *A. saccharum*. The high levels of *F. grandifolia* lead me

to hypothesize that this species will remain abundant throughout all sites of the forest sampled.

Observance of *A. saccharum* within the observed gaps was evidence that these two species have a greater probability of becoming abundant in intermediate and canopy positions (Hart and Grissino-Mayer 2009).

5. Conclusion

My study demonstrated that canopy gaps are clearly major drivers of forest composition, structure, and succession in mature, mesic *Quercus* stands in the southern Appalachian Highlands. For many areas across the region there is little quantitative data available regarding natural gap scale disturbance; but through an analysis of gap characteristics, gap formation, gap closure, and gap regeneration patterns, I have added valuable information about the development and succession pathways in secondary *Quercus* stands. I found the most common single gap formation mechanism to be snag-formed gaps, while wind formed gaps (i.e. windthrow and snapped stems) were more important. These gaps create unique microenvironments from the other two formation mechanisms, making this an important result for understanding the origin of canopy gaps. I documented the influence gap formation mechanisms have on the area of the gap, which ultimately contributes to the species that are able to colonize the gap. The projected closure mechanism was significantly related to the area of the gap whereby smaller gaps usually closed via lateral crown expansion and larger gaps typically closed by subcanopy recruitment. I hypothesize a threshold area of 200 m² in which the gap closure mechanism transitions from lateral crown expansion to subcanopy recruitment. Gaps projected to close by subcanopy recruitment demonstrated *Quercus* regeneration occurring on sites with relatively higher elevation, low understory competition, and adequate light levels. In most other gaps, the high importance values of both *F. grandifolia* and *A. saccharum* demonstrate the succession of these two species into intermediate and canopy classes. At these sites, the increased abundance of these mesic species could be at the behest of *Quercus* species. In conclusion, my study documented that natural gap

scale disturbances have a significant influence on the development and successional trajectories in mature *Quercus* stands of the southern Appalachian Highlands.

6. References

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