



Canopy gap dynamics and development patterns in secondary *Quercus* stands on the Cumberland Plateau, Alabama, USA

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ABSTRACT

Forest disturbances of various spatial extents and magnitudes shape species composition, structure, and stand development patterns. The disturbance regimes of most complex stage hardwood stands of the deciduous forests of eastern North America are typified by asynchronous and localized disturbance events. The overwhelming majority of gap-scale disturbance studies in hardwood forests of the region have analyzed late-successional stands. As such, there is a paucity of data on gap dynamics in hardwood stands prior to a complex developmental stage. We quantified biophysical characteristics of 60 canopy gaps in secondary *Quercus* stands on the Cumberland Plateau in Alabama to analyze gap-scale disturbance processes in developing systems. We found most gaps (90%) were caused by the removal of a single tree. Of the three gap formation mechanisms, snag-formed gaps were most common (40%). However, based on the number of uprooted and snapped stems we speculate that wind was also an important disturbance agent in these stands. Gap size and shape patterns were similar to what has been reported in other hardwood forests of the southern Appalachian Highlands. We did not find differences in gap size or shape based on formation mechanisms; a finding that may be related to the number of single-tree gap events. Gaps projected to close via subcanopy recruitment were significantly larger than those projected to close through lateral crown expansion. Most gaps (65%) were projected to close by lateral crown expansion of gap perimeter trees. However, the number of gaps projected to fill by subcanopy recruitment indicated the stands were approaching a transition in their developmental stage. Gap-scale processes modify residual tree architecture and stand structure. Through time these alterations result in progressively larger gaps, eventually reaching a size when most will fill by subcanopy recruitment, thus marking the complex stage of development. Gap capture by *Quercus* was restricted to relatively xeric sites that did not contain abundant shade-tolerant mesophytes in the understory. However, the majority of gaps contained abundant subcanopy *Fagus grandifolia*, *Acer saccharum*, and *Acer rubrum* leading us to project that the forest will undergo a drastic composition shift under the current disturbance regime. *Liriodendron tulipifera* was projected to capture several relatively small gaps illustrating the role of topography on gap closure mechanisms.

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1. Introduction

Forest disturbance events shape species composition and structure and drive development patterns. Disturbances are often classified according to their spatial extent and magnitude 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 (Oliver and Larson, 1996). Although exogenous disturbances occur throughout the region, the disturbance regimes of many old-growth hardwood stands in the deciduous forests of eastern North America are characterized by fine-scale, endogenous events (Lorimer, 1980; Barden, 1981; Runkle, 1981, 1982; Cho and

Boerner, 1991; Runkle, 2000). Indeed, it is these asynchronous and localized disturbances that create the complexity that defines old-growth structure in hardwood systems (Oliver and Larson, 1996; Frelich, 2002). At the stand-scale, canopy gaps create a patch-work mosaic of microsites comprised of different tree species, ages, diameters, heights, and crown spreads (Runkle, 1981; Canham and Marks, 1985; Phillips and Shure, 1990). By modifying fine-scale biophysical conditions, localized disturbances increase heterogeneity and biodiversity in forested environments (Putz, 1983; Abe et al., 1995).

Endogenous disturbance regimes and forest response to discrete events differ between forest developmental stages as composition, structure, and tree age distributions are markedly different. Although exogenous disturbance agents may not vary by stand age, responses of residual trees likely do (e.g. old trees may be less likely to respond to increased resources and growing space). Young

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secondary stands during the stem exclusion and understory reinitiation stages are characterized by high densities of relatively small individuals of similar age (Oliver and Larson, 1996). Intense competition for resources and self-thinning in developing secondary stands result in a high frequency of small canopy disturbance events (Clebsch and Busing, 1989; Hart and Grissino-Mayer, 2009). Theoretically, when a canopy individual dies adjacent trees are able to quickly capture the vacant growing space and close the canopy gap through lateral crown expansion, thereby altering tree size, tree architecture, and stand structure (Hart and Grissino-Mayer, 2008). Conversely, during the complex stage of development stands contain fewer individuals and have reduced competition and mortality rates leading to a lower frequency of canopy disturbance events (Zeide, 2005). Most canopy trees in complex stage hardwood stands have comparatively large crowns and when one of these individuals is removed from the canopy, a relatively large void is created and peripheral trees are often incapable of closing the gaps via lateral crown expansion (Tyrell and Crow, 1994; Yamamoto, 2000). These larger gaps should require a longer period to close because of their size, which increases the probability of a new individual recruiting to a dominant or codominant position through subcanopy ascension (Runkle, 1985; Rentch et al., 2003; Webster and Lorimer, 2005; Zeide, 2010).

The overwhelming majority of canopy gap research in hardwood forests of the eastern US and indeed the world has focused on stands in the complex stage of development (Yamamoto, 2000). As such, there is a dearth of data available on gap dynamics in hardwood stands prior to a complex developmental stage. Hence, we know relatively little about the role of gap-scale disturbance processes in the development of hardwood stands (Hart et al., 2011). Developing secondary stands (defined here as non-primeval forests prior to a complex stage of development) are representative of most of the deciduous forests of eastern North America as anthropogenic timber clearing significantly decreased throughout much of the region over a relatively uniform and short period in the early 1900s, creating large expanses of even-aged secondary stands (Whitney, 1994; Abrams, 2003; Dyer, 2006).

The ages of most hardwood stands in the North American Eastern Deciduous Forest make validating theoretical models on general disturbance characteristics and the influence of these events on hardwood forest development difficult. A central challenge is to document gap-scale disturbance processes in forests that represent various states of development. In *Quercus* systems of the southern Appalachian Highlands, canopy gap characteristics and their influence on forest development in stands that pre-date 1900 but have yet to reach the complex stage are not understood. The present study was conducted on the Sipsey Wilderness in Alabama because it is one of the few areas in the region known to support secondary *Quercus* stands of this age class (i.e. 110–130 years). Most *Quercus* stands in the region initiated 20–50 years later than those analyzed here. Thus, these systems may provide a model for the projected development of many *Quercus* stands in the region. The specific objectives of our study were to: (1) quantitatively describe gap characteristics and formation mechanisms; (2) document gap closure mechanisms and recruitment patterns; and (3) discern the role of localized canopy disturbance on composition, structure, and development in southern Appalachian *Quercus* stands that established prior to 1900.

2. Study area and methods

2.1. Study site

The Sipsey Wilderness is a 10,085 ha portion of the National Wilderness Preservation System maintained by the USDA Forest

Service (Fig. 1). The Sipsey Wilderness is situated within the 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 geology of the region is composed 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 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 typically acidic, well drained, and shallow (USDA, 1959). Study plots ranged in elevation from 656 to 955 m amsl and slopes ranged from 1–45% with a mean of 18%.

Thorntwaite (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: 5 °C; July mean: 26 °C). The frost-free period is ca. 220 days and extends from late-March to early-November (Smalley, 1979). Precipitation is distributed evenly throughout the year with no distinct dry season. Annual precipitation averages 1390 mm with monthly means of 135 and 113 mm for January and July, respectively (PRISM Climate Group, 2011). During winter, most precipitation events are of low intensity and are a result of frontal lifting, whereas summer precipitation is frequently the result of convective storms producing more intense rainfall and sometimes lightning and hail (Smalley, 1979).

Braun (1950) classified the Sipsey Wilderness as a transitional region between the *Quercus-Pinus* Forest to the south and the Mixed Mesophytic Forest to the north. On upland sites of the Cumberland Plateau, species composition is strongly influenced by topography and factors related to soil water availability (Hinkle, 1989). Cumberland Plateau forests are noted for high species richness and gamma diversity and contain over 30 tree species with the potential to reach the canopy (Hinkle et al., 1993). Zhang et al. (1999) classified 14 ecological communities on the Sipsey Wilderness ranging from xeric sites dominated by *Pinus virginiana* Mill to mesic sites dominated by *Fagus grandifolia* and *Acer saccharum* to sites with no overstory cover. *Quercus* was the most abundant genus across the Sipsey Wilderness and occurred in the majority of the delineated community types (Zhang et al., 1999).

2.2. Methods

We created a map using ArcGIS v. 9 from USDA field survey data containing information on species composition and establishment age of delineated stands. We used the map to ensure our field sampling was limited to stands classified as *Quercus* dominated that established prior to 1900. These stands established after the sites were last harvested in the late-1800s. We restricted our sampling in this manner to document the influence of gap-scale disturbance processes in mature *Quercus* stands and to elucidate the role of local disturbance on the initiation of complex structures in developing secondary stands. Within Sipsey Wilderness, several clusters or complexes of neighboring stands that met our criteria were located and sampled. These *Quercus* stands represented a relatively rare age class for the region and provided the unique opportunity to examine gap-scale disturbance processes at this stage of development (i.e. older than most secondary *Quercus* stands in the region, but not in a complex developmental stage). Non-gap forest vegetation was quantified using a total of twenty 0.05 ha fixed radius plots located randomly throughout the previously selected stands. In each plot we 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

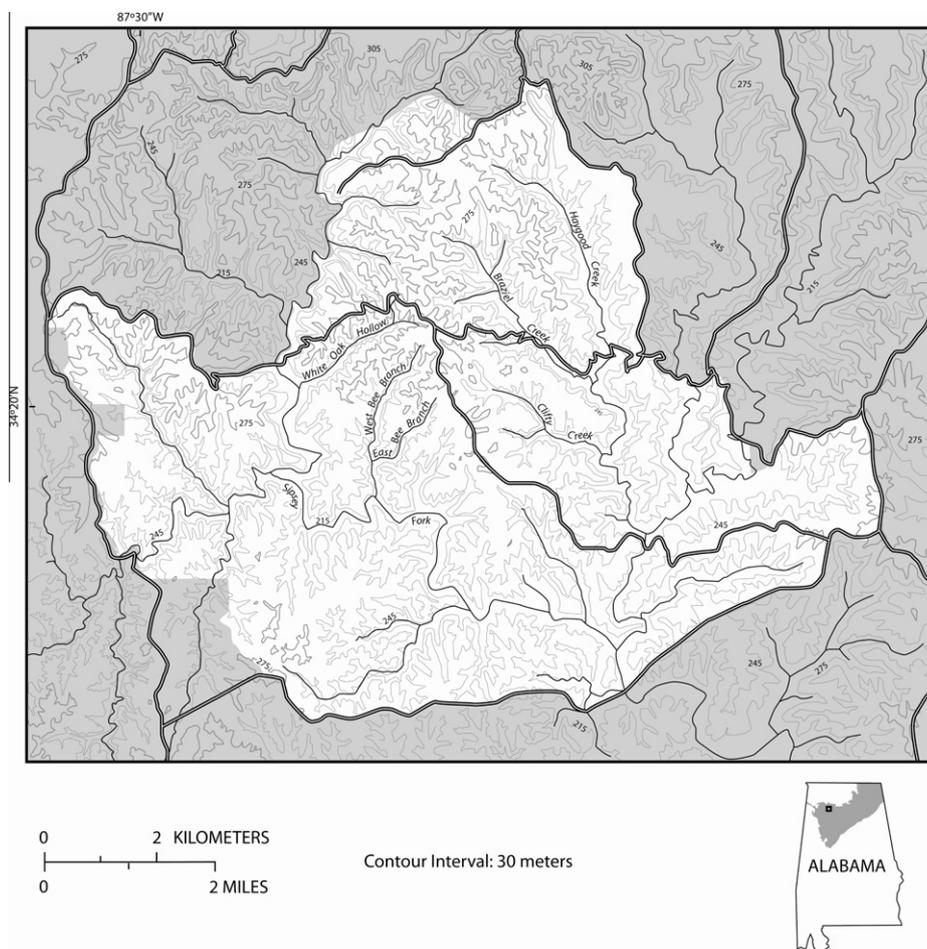


Fig. 1. Map of Sipsy Wilderness, Alabama. White area is the Sipsy Wilderness, thin lines are 30 m contour intervals, heavy lines are streams, and double lines are roads. Shaded portion on Alabama inset map is the Cumberland Plateau physiographic section.

direction of intercepted light (Oliver and Larson, 1996). 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 by walking transects through the selected stands. Transects were established from randomly selected points and were oriented parallel to slope contour. All gaps were sampled along mid-slope positions (from lower-middle to upper-middle positions) because this is where the *Quercus* stands with establishment pre-dating 1900 occurred in the Sipsy Wilderness. 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). We did not establish minimum or maximum gap size thresholds to ensure that an accurate representation of gaps was documented (Runkle, 1982; Hart and Grissino-Mayer, 2009). When we encountered a gap that met our criteria it was sampled regardless of biophysical characteristics thus, the first 60 gaps that met these criteria were quantified.

We 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 via the use of a vertical densitometer and visual estimations. 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 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 the formula of an ellipse (Runkle, 1982; Clinton et al., 1994). Gaps of the southern Appalachian Highlands are commonly elliptical in shape (Runkle, 1982, 1992; Clinton et al., 1993; Hart and Grissino-Mayer, 2009), and most gaps in the Sipsy Wilderness exhibited elliptical shapes, therefore this method was appropriate for our study.

Elevation, latitude, and longitude were recorded in the field using a handheld GPS receiver. Other physical site characteristics were recorded for each gap including percent slope, aspect, and average canopy height surrounding the gap. Canopy height was measured using a digital hypsometer with transponder and the mean was calculated from three canopy height measurements at each gap. 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 several techniques. Within gaps, individual stems and branches which appeared to have originated immediately following gap formation were identified. These small stems and branches were cut at their base and transported to the laboratory for age determination (Runkle, 1982; Hart and Grissino-Mayer, 2009). Increment core samples were collected from larger residual trees that we deemed would exhibit a notable increase in radial growth following gap formation (Hart et al., 2010; Rentch et al., 2010). In the laboratory,

all wood samples were processed and dated using standard dendrochronological techniques (Stokes and Smiley, 1996; Orvis and Grissino-Mayer, 2002). For small stems and branches we determined establishment dates. 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; Hart et al., 2010). In addition, we 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 five decay classes following the criteria of Pyle and Brown (1998). Thus, multiple techniques were used in combination to assign gap formation years.

The formation mechanism that created each gap was determined via observation of the gapmaker(s) and classified as originating from an uprooted stem (root network uplifted), a snapped stem (bole broken below the crown), or a snag (standing dead tree with crown intact; Putz, 1983; Clinton et al., 1993; Yamamoto, 2000). This classification was used to examine gap origins and differences in physical characteristics attributed to gap formation mechanisms. Gapmakers were classified to the lowest taxonomic level possible to examine species-specific mortality trends and overstory composition stability. The dbh of all gapmakers was recorded. Basal area (m^2) was calculated for all gapmakers and totaled by gap in order to determine the amount of overstory basal area lost during each event.

We characterized gap vegetation by documenting species and crown class for all stems ≥ 5 cm dbh within and comprising the perimeter of each gap. All stems ≥ 5 cm dbh were classified as being either perimeter trees (individuals within the expanded gap only) or interior trees (all individuals within the observed gap; Hart and Grissino-Mayer, 2009). Gap regeneration was characterized by tallying all saplings (woody stems < 5 cm dbh, ≥ 1 m height) within the observed gaps.

To document changes in forest composition and structure, we recorded the likely closure mechanism for each gap. Gaps were projected to close by either lateral crown expansion of surrounding canopy individuals or by the recruitment of a new individual(s) from the subcanopy (Taylor and Lorimer, 2003; Cole and Lorimer, 2005). For gaps projected to close by the height growth of a subcanopy tree we documented the species of the probable gap successor. 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). Documenting replacement trees is important for understanding future stand composition and analyzing the influence of canopy gaps on forest composition and development patterns (Taylor and Lorimer, 2003).

We calculated a ratio of length to width ($L:W$) for expanded and observed gaps to document gap shape patterns (Hart and Grissino-Mayer, 2009; Rentch et al., 2010). We also calculated diameter to height ratios ($D:H$) using gap width (W) as diameter and average canopy height for expanded and observed gaps (Marquis, 1965; Dey, 2002). These data provide 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 (two-tailed t -tests, one-way ANOVA with Scheffe post hoc tests, Pearson correlation analyses, linear regression) were performed using SAS v. 9.1 after being visually assessed for normality. For all trees sampled in the observed gap and total gap area (i.e. sum of expanded and observed areas per gap), we 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, we used relative frequency, relative density, and relative dominance values as vegetative descriptors. Intra-gap spacings of trees and saplings were calculated by dividing the number of these individuals by gap size.

3. Results

3.1. Forest composition and structure

The sampled stands on the Sipsey Wilderness were dominated by *Carya alba*, *Quercus prinus*, and *Quercus alba* (Table 1). Collectively these three species represented over 66% of the basal area. *Magnolia macrophylla* had the highest relative density value as the species represented ca. 19% of all stems ≥ 10 cm dbh in the sampled stands. In addition to the three most dominant species previously listed, *F. grandifolia* and *A. saccharum* exhibited the next highest densities. *Carya alba*, *Q. prinus*, *Q. alba*, and *M. macrophylla* were also the most important species in these stands. The canopy was dominated by *Quercus* with 87 dominant or codominant trees ha^{-1} . Only one *Quercus* individual was documented in an overtopped position. In contrast to the canopy, *M. macrophylla* was the most abundant species in the intermediate canopy position ($n = 49 ha^{-1}$). *Fagus grandifolia* and *Acer* species were abundant in intermediate ($n = 53 ha^{-1}$) and overtopped positions ($n = 21 ha^{-1}$). Only 14 *F. grandifolia* and *Acer* individuals per hectare were documented in the forest canopy. Notably, six *Liriodendron tulipifera* occurred in the forest canopy and the species was absent from intermediate and overtopped positions. *Carya alba* occurred on every sampled plot. Density of stems ≥ 10 cm dbh was 389 ha^{-1} and basal area was 23.97 $m^2 ha^{-1}$. The forest had a reverse J-shape diameter distribution as the number of stems gradually decreased with increased size. Mean canopy tree dbh was 35 cm \pm 12 (SD) and the largest tree was a *Q. prinus* with a dbh of 85 cm. The majority of stems occurred in the overtopped crown class (44%). Only 10% of trees ≥ 10 cm dbh in our study plots were overtopped. The distribution of codominant and dominant crown positions was relatively similar (25%: codominant and 21% dominant).

3.2. Gap and gapmaker characteristics

Snag-formed gaps were most common and accounted for 40% of the 60 total gaps. Uprooted and snapped-stem gaps accounted for 32% and 28% gaps, respectively. The mean size of expanded gaps was 199.5 $m^2 \pm 97.9$, with a maximum of 428.5 m^2 and a minimum of 39.6 m^2 . Mean size of observed gaps was 30.3 $m^2 \pm 23.6$. The maximum observed gap was 123.4 m^2 and the minimum was 3.3 m^2 (Fig. 2). The mean $L:W$ ratio for expanded gaps was 1.48:1 and for observed gaps was 2.07:1. Mean $D:H$ ratios were 0.52:1 and 0.19:1 for expanded and observed gaps, respectively. Expanded and observed gap size was not significantly different across gap formation mechanisms (Fig. 3). No significant differences occurred between the $L:W$ ratios for expanded and observed gaps. Likewise, $L:W$ ratios were not systematically different across gap formation mechanisms. The majority of canopy gaps (90%) were created by a single canopy individual. Only six gaps were formed by the death of multiple trees; of these six, four were the result of uprooting and two were formed by multiple snags. Single-tree gaps had a mean expanded area of 196.3 $m^2 \pm 97.8$, with a minimum of 39.6 m^2 and a maximum of 428.5 m^2 . Multi-tree gaps had a mean expanded area of 228.1 $m^2 \pm 84.9$ with minimum and maximum areas of 98.3 and 346.0 m^2 , respectively. Gaps created by a single gapmaker lost a mean basal area of

Table 1

Relative frequency (percent of plots in which species occurred), relative density (percent of total stems), relative dominance (percent of total basal area), and relative importance (IV; average of relative frequency, relative density, and relative dominance) for stems ≥ 10 cm dbh in 20 plots in Sipsey Wilderness, Alabama.

Species	Relative frequency	Relative density	Relative dominance	Relative IV
<i>Carya alba</i> (L.) Nutt.	100.00	14.65	22.74	45.80
<i>Quercus prinus</i> L.	80.00	14.40	21.78	38.72
<i>Quercus alba</i> L.	80.00	14.40	21.57	38.65
<i>Magnolia macrophylla</i> Michx.	80.00	19.02	6.44	35.15
<i>Acer saccharum</i> Marsh.	70.00	7.71	3.75	27.16
<i>Fagus grandifolia</i> Ehrh.	35.00	10.80	5.81	17.20
<i>Acer rubrum</i> L.	45.00	4.11	1.98	17.03
<i>Nyssa sylvatica</i> Marsh.	40.00	3.86	1.13	14.99
<i>Oxydendrum arboreum</i> (L.) DC.	35.00	3.60	1.50	13.37
<i>Liriodendron tulipifera</i> L.	30.00	1.54	5.15	12.23
<i>Quercus velutina</i> Lam.	20.00	1.29	3.26	8.18
<i>Carya glabra</i> (Mill.) Sweet	10.00	1.29	2.02	4.43
<i>Pinus taeda</i> L.	10.00	0.51	0.62	3.71
<i>Quercus rubra</i> L.	10.00	0.51	0.56	3.69
<i>Carpinus caroliniana</i> Walter	10.00	0.51	0.32	3.61
<i>Ostrya virginiana</i> (Mill.) K. Koch	10.00	0.51	0.22	3.58
<i>Cornus florida</i> L.	10.00	0.51	0.11	3.54
<i>Prunus serotina</i> Ehrh.	5.00	0.26	0.47	1.91
<i>Carya ovata</i> (Mill.) K. Koch	5.00	0.26	0.45	1.90
<i>Fraxinus americana</i> L.	5.00	0.26	0.13	1.80

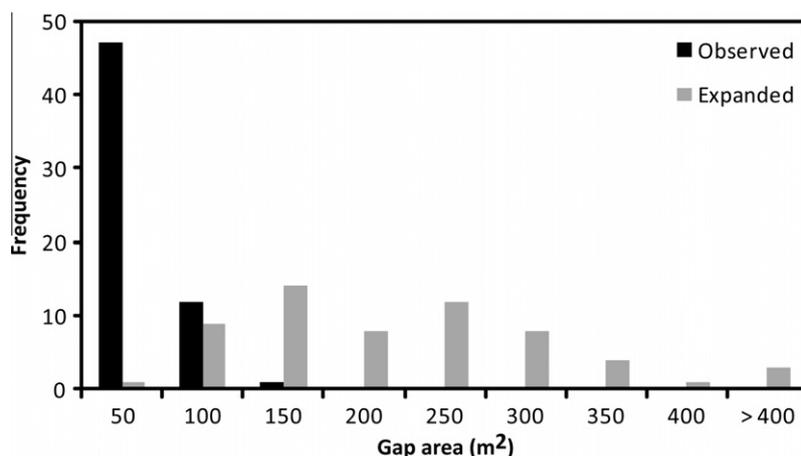


Fig. 2. Distribution of observed and expanded canopy gaps by 50 m² size classes in Sipsey Wilderness, Alabama.

0.13 m² ± 0.10, whereas gaps created by multiple trees lost a mean basal area of 0.25 m² ± 0.11. Expanded and observed gap size and basal area lost per event did not differ between single tree and multi-tree gaps. We found significant positive relationships between the basal area lost during a disturbance and both expanded gap ($r = 0.37$, $P = 0.004$) and observed gap sizes ($r = 0.37$, $P = 0.003$). We also found a significant positive relationship between the diameter of gapmakers and the expanded gap area ($r^2 = 0.13$, $P = 0.003$; Fig. 4).

Gap ages ranged from 3 to 28 years with an average age of 16.5 years (Fig. 5). 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 ($n = 4$). We identified 67 gapmakers that formed the 60 gaps. Of these 67 gapmakers, 54 individuals were identified to the species level, three only to the genus level, and 10 individuals were too decayed to be taxonomically classified with confidence. The 54 gapmakers identified to the species level represented a total of 11 species. *C. alba* was the most frequent gapmaker species accounting for 13 gaps. However, at the genus level, *Quercus* represented the largest number of gapmakers (44%). The average dbh of gapmakers was 37 cm ± 14. Mean gapmaker basal area lost per gap was

0.14 m² ± 0.11. The minimum basal area removed was 0.02 m² and the maximum was 0.41 m².

3.3. Gap closure and species composition

Of the 60 total gaps, 65% were projected to close via lateral crown expansion while the remaining 35% were projected to close through subcanopy recruitment. Expanded area of gaps projected to close via subcanopy height growth was significantly greater ($P < 0.01$) than that of gaps projected to close through lateral crown expansion (Fig. 6). Likewise, observed gap area was greater ($P < 0.001$) for gaps projected to close via subcanopy height growth compared to those projected to fill by lateral branch elongation (Fig. 6). Additionally, we found that the number of perimeter canopy trees (i.e. the number of trees required to complete the canopy around the void) was significantly greater ($P < 0.001$) for gaps projected to close by subcanopy recruitment than those projected to fill by lateral crown expansion. Projected gap closure was not significantly related to any of the following variables: average canopy height, $L:W$ ratio, $D:H$ ratio, intra-gap spacing of trees, or average diameter of canopy trees in the expanded gap.

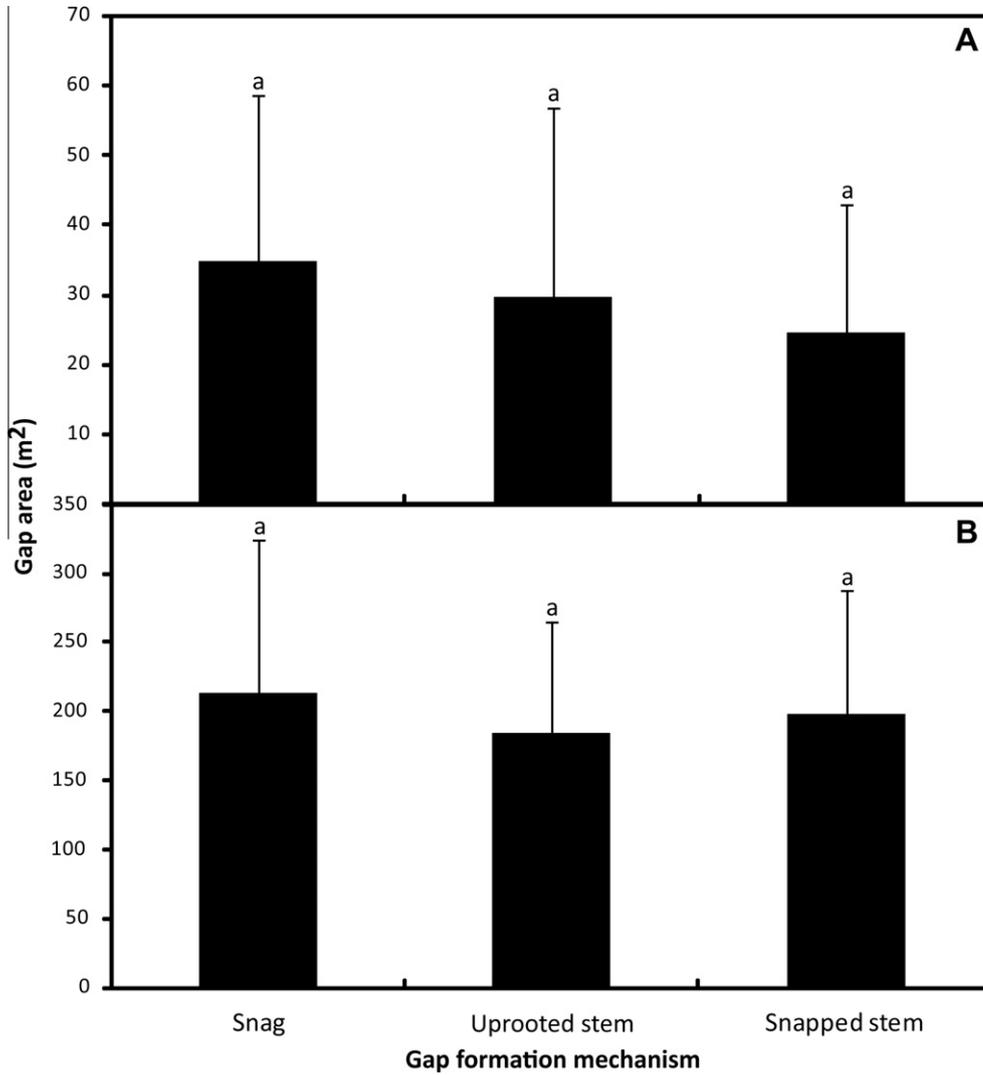


Fig. 3. Mean sizes (\pm SD) of (a) observed and (b) expanded gaps by gap formation mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant ($P < 0.05$) difference between gap origins as detected by ANOVA with Scheffe post hoc-testing.

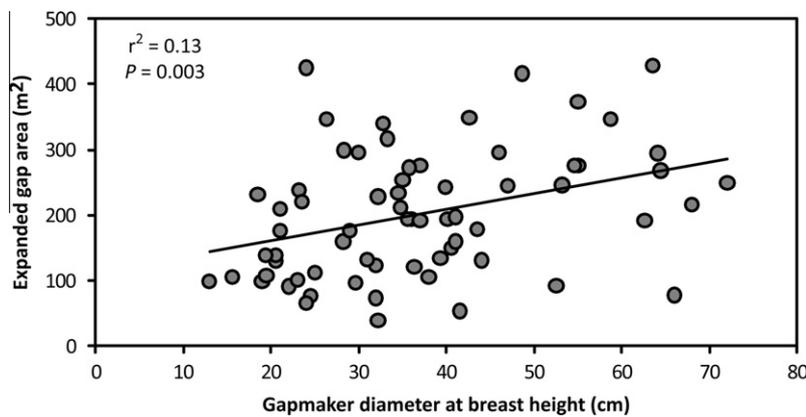


Fig. 4. Relationship between gapmaker diameter at breast height (cm) and expanded gap area (m^2) in Sipsey Wilderness, Alabama.

The mean number of trees within the expanded gap was 11.2 ± 4.7 with a minimum of four and a maximum of 31. The average number of individuals within the observed gap was 3.6 ± 2.2 with a minimum of zero individuals and a maximum of 10. No interior trees were documented in 10 of the 60 gaps. The

mean intra-gap spacing of trees was $14.4 m^2 \pm 5.0$ and ranged from 5.7 to 27.3 m^2 .

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

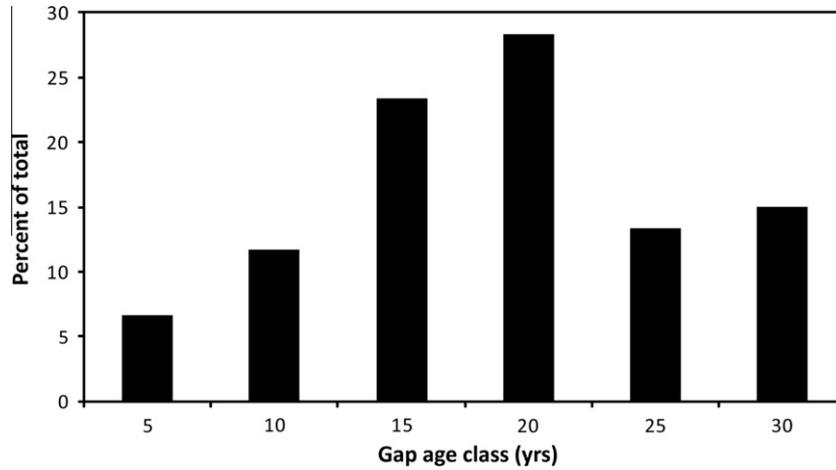


Fig. 5. Distribution of 60 canopy gaps by five-year age classes in Sipsey Wilderness, Alabama.

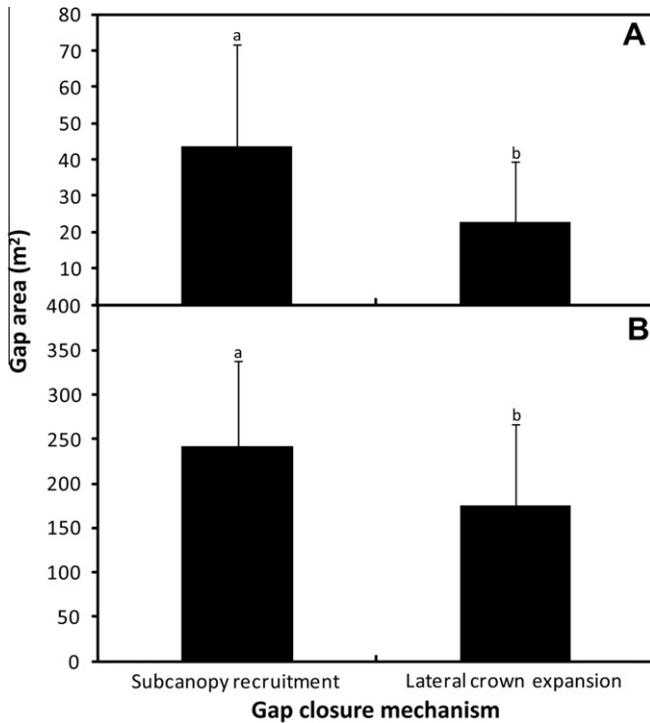


Fig. 6. Mean sizes (\pm SD) of (a) observed and (b) expanded gaps by gap closure mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant ($P < 0.05$) difference between gap closure mechanisms as detected by two-tailed t -tests.

L. tulipifera ($n = 7$) and *Q. alba* ($n = 6$). The other gap capturing species where *M. macrophylla* ($n = 2$), *F. grandifolia* ($n = 1$), *Carya cordiformis* ($n = 1$), *C. alba* ($n = 1$), *L. styraciflua* ($n = 1$), *Q. prinus* ($n = 1$), *Q. rubra* ($n = 1$), and *Ulmus rubra* ($n = 1$).

The composition and structure of gap perimeter vegetation and non-gap vegetation was similar. Species richness of trees (≥ 5 cm dbh) in observed gaps was 20. We documented one species in the tree layer of observed gaps that was not represented in the gap sapling layer (*Carya ovata*). *Fagus grandifolia* exhibited the highest relative frequency, relative density, and relative importance value of trees in observed gaps (Table 2). *Liriodendron tulipifera* had the highest relative dominance in observed gaps and was the second most important species. Within the observed gaps, *F. grandifolia* was followed by *M. macrophylla* and *A. saccharum* in

relative density. Combined, these three species represented over 42% of the total trees sampled in observed gaps. Species richness of the sapling layer was 36. We documented 15 sapling species in gaps that were not represented as gap trees. In the sapling layer, *F. grandifolia* and *A. saccharum* had the highest relative frequency and relative importance followed by *Nyssa sylvatica* and *Acer rubrum* (Table 3).

4. Discussion

4.1. Gap and gapmaker characteristics

The canopy gap sizes and shapes documented in *Quercus* stands on the Sipsey Wilderness were similar to what has been reported elsewhere in the southern Appalachian Highlands (Runkle, 1981; Wilder et al., 1999; Clinton et al., 1994). We anticipated that gaps caused by uprooting would be relatively large and linear and snag-formed gaps would be comparatively small and circular based on prior research in secondary *Quercus* stands on the Cumberland Plateau (Hart and Grissino-Mayer, 2009). However, we did not find differences in gap size or shape based on gap origin. A possible explanation for this finding may be the high number of uprooted gaps involving a single tree in the studied stands. Gaps formed by uprooting are more likely to involve two or more canopy trees compared to snag-formed gaps as the fall of the gapmaker may remove neighboring individuals (Yamamoto and Nishimura, 1999). However, if the uprooted gapmaker does not remove neighboring canopy trees the gap should not be significantly different in size or shape than gaps formed by other mechanisms (Bormann and Likens, 1979).

In our study, snag-formed gaps were the single most frequent cause of gap formation (40% of all gaps). Snag gaps have been shown to be common in other secondary *Quercus* stands of the southern Appalachian Highlands (Clinton et al., 1993, 1994). The relatively high percentage of snag-formed gaps documented, led us to speculate that drought was an important disturbance mechanism in the forest. Clinton et al. (1993, 1994) hypothesized that a severe drought in 1986 caused region-wide mortality within mid-elevation mixed *Quercus* forests in the southern Blue Ridge. In the southern Appalachians, snag-formed gaps are most common on xeric sites where water can be limited (McComb and Muller, 1983; Hart and Kupfer, 2011). Prolonged water stress depletes stored starch reserves making trees unable to maintain healthy functioning and more susceptible to killing agents including fungi *Armillaria mellea* Vahl ex Fr. and *Hypoxylon* species and insects

Table 2
Relative frequency (percent of gaps in which species occurred), relative density (percent of total stems), relative dominance (percent of total basal area), and relative importance (IV; average of relative frequency, relative density, and relative dominance) for all trees ≥ 5 cm dbh in 60 observed gaps in Sipsey Wilderness, Alabama.

Species	Relative frequency	Relative density	Relative dominance	Relative IV
<i>Fagus grandifolia</i>	36.67	23.89	15.65	25.40
<i>Liriodendron tulipifera</i>	20.00	7.78	15.90	14.56
<i>Quercus alba</i>	11.67	4.44	21.42	12.51
<i>Magnolia macrophylla</i>	20.00	9.44	3.75	11.07
<i>Acer saccharum</i>	16.67	8.89	3.76	9.77
<i>Ostrya virginiana</i>	18.33	8.33	0.44	9.04
<i>Nyssa sylvatica</i>	18.33	6.11	0.88	8.44
<i>Acer rubrum</i>	15.00	5.56	1.15	7.24
<i>Carya glabra</i>	11.67	3.89	4.39	6.65
<i>Carya alba</i>	6.67	2.22	8.76	5.88
<i>Cornus florida</i>	10.00	5.00	0.23	5.08
<i>Ulmus rubra</i> Muhl.	10.00	3.89	1.10	5.00
<i>Quercus prinus</i>	6.67	2.22	5.62	4.84
<i>Liquidambar styraciflua</i> L.	5.00	2.22	3.58	3.60
<i>Carpinus caroliniana</i>	6.67	2.22	0.22	3.04
<i>Quercus velutina</i>	1.67	0.56	5.98	2.73
<i>Carya ovata</i>	1.67	0.56	3.55	1.92
<i>Carya cordiformis</i> (Wangenh.) K. Koch	1.67	0.56	2.99	1.74
<i>Oxydendrum arboreum</i>	3.33	1.11	0.60	1.68
<i>Juniperus virginiana</i> L.	1.67	1.11	0.02	0.93

Table 3
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, Alabama.

Species	Relative Frequency (%)	Relative Density (%)	Relative IV (%)
<i>Fagus grandifolia</i>	53.33	20.76	37.05
<i>Acer saccharum</i>	51.67	9.38	30.52
<i>Nyssa sylvatica</i>	45.00	13.07	29.03
<i>Acer rubrum</i>	41.67	12.86	27.26
<i>Magnolia macrophylla</i>	30.00	5.06	17.53
<i>Ulmus rubra</i>	23.33	2.85	13.09
<i>Ostrya virginiana</i>	21.67	4.32	12.99
<i>Quercus alba</i>	20.00	4.74	12.37
<i>Tilia heterophylla</i> Vent.	20.00	4.53	12.27
<i>Carya alba</i>	18.33	3.48	10.91
<i>Carpinus caroliniana</i>	13.33	2.95	8.14
<i>Quercus prinus</i>	13.33	1.48	7.40
<i>Asimina triloba</i> (L.) Dunal	11.67	1.79	6.73
<i>Carya glabra</i>	8.33	2.95	5.64
<i>Cornus florida</i>	10.00	1.05	5.53
<i>Aesculus pavia</i> L.	6.67	2.11	4.39
<i>Liquidambar styraciflua</i>	6.67	0.74	3.70
<i>Quercus velutina</i>	6.67	0.74	3.70
<i>Carya cordiformis</i>	6.67	0.53	3.60
<i>Sassafras albidum</i> (Nutt.) Nees	5.00	0.84	2.92
<i>Callicarpa dichotoma</i> (Lour.) K. Koch	5.00	0.42	2.71
<i>Magnolia acuminata</i> (L.) L.	3.33	0.32	1.82
<i>Fraxinus americana</i>	1.67	1.16	1.41
<i>Celtis occidentalis</i> L.	1.67	0.32	0.99
<i>Juniperus virginiana</i>	1.67	0.32	0.99
<i>Ulmus alata</i> Michx.	1.67	0.21	0.94
<i>Betula nigra</i> L.	1.67	0.11	0.89
<i>Cladrastis kentukea</i> (Dum. Cours.) Rudd	1.67	0.11	0.89
<i>Hamamelis virginiana</i> L.	1.67	0.11	0.89
<i>Ilex opaca</i> Aiton	1.67	0.11	0.89
<i>Liriodendron tulipifera</i>	1.67	0.11	0.89
<i>Oxydendrum arboreum</i>	1.67	0.11	0.89
<i>Prunus serotina</i> Ehrh.	1.67	0.11	0.89
<i>Quercus muehlenbergii</i> Engelm.	1.67	0.11	0.89
<i>Quercus rubra</i>	1.67	0.11	0.89
<i>Lindera benzoin</i> (L.) Blume	1.67	0.11	0.89

and older trees (i.e. greater than 70 years of age) are more vulnerable (Clatterbuck and Kauffman, 2006). Although we speculate that drought-induced mortality explains some canopy gap events on the Sipsey Wilderness, we note that some snag trees died during pluvial conditions indicating that tree health decline was too advanced to be reversed by wet conditions or that drought-induced weakening was not the only snag forming agent in the sampled stands (Cook and Krusic, 2004).

Although snag-formed gaps represented the single most common origin, most gaps were formed by either uprooting or stem snapping. Indeed, most studies in southern Appalachian forests have found uprooted and snapped stems to be the most common gap formation mechanisms (Barden, 1979, 1981; Romme and Martin, 1982; Runkle, 1982; Hart and Grissino-Mayer, 2009). Because the majority of gaps were caused by uprooted or snapped stems we speculate that wind is an important disturbance agent in the sampled stands. This region experiences ca. 58 thunderstorms annually (Smalley, 1979). These events are associated with strong winds that have the potential to uproot and snap living and dead trees.

Carya alba was the most common gapmaking species. This species was also the most important species in the sampled stands. *Quercus* was the most common genus involved in gap formation. Likewise, the genus was the most important in the sampled stands. No species-specific mortality events were apparent and the most abundant and dominant taxa in the stands were those most commonly involved in gap formation. The average dbh of gapmakers was $37 \text{ cm} \pm 14$ and the average dbh of canopy trees in non-gap positions through the sampled stands was $35 \text{ cm} \pm 12$. The minimal range between the diameter of gapmakers and canopy trees and the relationship between gapmaking species and forest composition indicated that any individual in the canopy exhibited an equal probability of being removed (i.e. gapmakers were not larger than canopy trees in the stands and no species created an anomalously high number of gaps relative to their abundance in the community). Similar results were documented in other secondary hardwood forests on the Cumberland Plateau in Tennessee (Hart and Grissino-Mayer, 2009).

4.2. Gap closure and species composition

Expanded and observed gap sizes varied significantly by gap closure mechanisms. Gaps that we projected to close via lateral

Enaphalodes rufulus Haldeman and *Agilus bilineatus* Weber (Stringer et al., 1989; Clatterbuck and Kauffman, 2006). Infestation of these biotic agents can girdle roots and stems and cause crown dieback. Mortality typically occurs within 2–5 years after onset

crown expansion were smaller than those projected to close by subcanopy recruitment. Gaps closed by the height growth of a subcanopy individual must be sufficiently large so that they do not fill by lateral crown expansion before an understory tree has time to ascend to the main forest canopy (Runkle, 1982). The gaps projected to close by lateral crown expansion had an average expanded area of 175 m². In contrast, the mean size of gaps projected to close via subcanopy recruitment was 242 m². Based on these findings and an examination of our data we hypothesized that a gap size threshold existed in these mature *Quercus* stands whereby the probability of the projected closure shifted from lateral crown expansion to subcanopy recruitment when gaps approached ca. 240 m² (59% of subcanopy recruitment closures exceeded this size while only 18% of lateral expansion closures were greater than 240 m²). In young stands, stem density is high and the area occupied by a single tree crown is relatively small. As canopy trees are removed by self thinning and exogenous disturbances, the gaps created are relatively small compared to gaps in older forests (Clebsch and Busing, 1989; Yamamoto and Nishimura, 1999; Hart and Grissino-Mayer, 2008; Hart et al., 2011). These small canopy voids fill rapidly often by lateral crown expansion (Dahir and Lorimer, 1996). In complex stage stands, canopy trees occur at wider spacings and individual tree crowns occupy a larger proportion of the forest canopy. The gaps created by the removal of these trees would be large compared to those that occurred during early development (Oliver and Larson, 1996). As evidence of this pattern, in our study gapmaker diameter exhibited a significant positive relationship with gap size. Large gaps have a higher probability of being filled by the height growth of a subcanopy tree relative to small gaps (Dahir and Lorimer, 1996).

Based on the number of gaps projected to fill by subcanopy recruitment, we suggest these *Quercus* stands were in a transitional period in their structural development (i.e. moving from the understory reinitiation to the complex stage). Although still in the understory reinitiation stage, gap-scale processes increase the distance between canopy individuals so that individual tree crowns grow to comprise increasingly larger portions of the canopy. The future removal of these trees should result in progressively larger gaps, eventually to a size when most will fill by subcanopy recruitment. The point when most gaps are sufficiently large so that they fill by subcanopy recruitment marks the beginning of the complex stage of development. At this stage, the stands should exhibit structural characteristics that are typically used to define old-growth conditions (Oliver and Larson, 1996). The large gaps that characterize complex structure develop as a result of gap-phase processes that occur continuously throughout prior stages of development. The progression of increasing gap size eventually requires subcanopy recruitment to be the primary mode of gap closure. At this point, the complex stage has begun.

Interestingly, the mean size of canopy gaps reported from other hardwood stands of the southern Appalachian Highlands approximates the threshold observed in this study (Runkle, 1981; Clinton et al., 1994; Wilder et al., 1999). If this size threshold exists in other hardwood forests of the region, then gaps smaller than average may typically fill by lateral expansion and those larger than average may fill by subcanopy recruitment. We stress however, that factors such as gap shape and topography complicate gap filling beyond simply gap size. For example, gaps that are of the same size may represent very different shapes (e.g. linear vs. circular). In linear gaps (i.e. those with large *L:W* ratios) the distance between perimeter canopy trees along the long axis may inhibit subcanopy recruitment as the gap may fill via lateral expansion before an understory tree reaches the main forest canopy. More time would be required for a similarly sized, but circular gap to infill laterally. Thus, in this example the potential of gap capture by a subcanopy

tree would be greater in the circular gap of the same size. Slope gradient can also influence gap closure processes. On steep slopes the vertical structure of even young, secondary stands can be quite complex and subcanopy trees can capture gaps on steep slopes without growing to typical canopy tree height (Fig. 7).

Of the 21 gaps projected to close through subcanopy recruitment, eight were projected to be captured by a *Quercus* individual. The gaps projected to fill by height growth of a subcanopy *Quercus* had a mean expanded area of 297 m² and ranged in size from 121 to 429 m². Notably, five of the eight gaps projected to close by *Quercus* recruitment were formed by relatively large (mean dbh: 57 cm) *Quercus* individuals. The diameter of these trees was ca. 20 cm greater than the average of all other gapmakers sampled. All gaps projected to close by a *Quercus* individual occurred at upper-middle positions on exposed slopes (i.e. with southerly aspects). Although all sampled gaps occurred at upper-middle to lower-middle slope positions, aspect, landform curvature, and other factors varied considerably. Biophysical site factors, canopy disturbance characteristics, and their interactions likely had a strong influence on species composition of the gap environment (Abe et al., 1995; Hart and Kupfer, 2011). With one exception, gaps captured by a subcanopy *Quercus* individual had sparse sapling layers with few if any *F. grandifolia*, *A. saccharum*, or *A. rubrum*. These shade-tolerant species are known to outcompete *Quercus* in the

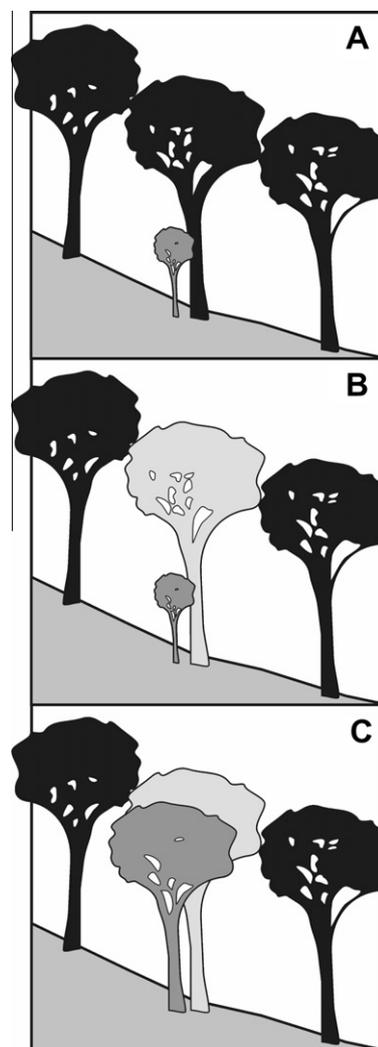


Fig. 7. Time series of: (a) canopy tree removal, (b) release of subcanopy individual, and (c) gap capture by subcanopy tree without reaching typical canopy tree height.

regeneration layer on productive sites (Lorimer et al., 1994), but these species are sparse on the most xeric sites (Abrams, 2005). On these exposed sites of the study area, *Quercus* dominance may be maintained through gap-phase processes.

L. tulipifera was projected to close seven of the documented gaps. In the southern Appalachians, regeneration of this shade intolerant species typically requires gaps $\geq 400 \text{ m}^2$ (Busing, 1994, 1995), but we note that some studies have documented its regeneration in smaller openings (e.g. Beck, 1970, 1988). Although the species is noted for its ability to recruit to the canopy in gaps, the gaps projected to close by *L. tulipifera* in this study had an average size of only 249 m^2 with a maximum size of just 317 m^2 . We did not document any *L. tulipifera* in the understory of the closed canopy environment; a finding expected for such a shade intolerant species. Thus, we suspect the species did not occur as advanced regeneration prior to gap formation. Most gaps projected to close by *L. tulipifera* were on sites with slopes greater than 20%. We speculate *L. tulipifera* was able to capture these gaps because individuals were not required to reach the typical canopy tree height to achieve a position in the main forest canopy, rather they only needed to reach the heights of the downslope canopy trees to capture the gaps (see Fig. 7). On level terrain, these relatively small gaps may have closed before *L. tulipifera* trees reached a canopy position.

The composition of species in canopy gap environments is a good predictor of future composition in forests dominated by gap-scale disturbance regimes (Runkle and Yetter, 1987). In the tree layer of gaps, *F. grandifolia* was the most important species. *Quercus alba* was the most dominant tree in gaps, but the species only represented ca. 4% of all gap trees and occurred in less than 12% of the gaps. Canopy gap formation is stochastic therefore understory density is a critical factor to determine if a tree is able to capture vacated growing space caused by overstory removal. Although localized canopy disturbances influence all forest strata, the microenvironmental modifications caused by these events are often most apparent in the sapling layer (Brokaw and Busing, 2000; Yamamoto, 2000). These influences are significant because the sapling layer contains the pool of species likely to recruit to larger size classes through gap-phase processes (Wilder et al., 1999; Taylor and Lorimer, 2003). The most important sapling species in gaps were *F. grandifolia*, *A. saccharum*, *N. sylvatica*, and *A. rubrum*. These species are all capable of withstanding periods of suppression and have been shown to respond positively to local canopy disturbance (Canham, 1985, 1990; Orwig and Abrams, 1994; Hart et al., 2010). Collectively, these species only captured one canopy gap (*F. grandifolia*), but because these species are shade-tolerant they may persist in the understory and recruit to larger size classes and eventually the canopy after future disturbances (Dahir and Lorimer, 1996; McClure et al., 2000; Taylor and Lorimer, 2003). Excepting the more xeric sites, gap-phase processes on the Sipsey Wilderness over time will favor shade-tolerant species which are abundant in the regeneration layer of gaps. Therefore, we project forest composition will change to include a much stronger component of *F. grandifolia*, *Acer* species, and other shade-tolerant taxa under a disturbance regime characterized by asynchronous and localized events.

5. Management implications

The replacement of *Quercus*–*Carya* with *Acer*–*Fagus* has been widely documented in the Central Hardwood Forest. Some researchers have postulated that this major shift in species composition is inevitable in the absence of silvicultural treatments (Abrams, 2005; Nowacki and Abrams, 2008). In order to retain the *Quercus* components to such forests, resource managers have

implemented a variety of silvicultural treatments including group selection harvesting which can mimic natural gap disturbance. With the group selection technique the size of the harvest-created canopy openings is critically important (Stringer, 2006). These canopy gaps must be large enough to increase light levels for mid-tolerant *Quercus*, without being excessively large to allow recruitment of shade-intolerant and fast-growing species such as *L. tulipifera*. Canopy openings that are too small will not allow enough light for *Quercus* recruitment and will favor the more shade-tolerant species which, in many stands, dominate the understory (Dey, 2002). Our results indicate that expanded gap sizes greater than ca. 240 m^2 were sufficiently large to allow understory trees to recruit to the canopy. However, for silvicultural operations gap size should likely be adjusted based on slope gradient and other biophysical site conditions. For example, *L. tulipifera* was able to capture gaps of only ca. 250 m^2 on relatively steep slopes indicating that inhibition of *L. tulipifera* recruitment may not be possible by creating small gaps alone. In these settings, competition removal by mechanical or chemical means may be required to recruit *Quercus* in harvest-created gaps.

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