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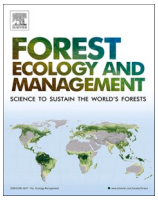

Canopy gaps increase species-dependent edge tree diameter growth in a mature southern Appalachian mixed hardwood forest

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ABSTRACT

Understanding the response of tree species to disturbance is critical as climatic variability is projected to shift disturbance regimes, species distribution, and carbon allocation in the eastern US. Altered resource availability and microclimatic drivers bordering canopy gap edges may enhance tree growth. Our objective was to evaluate how this gap edge effect varies across dominant species groups in a southern Appalachian mixed hardwood forest. We assessed the effect of silvicultural canopy gaps, 0.15–1.09 ha in area, on overstory tree diameter growth four years after gap harvest. Increment cores were collected from 288 mature trees across five species groups. Annual ring width was measured across an eight-year timespan to determine how percent change in average annual growth post-harvest varied with distance from gap edge compared to unmanaged control areas. We found that edge tree growth response was significantly greater than matrix and control tree response, with an average percent change in ring width of 48.1 ± 6.0 % at gap edge and 8.9 ± 4.1 % in the forest matrix. There were no significant effects from gap size or azimuth relative to gap center. Red maple had a higher growth response than oak groups, with hickory and tulip-poplar falling in between. These results highlight the importance of species composition in stand-level growth response to disturbance as diffuse-porous species like red maple and tulip-poplar use more water than ring-porous species like oaks.

1. Introduction

Disturbance is an ever-present element of temperate forest ecosystems. Across old-growth mesic forests in the Eastern United States, single-treefall canopy gaps encompass over 9.5 % of land area, with gap formation and closure estimated at approximately 1 % per year (Runkle, 1982). Intermediate- to high-intensity wind events constitute a variable yet highly influential disturbance factor in the region (Dale et al., 2001; Peterson, 2000). For example, windthrow following Hurricane Opal in 1995 created gaps that ranged in size from 0.2 to 1.1 ha in the Bent Creek Experimental Forest watershed in western North Carolina (Greenberg and McNab, 1998). The resulting structural heterogeneity introduced by disturbance events such as these plays an important role in carbon sequestration by increasing net primary productivity and maintaining rates of net ecosystem productivity as forests age (Curtis and Gough, 2018). The impacts of mid- to high-severity canopy disturbance on growth will become increasingly relevant as droughts and storms are projected to increase in frequency and severity over time (USGCRP, 2017).

Canopy gap creation alters the microclimate, both at gap edge and in the surrounding forest. Increases in available light (Canham et al., 1990) and soil temperature can occur up to 50 m past gap edge (Matlack, 1993). The effects of canopy gaps are less clear in the case of soil moisture, which has been observed to increase in the gap relative to the forest interior immediately post-harvest (Ritter et al., 2005) but may decrease at edge due to increased evapotranspiration. Canopy gaps also play a notable role as “nutrient hotspots”, increasing the bioavailability of nitrogen, which in conjunction with increased light and soil temperature correlates to increased microbial abundance at gap edge (Mladenoff, 1987; Scharenbroch and Bockheim, 2007).

The extent of these effects is influenced by the size and aspect of the gap. Trees in the northern hemisphere generally receive the highest levels of light along the northern gap edge, depending on gap size, aspect, and slope (Canham et al., 1990; Stan and Daniels, 2014), and are subject to corresponding changes in temperature, moisture, and vapor pressure deficit (Matlack, 1993). As gap size increases, so does the extent of light penetration into the surrounding forest, which in turn increases soil temperature (Abd Latif and Blackburn, 2010; Gray et al., 2012). In

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naturally formed treefall gaps, increased gap size has been reported to have a significant positive effect on solar radiation, soil moisture, and soil temperature (Abd Latif and Blackburn, 2010), as well as throughfall ammonium concentration, with decreases on microbial activity (Schliemann and Bockheim, 2014). Generally, these smaller gaps are considered the focus for gap studies, with 100 m^2 put forth as a proposed maximum threshold (Schliemann and Bockheim, 2011; Yamamoto, 1992). However, larger gaps over 0.01 ha formed by storm events (McNab et al., 2004; Mou and Warrillow, 2000) or silvicultural group selection (Shure et al., 2006) have been shown to result in canopy light and overstory/understory structures markedly different from smaller gaps (Hanson and Lorimer, 2007; Lhotka et al., 2018). In particular, large storm events such as hurricanes may shift maximum gap sizes substantially larger than the pre-hurricane levels, with examples reaching 18–34 times larger than pre-hurricane gap size (Xi et al., 2008) and up to 3.9 ha in size (McNab et al., 2004), significantly altering the forest structure across the landscape (Elliott et al., 2002). Whether microclimatic differences based on gap size persist at this scale demands further study.

Due to these changes in microclimate, gap edge tree diameter growth can be upwards of 24 % higher than forest matrix trees in temperate systems (Morreale et al., 2021; Pedersen and Howard, 2004). This effect is dependent on tree characteristics including size and species. Shorter overstory trees may respond more to canopy gaps than larger trees (Pedersen and Howard, 2004) due to their suppressed canopy position. In addition, species exhibit differences in growth rate in response to canopy gap disturbance (Trimble and Tryon, 1966), likely due to differing ranges of tolerance for environmental variables such as light and moisture (Grover et al., 2023; Pedersen and Howard, 2004). Differences in wood anatomy, which influence carbon allocation in response to changes in microclimate, may play an important role. Ring-porous species exhibit anisohydric stomatal behavior, resulting in relative insensitivity of growth rate in response to changes in soil moisture and light, whereas diffuse-porous species, being isohydric, are far more sensitive to such changes (Novick et al., 2022; Oren and Pataki, 2001).

Exploring the effects of disturbance across species groups is increasingly important as mesic species continue to become more dominant across the eastern US (Fei et al., 2011) and drought occurrences in the region increase in both frequency and severity (Vose and Elliott, 2016). Complex regeneration failures have led to declines in oak (*Quercus*) density across the eastern US (Nowacki and Abrams, 2008), leading to increased abundance of mesic species such as tulip-poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*) (Fei et al., 2011). Contemporary efforts to promote oak regeneration include harvesting large canopy gaps to increase light to the understory, promoting oak growth and regeneration (Lhotka and Stringer, 2013). The impacts of these gaps and gap sizes on edge tree growth may have important implications for stand-scale carbon sequestration and distribution. In previous research from the southern Appalachian region, both ring-porous species (oaks and hickory (*Carya*)) and diffuse-porous species (red maple and tulip-poplar) were sensitive to drought events, with ring-porous species showing higher drought sensitivity (Grover et al., 2023). This pattern contrasted from similar species groups in a nearby site (Elliott et al., 2015), likely reflective of the size and age differences of the individuals between the sites. Further investigation is needed to determine how this variation in species, size, and position translates to disturbance response in the southern Appalachians.

The objective of this study was to quantify the effect of silvicultural canopy gaps (0.1–1.3 ha) on overstory tree growth in a southern Appalachian mixed hardwood forest to quantify the response of species-specific diameter growth of trees at gap edge. We hypothesized that diameter growth in response to gap harvests would increase for gap edge trees, and that this response would vary by species, with oaks being less responsive than mesic species. Finally, we predicted that trees would exhibit larger responses in larger gaps and the northern gap edge would have the largest response due to increased light.

2. Methods

2.1. Site description

The study was carried out in the Southern Appalachian Femelschlag Experiment, a large-scale field experiment located in the Pisgah National Forest, Buncombe County, NC, USA (35°28′N, 82°40′W, Fig. 1). The site is within the Blue Ridge Physiographic Province of the Southern Appalachian Mountains, and ranges between 700 and 1070 m in elevation. The soils are shallow to very deep, well drained, moderately to extremely acidic Inceptisols and Ultisols, ranging in texture from fine sandy loam to gravelly loam with steep 10–90 % slopes (Web Soil Survey, 2023). The geology is predominantly felsic to mafic high-grade metamorphic biotite and granitic gneisses (Hadley and Nelson, 1971). The site is characterized by cool winters and longer, warm summers with average temperatures ranging between 3.8 and 8.8° C in January and 16.8 and 28.5° C in July (Fig. 2a). Annual precipitation averages ca 1143 mm and is relatively consistent per month (Candler and Station, 2020 Climate Normals; NCEI, NOAA). The area is characterized as a second-growth upland hardwood forest dominated (in rank order of basal area) by tulip-poplar, chestnut oak (*Quercus montana*), northern red oak (*Quercus rubra*), red maple, white oak (*Quercus alba*), and hickory (*Carya tomentosa, C. ovalis, C. glabra, C. cordiformis*) with mean ages ranging 95–150 years old (Grover et al., 2023).

The 60-ha study area was divided into harvest units. A single harvest treatment (large or small gaps) was applied to each unit and had approximately the same harvested area per unit, ~ 30 %. Experimental canopy gaps were harvested in January–April 2019. The management goals of the harvest were to increase oak-hickory regeneration and stand structural complexity. Merchantable trees within the proposed gaps were hand-felled and removed via skidders and forwarders. Non-merchantable trees were cut and remained on site as slash. During the growing season following harvest, June–August 2019, a midstory removal treatment was conducted across the whole harvest unit, under the remaining overstory canopy (Fig. 1). Non-mast producing trees with stems under 20 cm diameter at breast height (DBH) were targeted using a hack-and-squirt herbicide treatment (excluding oak, hickory, holly (*Ilex*) and dogwood (*Cornus*) species). The midstory removal treatment terminated approximately 356 stems ha^{-1} and 1.45 m^2 of basal area ha^{-1} across the harvest unit. Three areas adjacent to and located outside of the harvest unit that did not receive any silvicultural treatments were used as control units (Fig. 1).

2.2. Study design and data measurements

Two gaps within each harvest unit were randomly selected for intensive measurements. Selected large gaps ranged 0.78–1.09 ha in size and small gaps ranged 0.15–0.25 ha. Likewise, two plots per control unit were randomly selected for intensive measurements. In total, eighteen plots were included in this study: six large gaps, six small gaps, and six controls (Fig. 1). Gap boundaries, i.e., gap edges, were defined using the stems of trees > 20 cm DBH surrounding the canopy opening. Trees with stems near the gap boundaries and with crowns that received extra direct light from the canopy gap were defined as edge trees. The forest matrix was defined as the area surrounding the gaps and located within 25 m of each gap edge. The study design included factors of treatment (three levels), zone (two levels), and species (five levels). Treatment levels included large gap, small gap, and control. Within gap treatments, zone was defined by position relative to the canopy gap in two levels, gap edge trees (hereafter “edge”) and forest matrix trees (hereafter “matrix”). Matrix trees were located within 25 m of gap edge and received no additional direct light to their crown from the gap. Five species groups (hereafter “species”) were studied: red maple, hickory (*Carya* spp.), tulip-poplar, red oak group (*Q. coccinea, Q. rubra, Q. velutina*), and white oak group (*Q. alba, Q. montana*).

A tree inventory was conducted in October 2021, where for all

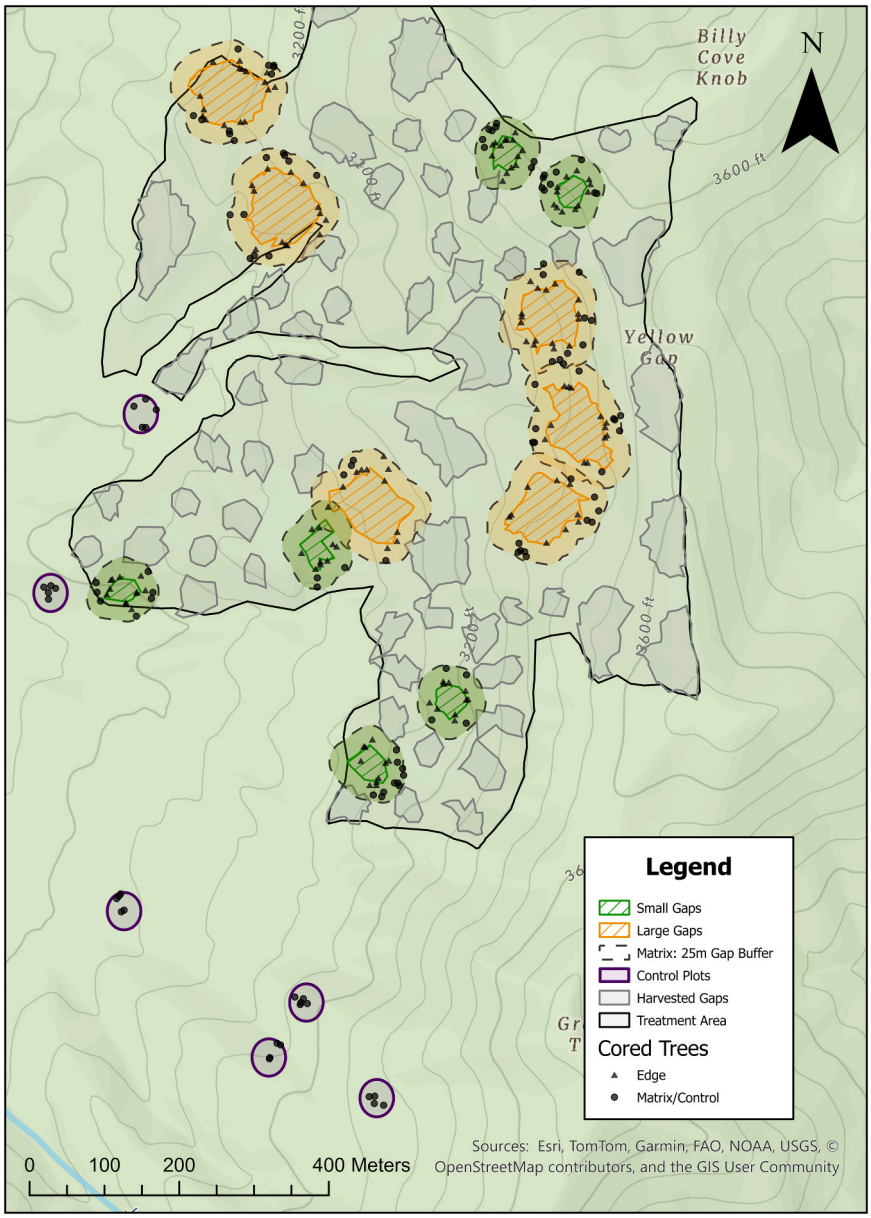

Fig. 1. Site map of the Southern Appalachian Femelschlag Experiment within the Pisgah National Forest in the Southern Appalachian Mountains, near Asheville, NC, USA. Within the treatment area, experimental canopy gaps of two sizes were harvested and a midstory removal was conducted in 2019. Cored trees in selected gaps and control plots are shown; symbols distinguish between trees at gap edges versus matrix or control trees. Control plots lay outside the treatment area, boundaries shown.

overstory trees ≥ 12.7 cm DBH within 25 m of the gap edges extending into the forest matrix and within 25 m of control plot centers the geolocation, species, DBH, and crown class were recorded. Crown class was categorized as dominant/codominant, intermediate, or suppressed. The stem inventory was used to select a subset of trees to core by dividing the zones in gap treatments into geographically based quadrants, with two quadrants for matrix (North/East and South/West) and four quadrants for edge (North, East, South, and West). One tree of each species was selected in each zone and quadrant, where available, for a possible total of up to 30 trees per gap plot. In each control plot, one tree was selected per species. Where multiple candidate trees were available, DBH was taken into consideration to capture a representative range per species. In total, the subset of trees to core included 146 from edge, 96 from matrix, and 29 from control. Subject tree DBH distributions varied by species (Table 1) which was representative of species DBH distributions across the site (Fig. S1). Metrics of distance from gap edge and azimuth from gap center were extracted for trees in gap treatments using GIS tools, i.e. Near (ArcMap Pro 3.0, ESRI, 2022).

Tree cores were collected in May–June 2023, five growing seasons post-harvest. One core was collected per tree at breast height using an increment borer, perpendicular to slope direction. The cores were preserved in paper straws before being glued to mounting boards and sanded until the rings were clearly visible. Growth increments were captured using one of two methods: a Velmex linear encoder with an Amscope stereo microscope and MeasureJ2X software (VoorTech Consulting, Holderness, NH), and CooRecorder software (Cybis Elektronik & Data AB) using images collected by scanner. Ring widths between 2015 and 2022 were measured to compare the 4-year time periods pre- and post-harvest. Cross-dating was not possible for this short time range. Confidence in the accuracy of ring years came from the fact that cores were collected from the same site, year, and season, and contained bark.

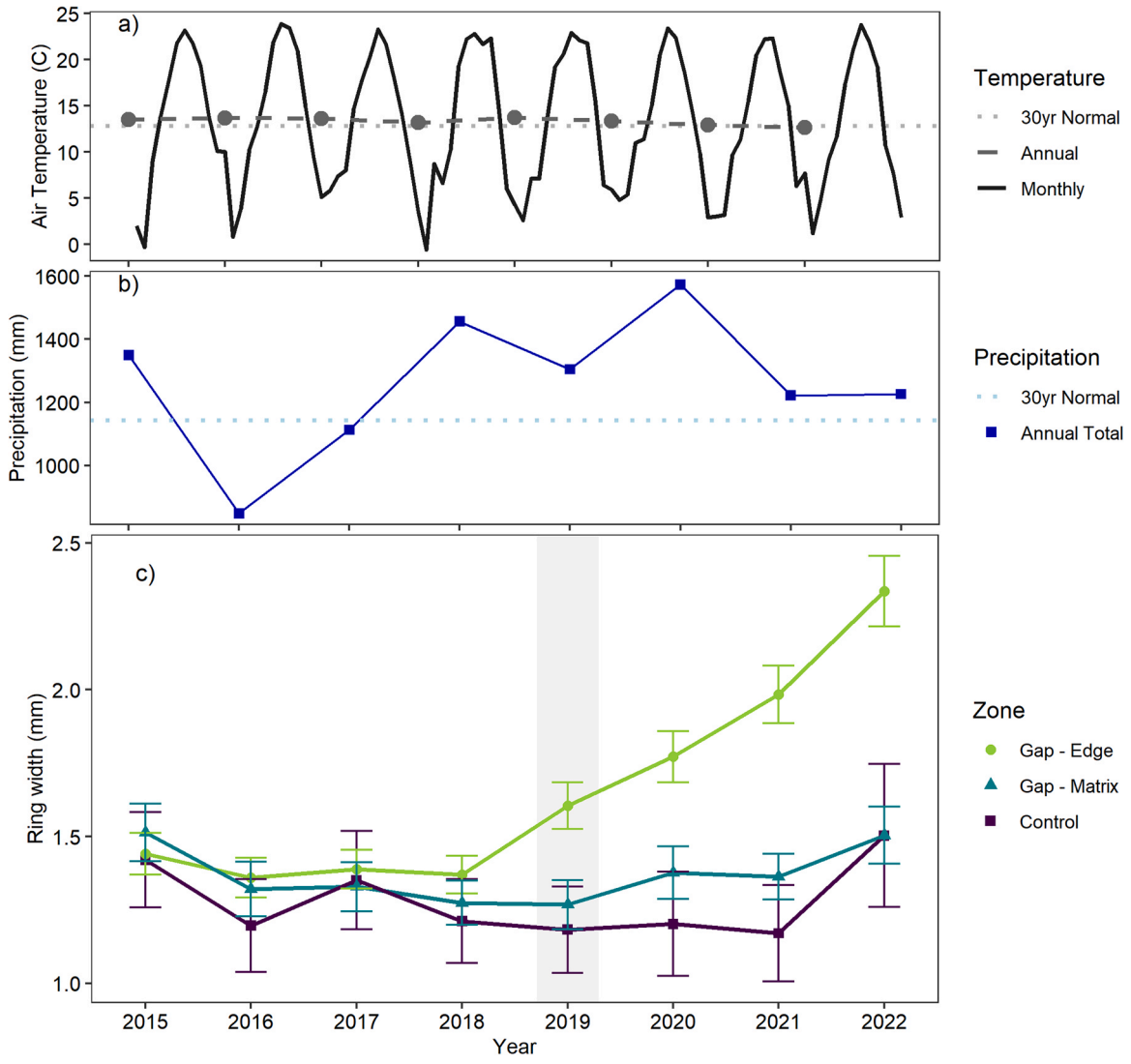

Fig. 2. Annual a) average air temperature, b) total precipitation (30-year norms for temperature and precipitation shown as dotted lines) and c) average ring width (+/− SE) of dominant trees by zone. Outliers were excluded. Harvest occurred in 2019, denoted by shaded area. Climate data from Candler 1 W weather station, NC State Climate Office [accessed 12/06/2024].

Table 1
Diameter at breast height (DBH) and sample size for each species group. Diameter (cm) was measured in 2022, four years after harvest. In total, N = 271; 17 outliers were removed. Species differ in diameter distribution ($P < 0.001$); Tukey HSD order letter report shows differences between species.

			DBH (cm)		
Latin names	**Species Group**	**n**	**Range**	**Mean**	
Acer rubrum	Red maple	63	13.5–56.1	31.8	C
Carya spp. *(C. tomentosa, C. ovalis, C. glabra)*	Hickory	47	15.1–64.4	29.8	C
Liriodendron tulipifera	Tulip-poplar	62	13.5–93.3	49.3	B
Quercus rubra, Q. velutina, Q. coccinea	Red Oak Group	47	14.4–112.4	60.1	A
Quercus alba, Q. montana	White Oak Group	49	23.1–100.5	55.4	AB

2.3. Analysis

Change in growth rate post-harvest was calculated as the percent change in average annual ring width:

$$\%\Delta RW = 100 \times (RW_{post} - RW_{pre}) / RW_{pre} \quad (1)$$

where RW_{pre} and RW_{post} represented average annual ring width pre- (2015–2018) and post-harvest (2019–2022), respectively. Cores yielding %ΔRW values outside a 95 % confidence interval were re-measured to validate. Outliers were defined as values outside a 95 % confidence interval for each species, treatment, and position, and were removed (n = 17). All remaining cores (n = 271) were retained for analysis.

To test gap harvest effects on tree growth rate, %ΔRW was compared across gap sizes and zones as well as to a control. Due to the unbalanced factorial study design of zone and treatment, three linear mixed models were used to draw pairwise comparisons between: 1) edge versus matrix, 2) edge versus control, and 3) matrix versus control. Model 1 included only gap treatments, e.g., only edge and matrix zones, and tested the effects of zone, treatment, covariates, and all possible interactions in the following equation:

$$\%\Delta RW = Species + TRT + Zone + Azimuth + DBH + CrownClass + Species \times TRT + TRT \times Zone + Species \times Zone + TRT \times Species \times Zone + \varepsilon_p \quad (2)$$

where species had five levels, treatment (TRT) had two levels (large gap and small gap), zone had two levels (edge and matrix), azimuth and DBH (cm) were continuous variables, crown class had three levels (dominant/codominant, intermediate, suppressed), and ε_p was the random error associated with plot. The response variable, %ΔRW, was shifted and log transformed to meet model assumptions. Model 2 included only edge and control trees and tested the effects of treatment, covariates, and all possible interactions in the following equation:

$$\%\Delta RW = Species + TRT + DBH + CrownClass + Species \times TRT + \varepsilon_p \quad (3)$$

where species had five levels, treatment (TRT) had three levels (large gap, small gap, and control), DBH (cm) was a continuous variable, crown class had three levels (dominant/codominant, intermediate, suppressed), and ε_p was the random error associated with plot. The response variable, %ΔRW, was shifted and log transformed to meet model assumptions. Model 3 included only matrix and control trees and was otherwise identical to model 2 (Eq. 3). Treatment, species, zone, azimuth, DBH, and crown class were fixed effects. Azimuth was included as a continuous variable after transformation, where values were first folded (i.e., shifted so that North was equal to 0, East was equal to −90, South was equal to 180 and −180, and West was equal to 90), then squared. The resulting azimuth variable represented trees north of gap center as small values and trees south of gap center as large values, with trees east and west of gap center having similar values to each other.

To test if the matrix tree growth response changed based on distance from the gap edge, we used the following linear mixed model:

$$\%\Delta RW = Species + Distance\ from\ Edge + \varepsilon_p \quad (4)$$

where species had five levels, distance from edge (m) was a continuous variable ranging 3–25 m, and ε_p was the random error associated with plot. Edge and control trees were excluded. The response variable, %ΔRW, was shifted and log transformed to meet model assumptions. To assess if edge tree growth response differed by tree size (DBH) within species, we used the following linear mixed model:

$$\%\Delta RW = Species + TRT + DBH + Species \times TRT + Species \times DBH + TRT \times DBH + Species \times TRT \times DBH + \varepsilon_p \quad (5)$$

where species had five levels, treatment (TRT) had two levels (large gap, small gap), DBH (cm) was a continuous variable, and ε_p was the random error associated with plot. The response variable, %ΔRW, was shifted and log transformed to meet model assumptions.

$$BAI = BA_t - BA_{t\text{-}1} = \pi \times (r_t^2 - r_{t\text{-}1}^2) \quad (6)$$

Where BAI ($cm^2 yr^{-1}$) represented the current yr, t − 1 represented the previous year, and r is the radius (cm) at breast height from diameter reconstructed backwards through time using the ring widths from the tree cores subtracted from the measured DBH. An average BAI was calculated across years pre- and post-harvest for each tree. Using BAI as the response variable and all species combined, we used two linear mixed models to test for the fixed effects of treatment and time (pre-treatment versus post-treatment) with plot as a random effect for 1) matrix and control trees, and 2) matrix and edge trees. To test for differences between matrix in large and small gaps and control trees over time the following model was used:

$$BAI = TRT + Time + TRT \times Time + \varepsilon_p \quad (8)$$

where treatment (TRT) had three levels (large gaps, small gaps, and controls), time had two levels (pre- and post-treatment), and ε_p was the random error associated with plot. The response variable, BAI, was shifted and log transformed to meet model assumptions. To test for differences between matrix and edge trees over time the following model was used:

$$BAI = TRT + Time + Zone + TRT \times Time + Zone \times Time + \varepsilon_p \quad (9)$$

where treatment (TRT) had two levels (large gaps and small gaps), time had two levels (pre- and post-treatment), zone had two levels (matrix and edge), and ε_p was the random error associated with plot. The response variable, BAI, was shifted and log transformed to meet model assumptions. Across all models, simple effects were used to examine significant interactions. A Tukey HSD post-hoc test was performed where $P < 0.05$ to show differences between groups. Residuals were visually examined using quantile-to-quantile plots and fitted versus residual plots to ensure models met assumptions of normality and homoscedasticity. Random effects variance components for all models are reported in Table S1. Analyses were conducted in R 4.5.0 (R Core Team, 2025) and the *lme4* package (Bates et al., 2015).

3. Results

Annual ring width increment averaged across all species groups fluctuated on a year-by-year basis for all three zones (Fig. 2c). For control and matrix trees, ring width increment remained largely constant across all 8 years, with matrix slightly higher than control in most years. The average increment for edge trees remained close to matrix and control pre-harvest (from 2015 to 2018), but in the subsequent 4 years post-harvest it diverged, increasing in near-linear fashion. Trees ranged in DBH from 13.5 to 112.4 cm (Table 1). Diameter varied significantly by species, with the red oak group ranking highest in both mean DBH and variability, while hickory had the lowest mean value and red maple, which had the second-lowest mean DBH, had the lowest variability ($P < 0.001$, Table 1). A Tukey post-hoc test showed that red maple and hickory were statistically similar, while tulip-poplar and the red oak group were both unique, and the white oak group lay in between the two averaging at 55.4 cm. DBH also differed by crown class, such that suppressed trees ranged 13.5–39.8 cm, intermediate trees ranged 13.5–72 cm, and dominant/codominant trees ranged 25.3–112.5 cm.

Growth responses differed significantly between edge and matrix zones ($P < 0.001$) and to different degrees dependent on the species group ($P = 0.06$, Table 2, Model 1). All except the red oak group showed a significantly higher %ΔRW at edge compared to the matrix ($P < 0.05$; Fig. 3). Other factors including gap size (treatment), azimuth, crown class, and diameter did not exhibit significant influence on growth. At edge, red maple displayed the highest mean response, 74.4 %, which was 3.6 times higher than in the matrix. Red maple %ΔRW was significantly greater than both oak groups. The red oak group had the lowest mean %ΔRW value at edge, 20.0 %. Hickory had the most variable response at edge, with upper and lower outliers and a high standard deviation (64.7).

Between gap edge and control, the effect of treatment differed by species ($P < 0.01$, Table 2, Model 2). Red maple growth response was highest at the edge of large gaps (97 %) relative to controls (−22 %) or small gaps (73 %) reflecting the greater influence of the larger gap size. Tulip-poplar response, however, was highest for edge trees at small gaps (69 %) versus controls (9 %) and large gaps (39 %). Differences among species were most pronounced in large gaps ($P < 0.001$) where red maple responded more than other species, with the exception of hickory.

Growth was not different among gap size (treatment), species, DBH, or crown class when comparing matrix and control zones (Table 2, Model 3). In the linear model for all matrix trees, neither distance from edge nor species significantly influenced %ΔRW (Table 3). There was no effect of DBH for all trees (Table 2) or for only edge trees when species was also included in the model (Table 3). Without species in the model, however, edge trees with smaller DBH had growth responses which were generally higher, with greater variation, than larger trees ($N = 145$, $P < 0.001$, Fig. 4). This corresponds to the significant differences in DBH by species group as seen in Table 1, with red maple and hickory

Table 2
Statistical summary of fixed effects for three models (Eqs. 2 and 3) using log transformed percent change ring width (%ΔRW) as the response variable. Model number shows the zones included in each model. Five species groups (Sp) were tested: red maple, hickory, tulip-poplar, red oak group, and white oak group. Treatment (TRT) included a maximum of three levels, i.e., large gaps, small gaps, and control, and model 1 excluded controls. Zone included edge and matrix. Azimuth from gap center was a continuous variable transformed to distinguish between northness and southness. Diameter at breast height (DBH) was a continuous variable. Crown class represented three categories: dominant/codominant, intermediate, suppressed. Bold values indicate $P < 0.05$.

Model	DF	F	P
1: Edge & Matrix			
Species (Sp)	4	1.9153	0.1090
Treatment (TRT)	1	0.0137	0.9094
Zone	1	40.6492	**< .0001**
Azimuth	1	1.7347	0.1892
DBH	1	0.1738	0.6772
CrownClass	3	0.1195	0.8874
Sp × TRT	4	1.1029	0.3561
TRT × Zone	1	0.7805	0.3780
Sp × Zone	4	2.2511	0.0647
TRT × Sp × Zone	4	1.5887	0.1785
2: Edge & Control			
Sp	4	0.9773	0.4217
TRT	2	15.624	**< .0001**
DBH	1	0.1124	0.7380
CrownClass	3	0.3674	0.6932
Sp x TRT	8	2.7573	**0.0071**
3: Matrix & Control			
Sp	4	1.9096	0.1148
TRT	2	1.6212	0.2361
Sp x TRT	8	1.7121	0.1050
DBH	1	0.2662	0.6070
CrownClass	2	0.2223	0.8011

Note: Factors are described in further detail in Section 2.2. Models are described further in Section 2.3.

Table 3
Statistical summary of fixed effects for two models (Eqs. 4 and 5) using log transformed percent change ring width (%ΔRW) as the response variable. Model headings show the zones included in each model. Five species groups (Sp) were tested: red maple, hickory, tulip-poplar, red oak group, and white oak group. Distance from edge was a continuous variable ranging 3–25 m. Treatment (TRT) included only large gaps and small gaps. Diameter at breast height (DBH) was a continuous variable. Bold values indicate $P < 0.05$.

	Fixed Effects	DF	F	P
Matrix				
	Species	4	1.3172	0.2703
	Distance from Edge	1	0.0177	0.8946
Edge				
	Treatment (TRT)	1	1.8778	0.1730
	Species (Sp)	4	0.8883	0.4731
	DBH	1	0.1431	0.7059
	TRT × Sp	4	0.5603	0.6919
	TRT × DBH	1	1.0713	0.3026
	Sp × DBH	4	0.1937	0.9413
	TRT × Sp × DBH	4	0.2683	0.8979

Note: Factors are described in further detail in Section 2.2. Models are described further in Section 2.3.

constituting most of the smaller trees, and tulip-poplar and both oak groups having relatively higher DBH values.

Increases in annual basal area increment before and after harvest were only evident in edge trees ($P = 0.055$; Table 4), which increased by 8 cm^2 between pre- and post-harvest (Fig. 5). There were no differences between time periods for matrix zones ($P = 0.97$) or unharvested controls (Fig. 5).

4. Discussion

Annual average temperatures remained relatively consistent over the 8-year period at the nearest weather station (Fig. 2a; Candler 1 W, NC Station 1991–2020 Climate Normals; NCEI, NOAA). Precipitation did fluctuate, with its lowest point over the 8-year period in 2016 and highest in 2020, which may account for the dip in average ring width increment in 2016 (Fig. 2c). Otherwise, there is little apparent connection between precipitation and annual growth for any of the three zones, lending confidence to the growth response being due to harvest.

The average percent change in ring width after gap harvest for edge trees (48 %) was over five times higher than matrix trees (8.9 %), while the error bounds for the control trees (−4.6 %) included zero, supporting our first hypothesis. While some matrix trees showed a marginal

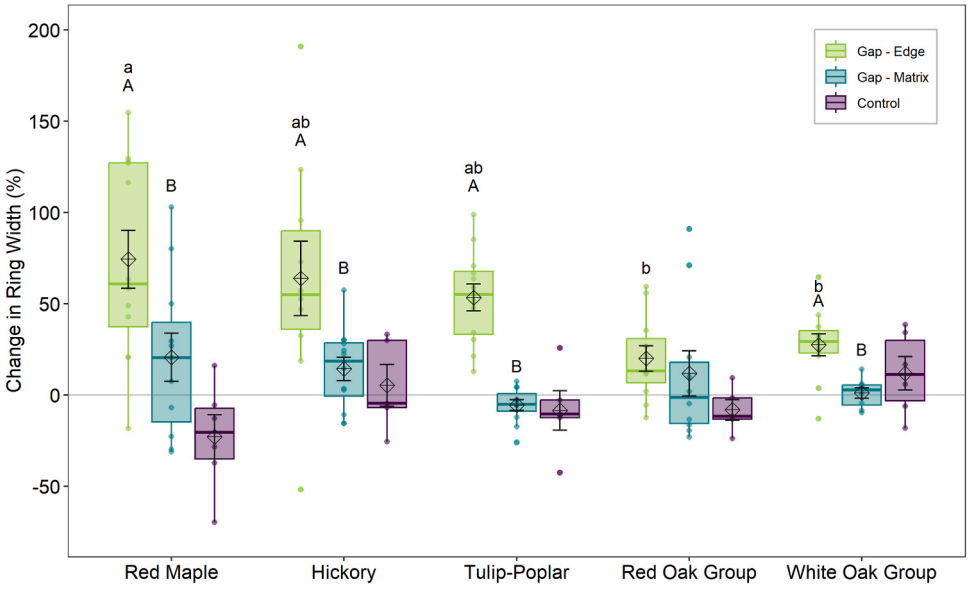

Fig. 3. Percent change in average annual ring width post-harvest (%ΔRW) by species. Points show average responses of trees per plot (replicates) from a total of 271 trees. Boxes encompass 50 % of the data; the central line represents the median, and whiskers represent the remaining 25 % above and below the box. Outliers are shown as points above or below the whiskers. Grey diamonds show group means +/− SE. Tukey HSD order letters are shown in uppercase where zone effect has $P < 0.05$, and in lower case for edge trees to show differences between species. Detailed model results in Table 2.

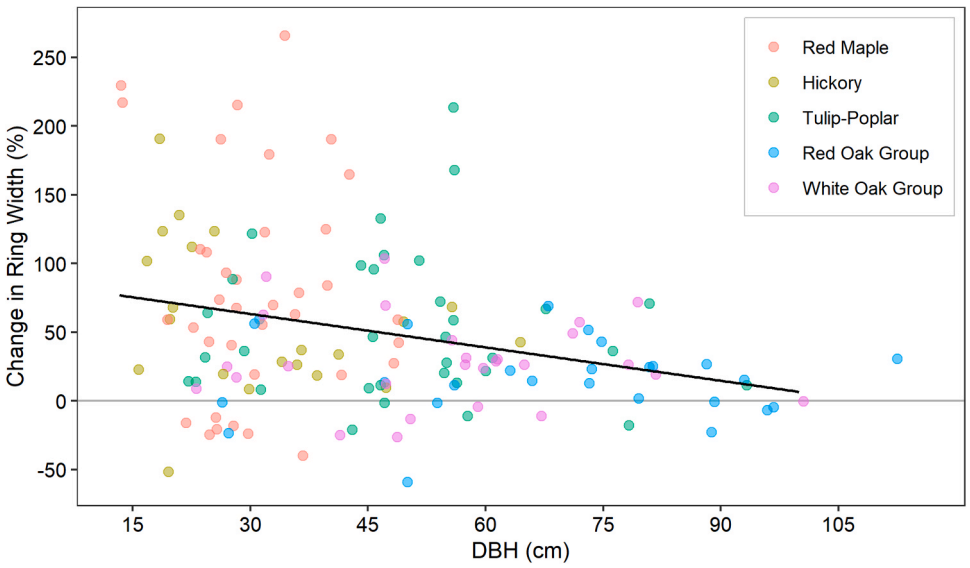

Fig. 4. Edge tree change in ring width increased more for smaller trees. Linear regression shown (N = 145, $P < 0.001$). DBH was correlated with species (see Table 1).

Table 4
Statistical summary of fixed effects for two models (Eqs. 8 and 9) testing effects on log transformed basal area increment (BAI) over time (pre- vs. post-harvest). Model heading shows the zones included in each model. Treatment (TRT) included a maximum of three levels, i.e., large gaps, small gaps, and control. Zone included edge and matrix. Bold values indicate $P < 0.05$.

Fixed Effects	DF	F	P
Matrix & Control			
TRT	2	0.7016	0.5314
Time	1	0.0114	0.9152
TRT × Time	2	0.0825	0.9208
Matrix & Edge			
TRT	1	1.2118	0.3032
Time	1	6.6074	**0.0105**
Zone	1	15.0536	**0.0001**
TRT × Time	1	0.0063	0.9366
Zone × Time	1	3.7068	0.0548

Note: Factors are described in further detail in Section 2.2. Models are described further in Section 2.3.

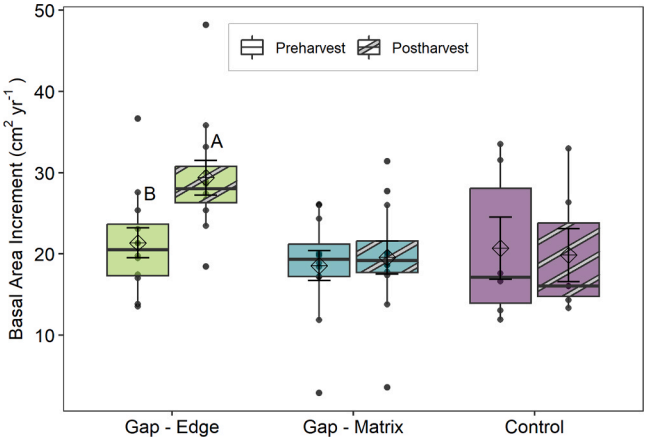

Fig. 5. Comparison of average tree basal area increment pre- and post-harvest by zone for all species combined. Points represent plot average response (replicates). Solid color denotes growth pre-harvest (2015–2018); hashed pattern denotes post-harvest (2019–2022). Boxes encompass 50 % of the data; the central line represents the median, and whiskers represent the remaining 25 % above and below the box. Diamonds show group means +/− SE. Order letters from Student t test shown where $P < 0.05$.

increase in growth compared to control trees, the pattern was inconsistent ($P = 0.29$). This suggests that some matrix trees may have received marginally more access to additional resources post-harvest, such as light, water, nutrients, and release from belowground competition due to the midstory removal treatment that was applied across the matrix area, unlike the unmanaged control areas. This may also be reflective of variation between individual trees as the control sample size was lower than matrix zones in gap plots. When excluding edge trees, we found no effect of distance from edge on matrix tree growth within 25 m of gap edge. This is contrary to another forest edge study that found diameter increases up to 10 m (York and Battles, 2008) and 60 m into the forest matrix (Chen et al., 1992). This may be due to the proximity of harvested gaps to each other. Some gaps had matrix buffers which were in close proximity or even overlapping, meaning that some matrix trees may have received marginal increases in available light and below-ground resources from more than one gap (Fig. 1). In addition, delineation of gap edge using 20 cm DBH tree stems is not a perfect proxy for resource (i.e., light) availability due to variability in density and width of tree crowns, gap aspect, and slope. Our forest matrix delineation of 25 m may not have been far enough away from gap edges to see a distance from edge response. However, the management goals of the experimental gap harvest that guided the harvest layout and resulting proximity of gaps to each other did not allow for longer distances from edge. As such, the growth response of the forest matrix as represented here is a reasonable assessment of this harvest type.

This increase in growth for edge and matrix trees may continue to diverge from control trees over time. Following gap creation, %ΔRW of edge trees increased in a near-linear fashion over the following four years, offering no indication of the expected duration and magnitude of edge response (Fig. 2c). Gray et al. (2012) found that increases in average annual growth increment persisted up to 16 years after gap formation in mature and old-growth western hemlock (*Tsuga heterophylla*) - Douglas-fir (*Pseudotsuga menzieseii*) dominated forests of the coastal Pacific Northwest, while Stan and Daniels (2010) found a median duration of edge release ranging from 23 to 37 years in old-growth western redcedar (*Thuja plicata*) - western hemlock forests of coastal British Columbia.

All species groups experienced a boost in diameter growth at gap edge compared to control trees, although species response differed

widely in magnitude, similar to observations in other systems across the eastern United States (Arseneault et al., 2011; McDonald and Urban, 2004). The interaction between zone and species supported our second hypothesis. The mesic species groups (red maple and tulip-poplar) had a higher mean %ΔRW at edge compared to both oak groups. Our finding that hickory had a similarly high response contrasts with a past study which found that shagbark hickory (*Carya ovata)* had a minimal response at edge relative to red maple and tulip-poplar (Pedersen and Howard, 2004), although that may speak to differences within the hickory genus as our study did not include shagbark. The difference in edge response observed between the two oak groups indicates that although white oaks may have slower diameter growth relative to red oaks (Shifley and Smith, 1982) they may experience a greater relative advantage post-disturbance. This is reflected to a marginal extent in our data, as the red oak group had a slightly higher average annual ring width increment at edge than the white oak group during both the pre- and post-harvest periods, but the latter group had a greater relative increase post-harvest (Fig. S2).

While differences in growth by species groups largely responded as expected, this could have been partly confounded by the species groups' differences in age and DBH. At the site, red maple and tulip-poplar were generally smaller and younger than the oak groups, while hickory trees were small but more variable in age (Grover et al., 2023, Table 1). The observed marginal negative correlation between DBH and %ΔRW across species groups is consistent with past literature which found that DBH marginally affected growth rate in response to edge release, with smaller trees having a greater response (Pedersen and Howard, 2004; Vitali et al., 2016). This correlation could be attributed to the increased light competition experienced by smaller trees, granting them a higher relative response after disturbance. A study conducted on edge tree growth in spruce, fir, and beech trees in the northern Alps found that the negative relationship between DBH and growth was species-dependent, pointing to differences between species in shade tolerance and competitiveness as growth factors (Biber and Pretzsch, 2022). However, we found no significant effect of DBH on growth response within species groups, which may indicate that other species-dependent characteristics served as more influential drivers of growth response at our site. For example, variation in soils or rooting depth across the site, which was not accounted for in this study, may play a role in growth differences by individual or species (McDonald and Urban, 2004). Regarding crown class, another factor associated with size and growth response (Dyer et al., 2010), a study in the Pacific Northwest found a 111 % increase in growth from understory trees compared to 39 % in overstory trees (Gray et al., 2012). Our sampled trees did vary by crown class, but there was no associated correlation to %ΔRW within species (Fig. S3).

Edge tree growth did not vary significantly by gap size or azimuth from gap center, which did not support our third hypothesis. This contrasts with a study that found that regeneration in 0.46 ha silvicultural gaps supported higher long-term average diameter growth in oak, tulip-poplar, and red maple compared to 0.16 ha gaps (Lhotka et al., 2018), but complements the lack of response reported in pine, spruce, and fir adjacent to 0.1–0.6 ha selection cuttings in Finland that were not affected by gap size or azimuth (Repola and Valkonen, 2025). The similarity seen across gap sizes could be due to the relatively large areas harvested at this site (0.15–1.1 ha), compared to individual treefall gaps, which have a median area of 0.02 ha (Pedersen and Howard, 2004). Other studies reporting weak influences of gap size suggest that changes in soil moisture drive the response in more vigorous growing conditions characteristic of mature forests as opposed to light (Gray et al., 2012; York and Battles, 2008). Azimuth relative to gap center was not significant, nor was there any apparent correlation to hypothesized light availability (Fig. S3). We expected azimuth from gap center to influence growth responses due to greater light availability along the northern gap edge (Canham et al., 1990; Stan and Daniels, 2014). The effects of azimuth from gap center on light infiltration at gap edge may have been subdued by the large slopes of the gaps, the already high light due to the south or southwest aspect of the gaps, as well as the larger gap sizes relative to tree height. The lack of growth differences by position around the gap was similar to other studies in mature forests (Pedersen and Howard, 2004) but this has been shown to vary by the successional stage of the forest and canopy position of the trees (Gray et al., 2012). Future analyses may shed more light on the magnitude and duration of growth responses and potential differences by gap size (Arseneault et al., 2011; Biber and Pretzsch, 2022).

5. Management implications and conclusions

Gap edge trees experienced an increase in annual diameter growth rate in response to gap harvests. We found that gap effect varied by species, but not direction from gap center or gap size. There was no significant negative correlation between DBH and annual ring width, although DBH was associated with species. Averaged across species, edge trees had a 33 % increase in basal area increment post-harvest, followed by a marginal 3 % increase for matrix trees and −6 % decrease for control trees (Fig. 5). The temporal implications of these increases will be important to monitor.

The species-specific edge growth responses highlight the role of stand-level disturbance as a driver for overstory tree growth and species composition in mixed hardwood forests. As mesic species (red maple and tulip-poplar) as well as hickory experienced a greater response at gap edge compared to oaks, this could indicate that as disturbance occurs, these species are more likely to outcompete oaks in the overstory through crown expansion and may contribute more to stand-level net carbon storage. This is especially pertinent considering that mesic species are diffuse-porous, granting them a lower water use efficiency than ring-porous species groups such as oak (Caldwell et al., 2016). As these species experience higher growth releases in response to disturbance, mesophication may be exacerbated and stand-level drought resilience may be negatively affected in response to projected increases in the frequency and severity of drought in the southern Appalachian region (Vose and Elliott, 2016). Further intervention may be required to promote oak overstory competitiveness, drought resilience, and productivity in the southern Appalachians.

CRediT authorship contribution statement

Shriya C. Reddy: Writing – original draft, Investigation, Data curation. **Morgan L. Arteman:** Writing – review & editing, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Jodi A. Forrester:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Tara L. Keyser:** Writing – review & editing, Supervision, Funding acquisition.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Shriya Reddy reports financial support was provided by Doris Duke Charitable Foundation. Jodi Forrester reports financial support was provided by National Institute of Food and Agriculture. Jodi Forrester reports financial support was provided by USDA Forest Service Southern Research Station. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123008.

Data availability

Data will be made available on request.

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