GAP-SCALE DISTURBANCE PROCESSES

IN LONGLEAF PINE (*PINUS PALUSTRIS*

MILL.) WOODLAND

by

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ABSTRACT

Forest disturbances influence stand succession and developmental patterns. The most localized and frequent disturbances, gap-scale events, remove large branches, individual trees, orsmall groups of overstory trees. The formation of canopy gaps can lead to an increase in resources including light and growing space for the residual stems in proximity to the gap. Longleaf pine (*Pinus palustris*) has experienced a 95% range decline since European settlement.Longleaf pine establishment and recruitment has been found to be enhanced by canopy gaps.

Gap-scale disturbance processes have been studied in Coastal Plain longleaf pine ecosystems, but not in montane longleaf pine woodlands. To better understand gap-scale processes in montane longleaf pine woodlands, I sampled 50 canopy gaps and 20 non-gap (i.e. reference) plots at Reed Brake Research Natural Area in the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA. I collected data on canopy gap characteristics including canopy gap formation mechanisms, closure mechanisms, and canopy gap and non-gap species composition. Increased understanding of gap-scale processes in longleaf pine woodlands will allow for better management of these endangered ecosystems. The most common canopy gap formation mechanism among sampled gaps was snags (38%) followed by snaps (32%), and the majority of canopy gaps were formed by the death of a single tree (64%). The most common closure mechanism was lateral crown expansion (74%), and longleaf pine was the most commonspecies predicted to capture canopy gaps. I used LiDAR data to examine canopy gap size and gap fraction across the study area. The average area of

observed canopy gaps sampled, and the average observed area of LiDAR detected gaps were similar (75 m^2, and 76 m^2 respectively). For canopy gap, and non-gap plots, the most important tree species was longleaf pine, the most important sapling species was *Vaccinium arboretum*, and the most important seedling species was also *Vaccinium arboretum*. Based on these results, I predict that under the current disturbance regime longleaf pine will remain the dominant species in this stand. This study increased our knowledge of longleaf pine woodland gap fraction, as well as the composition ofcanopy gaps and non-gap areas.

LIST OF ABREVIATIONS AND SYMBOLS

°C   Celsius

cm   Centimeter

dbh   Diameter at breast height

ha   Hectare

m   Meter

mm   millimeter

km   Kilometer

p   Probability of occurrence under the null hypothesis of obtaining a value as extreme or more extreme than the observed value

LiDAR   Light Detection and Ranging

USDA   United States Department of AgricultureNRCS Natural Resources Conservation Service

%   Percent

=   Equal to

>   Greater than

≥   Greater than or equal to

<   Less than

≤   Less than or equal to

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INTRODUCTION

All forest disturbance events may be classified along a severity gradient by size, magnitude, and return interval into one of three categories: catastrophic, intermediate-severity, or gap-scale disturbances (Oliver and Larson, 1996; Hart and Kleinman, 2018). Catastrophic disturbances remove almost all overstory stems in a stand, and typically have long return intervals. Intermediate-severity disturbances span the large range between gap-scale and catastrophic events (Cowden et al., 2014). In many forest types, intermediate-severity disturbances have return intervals of ca. 20–50 years (Hart and Kleinman, 2018) The most localized and frequent disturbances are gap-scale events that remove large branches, individual trees, or small groups of overstory trees. The death of a canopy tree may lead to an increase in available resources for residual stems including increased light in the understory, growing space, and soil moisture (Runkle, 1982; Canham, 1988; Poulson and Platt, 1989; Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Hart and Grissino-Mayer, 2008; Weber et al., 2014). These biophysical modifications may allow for increased tree establishment and recruitment in canopy gaps thereby driving successional and stand development patterns (Runkle, 1984; Spies et al., 1990; Lertzman, 1992; Oliver and Larson, 1996).

The original range of longleaf pine (*Pinus palustris* Mill.) expanded over nearly 37 million hectares from Texas to Virginia USA, but its distribution decreased ca. 95% following European settlement (Frost, 1993). Multiple factors such as the production of naval stores, grazing pressure, fire suppression, and land-use changes, resulted in the loss of longleaf pine

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dominance throughout its range. Mature longleaf pine were damaged for the naval stores industry, while recruitment failed as a result of grazing pressure and fire suppression. Many sites historically dominated by longleaf pine were converted to loblolly pine (*Pinus taeda*) plantations as this species grows faster, and thus was preferred in the forest products industry (Frost, 1993). Loblolly pine plantations have a different stand structure than longleaf pine ecosystems and supports less biodiversity (Jeffries et al., 2010; Zobrist et al., 2005). Longleaf pine ecosystems support relatively high levels of biodiversity in the understory and can have up to 50 different species per m^2 when burned at regular intervals (Hardin and White, 1989; Kirkman et al., 2001).

Fire maintained longleaf pine stands generally have a savanna or woodland structure. Savannas, defined as open grasslands with trees and shrubs interspersed, with non-overlapping crowns (McGuire et al., 2001), and woodlands defined as stands with 30–80% crown cover (Dey and Kabrick, 2015), are not light limited relative to closed canopy forests. Nonetheless, studies have documented the importance of canopy gaps in regulating light levels in longleaf pine savannas and woodlands (Battaglia et al., 2003; McGuire et al., 2001; Palik et al., 1997).

Increased light from the formation of canopy gaps has been shown to increase growth and recruitment of longleaf pine seedlings (Pecot et al., 2007; Gagnon et al., 2003; Varner et al., 2003). Pecot et al., (2007) found longleaf pine seedlings that received light levels over 35% were able to establish and survive with only 13% initiating height growth, while seedlings receiving light levels over 60% were more likely to initiate height growth. In longleaf pine canopy gaps seedlings are often clustered near gap centers (Platt et al., 1988; Brockway and Outcalt, 1998). In the absence of stand replacing disturbances, regeneration clusters in canopy gap microenvironments can result in complex stand structures with multiple age classes (Oliver and Larson, 1996; Palik and Pederson, 1996; Jack and Pecot, 2018). The underlying mechanism, or

mechanisms, for increased regeneration of longleaf pine in canopy gaps is still unclear, though studies have indicated the pattern is likely related to increased light and growing space associated with gap formation (Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Battaglia et al., 2002). Another possible cause for increased seedling and sapling density (Brockway and Outcalt, 1998) and growth (Palik et al., 2003; Boyer, 1963) in canopy gaps is reduced competition from mature trees. Brockway and Outcalt (1998) determined the main competition for longleaf pine seedlings was from roots of mature longleaf pine trees that inhibit seedling establishment (i.e. the seedling exclusion zone). In longleaf pine ecosystems the seedling exclusion zone along the gap perimeter has been shown to restrict seedling establishment within ca. 15 m of the gap edge (Brockway and Outcalt, 1998; Boyer, 1963). Gap partitioning provides an area of decreased competition in the center of the canopy gap, outside the seedling exclusion zone, resulting in increased seedling establishment.

Low intensity surface fires maintain longleaf pine dominance and woodland structure (Wahlenberg, 1946; Boyer, 1979). These fires also enhance ground flora diversity in these ecosystems (Jin et al., 2019; Kleinman and Hart, 2018; Brockway et al., 2005; Glitzenstein et al., 2003). Longleaf pine are fire adapted, allowing them to better tolerate low intensity surface fires relative to many co-occurring trees (Wahlenberg, 1946; Boyer, 1979). Longleaf pine needles are an important fuel source in longleaf pine ecosystems as they provide fine fuels with a high resin content and create a continuous fuel bed (Mitchell et al., 2009). Herbaceous and select oak (*Quercus*) species in longleaf pine ecosystems have been found to burn similarly to longleaf pine needles, meaning there may be less of a difference in fire behavior between non-gap forest and canopy gap microenvironments (Emery and Hart, 2020). Overstory density has also been linked to the distribution and abundance of pine needle litter (Dell et al., 2017). Canopy gaps may cause changes in fuel loads throughout a stand and impact fuel bed continuity, which often corresponds to

the spatial distribution of canopy trees (Mitchell et al., 2009). Canopy gap and closed canopy environments may also have different fuel sources and fuel bed compositions (Mitchell et al., 2006; Mugnani et al., 2019). Although pine litter loading may be relatively low in canopy gaps herbaceous fuels, and seedling and sapling density may be higher. Herbaceous species and the litter of select hardwood species in longleaf pine ecosystems may be flammable, but the change of fuel composition in canopy gaps could lead to a decrease in the effectiveness of prescribed burns, as fire intensity and temperature may decrease (Jacqmain et al. 1999; Emery and Hart, 2020; Emery et al., 2020). Decreased fire intensity could result in stand composition changes as fire sensitive species may not be removed and could then outcompete fire resistant species (Platt et al., 1988; Mitchell et al., 2009; Loudermilk et al., 2011). However, Robertson et al., (2019) examined longleaf pine recruitment in canopy gaps and found that over a period of 13 years and 11 prescribed fires, on a 1–2-year rotation, there was increased recruitment in canopy gaps that did not burn in one or more fires. Being burned later allowed longleaf pine seedlings growing in canopy gaps more time to increase their root collar diameter and height growth before fire exposure, which increased survival (Boyer, 1963; Grace and Platt, 1995). O'Brien et al, (2008) also found that growing season fires may negatively impact longleaf pine seedling height, finding that seedlings in litter removal plots were significantly taller than those in control or increased litter plots. Thus, altered fuel conditions and fire behavior in cany gaps may facilitate seedling survival of longleaf pine. However, burning is still important for longleaf pine in canopy gaps as Robertson et al., (2019) found that longleaf pine recruitment was lower in canopy gaps that had not burned at all over a 13-year period.

Prior studies have quantified and analyzed gap-scale disturbance processes in Coastal Plain longleaf pine ecosystems (e.g., Brockway and Outcalt, 1998; McGuire et al., 2001, Palik et al., 1997; Gagnon et al., 2004) however, no studies have quantified canopy gaps in montane longleaf pine woodlands. Coastal Plain longleaf pine ecosystems are distinct from montane longleaf pine

systems by their stand structure, species composition, and topography (Beckett and Golden, 1982; Hammond et al., 2015; Klaus et al., 2020). Coastal Plain longleaf pine generally grow in savannas, with wider spacing between trees and lower basal area values. Montane longleaf pine usually occur in woodlands, where tree density is higher and basal area values are higher, though the canopy may still not be completely closed. Coastal Plain longleaf pine savannas are less light limited than longleaf pine woodlands, however neither are as light limited as forest structures. Coastal Plain longleaf pine stands are nearly monospecific, whereas the canopy of montane longleaf pine woodlands often contain small contributions from other tree taxa, such as oak and hickory (*Carya*) species (Edwards et al., 2013, Klaus et al., 2020). Coastal Plain topographic gradients are gentle as the landscape is relatively flat to gently rolling.

Montane topographic gradients are generally steep with higher relief and more complex terrain (Peet and Allard, 1993; Beckett and Golden, 1982). Knowledge of gap-scale disturbance patterns and processes in longleaf pine woodlands can be used to inform silvicultural systems. For example, entries could be based on natural patterns of canopy disturbance and stand development typical of montane longleaf pine woodlands. A natural disturbance-based silviculture approach may enhance ecosystem adaptation potential which is hypothesized to become increasingly important as perturbations and stresses are expected to increase in accord with global changes (Seidl et al., 2017; D'Amato and Palik, 2021).

The overarching goal of this study was to quantify gap-scale disturbance patterns and processes in a montane longleaf pine woodland. The specific objectives of this study were to: (1) examine canopy gap formation mechanisms and quantify gap characteristics, (2) document gap closure mechanisms and canopy recruitment patterns, (3) examine the impacts of canopy gaps on species composition and stand structure, and (4) quantify the frequency, size, and spatial distribution of canopy gaps through a montane longleaf pine woodland.

I hypothesized that canopy gaps will be formed mostly by snags when compared to snaps and uproots. I also hypothesized that canopy gaps would have shallower litter depths than reference plots, non-gap plots, and that they would have more seedlings and saplings than reference plots. I also hypothesized that within canopy gaps there would be more seedlings and saplings of both longleaf pine and other species than there were in non-canopy gap areas. I anticipated that more canopy gaps would be closed through lateral capture then by understory capture, and the smaller canopy gaps would be more likely to be closed by lateral capture then larger canopy gaps. I hypothesized that longleaf pine would be the most common species to capture canopy gaps, with the next most common being oak species. I also hypothesized that more of the study area would be in closed canopy conditions then in canopy gaps.

METHODS

Study Site

This study was conducted in the Reed Brake Research Natural Area on the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA. The forest is managed for the restoration and maintenance of longleaf pine on appropriate sites (USDA Forest Service, 2005). The study site occurs in the Fall Line Hills, which represents the boundary between the Appalachian Highland physiographic provinces and the Coastal Plain (Shankman and Hart, 2007). The study site supports species characteristic of both Coastal Plain and Appalachian Highland forest communities (Kleinman and Hart, 2017; Cox and Hart, 2015). The climate of the study area is classified as humid mesothermal, with hot summers and mild winters (Thornwaite, 1948). The average yearly precipitation for the area is 1,376 mm, with the highest average amount of precipitation in February (138 mm) and the lowest average monthly precipitation in October (86 mm). The average yearly temperature is 17.1 °C, with the lowest average monthly temperature occurring in January at 6.5 °C, and the highest average monthly temperature occurring in July at 26.9 °C (30-year normal, PRISM, 2020). Soils of the study site are mainly the Maubila-Smithdale complex (USDA NCRS, 2020). The Maubila soil series typically forms on hillslopes and is moderately well drained, with a 5 cm deep flaggy loam A horizon and clay Bt and C horizons. The Smithdale series also forms on hillslopes and is well drained with Ap and E horizons of sandy loam to 33 cm deep and a Bt1 horizon of sandy clay loam and a Bt2 horizon of sandy loam (USDA NRCS, 2020

Field Methods

      I sampled twenty 0.05-ha circular non-gap reference plots to quantify and compare species composition and stand structure measures with canopy gap plots. Reference plots were installed and inventoried in the same Forest Service- delineated compartment in the Reed Brake Research Natural Area to ensure similar biophysical site conditions. Reference plots were interspersed with canopy gap plots and care was taken to be sure no part of the reference plot was within or bordering a canopy gap.
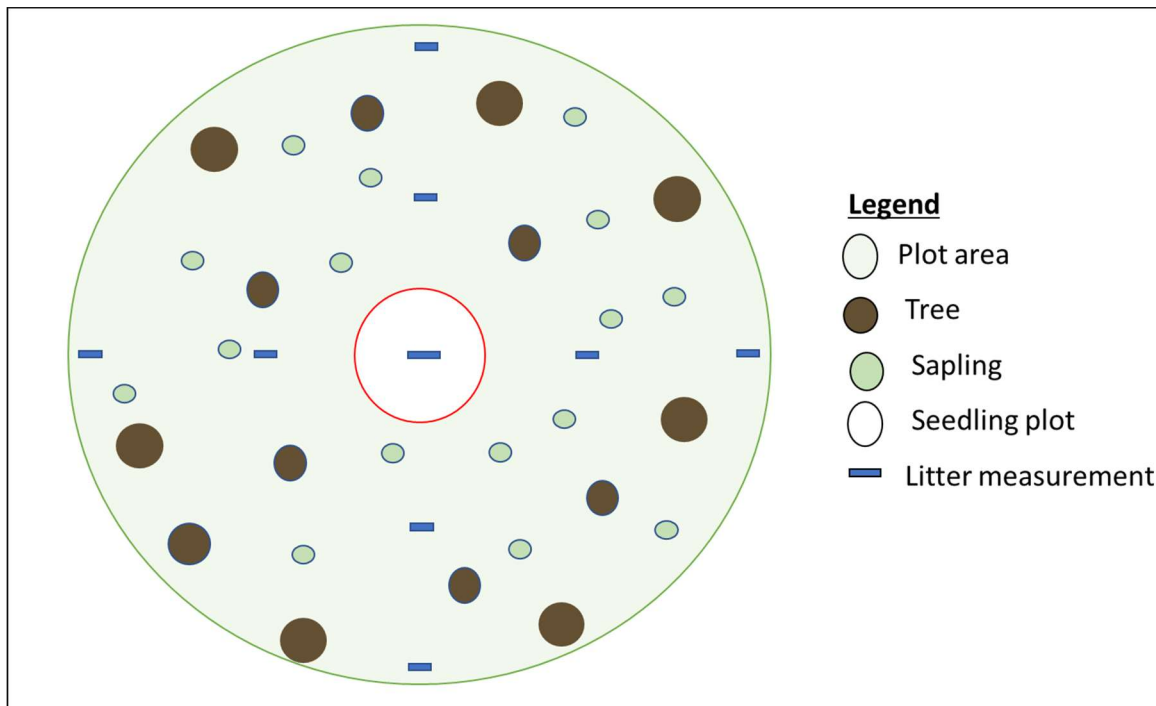
Figure 1: Example of a reference (non-gap) plot. Including trees, and saplings. Also indicates approximate locations of seedling plots and litter depth measurements.

      On each reference plot, all trees (live woody stems > 10 cm diameter at breast height (dbh, 1.37 m above the root collar)) were identified by species and dbh and crown class were recorded. Crown class categories (dominant, co-dominant, intermediate, overtopped) were determined by examining the direction and amount of light intercepted by the tree crown (Oliver

and Larson, 1996). Saplings (live woody stems ≥ 1 m height, ≤10 cm dbh) were tallied by

species. Seedlings (live woody stems < 1 m in height) were tallied by species in a 10 m² nested

plot located in the center of the 0.05 ha reference plot. Percent ground cover was estimated for

rocks, gravel, bare ground, coarse woody debris (CWD, deadwood with a diameter ≥ 10 cm),

fine woody debris (FWD, dead wood with a diameter < 10 cm), pine litter, hardwood litter,

grass, and forb cover to the nearest 1% (Anderson, 1986). Litter depth was recorded to the

nearest 0.01 cm at nine locations in the plot, one at plot center, and one at 6.31 m from plot

center and 12.62 m from plot center in each cardinal direction. For each plot the slope gradient,

slope aspect, microscale curvature (linear, concave, convex), and topographic position (ridge,

shoulder, backslope) were recorded.
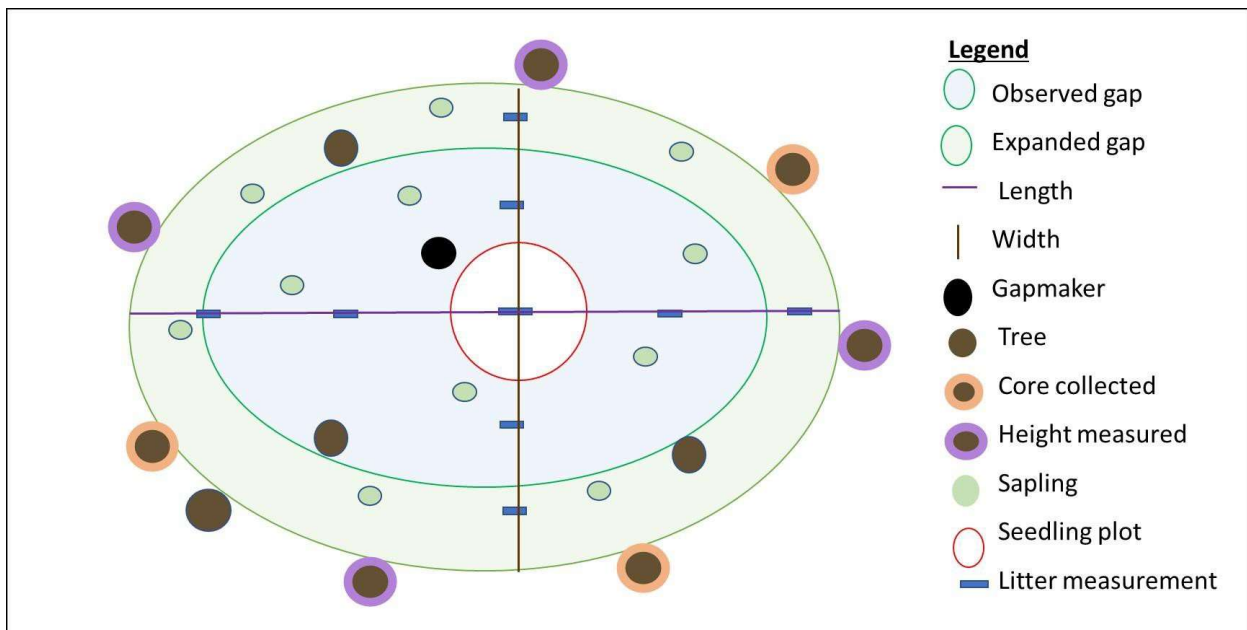
Figure 2: Example of a canopy gap plot. Including observed and expanded gaps, length and width measurements, trees, saplings, and seedling plot. Also indicates approximate locations of litter depth measurements.

Canopy gaps were also sampled in the Reed Brake Research Natural Area. In this region,

longleaf pine is dominant on upper slopes, and on south to west facing mid-slopes, while

lowerslopes are more often dominated by hardwood species (Beckett and Golden, 1982; Cox and

Hart, 2015). Therefore, canopy gaps were only sampled on upper slopes and at south to west facing mid-slope positions. To locate the 50 canopy gaps, I established and subsequently walked transects through longleaf pine dominated stands within the Reed Brake Research Natural Area. To be sampled, canopy gaps had to meet two criteria: a discernable void in the canopy caused by the removal of a canopy tree, and the presence of a gapmaker (i.e., the dead tree or trees that caused the canopy gap to form). Each canopy gap along the transects that met these criteria was sampled. Canopy gap voids that did not contain visible gapmakers were not sampled since we could not be certain if they were canopy gaps created by the death of canopy trees, or open portions of the woodland canopy unassociated with tree mortality. Likewise, if a canopy gap had more than one gapmaker of the same species but in different decay classes, the canopy void was not sampled. Gapmakers of the same species with different decay classes may have resulted from different disturbance events, and it would have been difficult to separate the effects of each discrete disturbance (Runkle, 1992).

For each canopy opening, I sampled the observed and expanded gap areas. The observed gap was defined as the area directly under the canopy void (i.e., unrestricted from above), and the expanded gap was defined as the entire area extending to the bases of the canopy gap perimeter trees (Runkle, 1982; Hart, 2016). Canopy gap length was measured as the greatest distance (i.e., longest axis) of the observed and expanded gaps. The width was the longest distance of the observed and expanded gaps perpendicular to the length. Observed and expanded gap length and width were measured using a hypsometer and transponder. The coordinates for each plot center were recorded using a Trimble Juno T/5 GPS unit. The microscale curvature,topographic position, slope aspect, and slope gradient were also measured for each plot with a clinometer and sighting compass.

The number of gap perimeter trees was recorded to determine how many canopy trees had the potential to close the canopy gap through lateral branch growth. The border of each canopy gap plot was defined by the perimeter trees, which I denoted by observing the canopy and determining which tree crowns constituted the boundaries of the gap. The dbh of all trees (woody stems > 10 cm dbh) within the canopy gap were recorded, including perimeter trees. Each tree was recorded as being a perimeter tree (making up the boundary of the expanded gap), or located in the observed (i.e., directly beneath the canopy void), or the expanded gap (i.e., in the gap, but not beneath the canopy void) depending on spatial location. The crown class and species were also recorded for each tree consistent with the methods used on the reference plots. The formation mechanism of each canopy gap was recorded as a snag (standing dead tree with mostly intact crown), snap (broken bole), or uproot (uplifted root network). In the case of multiple gapmakers, all formation mechanisms were recorded. The dbh (for snags), or the diameter 1.37 m from the root collar (for downed logs), species, and decay class of each gapmaker was recorded. The decay class was assigned based on Ulyshen et al. (2018) which was developed specifically for longleaf pine. This system includes seven decay classes for coarse downed woody debris, and five for standing dead wood. The decay classes were later used to facilitate the determination of canopy gap formation age. To calculate the average height of the canopy surrounding the canopy gap, I measured the height of four perimeter canopy trees, one in approximately each cardinal direction, using a hypsometer and transponder.

In each canopy gap, saplings were tallied by species and recorded as being either within the expanded or observed gap. Seedlings were tallied by species in a nested 10 m^2 circular plot placed at canopy gap center. Canopy gap center was defined as the intersection point of gap length and width axes. Percent ground cover were estimated for rocks, gravel, bare ground,

CWD, FWD, pine litter, hardwood litter, grass, and forb cover to the nearest 1% (Anderson, 1986). Litter depth measurements were taken in nine locations through the plot to the nearest 0.01 cm. One measurement was taken at plot center and four measurements were taken equidistant along the length and width from the center. Changes in forest composition were examined by recording the likely canopy gap closure mechanism: lateral capture or understory capture (Taylor and Lorimer, 2003). Lateral capture occurred when branches from the surrounding canopy gaps were likely to grow into the canopy gap and close the void. Understory capture occurs when stems growing in the canopy gap grow into the canopy and close the void. Understanding what species were likely to capture the gap increases our understanding of stand composition changes over time and provides information on gap-phase succession in these systems.

To help determine canopy gap age, an increment borer was used to remove a core from three gap perimeter trees, or trees growing within the canopy gap, that I deemed had likely experienced an increase in radial growth coincident with canopy gap formation. Trees were cored 50 cm above the ground. Once the core was collected it was placed in a paper straw and returned to the laboratory to air dry.

Analytical Methods

Once dried all tree cores were mounted with cells vertically aligned, and sanded, so the rings could clearly be seen (Stokes and Smiley, 1996). Annual rings on each sample were dated to the calendar year of formation by examining them under a stereo zoom macroscope. For samples that did not contain pith but showed substantial ring curvature, pith estimators were used (Villalba and Veblen, 1997). The raw-ring widths of the most recent 30 years (1990 to 2021) were then measured to the nearest 0.001 mm using a Velmex measuring stage (Velmex Incorporated 2009) interfaced with Measure J2X software (Voor Tech Consulting 2008). To

determine year of canopy gap formation, I calculated anomalous growth, which indicated a canopy release event. For a given year the median of the preceding ten years was calculated and compared to current year ring width. If the difference was over 25%, that year was determined to have exhibited a release event (anomalous increase in growth). If at least two of the three samples for a canopy gap showed a release in the same year ($\pm$ 1 year), that year was determined to be the canopy gap formation year. Line graphs of ring widths were made for each canopy gap to visually assess growth trends and elucidate dramatic increases in growth. Gapmaker decay class was also used when determining canopy gap formation age. If there were multiple release dates derived from the samples, the decay class allowed us to determine the most likely formation date from the likely gapmaker age.

To test my hypotheses about gapmakers, species composition, litter depths, and gap closure, I compared the characteristics of canopy gaps to each other and to reference plot characteristics. All data used were assessed for normality and homogeneity of variances and using those results the correct test was chosen. Kruskal-Wallis tests were used to determine if there was a significant difference in mean canopy gap size and gap formation mechanism (snap, snag, uproot), basal area lost and canopy gap closure mechanism (lateral or understory capture), canopy gap size and the number of gapmakers forming a canopy gap, the mean basal area lost between canopy gaps formed by single gapmakers or multiple gapmakers, and to compare the diameter of single-tree gapmakers gaps and the mean diameter of multi-tree gapmaker gaps. To examine the relationship between the basal area lost and the size of canopy gaps a Pearson correlation was used. The Pearson correlation was used for the basal area lost and expanded gap size as well as for the basal area lost and the observed gap size, with the independent variable being the expanded or observed gap size and the dependent variable being the basal area lost.

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Another Kruskal-Wallis test was used to find a significant difference in the mean between the observed and expanded gap area and the number of perimeter trees. A Mann-Whitney test was used to find a significant difference in litter depth between canopy gap plots and reference plots. All statistical tests were performed in the program SPSS Statistics (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 28.0, Armonk, NY: IBM Corp.).

To understand differences between canopy gap plots and reference (non-gap) plots, the density (number of stems), relative density (density of one species as a percent of the total), dominance (basal area, measured in m^2 per hectare), relative dominance (dominance of one species as a percent of the total), and relative importance values (combination of relative density and relative dominance) were calculated for all species. For the saplings and seedlings in each plot type the density and relative density were calculated. Shannon diversity was calculated for all trees, saplings, and seedlings.

To help quantify gap shape, length to width ratios (L:W) were calculated for both expanded canopy gaps and observed canopy gaps. Pearson correlations were then used to determine if there was a significant difference between the L:W ratios between expanded and observed canopy gaps. A Kruskal-Wallis test was used to determine if there was a difference between the L:W ratios of observed and expanded canopy gaps by canopy gap formation mechanism, or by canopy gap closure mechanism. A Kruskal-Wallis test was also used to determine if there was a difference between the L:W ratio and the number of gapmakers.Diameter to height (D:H) ratios were also calculated for the expanded and observed canopy gaps. The width of the canopy gaps was used as the diameter measurement and the average height from the four canopy trees measured at each gap was used for the height measurement. A Pearson correlation was used to determine if there was a difference between the

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D:H ratios for expanded canopy gaps and observed canopy gaps. A Kruskal-Wallis test was used to determine if there was a difference between the D:H ratios of observed and expanded canopy gaps by canopy gap closure mechanism.

LiDAR Methods

To determine the size, density, and spatial distribution of canopy gaps throughout the study site I used a canopy height model created from LiDAR data. LiDAR data are collected using laser pulses and their reflected return signals, to generate a point cloud (Beland et al., 2019). The discrete point cloud can then be used to create a digital terrain model (DTM) and a digital surface model (DSM). I used these returns to create a canopy height model (CHM) by subtracting the first returns (high points) and the ground returns (low points). Low elevation areas were removed (< 100 m), leaving the mid and upper slopes that are dominated by longleaf pine. The LiDAR data I used were collected in 2019 via the National Ecological Observatory Network (NEON) using an Optech Gemini LiDAR system and downloaded from the NEON database for use (NEON, 2022; NEON, 2021). The digital surface model and digital terrain model were mosaicked into a spatially uniformed grid, with a 1 m resolution, and were distributed in 1 km by 1 km tiles. NEON collects LiDAR during the growing season, allowing for detection of canopy gaps (NEON, 2022).NEON LiDAR data are grouped into 1 km by 1 km tiles, and 42 of the sampled canopy gaps occurred within a single tile. The remaining eight gaps occurred in an adjacent tile.

Therefore, the LiDAR data in the tile with 42 canopy gaps was used to examine LiDAR detected canopy gaps and quantify the gap fraction. To ensure there were no edge effects from anthropogenic features, a 10 m buffer was established along abandoned logging roads within the

study area. No canopy gap plots inventoried occurred within these buffer zones. The modified CHM with lower elevations and road buffer removed were analyzed in R, where the package ForestGapR was used in R (Silva et al., 2019). I used the package to set parameters to find different sized canopy gaps. The canopy gaps found using the parameters can then be converted into shapefiles, which can be used in ArcGIS. LiDAR only detected observed canopy gaps, as expanded canopy gaps are beneath the forest canopy, so the parameters I used were based on my observed gap characteristics. The parameters I used were 5 m in height (Koukoulas and Blackburn, 2004), and gaps with an area from 25–300 m^2 or less. The parameters used were similar to those found when sampling canopy gaps in Reed Brake Research Natural Area. The canopy gap fraction calculated from these results did not use larger gaps, so a gap fraction calculated using larger gaps would likely have different results.

Gapmaker and Canopy Gap Characteristics

Snags were the most common formation mechanism representing 38% of sampled canopy gaps. Snaps formed 32% of canopy gaps, while a combination of snags and snaps formed 24% of canopy gaps. Uproots comprised only 2% of canopy gaps, and a mix of snaps and uproots created 4% of canopy gaps (Figure 1). No significant difference was found between canopy gap sizes from different formation mechanisms for the expanded ($H(3) = 1.105$, $p = 0.776$) or observed gap ($H(3) = 0.900$, $p = 0.826$). I recorded 96 total gapmakers, and 95 of them were longleaf pine. The remaining gapmaker was a southern red oak (*Quercus falcata*), which was a snag. Mean expanded gap area was 187 m^2 ± 116.26 (SD) m^2 with a maximum of 479 m^2 and a minimum of 48 m^2. The mean observed gap area was 75 m^2 ± 62.36 m^2, with a maximum of 255 m^2, a minimum of 3 m^2.
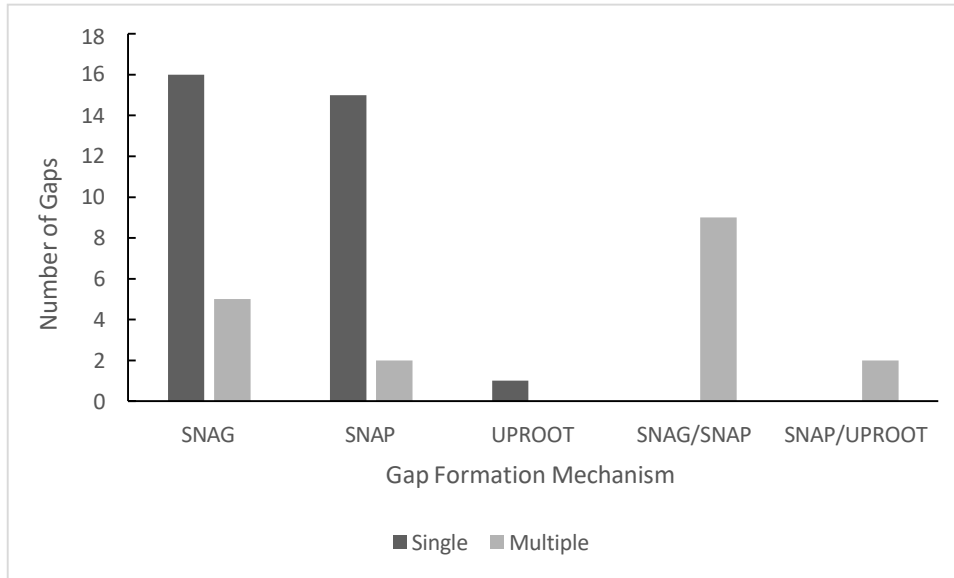
Figure 3: Canopy gap formation mechanisms in a montane longleaf pine woodland, by single gapmaker or multiple gapmaker gaps, and the number of canopy gaps formed by each mechanism. Canopy gaps can be formed by snags (standing dead trees), snaps (snapped boles), and uprooted stems. When canopy gaps with multiple gapmakers were formed by more than one mechanism both were recorded (snag/snap, snap/uproot).

The majority (64%) of canopy gaps were single tree events, 20% of canopy gaps were formed by two gapmakers, and 16% of documented canopy gaps were formed by three or more gapmakers (Figure 2). Canopy gaps formed by the death of nine canopy trees were found twice, representing the most gapmakers found in a single gap in this study. The mean basal area lost in canopy gaps formed by single gapmakers was 0.12 m^2/ha ± 0.04, with a minimum of 0.07 m^2/ha, and a maximum of 0.24 m^2/ha. For multiple gapmaker (2–9 tree gaps) canopy gaps the mean basal area lost was 0.34 m^2/ha ± 0.25, with a minimum of 0.09 m^2/ha, and a maximum of 0.87 m^2/ha. Multiple gapmaker canopy gaps lost a significantly higher basal area than single gapmaker canopy gaps (H(1) = 19.434, p < 0.001). The dbh of gapmakers in single gapmaker canopy gaps was significantly higher than the average dbh of gapmakers in multiple gapmaker canopy gaps (H(1) = 6.238, p < 0.013). No significant difference was found between the expanded gap area and the basal area lost (r = 0.179, p = 0.214), and there was also not a

relationship between the observed gap area and the basal area lost ($r = 0.089$, $p = 0.538$). No

significant difference was found between the number of gapmakers and the size of the expanded

gap ($H(6) = 5.081$, $p = 0.533$).

Table 1: Mean, minimum, maximum, and standard deviation ± are shown for single gapmaker expanded and observed gaps, as well as for multiple gapmaker expanded and observed gaps in Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

	Mean (m²)	Minimum (m²)	Maximum (m²)	SD (m²)
Single Gapmaker Expanded Area	188.56	49.68	478.79	120.25
Single Gapmaker Observed Area	77.95	16.32	254.89	64.87
Multiple Gapmaker Expanded Area	184.85	48.39	409.77	112.16
Multiple Gapmaker Observed Area	68.4	3.09	187.04	58.94

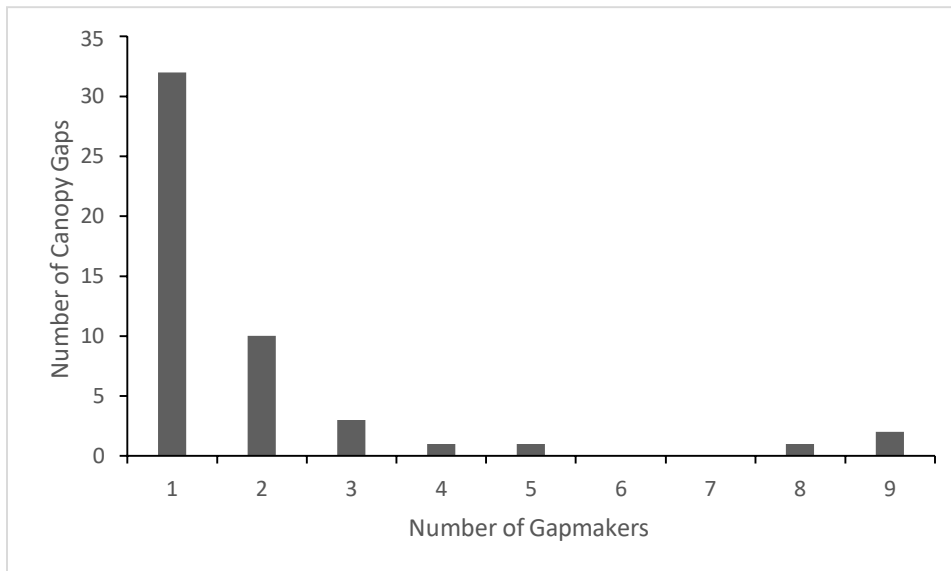**Figure 4:** The number of gapmakers in a single canopy gap ranged from a single gapmaker to nine gapmakers. Single gapmaker canopy gaps were the most common among gaps sampled. None of the sampled gaps contained six or seven gapmakers.

Out of the 50 canopy gaps studied, 41 were confidently dated to a formation year. Of the

remaining nine canopy gaps, seven were unable to be confidently date to a formation year as

there was not a common release year observed in two or more of the collected cores. The

formation years of the two other canopy gaps were estimated to be over 20 years old, but their

exact formation year could not be determined with confidence. The most common canopy gap

formation year was 2005, with 22% of sampled canopy gaps forming that year (Figure 3). The

next two most common canopy gap formation years were 2016 and 2011 each with 10% of

sampled canopy gaps forming in those years.
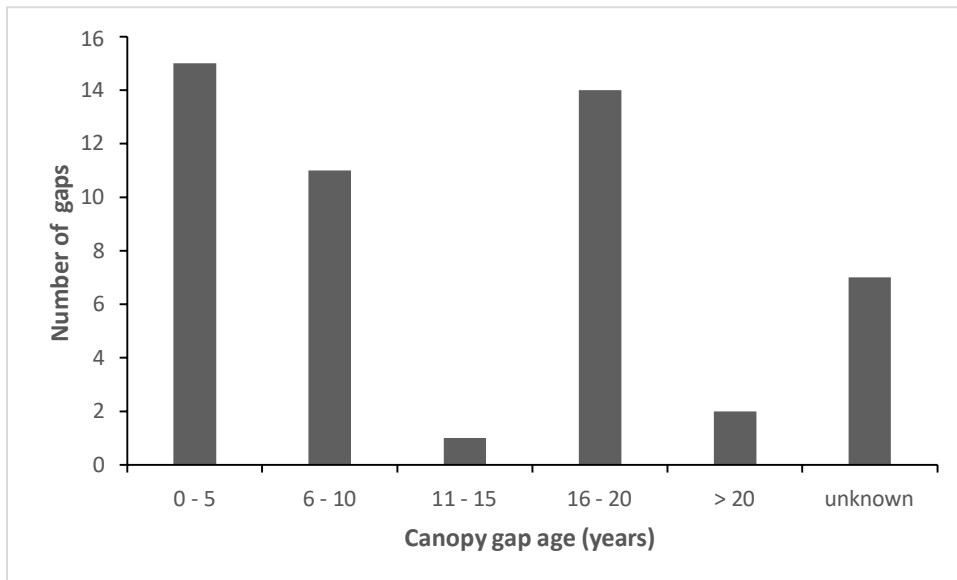
Figure 5: Canopy gap ages were sorted into in five-year bins based on tree core analysis
and gapmaker decay class. The unknown canopy gap ages resulted from a lack of a
common formation year between at least two of the cores taken for that specific canopy
gap.

A significant difference in litter depth was found between canopy gap plots and reference

plots ($p = < 0.001$). The average litter depth in canopy gap plots was 0.99 cm ± 0.76, with a

minimum of 0.00 cm, a maximum of 6.00 cm, while most plots had averages under 1.00 cm. The

average litter depth in reference plots was 1.54 cm ± 0.68, with a minimum of 0.10 cm, a

maximum of 4.10 cm and the litter depth average for all but one reference plot was over 1.00 cm.

Pine litter had the highest average cover in both canopy gap plots and reference plots with an

average cover of 63% and 80% respectively. The next highest average cover came from forb cover with 19% in canopy gap plots and 13% in reference plots. Grass was the third highest cover with 8% in canopy gap plots and 2% in reference plots.

The mean L:W for expanded canopy gaps was 1.59:1 ± 0.57:1, a minimum of 0.87:1, a maximum of 3.43:1. For the observed canopy gap the mean L:W ratio was 2:1 ± 2.54:1, with a minimum of 0.7:1, a maximum of 15.72:1. A significant difference was found between the L:W ratios for expanded and observed gaps (r = 0.355, p = 0.012). No significant difference was found between the L:W ratio and the gap formation mechanism for either the expanded gap (H(3) = 3.052, p = 0.384) or the observed gap (H(3) = 4.882, p = .181). No significant difference was found between the L:W ratios and the canopy gap closure mechanism for the expanded gap (H(3) = 1.136, p = 0.768) or the observed gap (H(3) = 2.639, p = 0.451). No significant difference was found between the L:W ratio and the number of gapmakers for the expanded gap (H(6) = 5.737, p = 0.453) or the observed gap (H(6) = 3.590, p = 0.732). Diameter height ratios (D:H) were also calculated for expanded and observed gaps. The mean D:H for expanded canopy gaps was 2.3:1 ± 0.13:1, with a minimum of 1.07:1, a maximum of 5.8:1. The mean D:H for observed canopy gaps was 5.01:1 ± 7.16:1, a minimum of 1.67:1, a maximum of 50:1. A significant difference was found between the D:H ratios for expanded and observed gaps (r = 0.326, p = 0.021). No significant difference was found between the closure mechanisms for the expanded gap D:H ratio (H(3) = 5.991, p = 0.112). A significant difference was found between the closure mechanisms for the observed gap D:H ratio (H(3) = 9.013, p = .0.29). Canopy gaps were determined to be primarily elliptical in shape based on L:W ratios.

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Forest Composition

Longleaf pine was the dominant tree species across canopy gap plots with 96% of the basal area. The next most dominant species, southern red oak, had a much lower density than longleaf pine, with just over 1% of the basal area. The third most dominant tree species was blackjack oak (*Quercus marilandica*) with less than 1% of the basal area. The three most dominant species were also the species with the highest importance values with 95%, 1%, and 1% respectively (Table 1). Canopy gap plots contained nine tree species with a Shannon Diversity of 0.39. Longleaf pine was also the dominant tree species in reference plots with a basal area of 98%. For the reference plots, loblolly pine was the second most dominant with just under 1% of the basal area, and the third most dominant tree species was post oak (*Quercus stellata*) with under 1%. These three species were also the three species with the highest importance values with 96%, 1%, and under 1% respectively (Table 2). Reference plots contained nine tree species as well, with a Shannon Diversity of 0.31. Hardwood species comprised only 3% of the basal area of the canopy gap plots and only 1% of reference plot basal area. Pine species made up 97% of the basal area in canopy gap plots and 99% of the basal area of reference plots. Oak species comprised 2% of basal area in canopy gap plots and under 1% of basal area in reference plots.

Table 2: Density, relative density, dominance, relative dominance, and relative importance (average of relative density and relative dominance) values for canopy gap and reference (non-canopy gap) plots in Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

Species	Gap Density/ ha	Gap Relative density	Gap Dominance (m²/ha)	Gap Relative Dominance	Gap Relative Importance	Reference Density/ ha	Reference Relative density	Reference Dominance (m²/ha)	Reference Relative Dominance	Reference Relative Importance
Pinus palustris	32.80	93.03	3.65	96.03	94.53	387.00	94.62	31.90	98.17	96.39
Quercus falcata	0.43	1.21	0.05	1.41	1.31	1.00	0.24	0.01	0.03	0.14
Quercus marilandica	0.53	1.52	0.03	0.73	1.12	3.00	0.73	0.09	0.29	0.51
Pinus taeda	0.43	1.21	0.03	0.74	0.98	5.00	1.22	0.21	0.63	0.93
Quercus stellata	0.43	1.21	0.02	0.42	0.81	4.00	0.98	0.12	0.37	0.67
Carya tomentosa	0.21	0.61	0.00	0.11	0.36	1.00	0.24	0.02	0.08	0.16
Nyssa sylvatica	0.21	0.61	0.00	0.05	0.33	-	-	-	-	-
Oxydendrum arboreum	0.11	0.30	0.01	0.27	0.29	2.00	0.49	0.02	0.06	0.27
Quercus alba	0.11	0.30	0.01	0.24	0.27	-	-	-	-	-
Quercus laevis	-	-	-	-	-	4.00	0.98	0.03	0.08	0.53
Pinus Virginiana	-	-	-	-	-	2.00	0.49	0.10	0.30	0.40
Total	35.25	100	3.80	100	100	409	100	32.50	100	100

Canopy gap plots contained 32 different species in the sapling size class with a Shannon Diversity of 1.50, and reference plots contained 16 different species with a Shannon Diversity of 1.38. The sapling species with the highest relative density in the canopy gap plots was farkleberry (*Vaccinium arboretum*) with 60%. Sweetgum (*Liquidambar styraciflua*) was the sapling species with the second highest relative density with 9% and sourwood (*Oxydendrum arboretum*) had the third highest relative density at 8% (Table 3). Sapling relative density for reference plots was similar, with farkleberry having the highest relative density at 58%. The sapling species with the second highest relative density was sourwood with 21%, and blackgum (*Nyssa sylvatica*) had the third highest relative density with 5% (Table 4). In canopy gap saplings, longleaf pine had the eighth highest relative density with 1%, and for reference plot saplings it had the fifth highest relative density with 4%.

Table 3: Density and relative density for saplings (≥ 1 m tall, ≤ 10 cm dbh) in canopy gap and reference (non-gap) plots in Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

Species	Gap Density/ha	Gap Relative Density	Reference Density/ha	Reference Relative Density
Vaccinium arboreum	119	59.81	823	58.00
Liquidambar styraciflua	18	8.84	62	4.37
Oxydendrum arboreum	16	8.30	305	21.49
Symplocos tinctoria	16	7.92	33	2.33
Rhus copallinum	14	6.90	18	1.27
Diospyros virginiana	5	2.69	-	-
Acer rubrum	2	1.24	40	2.82
Pinus palustris	2	1.02	50	3.52
Quercus marilandica	1	0.70	-	-
Ditrysinia fruticosa	1	0.54	-	-
Nyssa sylvatica	1	0.48	67	4.72
Vaccinium stamineum	1	0.27	3	0.21
Cornus florida	1	0.22	1	0.07
Quercus falcata	1	0.22	1	0.07
Carya tomentosa	0	0.16	-	-
Quercus laevis	0	0.16	8	0.56
Quercus alba	0	0.11	-	-
Quercus nigra	0	0.11	-	-
Quercus margaretta	0	0.11	-	-
Amelanchier arborea	0	0.05	-	-
Callicarpa americana	0	0.05	2	0.14
Magnolia virginiana	0	0.05	-	-
Quercus coccinea	0	0.05	-	-
Pinus taeda	-	-	4	0.28
Quercus hemisphaerica	-	-	1	0.07
Quercus stellata	-	-	1	0.07
Total	**198**	**100**	**1419**	**100**

A similar number of seedlings per hectare were found in canopy gap plots compared to reference plots, though canopy gap plots had more. Canopy gaps had a total of 20 seedling species with a Shannon Diversity of 1.26, and reference plots had a total of 17 seedling species with a Shannon Diversity of 1.37 (Table 5). For both canopy gap and reference plots farkleberry

was the most common seedling species, with 3183 seedlings per hectare in canopy gap plots and 2550 seedlings per hectare in reference plots. The second most common seedling species for both plot types was longleaf pine, with 1098 seedlings per hectare for canopy gap plots and 1095 seedlings per hectare in reference plots. The total number of seedlings per hectare in canopy gap plots was 5147, and reference plots had a total of 5120 seedlings per hectare.

Table 4: Density and relative density for seedlings in gap and reference (non-canopy gap) plots in Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA.

Species	Gap Density/ha	Gap Relative Density	Reference Density/ha	Reference Relative Density
Vaccinium arboreum	3183	61.84	2550	49.80
Pinus palustris	1098	21.33	1095	21.39
Pinus taeda	409	7.94	335	6.54
Symplocos tinctoria	104	2.03	30	0.59
Rhus copallinum	74	1.45	10	0.20
Diospyros virginiana	55	1.07	-	-
Liquidambar styraciflua	49	0.95	-	-
Quercus falcata	34	0.66	15	0.29
Nyssa sylvatica	21	0.41	10	0.20
Vaccinium stamineum	19	0.37	10	0.20
Quercus coccinea	17	0.33	5	0.10
Quercus stellata	17	0.33	-	-
Carya glabra	13	0.25	-	-
Oxydendrum arboreum	13	0.25	20	0.39
Quercus nigra	13	0.25	-	-
Acer rubrum	11	0.21	5	0.10
Quercus alba	9	0.17	-	-
Quercus marilandica	4	0.08	25	0.49
Carya tomentosa	2	0.04	5	0.10
Quercus laevis	2	0.04	20	0.39
Gaylussacia dumosa	-	-	965	18.85
Asimina triloba	-	-	10	0.20
Ilex opaca	-	-	10	0.20
Total	**5147**	**100**	**5120**	**100**

Gap Closure Mechanism

I estimated that 74% of canopy gaps would close through lateral crown expansion. I predicted that 22% of canopy gaps would close through understory capture, and 4% of canopy gaps were predicted to close by a combination of lateral and understory capture (Figure 4). A combination of closure methods were chosen for these gaps because part of the canopy void was projected to close through lateral expansion, but the gap was also projected to allow for the accession of an understory tree to the canopy layer. The two gaps with combination closure mechanisms were also the largest of the canopy gaps sampled. Out of the 13 canopy gaps predicted to close through understory capture, eight (62%) of them were predicted to be capture by longleaf pine. In the remaining two canopy gaps there was no clear species likely to capture the gap as there were many saplings and multiple species had the potential to capture the gap. For the remaining three canopy gaps, it was determined that one would be captured by sweetgum, one would be captured by loblolly pine, and one would be captured by post oak. I found there was no significant difference between the basal area lost and the predicted closure mechanism ($H(3) = 5.106$, $p = 0.164$). I also found no significant difference between the expanded gap area and closure mechanism ($H(3) = 3.218$, $p = 0.359$).
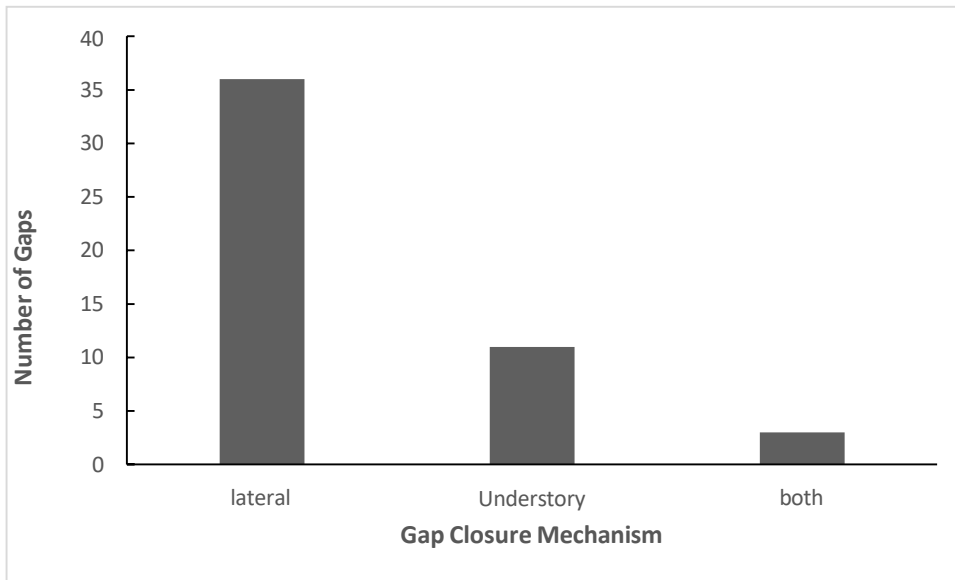
Figure 6: Canopy gaps can close through lateral capture, understory capture, or a mixture of both. Lateral capture was the more common closure mechanism for the canopy gaps sampled.

LiDAR Detected Canopy Gaps

The canopy gap area parameters (25 m^2 through 300 m^2) allowed for the capture of the small canopy gaps in the canopy height model. The 5 m height threshold captured only canopy gaps with low vegetation (under 5 m), which allowed for the exclusion of canopy openings with taller vegetation (like saplings or shorter trees) growing within them. Using the canopy height model, I detected 742 observed canopy gaps. The average observed canopy gap area was 76 m^2 ± 59.89, with a minimum of 25 m^2, and a maximum of 298 m^2. Using the output data from the CHM, I determined there was an average of 11 canopy gaps per hectare. An average area of 836 m^2 (8%) per hectare was in observed canopy gaps of this size.
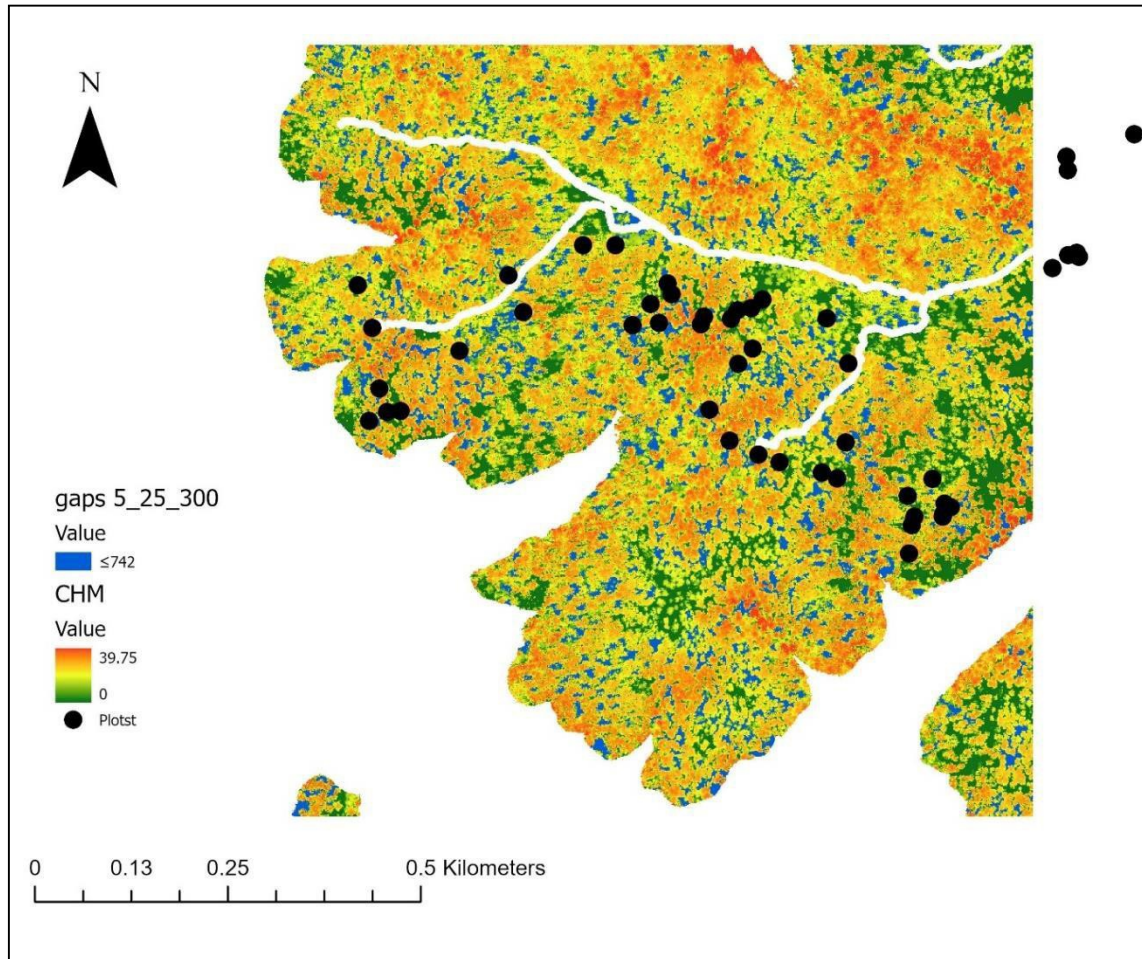
Figure 7a: A map of Reed Brake Research Natural Area, Oakmulgee Ranger District, Talladega National Forest, Alabama, USA. This is the full canopy height model, with canopy gaps in blue. Black dots represent canopy gap plots. The white area within the canopy height model is the 10 m buffer of the removed roads.
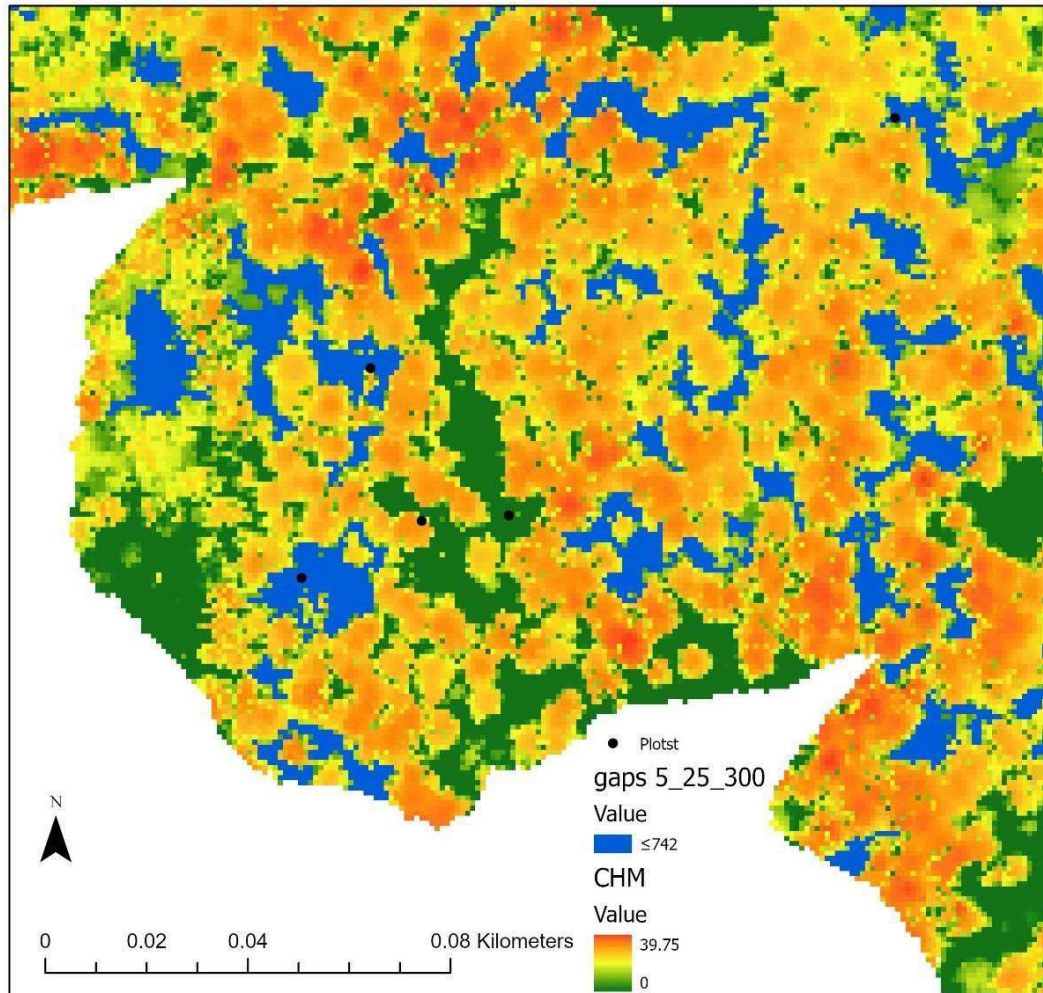
Figure 7b: A section of the canopy height model created in ArcGIS for a longleaf pine woodland in part of Reed Brake Research Natural Area, in the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA. Blue areas indicate canopy gaps found through GapForestR with an area between 25 m^2 and 300 m^2, and the black dots represent canopy gap plots. The color ramp represents the normalized height of LiDAR returns from 0 m (ground) to
39.75 m (tallest canopy tree).

DISCUSSION

Physical Canopy Gap Characteristics

The majority of canopy gaps in this longleaf pine woodland were formed by snags, with snapped stems being the second most common and uprooted stems being the least common. Compared to loblolly pine, longleaf pine is more susceptible to stem snapping and uprooting when exposed to strong winds (Rutledge et al., 2021; Johnsen et al., 2009). Multiple studies have examined snags in longleaf pine stands, which are often the result of lightning strikes, insects, or fire mortality, and can be important for wildlife and fire ignition (Ulyshen et al., 2018; Mitchell et al., 2009; Outcalt, 2008; Blanc and Walters, 2007; Landers and Boyer, 1999; Platt et al., 1988). I calculated snag density for my study area and found that there were 5 snags/ha (all snags were longleaf pine, except for a single southern red oak). Landers and Boyer (1999) found a snag density of 7 snags/ha for old growth longleaf pine stands, while Varner et al., (2003) found a snag density of 9–11 snags/ha for old growth longleaf pine stands. Although snag density in this montane, longleaf pine woodland was lower than that reported in other studies, those investigations were conducted in older (i.e. old growth) stands, and differences may be related to stage of stand development.

The high frequency of snag formed canopy gaps found in my study may have been caused by southern pine beetle (*Dendroctonus frontalis* Zimm.) activity. Out of 50 plots, 20 showed beetle activity on gapmakers, and 13 of those 20 canopy gaps were formed fully or partially by snags. Southern pine beetle activity was detected in Alabama counties containing the Oakmulgee Ranger District in 1992, 1995, 1997–2002, 2004–2007, and 2016–2018, (only

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reports from 1990 to 2018 were examined, reports after 2018 were not yet available) (U.S. Forest Service, 2022). Canopy gaps created by gapmakers with evidence of beetle activity formed in 2004, 2005, 2010, 2011, 2012, 2014, 2016, 2018, and 2019. Reports of southern pine beetle activity in counties containing the Oakmulgee Ranger District may not mean there was damage in the National Forest, or in Reed Brake Research Natural Area, only that beetle activity was nearby. Longleaf pine has been found to have a lower mortality rate when exposed to southern pine beetle relative to loblolly pine (Martinson et al., 2007). Originally it was hypothesized this enhanced resistance was a function of increased resin flow in longleaf pine. However, subsequent research showed resin flow was not significantly different between longleaf pine, loblolly pine, and shortleaf pine and suggested stand management (i.e., frequent, low intensity fires and lower stocking with a relatively open canopy) may explain reduced mortality by southern pine beetle (Knebel and Wentworth, 2007; Martinson et al., 2007).

Canopy gaps with multiple gapmakers were formed from a significantly higher loss of overstory basal area than canopy gaps with a single gapmaker. Richards and Hart (2011) also found that canopy gaps with multiple gapmakers lost a higher basal area, although that study was focused on oak systems. Weber et al., (2014), which was focused on oak-pine systems, found the same result. Although the basal area lost in canopy gaps differed by number of gapmakers there was no significant difference between basal area lost and canopy gap area. Weber et al., (2014) did find a significant difference between basal area lost and expanded and observed gap size, which could be the result of the oak-pine, closed canopy system compared to the more open longleaf pine woodland structure studied here. Canopy gaps formed from multiple gapmakers had a marginally smaller mean observed and expanded area than gaps formed from a single gapmaker. Although the difference was not significant, it was still unexpected. A possible

explanation for this result is that diameter of gapmakers in single gapmaker formed canopy gaps was significantly greater than the mean diameter of gapmakers in multiple gapmaker formed canopy gaps. Tree diameter is related to crown volume and thus, some of the single tree formed gaps were caused by mortality of large trees that represented a relatively large portion of the canopy. In contrast, gapmakers in some multi-tree gaps were relatively small and therefore, constituted smaller portion of the forest canopy.

Canopy gap ages ranged from over 20 years to 1 year. Out of 50 canopy gaps sampled, seven canopy gaps had unknown ages, as there was no agreement on the formation year between multiple cores taken for those canopy gaps. It is likely that canopy gaps in this system remain open for ca. 20–25 years as no canopy gaps were determined to be older. Canopy openings without gapmakers were found while walking transects but were not sampled because they did not meet my established canopy gap criteria. This could be an indication of old canopy gaps where the gapmaker had decomposed completely, but more likely indicates intermediate-severity disturbance. The average age of canopy gaps was 10 years (formed in 2011), and the most common age was 16 years (formed in 2005). If canopy gaps are being formed and closed at the same rate gap fraction is in equilibrium (Himes and Rentch, 2013). If this is the case there should be a greater number of young canopy gaps, and fewer old canopy gaps (Hart, 2016). Based on the canopy gap age distribution found in my sampled gaps the study site gap fraction is not in equilibrium. I suspect my inability to confidently assign a formation year to seven canopy gaps was the result of the trees selected for sampling. In these seven cases, the trees selected did not show a significant response to canopy gap formation, and as a result the formation year could not be confidently identified.

My hypothesis that reference plots would contain greater litter depth, as they would have a higher overstory density leading to more litter production, was correct. Overstory density in longleaf pine stands has been shown to be a strong predictor of pine needle litter (Dell et al., 2017). A lower cover of pine litter and higher cover of forbs and grasses in canopy gaps compared to reference plots is likely a result of decreased pine overstory, and increased light for understory plants in canopy gaps (McGuire et al., 2001). This would also likely influence fire behavior, causing reference plots, with their higher fuel loads to have different fire effects than canopy gap plots, which contain lower fuel loads (Mitchell et al., 2009). Increased litter depths will likely lead to higher mortality for fire-sensitive species as increased fuel will lead to hotter fires which will cause stem cambium to reach 60° C, the temperature whereby mortality occurs (Varner et al., 2005; Bigelow and Whelan, 2019). Consequently, competition reduction from prescribed fire may explain the increased density of longleaf pine saplings in reference plots compared to canopy gap plots.

L:W ratios can be used to understand variation in canopy gap shapes and microenvironments which could be influenced by canopy gap formation mechanisms (Hart and Grissino-Mayer, 2008). However, as there was no significant difference between L:W and formation mechanism, the canopy gap formation mechanisms in the study area did not significantly influence L:W ratios. Canopy closure mechanisms could also be influenced by L:W ratios, as gaps with different L:W ratios can have different light entrance levels (De Lima et al., 2013). This could influence the closure mechanism as canopy gaps with a lower width could be more likely to close through lateral capture. However, there was no significant relationship between L:W ratios and canopy gap closure mechanisms. The number of gapmakers forming a gap also did not have a significant impact on L:W ratios indicating gapmaker numbers did not

have an impact on gap shape. The L:W ratio was found to be significant for expanded and observed canopy gap areas, indicating that gap area had an impact on L:W. Holeksa and Cybulski (2001) found gap shape (which relied on canopy gap L:W ratios) was significantly related to gap area in a subalpine spruce forest. They found that larger canopy gaps tended to have a more elongated shape. In contrast, Richards and Hart, (2011) and Weber et al., (2014), did not find a significant difference between L:W ratios in expanded and observed canopy gaps, though that may have been a result of the closed canopy forest structure of their study areas. De Lima et al. (2013) found no evidence of L:W ratios being linked to gap size in seasonal and rainforest stands in Brazil.

D:H ratios were also calculated for more information on canopy gap microenvironments as D:H can influence the amount of light entering a canopy gap (Canham et al., 1990). No significant relationship was found for the canopy closure mechanism for D:H ratio and expanded canopy gap area. However, there was a significant relationship between the canopy closure mechanism and the D:H ratio and observed canopy area. This indicates that the D:H ratio had an impact on the canopy gap closure mechanisms in observed, but not expanded canopy gaps. For example, a greater height could result in canopy gaps more prone to lateral closure as understory stems would have to grow taller to reach the canopy. A significant difference was found between the D:H ratios of expanded and observed canopy gaps, which is intuitive as the diameters of these would be different. Similarly, Weber et al., (2014) found a significant difference between the D:H ratios of expanded and observed canopy gaps in oak-pine stands.

Gap Composition and Structure

Tree density was higher in reference plots than in canopy gap plots. This was likely a result of most recorded trees in canopy gap plots being perimeter trees, with few trees growing in the observed or expanded gaps. Seedling density in canopy gap plots and reference plots was similar. However, since there was a higher number of saplings in reference plots compared to canopy gap plots, but both

had similar seedling numbers, seedlings in reference plots may be more likely to recruit to the sapling stage. This could be a result of decreased competition as fires through non-gap forest, with more even fuel beds, may result in increased hardwood death (Platt et al., 1988; Mitchell et al., 2009).

Species diversity was higher in canopy gap plots than in reference plots for both seedlings and saplings. I found there were only marginally more longleaf pine seedlings per hectare in canopy gap plots compared to reference plots. In contrast there were more longleaf pine saplings found in reference plots than in canopy gap plots. Canopy gap plots containing a higher number of species is likely a result of more sunlight and growing space being available in these microenvironments (Brockway and Outcalt, 1998; Palik et al., 1997; McGuire et al., 2001; Runkle, 1982). Hardwood saplings were more abundant than longleaf pine or other pine species saplings in both canopy gap and non-gap plots. Pecot et al. (2007) found that advance hardwood regeneration in longleaf pine canopy gaps had the advantage of established root systems that allow for faster vertical growth. However, with recurring surface fires, hardwoods should disproportionately be maintained in the seedling and sapling size categories as they will continually be top killed (Boyer, 1979; Bigelow and Whelan, 2019). The success of top killing can vary depending, in part, on species and stem size (which can impact bark thickness and bud height) and fire behavior (which can influence the temperatures to which stems are exposed).

Canopy Gap Closure

The majority of canopy gaps were projected to close through lateral crown extension. Longleaf pine was the species most likely to capture canopy gaps through lateral extension, or understory growth. Though there was a high species diversity of saplings in each canopy gap relative to reference plots, only four gaps in total were predicted to be captured by a species other than longleaf pine. The canopy gap predicted to be capture by sweetgum had a low, wet area within it, where fire likely was not able to burn evenly and top kill all the hardwoods. Loblolly pine was predicted to capture one of

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the canopy gaps, and in that canopy gap two of the perimeter trees were also loblolly pines. The remaining two canopy gaps were predicted to be captured by oaks, and in these canopy gaps, two of the perimeter trees were oak species. This indicates that, under the current disturbance regime, longleaf pine will likely continue to be the dominant species in the study area, even though there are other species represented in the canopy gaps. Recurring low intensity fires disproportionality kill shoots of fire-sensitive species which benefits fire-tolerant longleaf pine by reducing competition (Jin et al., 2019; Outcalt and Brockway, 2010; Platt et al., 1988).

I hypothesized that smaller canopy gaps would be more likely to close through lateral crown expansion and larger canopy gaps would be more likely to close by understory capture. Smaller canopy gaps could have been more likely to be captured by lateral expansion as there would be a smaller canopy void to fill. Larger canopy gaps could have been more likely to be captured by understory growth as they may take longer to close, resulting in more time for understory stems to grow into the canopy (Pedersen and Howard, 2004). However, the canopy gap closure mechanism was not impacted by gap area or basal area lost and both the largest and smallest canopy gaps documented were predicted to close through understory capture. This indicates that the canopy gaps sampled did not have a large enough area, or did not lose enough basal area, to influence the canopy closure mechanism. Lertzman (1992) found the closure mechanism is reliant on the presence of advance regeneration in the canopy gap, determining that the species with a greater abundance of saplings in the understory was most likely to fill the canopy void. I also predicted that, no matter the size, canopy gaps with a greater number of perimeter trees would be more likely to close through lateral extension, as more canopy trees would be able to extend branches into the gap. However, there was no significant difference found between the number of perimeter trees and the canopy gap closure mechanism. This indicates that having more perimeter trees or having a greater gap area did not predispose a canopy gap to close through lateral extension or understory capture. The number of gap perimeter trees is likely influenced by stand

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density and the crown area of the gapmaker. Stands with a higher tree density would result in more gap perimeter trees, and older stands with lower tree densities would likely have fewer gap perimeter trees.

LiDAR Detected Gaps

I used LiDAR data to determine the total area of the CHM and the total area of the LiDAR detected observed gaps. Using LiDAR to calculate gap fraction allowed for the removal of bias from sampling only the gaps found along a transect (Runkle, 1992). It also allowed for all gaps within the set parameters in the study area to be included, which may have led to a more accurate gap fraction calculation. The canopy gap areas for the sampled gaps and the LiDAR detected gaps were similar, with the average area of LiDAR gaps being 76 m^2 and the average area of the observed canopy gaps being 75 m^2 indicating that LiDAR canopy gaps were properly detected. Larger canopy gaps (300– 3250 m^2, average 144 m^2) were also detected with LiDAR, and large openings without gapmakers were observed during field data collection. Multiple studies have proposed thresholds to differentiate between gap-scale and intermediate-severity disturbances which have ranged from 500 m^2 to 1000 m^2 or more (Hart and Kleinman, 2018). Hart and Kleinman (2018) recommend that the best way to differentiate between gap-scale and intermediate-severity disturbances is to use the D:H, starting with a D:H value of 2.0. The large openings indicate the presence of intermediate-severity disturbances. LiDAR detected gaps appear relatively elliptical, which agreed with the L:W ratios calculated for the sampled canopy gaps indicating sampled gaps were elliptical.

Canopy gaps were clustered together in some parts of the study area, while they were dispersed in other areas, which could be an indication of intermediate-severity disturbances. Many of the LiDAR detected canopy gaps were also connected, causing LiDAR to label an open area a single canopy gap, while from the ground I may have determined the same area to be broken up into multiple gaps. Although the average area of LiDAR and observed canopy gaps was similar this could have still resulted in a low count of canopy gaps in the LiDAR data, however the total canopy gap area was

likely not affected. Longleaf pine canopy gap fraction has not been calculated so I compared my results to other forest types. Kneeshaw and Bergeron (1998) found canopy gap fraction in a 234-yr-old fir dominated forest to be ca. 40%, which was similar to canopy gap fractions found in other coniferous forests which had an average of 30– 40%. Hart and Grissino-Mayer (2008) used transects to quantify gap fraction in a closed canopy oak system and found 6% of their area to be in observed canopy gaps with a total of 600 m^2 in observed canopy gaps. Although the stand structure is different (closed canopy oak stands vs pine woodlands), this was similar to the fraction of gaps found in our study at 8%. In an oak woodland in Kansas, Cory et al., (2019) found a canopy gap frequency of 4.1 gaps per 1 km linear transect for expanded gaps (estimated to be a gap fraction of ca 4% based on average gap size and average number of gaps per transect). Koukoulas and Blackburn, (2004) used LiDAR data to quantify canopy gaps in an oak-beech forest and found that most gaps were small, approximately 250 m^2, similar to the parameters I used. They found that there were approximately 10 canopy gaps per ha, which was similar to my result of 11 canopy gaps per ha. Although the stand structure was different, the results indicate that smaller canopy gaps are relatively common.

CONCLUSION

The results of this study provide information on canopy gap characteristics and recruitment in a montane longleaf pine woodland. The predominant gapmaker species in sampled gaps was longleaf pine and most canopy gaps were also predicted to be closed by longleaf pine through lateral crown expansion. Similarly, canopy gaps predicted to close through understory capture were most likely to be captured by midstory stems, which could indicate that, in canopy gaps of the sampled size, understory recruitment to the canopy is low. As all canopy gaps sampled had observed areas < 300 m^2 this could indicate that gaps of that size were generally too small for much canopy recruitment to occur. Although there was little canopy recruitment, longleaf pine is still likely to remain the dominant species under the current disturbance regime, as there was also little hardwood canopy recruitment.

Although many of the gaps sampled in this study were formed from the death of a single tree, the results of the LiDAR data indicate that there are larger gaps, which likely resulted from intermediate-severity disturbances (Hart and Kleinman, 2018). To increase longleaf pine recruitment in this stand, larger canopy gaps than those sampled here (> 300 m^2), could be created. This could be achieved by mimicking intermediate disturbances, as the resulting larger canopy gaps could have more growing space for canopy recruitment. The area of the observed canopy gaps sampled ranged from 3–255 m^2, but other studies on longleaf pine canopy gaps have suggested larger gaps with areas over 1200 m^2 or an area of 1400 m^2, and diameters ≥ 40 m, to increase recruitment (Gagnon et al., 2004; Palik et al., 1997; Brockway and Outcalt, 1998).

Larger gaps and continued prescribed fire would allow for increased longleaf pine recruitment and continued hardwood control likely leading to increased longleaf pine canopy recruitment.

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