Influence of gap-scale disturbance on developmental and successional pathways in *Quercus-Pinus* stands

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ABSTRACT

Quercus-Pinus forests of the eastern USA cover millions of hectares and span a variety of ecoregions. Understanding the influence of natural disturbance on developmental and successional pathways is important for managers that wish to sustain *Pinus* spp. in these mixtures. Quantifying developmental and successional patterns in this forest type can help assess the need to actively manage natural processes and inform silvicultural prescriptions to achieve management goals. Little research has been conducted on natural, gap-scale disturbance processes in *Quercus* stands with strong components of *Pinus taeda*, *Pinus virginiana*, and *Pinus echinata*. We examined 60 canopy gaps in a *Quercus-Pinus* forest on the southern Cumberland Plateau in Alabama to document gap formation, closure, and other characteristics and to analyze the influence of localized disturbance on development and succession. The majority of gapmaker trees (56%) were *Pinus* individuals and 44% were hardwoods. Most gaps (58%) closed by height growth of subcanopy trees. The majority of these gap filler taxa were hardwoods: *Quercus* (39%), *Carya* (14%), *Nyssa sylvatica* (12%), and other hardwoods (15%), with *Pinus* representing 14%. The number of *Pinus* gapmakers and the number of gaps projected to fill by subcanopy recruitment of hardwoods indicated the forest was in the latter stages of a composition shift from *Pinus* to a much stronger *Quercus* component. Significant positive relationships existed between gap size and sapling diversity ($r^2 = 0.15$, $P = 0.002$), tree diversity ($r^2 = 0.21$, $P = 0.0002$), and total stem diversity ($r^2 = 0.29$, $P < 0.0001$) indicating a positive relationship may exist between gap size and diversity on xeric ridge tops where shade-tolerant species are less competitive. We speculated the ridge top positions contributed to the relatively high gap formation rates noted in this study. *Pinus* composition was found to be patchy, indicating a gap-based approach may be used to manage for *Pinus* recruitment in hardwood dominated systems.

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1. Introduction

Forests are subject to disturbance events which shape developmental patterns and successional pathways. Disturbance extent and magnitude vary widely from catastrophic, stand-scale to highly localized, gap-scale events (Oliver and Larson, 1996). Localized, gap-scale events are the most common natural disturbances in eastern USA forests (Runkle, 1985). These disturbances create structural changes associated with older forests by increasing large woody debris inputs, creating pit and mound topography, releasing understory trees from suppression, providing sites for new germinants, promoting multi-aged structures, and allowing for canopy expansion that leads to large canopy trees at wide spacings

(Oliver and Larson, 1996; Frelich, 2002; Richards and Hart, 2011). Localized disturbances can also shift species composition to shade-tolerant, late-seral species (Goebel and Hix, 1996, 1997; Hart and Grissino-Mayer, 2009).

The influence of natural gap-scale disturbance processes on development and succession has been described for both secondary and old-growth hardwood stands of the temperate zone (e.g. Lorimer, 1980; Barden, 1981; Runkle, 1982, 2000; Cho and Boerner, 1991; Yamamoto and Nishimura, 1999, 2000; Zeibig et al., 2005; Mountford et al., 2006; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011; Petritan et al., 2013). However, few studies have quantified natural canopy gap formation in upland *Quercus* stands with a canopy component of *Pinus taeda*, *Pinus virginiana*, and *Pinus echinata* in the Central Hardwood Forest (Rantis and Johnson, 2002; Stambaugh et al., 2002; Stambaugh and Muzika, 2007); a forest type that spans millions of hectares throughout the

eastern USA (Smith and Darr, 2004). Thus, there is a paucity of quantitative information on natural canopy disturbances and their influence on developmental and successional pathways in these *Quercus-Pinus* systems.

Although developmental and successional patterns in mixed hardwood stands and *Quercus-Pinus* stands are both influenced by gap-scale disturbance processes, forest response to these discrete events may vary by forest type. For example, in the Central Hardwood Forest *Pinus* spp. typically have more narrow crowns with stronger apical dominance compared to co-occurring hardwoods; *Pinus* stems may also extend above the main hardwood canopy (i.e. an emergent layer). Differences in crown and height characteristics of canopy trees may result in different gap characteristics, such as size and shape, which in turn influence gap closure mechanisms. Gap formation and closure are important controls on development and succession (Rentch et al., 2003; Webster and Lorimer, 2005; Hart and Grissino-Mayer, 2009; Zeide, 2010).

The theoretical basis for successional pathways in *Quercus-Pinus* forests of the eastern USA has been established (e.g. Billings, 1938; Oosting, 1942; Braun, 1950; Quarterman and Keever, 1962; Halls and Homesley, 1966; Nicholson and Monk, 1975; Switzer et al., 1979; Peet and Christensen, 1980; Christensen and Peet, 1981, 1984; Christensen, 1989). At crown closure, shade-intolerant *Pinus* individuals typically dominate the canopy. *Pinus* stems are sparse to non-existent in the understory strata of these closed canopy stands and mortality of canopy *Pinus* provides the opportunity for the more shade-tolerant hardwoods to recruit to larger size classes and ascend to canopy positions. It may be understood that in the absence of broad-scale disturbances, gap-scale disturbance processes drive this successional trajectory, but we lack a clear mechanistic understanding of the transition from *Pinus* to hardwood dominance in these systems. A mechanistic understanding of this process is required for managers interested in maintaining a *Pinus* component in stands with an understory stocked by more shade-tolerant hardwoods, promoting mixtures of hardwoods in managed *Pinus* systems, or altering composition toward hardwood dominance.

In the Central Hardwood Forest, managers increasingly wish to maintain a *Pinus* component in stands transitioning to hardwood dominance (Hart et al., 2012) for a variety of reasons such as biodiversity, fuels, drought tolerance, commodity production, and restoration objectives. *Pinus* stems provide a pathway for change within a forest system dominated by hardwood species because they increase the heterogeneity of the canopy, may have high live crown ratios, year-round foliage, and relatively acidic litter, wood, and bark (Harmon et al., 1986; Schulte et al., 2007; Fahey and Lorimer, 2013). *Pinus* trees contribute to the maintenance of diverse wildlife communities by providing habitat suitable for many wildlife species that are associated with mature *Pinus* trees such as *Picoides borealis* Vieillot, *Sitta pusilla* Latham, and *Setophaga pinus* Wilson (Johnston and Odum, 1956; Dickson, 1982; Buckner, 1982; Owen, 1984). *Pinus* needles are highly flammable and encourage the spread of fire compared with some hardwood litter (Kane et al., 2008; Ellair and Platt, 2013). *Pinus* individuals may also contribute large coarse woody debris, and offer economic value in the form of wood products. Without active management or the absence of stand initiating or perhaps intermediate-scale disturbances, the *Pinus* component in many *Quercus-Pinus* systems in the eastern USA will be lost or greatly diminished (Rantis and Johnson, 2002; Guyette et al., 2007; Stambaugh and Muzika, 2007; Hart et al., 2012). By quantifying the driving mechanisms of development and succession in *Quercus-Pinus* stands, we can provide the tools required to actively manage natural processes and to develop or refine silvicultural prescriptions.

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

2. Study area and methods

2.1. Study area

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

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

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

2.2. Methods

To identify potential study stands, we used georeferenced field survey data provided by the USDA Forest Service, Bankhead Ranger District staff to locate *Quercus-Pinus* forest types in the Sipsey Wilderness. Society of American Foresters forest cover types 13 and 16 were used (Eyre, 1980). All suitable stands were then visited for reconnaissance. We avoided sampling stands recently damaged by disturbance agents that resulted in intermediate-levels of

disturbance (i.e. disturbances larger than the gap scale) because our goal was to document the influence of natural gap-scale disturbance processes on developmental and successional pathways rather than analyze broader-scale disturbance processes. All stands were located along ridge top positions. Non-gap forest vegetation was quantified using twenty 0.05 ha fixed-radius plots located randomly throughout the 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 direction of intercepted light (Oliver and Larson, 1996). To document stand age, increment core samples were taken from two trees per non-gap plot that we estimated would have been the oldest individuals based on visible characteristics (Pederson, 2010). These data were used to establish composition and structural measures of the sampled stands and to examine the influence of gaps on these characteristics.

Canopy gaps ($n = 60$) were located along transects throughout the study stands using the line-intercept method (Runkle 1982, 1985, 1992; Veblen, 1985). The fraction of land area in both the expanded and observed canopy gaps was calculated by dividing the transect distance in gaps by total transect length (Runkle 1985, 1992). Gaps were defined as locations with: (1) a noticeable void in the main forest canopy, (2) leaf height of the tallest gap stems less than three-fourths the height of the adjacent canopy, and (3) presence of a gapmaker (Taylor and Lorimer, 2003). No minimum gap size threshold was used to ensure an accurate representation of gaps was documented (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). When we encountered a gap that met the criteria listed above it was sampled regardless of biophysical characteristics. Thus, the first 60 gaps that met these criteria were sampled.

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

Elevation, latitude, and longitude were recorded in the field using a handheld GPS device. Other physical site characteristics were recorded for each gap including percent slope, aspect, and average canopy height surrounding the gap. The number of perimeter canopy trees was recorded for each gap to analyze the number of individuals required to complete the canopy surrounding gaps and the number of canopy individuals with the potential to close the gaps through branch elongation (Runkle, 1982). Gap age was determined using a variety of techniques. Increment core samples were taken from larger residual trees hypothesized to show increased radial growth rates coincident with gap formation (Hart et al., 2010; Rentch et al., 2010). Within gaps, individual stems and branches which appeared to have formed immediately following gap formation were cut at their base and transported to the laboratory to determine the establishment date (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). In the laboratory, all wood samples were processed and dated using standard dendrochronological techniques (Stokes and Smiley, 1996; Orvis and Grissino-Mayer, 2002). Tree-ring series

on the increment core samples were visually analyzed for sudden and anomalous increases in radial growth (Runkle, 1982; Hart and Grissino-Mayer, 2009; Richards and Hart, 2011). Furthermore, 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 four decay classes following the criteria of Jones and Daniels (2008). Thus, multiple techniques were used in combination to assign gap formation years.

Canopy gaps can be created by several different mechanisms that cause overstory tree mortality. Different gap formation mechanisms may have different effects on biotic and abiotic forest conditions. For this reason, gap formation mechanisms were determined by observation of gapmaker and classified into one of three categories: snag (standing dead tree with crown intact), uprooted stem (root network uplifted), or snapped stem (bole broken below the crown; Putz, 1983; Clinton et al., 1993; Yamamoto, 2000). Gapmakers were taxonomically classified to quantify any species-specific overstory mortality patterns. The dbh of all gapmakers was recorded to determine the amount of overstory basal area (m^2) lost during each event and provide information on the amount of basal area naturally removed through gap-scale processes.

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

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

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

All statistical tests were performed with SAS v. 9.3. All data were visually assessed and statistically analyzed for normality and variance. Two-tailed *t*-tests were used to examine relationships between gap closure mechanisms and the following characteristics: observed and expanded gap sizes, number of perimeter trees surrounding each gap, number of perimeter trees that were *Pinus* surrounding each gap, D:H ratio for expanded gaps, D:H ratio for observed gaps, intra-gap tree density, average canopy height, and L:W ratios for both observed and expanded gaps. Two-tailed *t*-tests were also used to analyze relationships between taxonomic classification of gapmaker (*Pinus* v. hardwood) and the following characteristics: observed gap area, expanded gap area, L:W ratio of observed gaps, and L:W ratio of expanded gaps. Finally, two-tailed *t*-tests were used to examine the relationship between the L:W ratio of observed gaps and L:W ratio of expanded gaps.

Pearson correlation analysis and linear regression were used to analyze relationships between observed and expanded gap sizes with gapmaker diameter at breast height and basal area lost during a gap-scale disturbance. Both Pearson and Spearman rho correlation analyses were used to test for relationships between expanded gap sizes and density and diversity of saplings, trees, and total stems within each gap. Linear regression analysis was subsequently used to examine relationships between diversity of saplings, trees, and total stems and expanded gap area.

We used ANOVAs with a Scheffe post hoc tests to analyze relationships between gap formation mechanisms (snag, uprooted stem, or snapped stem) and the following characteristics: observed gap size, expanded gap size, L:W ratio of observed gap, L:W ratio of expanded gap, and diversity of saplings, trees, and total stems within each gap. Finally, a chi-square analysis was used to determine relationships between taxonomic classification of gapmaker and gap closure mechanisms and a Fisher's exact test was used to determine relationships between taxonomic classification of gapmaker and gap formation mechanisms.

3. Results

3.1. Forest composition and structure

Mean establishment year of the 40 trees used to document stand age was 1899 ± 14.0 years (SD). The oldest stem was a *P. taeda* with a dbh of 58 cm that established in 1884, and the youngest tree was also a *P. taeda* with a dbh of 31 cm that established 1920. Sampled stands on the Sipsey Wilderness were dominated by *Quercus alba*, *P. taeda*, and *Quercus prinus* (Table 1), collectively representing 78% of the basal area. The next most dominant taxa were *Oxydendron arboreum*, *Quercus rubra*, *Carya* spp., *Liriodendron tulipifera*, *P. virginiana*, *Nyssa sylvatica* and *Quercus falcata*, cumulatively compromising 20% of the basal area. Basal area of all stems ⩾10 cm dbh was 28.13 m^2 ha^{-1}. *Q. alba* (n = 112 ha^{-1}) and *Q. prinus* (n = 81 ha^{-1}) were the most abundant species, representing 53% of all stems ⩾10 cm dbh in the sampled forest. *P. taeda* (n = 35 ha^{-1}) had the next highest density, representing 10% of all stems.

Of the 12 trees ha^{-1} with dominant positions in the forest canopy, 10 were *P. taeda* individuals and the other two were *L. tulipifera* and *Q. rubra*. The largest tree documented on a non-gap plot was a *P. taeda* with a dbh of 76 cm. Average dbh for trees in a dominant canopy position was 61 cm ± 9. The majority of stems (56%) occurred in the codominant crown class. The codominant canopy position was occupied by *Q. alba* (n = 86 ha^{-1}), *Q. prinus* (n = 49 ha^{-1}), *P. taeda* (n = 25 ha^{-1}), *P. virginiana* (n = 12 ha^{-1}), and *Q. rubra* (n = 11 ha^{-1}). Mean dbh for trees in the codominant canopy position was 35 cm ± 10. *Q. prinus* was the most abundant species in the intermediate canopy position (n = 33 ha^{-1}), followed by *O. arboreum* (n = 31 ha^{-1}), *Q. alba* (n = 26 ha^{-1}), *N. sylvatica* (n = 18 ha^{-1}) and *Carya* spp. (n = 11 ha^{-1}). Only one *Pinus* stem, i.e., *P. virginiana*, was found in an intermediate position and the genus was absent from the overtopped position.

3.2. Gap fraction, gap, and gapmaker characteristics

Total transect length was 3.0 km, with 28.0% of the total length in expanded and observed gaps, and 11.5% in observed gaps only. Standardized to the hectare level, 2800 m^2 ha^{-1} were in expanded gaps and 1150 m^2 ha^{-1} were in observed gaps. Gap ages ranged from 2 to 29 years with an average age of 11 years ± 6 (Fig. 1).

We documented 74 gapmakers that formed the 60 studied gaps. *Pinus* individuals represented 56% of gapmakers and the remaining 44% were hardwoods. Only two species of *Pinus* gapmakers were found, *P. taeda* (n = 32) and *P. virginiana* (n = 9). Out of the 33 hardwood gapmakers, 31 were *Quercus*. *Q. prinus* (n = 13) and *Q. rubra* (n = 10) accounted for the majority of *Quercus* gapmakers and *Fagus grandifolia* and *L. tulipifera* were the only two non-*Quercus* gapmaking hardwood species we documented. Taxonomic classifi-

Table 1

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

| Species	Density (ha^{-1})	Relative density (%)	Dominance (m^2 ha^{-1})	Relative dominance (%)	Relative importance (%)
Quercus alba L.	112	30.94	8.51	30.27	30.60
Quercus prinus L.	81	22.38	5.46	19.41	20.89
Pinus taeda L.	35	9.67	7.86	27.93	18.80
Oxydendrum arboretum (L.) DC.	33	9.12	0.56	2.00	5.56
Quercus rubra L.	12	3.31	1.46	5.19	4.25
Carya spp.	19	5.25	0.80	2.86	4.06
Liriodendron tulipifera L.	11	3.04	1.19	4.23	3.63
Pinus virginiana Mill.	13	3.59	0.97	3.43	3.51
Nyssa sylvatica Marshall	19	5.25	0.25	0.88	3.06
Quercus falcata Michx.	6	1.66	0.46	1.64	1.65
Magnolia macrophylla Michx.	5	1.38	0.07	0.23	0.81
Fagus gradifolia Ehrh.	5	1.38	0.05	0.19	0.79
Quercus velutina Lam.	2	0.55	0.19	0.68	0.61
Quercus stellata Wangenh.	2	0.55	0.15	0.52	0.54
Acer rubrum L.	2	0.55	0.02	0.08	0.32
Pinus echinata Mill.	1	0.28	0.07	0.26	0.27
Prunus serotina Ehrh.	1	0.28	0.02	0.07	0.17
Fraxinus americana L.	1	0.28	0.01	0.05	0.16
Sassafras albidum (Nutt.) Nees	1	0.28	0.01	0.05	0.16
Cornus florida L.	1	0.28	0.01	0.03	0.15
Total	362	100.00	28.13	100.00	100.00
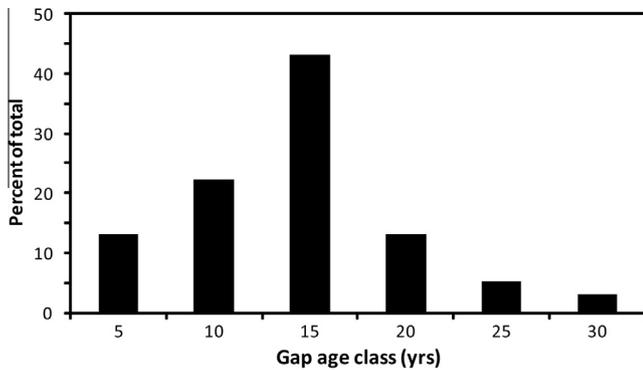
Fig. 1. Age distribution of 60 canopy gaps by five-year age classes in the Sipsey Wilderness, Alabama.

cation of gapmaker (*Pinus* v. hardwood) was not significantly related to the following variables: expanded gap area ($t(43) = 0.85$ $P = 0.4001$), observed gap area ($t(43) = 1.19$, $P = 0.2396$), $L{:}W$ ratio of expanded gap ($t(43) = 0.95$, $P = 0.3463$), or $L{:}W$ ratio of observed gap ($t(43) = 1.36$, $P = 0.1798$). Mean size of expanded gaps was 226 $m^2 \pm 113$. The largest expanded gap was 488.8 m^2 and the smallest was 75 m^2. The mean size of observed gaps was 55 $m^2 \pm 47$, with a maximum of 202 m^2 and a minimum of 4 m^2. Mean $L{:}W$ ratios of expanded gaps and observed gaps were 1.44:1 and 1.84:1, respectively. The mean $D{:}H$ ratio for expanded gaps was 0.53:1 and for observed gaps was 0.23:1. The majority of canopy gaps were formed by snapped stems (53%) followed by snags (27%) and uprooted stems (20%). Expanded gap size (ANOVA: $df = 2$, $F = 2.30$, $P = 0.1093$) and observed gap size (ANOVA: $df = 2$, $F = 1.21$, $P = 0.3064$) were not statistically different across gap formation mechanisms (Fig. 2). Likewise, $L{:}W$ ratio of expanded gaps (ANOVA: $df = 2$, $F = 0.74$, $P = 0.4823$) and observed gaps (ANOVA: $df = 2$, $F = 3.04$, $P = 0.0556$) did not significantly differ by the mode of gap formation. However, the $L{:}W$ ratios of observed gaps were significantly greater ($P = 0.005$) than $L{:}W$ ratios of expanded gaps.
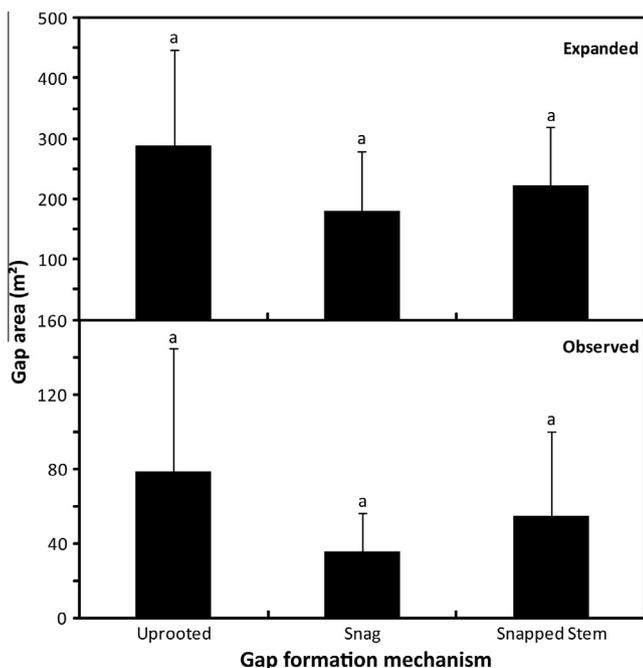

Fig. 2. Mean sizes (±SD) of observed and expanded canopy gaps by gap formation mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant ($P < 0.05$) difference between gap origins as detected by ANOVA with Scheffe post hoc testing.

All gaps were caused by the death of one or two trees. Single tree gaps represented 73% of all gaps and two-tree gaps accounted for 27%. Gaps created by a single tree had a mean expanded area of 199 $m^2 \pm 91$ and a mean observed area of 42 $m^2 \pm 31$. Two-tree gaps had mean areas of 298 $m^2 \pm 143$ and 86 $m^2 \pm 62$ for expanded and observed gaps, respectively. Mean basal area lost for single tree and multi-tree events was 0.16 $m^2 \pm 0.08$ and 0.30 $m^2 \pm 0.15$, respectively. Significant positive relationships were found between basal area lost during a disturbance and both expanded gap ($r = 0.48$, $P = 0.0001$) and observed gap sizes ($r = 0.52$, $P \leqslant 0.0001$). Significant positive relationships were also found between gap-maker dbh and expanded gap size ($r = 0.41$, $P = 0.006$) (Fig. 3). Average dbh of *Pinus* and hardwood gapmakers was 43 cm ± 12 and 41 cm ± 8, respectively, with an overall average dbh of 43 cm ± 11.

3.3. Density and diversity within gaps

The mean number of canopy trees that bordered gaps was 6.3 ± 1.9, ranging between three and 11. The mean number of trees $\geqslant 5$ cm dbh within expanded gaps was 6.3 ± 4.9 with a maximum of 23 and a minimum of zero. The mean number of trees $\geqslant 5$ cm dbh in the observed gap was 5.9 ± 5.2 with a maximum of 25 and a minimum of zero. The mean number of trees $\geqslant 5$ cm dbh in both the expanded and observed gap was 12.3 ± 9.1. The mean intra-gap density of trees for the observed and expanded gap environments was 26.6 $m^2 \pm 19.9$ and ranged from 8.62 to 102.41 m^2.

In the observed gap, species richness of trees $\geqslant 5$ cm dbh was 26. *N. sylvatica* was the most abundant of all trees $\geqslant 5$ cm dbh in observed gaps (13.9%) followed by *F. grandifolia* and *Q. alba*. The most dominant species were *Q. alba* and *Q. prinus* (Table 2). *P. virginiana* and *P. taeda* represented only 5% and 1% of observed gap trees, respectively. Average Shannon diversity (H') of all trees in both the expanded and observed gaps was 1.48 ± 0.58 with a maximum of 2.48 and a minimum of zero.

Observed gaps contained 39 different species in the sapling layer. *Acer rubrum* had the highest relative density, representing 37% of all sapling stems. *Carya* spp. had the next highest relative density (9%). The average number of saplings in observed gaps was 34 ± 23. Mean sapling diversity (H') was 1.68 ± 0.41. Maximum sapling diversity was 2.52 and the minimum was 0.41. Mean total diversity for all stems $\geqslant 1$ m was 2.03 ± 0.30 with a maximum of 2.75 and a minimum of 1.39. Significant positive relationships were found between gap size and number of saplings ($r_s = 0.79$, $P < 0.0001$), trees ($r_s = 0.69$, $P < 0.0001$), and total stems ($r_s = 0.84$, $P < 0.0001$). Positive relationships also existed between gap size and sapling diversity ($r^2 = 0.15$, $P = 0.002$), tree diversity ($r^2 = 0.21$, $P = 0.0002$), and total stem diversity ($r^2 = 0.29$, $P < 0.0001$) (Fig. 4).
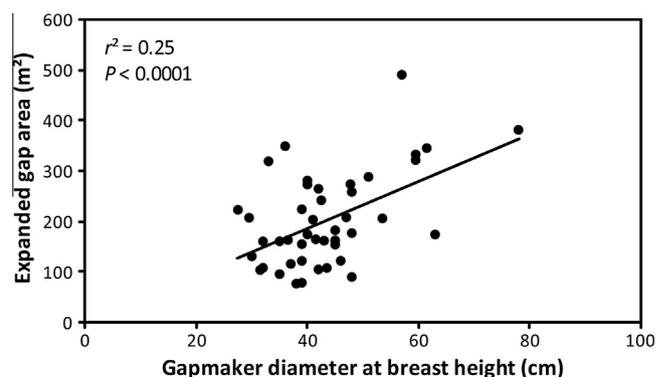

Fig. 3. Relationship between gapmaker diameter at breast height (cm) and expanded gap area (m^2) in Sipsey Wilderness, Alabama.

Table 2
Density, dominance, and relative importance (average of relative density and relative dominance) for all trees ⩾5 cm dbh in 60 observed canopy gaps in Sipsey Wilderness, Alabama.

Species	Density (ha^{-1})	Relative density (%)	Dominance (m^2 ha^{-1})	Relative dominance (%)	Relative importance (%)
Quercus alba	111	11.67	3.02	23.04	17.35
Nyssa sylvatica	132	13.88	0.95	7.28	10.58
Quercus prinus	60	6.31	1.88	14.32	10.32
Fagus grandifolia	114	11.99	1.01	7.68	9.84
Pinus virginiana	51	5.36	1.25	9.57	7.47
Carya spp.	57	5.68	0.99	7.36	6.52
Acer rubrum	90	9.46	0.33	2.53	6.00
Oxydendrum arboreum	45	4.73	0.66	5.05	4.89
Cornus florida	63	6.62	0.30	2.28	4.45
Magnolia macrophylla	42	4.42	0.35	2.64	3.53
Amelanchier arborea (Michx. f.) Fernald	39	4.10	0.27	2.06	3.08
Pinus taeda	12	1.26	0.49	3.71	2.49
Prunus serotina	27	2.84	0.24	1.83	2.34
Quercus rubra	15	1.58	0.20	1.50	1.54
Fraxinus americana	18	1.89	0.14	1.07	1.48
Quercus velutina	6	0.63	0.30	2.25	1.44
Liriodendron tulipifera	12	1.26	0.20	1.52	1.39
Ostrya virginiana (Mill.) K. Koch	18	1.89	0.10	0.80	1.34
Ilex opaca Aiton	12	1.26	0.06	0.43	0.85
Quercus falcata	3	0.32	0.14	1.06	0.69
Quercus stellata	3	0.32	0.10	0.80	0.56
Juniperus virginiana L.	6	0.63	0.06	0.47	0.55
Sassafras albidum	6	0.63	0.04	0.28	0.45
Ulmus alata Michx.	3	0.32	0.03	0.20	0.26
Vaccinium arboreum Marshall	3	0.32	0.01	0.05	0.18
Acer saccharum Marsh.	3	0.32	0.01	0.05	0.18
Total	955	100.00	13.11	100.00	100.00

3.4. Gap closure and recruitment

The majority (58%) of gaps were projected to close via subcanopy recruitment and 42% were projected to close via lateral crown expansion. The gaps projected to close by lateral crown expansion and subcanopy recruitment had average expanded areas of 162 m^2 and 242 m^2, respectively (Fig. 5). The following variables were significantly greater for gaps projected to close via subcanopy recruitment: expanded gap area (t(58) = 4.88, P < 0.0001), observed gap area (t(58) = 5.01, P < 0.0001), number of perimeter trees surrounding each gap (t(49) = 2.77, P = 0.008), the number of perimeter trees that were *Pinus* surrounding each gap (t(55) = 3.18, P = 0.002), the $D{:}H$ ratio for expanded gaps (t(58) = 3.21, P = 0.002), and the $D{:}H$ ratio for observed gaps (t(58) = 3.69, P = 0.0005). Intra-gap spacing of trees was significantly greater (P = 0.03) for gaps projected to close via lateral crown expansion. Gap closure was not significantly related to average canopy height (t(58) = 1.07, P = 0.2911) or $L{:}W$ ratio of the expanded gap (t(58) = 0.29, P = 0.7718), or the observed gap (t(58) = 0.36, P = 0.7210).

Of the 35 gaps projected to close via subcanopy height growth, *Quercus* was the most common gap filling genus, projected to capture 25% of these gaps. Other gap filling taxa were *Carya* spp. (14%), *N. sylvatica* (12%), *F. grandifolia* (10%), *P. virginiana* (8%), *P. taeda* (6%), *A. rubrum* (4%), followed by *L. tulipifera*, *Prunus serotina*, *Fraxinus americana*, and *Quercus stellata* (2% each). Gaps projected to close by a *Quercus* individual had an average expanded gap area of 276 m^2 ± 104 and gaps projected to close by a *Pinus* stem had a mean expanded area of 273 m^2 ± 114.

4. Discussion

4.1. Gap fraction, gap, and gapmaker characteristics

Data regarding the fraction of land area within a gap environment in *Quercus-Pinus* systems is of the Central Hardwood Forest is lacking. Bottero et al. (2011) found that stands with a strong *Picea* and *Abies* component in the canopy had a greater percentage of the stand in a gap environment compared to stands with a dominant hardwood canopy. They speculated that since *Picea* and *Abies* have less capacity for lateral crown growth, a higher gap fraction is expected for stands with a low hardwood component in the canopy layer. The *Pinus* spp. in our study also are relatively less capable than most co-occurring hardwoods at extending their crowns laterally, and our results show a high portion of sampled stands within a gap environment compared to what has been reported elsewhere in the region (Runkle, 1982; Hart and Grissino-Mayer, 2009; Rentch et al., 2010). Although gap fraction was high, our results also show that gap sizes were similar to those found in other studies (Runkle, 1982; Hart and Grissino-Mayer, 2009; Rentch et al., 2010; Richards and Hart, 2011) thus, the gap formation rate in the sampled stands, which were located on ridge tops, was comparatively high. Ridge tops in this region typically have thin soils and experience strong winds compared to lower slopes; both of these factors would lead to a greater probability of windthrow and thus, relatively high gap formation rates.

Frequency of gap formation varies with stand age (Hart and Grissino-Mayer, 2009). Typically young stands have a relatively high frequency of localized gap-scale disturbances and frequency declines with stand maturity. The average gap formation rate in stands throughout the eastern USA is 0.5–2% year^{-1} (Runkle, 1985), and if the amount of canopy opening per year equals the amount closing per year the stand would be in a state of dynamic equilibrium. However, this state may be rarely observed as a result of punctuated stand-wide disturbances (Richards and Hart, 2011; Himes and Rentch, 2013). If these stands were in dynamic equilibrium, we would expect a high frequency of young gaps whose numbers would decline with stand age as canopy voids close. However, there were unusually high rates of canopy disturbance events in the 15–20 year gap age classes, indicating gap formation rates were in a state of disequilibrium. We did not see evidence of *Dendroctonus frontalis* Zimmermann damage to explain the high frequency of gaps at that period. Interestingly, Richards and Hart (2011) also noted a similar gap age distribution in mesic *Quercus* stands of the Sipsey Wilderness.
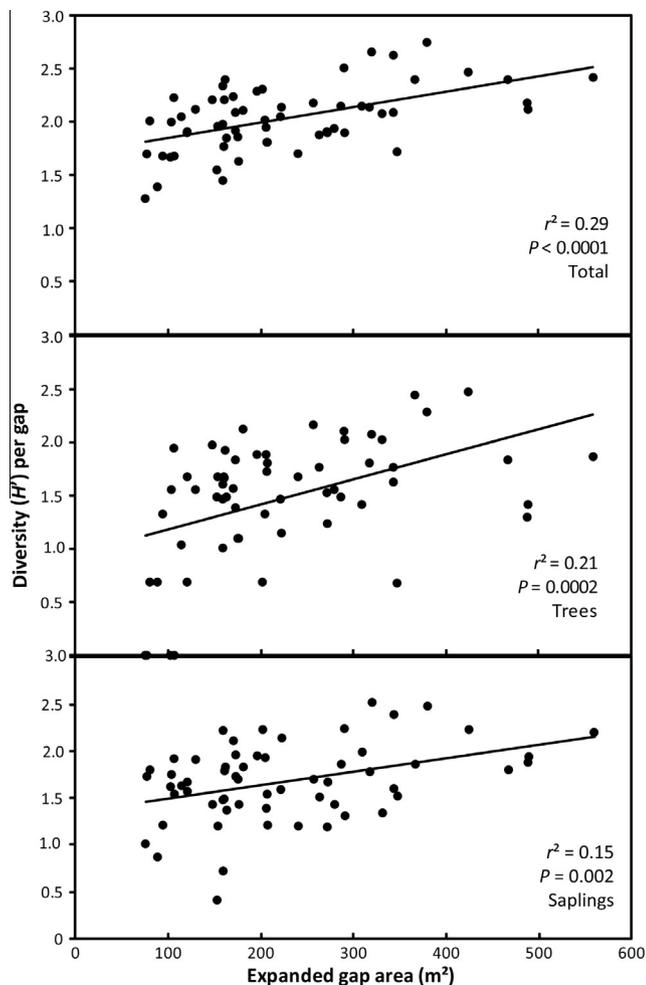
Fig. 4. Relationships between diversity values for saplings (>1 m height, <5 cm dbh), trees (⩾5 cm dbh), and total stems (all woody stems ⩾1 m height) and expanded gap area in Sipsey Wilerness, Alabama.

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

Snapped-stems were the most frequent cause of gap formation, representing 53% of all gaps and, out of gaps formed from the death of a *Pinus* individual, snapped stems accounted for 67% of canopy gaps. Jones et al. (1981) reported that *Pinus* trees were more likely to become snags, however we found only 6% of *Pinus* gapmakers stood as snags. A possible reason could be gap age. Conner and Saenz (2005) observed a 90% loss of *Pinus* snags with a dbh >40 cm 10 years after tree death. In our study, the average dbh of *Pinus* gapmakers was 43 ± 12 and the average age for each gap formation mechanism was: uprooted 10 ± 5, snag 10 ± 6, and snapped stem 12 ± 6. Snapped and uprooted stems in our study may have stood as snags before falling from a wind disturbance.
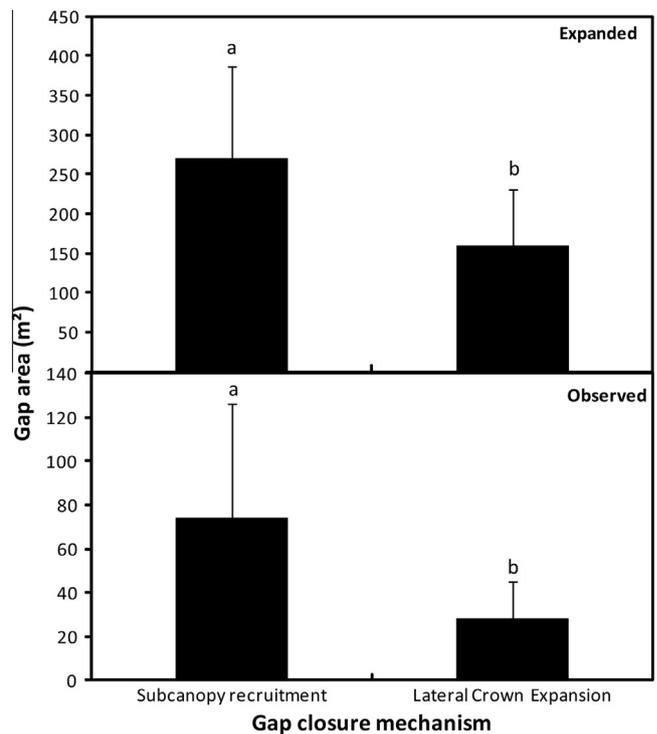

Fig. 5. Mean sizes (±SD) of observed and expanded gaps by gap closure mechanism in Sipsey Wilderness, Alabama. Different letters indicate a significant (P < 0.0001) difference between gap closure mechanisms as detected by two-tailed t-tests.

4.2. Density and diversity within gaps

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

4.3. Gap closure, recruitment, and succession

Gaps that were projected to close via lateral crown expansion were smaller than those projected to close through subcanopy recruitment. Gaps closed by the height growth of subcanopy individuals need to be sufficiently large to prevent closing through the lateral extension of neighboring canopy tree crowns, thus, allowing

an understory tree time to ascend to the canopy (Runkle, 1982). Gaps projected to close via subcanopy height growth had a mean gap size of 242 m², which is similar to the subcanopy recruitment threshold reported in Richards and Hart (2011). Compared to hardwoods, *Pinus* crowns are more narrow and conical, and allow more light to reach the understory and midstory layers. On the North Carolina Piedmont, Swan and Lieth (1976) found *Quercus* stands had 59% lower insolation than *Pinus* stands, but only 15% more basal area. In our study, the crowns of hardwood trees appeared to be taking advantage of this additional light penetration through the canopy. Gaps projected to close by lateral crown expansion as a result of a *Pinus* gapmaker had a mean area of 174 m². In contrast, the mean size of gaps projected to close via lateral crown expansion as the result of a hardwood gapmaker had a mean expanded gap area of 150 m². Perhaps hardwood crowns adjacent to *Pinus* canopy trees may extend further laterally than they would if they were adjacent to another canopy hardwood tree. Being adjacent to a dominant *Pinus* individual may allow hardwoods stems to capture wider gaps through lateral expansion than what they could capture if they had a hardwood neighbor.

Gap-scale events are the most frequent canopy disturbance events within this forest. Forests dominated by localized gap-scale disturbances typically favor shade-tolerant species (Henry and Swan, 1974; Dahir and Lorimer, 1996; Taylor and Lorimer, 2003) and species composition within gaps is a good predictor of future forest composition under the current disturbance regime (Runkle and Yetter, 1987). In our study, we found that 14 of the 35 gaps projected to close through subcanopy recruitment were filled by *Quercus* individuals. *Quercus* was also the most dominant genus of trees ⩾5 cm dbh in observed gaps, representing 37% of the basal area. *Acer rubrum* accounted for 37% of the stems in the sapling layer; *Quercus* individuals represented 13%. We suggest that under the current gap-based disturbance regime, the existing *Q. alba*, *P. taeda*, and *Q. prinus* canopy will yield dominance to the present-day intermediate canopy class dominated by *Q. prinus* and *Q. alba*. Continuing along this successional pathway under a gap-scale disturbance regime without intermediate- or stand-scale disturbance events, the current sapling layer, comprised mostly of *A. rubrum*, would be the next cohort to grow into canopy positions.

Pinus spp. were not regenerating nor were they recruiting into canopy positions and few *Pinus* saplings were present in the regeneration layer; only 12 *Pinus* saplings ha⁻¹ in observed gaps (<1% relative density). Of the 35 gaps projected to close via subcanopy height growth, only four gaps were projected to fill by recruitment of *Pinus* individuals. Unlike more shade-tolerant species, regeneration and recruitment of shade-intolerant *Pinus* spp. typically require large gaps and suitable seedbeds (Palik and Pederson, 1996; Brockway and Outcalt, 1998; McGuire et al., 2001; Gagnon et al., 2003; Stambaugh and Muzika, 2004). In a study examining relationships between canopy openness and *P. echinata* regeneration, Stambaugh and Muzika (2004) observed that the maximum number of *P. echinata* seedlings regenerating was eight times higher in larger gaps (1700 m²) than smaller gaps (400 m²). Larger gaps increase the potential for *Pinus* regeneration as they receive more insolation. Large gaps may also have higher temperatures at the forest floor which may accelerate litter decomposition (Liming, 1945). Reduced leaf litter provides more bare mineral soil, thought to be a requirement for seedling establishment of the *Pinus* species documented here (Skeen, 1976; Rantis and Johnson, 2002; Coleman et al., 2008) although Duncan and Linhoss (2005) found *P. virginiana* could germinate in thin layers of litter.

Little data are available on the relationships between gap-scale disturbances and regeneration and recruitment for *P. taeda*, *P. virginiana*, and *P. echinata* that co-occur with hardwoods. Considerably more research has been conducted to document the effects of gap-scale disturbances on *P. palustris* Mill. regeneration and recruitment. *Pinus palustris* is considered less shade tolerant than *P. taeda*, *P. virginiana*, and *P. echinta* (Wahlenberg, 1960; Eyre, 1980) and grows slower early in life (Fowells, 1965). As *P. palustris* is considered less tolerant of shade and has a slower early growth rate than *P. taeda*, *P. virginiana*, and *P. echinata*, gap sizes that translate to regeneration and recruitment of *P. palustris* may also lead to regeneration and recruitment of these other *Pinus* spp. Brockway and Outcalt (1998) suggested gaps to regenerate *P. palustris* be at least 40 m in diameter and for unobstructed growth of *P. palustris* reproduction, Palik et al. (1997) recommended a minimum gap size of ca. 1400 m². McGuire et al. (2001) was successful with artificially created expanded gaps >1100 m². Vegetation response to gap size may differ by species, forest type, and stand age, so gap sizes that promote *P. palustris* regeneration may not necessarily encourage the same for *P. taeda*, *P. virginiana*, and *P. echinata*.

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

5. Management implications

The size and shapes of gaps found in this study promoted hardwood regeneration and canopy recruitment of subcanopy hardwood stems. Although over half of the canopy gaps documented in this study were caused by the removal of a *Pinus* tree, hardwood species, specifically *Q. alba* and *Q. prinus*, were the most likely species to capture canopy gaps. Of the 60 gaps sampled, only four were projected to close through the subcanopy recruitment of *Pinus* individuals. This forest was in the latter stages of the transition from *Pinus* to hardwood dominance assuming no intermediate- or stand-scale disturbances. In the absence of silvicultural treatments, we hypothesize the *Pinus* component of this system will continue to decrease under the current disturbance regime.

Maintaining a *Pinus* component alongside hardwoods is difficult because the most common disturbances in these forests, gap-scale events, favor more shade-tolerant species. In sampled stands, the characteristics that are hypothesized to promote regeneration of shade-intolerant *Pinus* individuals, namely gap sizes >1400 m², bare mineral soil, and a low density of hardwood competition, were largely absent. To maintain a *Pinus* component, managers would likely need to create canopy gaps larger than those documented here. Multi-tree gaps are part of the historical disturbance regime in *Quercus-Pinus* forests of this region and these gaps can be large enough to regenerate and recruit these *Pinus* spp. (Hart et al., 2012). Group selection and variable retention harvests may provide the conditions needed to regenerate and recruit shade-intolerant *Pinus* spp. while at the same time mimicking natural disturbance processes.

Our results combined with field observations revealed that *Pinus* stems were clustered in these stands, giving credence to the idea that a gap-based approach may be used to manage for these *Pinus* species in systems dominated by hardwoods. Thus,

uniform silvicultural treatments may not be required to maintain or recruit *Pinus* spp. Based on our results and those of other studies (e.g. Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Gagnon et al., 2003) expanded gap areas should be >1400 m^2 with a *D:H* ratio of at least 1.5:1. These treatments should be centered around existing *Pinus* cohorts. Residual *Pinus* stems should remain within each group selection as a seed source and hardwood stems <1.5 m in height may remain to maintain the hardwood component, however, basal area of stems within the group selection should not exceed 17 m^2 ha^{-1} (Cain, 1993; Murphy et al., 1993; Shelton and Murphy, 1994; Shelton and Cain, 2000). Competition reduction methods, such as fire and herbicide application, should follow these group selections to inhibit hardwood reproduction. If there is no existing *Pinus* composition, or if a stronger *Pinus* component is desired, seedlings may be planted after the site is prepared with prescribed fire. Planting should be done at wide spacings ranging between 3 × 3 m and 4.5 × 4.5 m (Phillips and Abercrimbie, 1987; Waldrop, 1997). This would mean planting roughly 66–156 seedlings inside a 1400 m^2 gap. Planted seedlings should be able to overtop residual hardwood stems that are <1.5 m in height in ca. 4–7 years (Phillips and Abercrimbie, 1987; Waldrop, 1997).

Group selection and variable retention harvest methods can also be used by managers who wish to promote mid-tolerant hardwood species, such as *Quercus* and *Carya*, in a stand comprised of a *Pinus* overstory and a hardwood understory. To promote mid-tolerant taxa, light levels should be increased, but excessive canopy removal should be avoided. Too much canopy removal may favor recruitment of shade-intolerant *Pinus* spp. while too little canopy removal may favor more shade-tolerant species such as *Acer* (Dey, 2002). Based on our results in stands with *Quercus* developing in the understory of *Pinus*, but with the next generation trending toward *Acer*, we suggest gaps sizes greater than ca. 250 m^2 with a *D:H* ratio of ca. 1.0 be used for *Quercus* recruitment. Gaps of this size were large enough to promote subcanopy recruitment of understory trees into the canopy and similar sizes have been recommended for *Quercus* regeneration by others (Marquis, 1965; Dey, 2002; Richards and Hart, 2011). However, because the seedling and sapling layers of sampled stands were dominated by *Acer* spp., competition reduction measures such as fire or herbicidal application should be used in conjunction with these harvests (Schweitzer and Dey, 2011). Group selection or variable retention harvests would result in patches of even-aged trees within a stand and would result in multiple age classes across a single stand (O'Hara and Nagel, 2013).

Acknowledgements

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