Canadian Journal of Forest Research

OPEN ACCESS | Research Article

Light patterns align with successful *Quercus* and *Carya* regeneration but reveal continued challenges in managing dry-mesic southern Appalachian upland hardwood forests

David K. Schnake[a,b], **Jodi A. Forrester**[a], **Tara L. Keyser**[c], **and Andrew J. Sánchez Meador**[d,e]

[a]Department of Forestry and Environmental Resources, College of Natural Resources, North Carolina State University, Raleigh, NC, US; [b]The Nature Conservancy, Arlington, VA, US; [c]United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, US; [d]Ecological Restoration Institute, College of the Environment, Forestry, and Natural Sciences, Northern Arizona University, Flagstaff, AZ, US; [e]School of Forestry, College of the Environment, Forestry, and Natural Sciences, Northern Arizona University, Flagstaff, AZ, US

Corresponding author: **David K. Schnake** (email: David.Schnake@tnc.org)

Abstract

Field experiments of gap-based silviculture have provided inconsistent evidence that these approaches are effective in regenerating shade midtolerant oaks (*Quercus* spp.) and hickories (*Carya* spp.) in upland deciduous forests of the southern Appalachian Mountains, USA. We measured tree regeneration in a long-term field demonstration containing 13- and 30-year-old harvest gaps to evaluate the response of regeneration to group selection harvesting. Oak and hickory regeneration was mapped within the gaps to allow testing for evidence of spatial partitioning among these species. Mixed mesophytic hardwood species accounted for nearly 75% of the regeneration density in both sets of gaps. However, the average combined densities of regenerated oaks and hickories exceeded 900 trees per hectare across all gaps. Oak and hickory regeneration was clustered in the western portion and edges of the 13-year-old gaps but randomly distributed throughout 30-year-old gaps. Light was a significant driver for the spatial partitioning of oaks and hickory regeneration, but other unmeasured factors like interspecific competition from mesophytic hardwoods likely also exerted influence. These results show that oaks and hickories can be regenerated using gap-based silviculture and that their densities may temporarily be highest along the periphery of the gap environment.

Key words: silviculture, group selection, oak, upland hardwood, gap dynamics

Résumé

Les expériences de terrain sur la sylviculture basée sur les trouées ont fourni des preuves incohérentes que ces approches sont efficaces pour régénérer les chênes (*Quercus* spp.) et les caryers (*Carya* spp.) tolérants à l'ombre moyenne dans les forêts décidues des hautes terres des montagnes Appalaches du Sud, aux États-Unis. Nous avons mesuré la régénération des arbres dans une démonstration de terrain à long terme contenant des trouées de récolte de 13 et 30 ans pour évaluer la réponse de la régénération à la coupe par sélection en groupe. La régénération des chênes et des caryers a été cartographiée dans les trouées pour tester la preuve de la partition spatiale parmi ces espèces. Les espèces de feuillus mésophytiques mélangées représentaient près de 75% de la densité de régénération dans les deux ensembles de trouées. Cependant, les densités moyennes combinées des chênes et des caryers régénérés dépassaient 900 arbres par hectare dans toutes les trouées. La régénération des chênes et des caryers était regroupée dans la partie ouest et les bords des trouées de 13 ans, mais distribuée de manière aléatoire dans les trouées de 30 ans. La lumière était un facteur significatif pour la partition spatiale de la régénération des chênes et des caryers, mais d'autres facteurs non mesurés comme la compétition interspécifique des feuillus mésophytiques exerçaient probablement également une influence. Ces résultats montrent que les chênes et les caryers peuvent être régénérés en utilisant la sylviculture basée sur les trouées et que leurs densités peuvent être temporairement les plus élevées le long de la périphérie de l'environnement de la trouée. *[Ceci est une traduction fournie par l'auteur du résumé en anglais.]*

Mots-clés : sylviculture, coupe par groupes, chêne, feuillus des hautes terres, dynamique des trouées

Introduction

Upland mixed hardwood forests of the southern Appalachian Mountains of the eastern United States are subject to a mixed-severity gap-scale disturbance archetype (Palik et al. 2020). Small canopy gap-scale (<500 m^2 in expanded gap area (Runkle 1982, 1985)) disturbances occur frequently due to fire, drought, wind, ice, and forest pests and disease and these disturbances are infrequently yet meaningfully punctuated by mostly wind-driven disturbances of intermediate extent and severity (Greenberg and McNab 1998; McNab et al. 2004; Hart 2016). Recurrent low-severity understory fire also regularly altered understory composition, structure, and light conditions and favored regeneration of fire adapted species with midtolerance of shade (McEwan et al. 2011). The combination of these disturbance regimes and highly variable edaphic and microclimatic conditions due to the complex topography characteristic of the mountainous terrain has for centuries supported the regeneration and eventual canopy dominance of various species of upland oaks (*Quercus* spp.) and hickories (*Carya* spp.) (Yarnell 1998; Simon et al. 2005; Greenberg et al. 2016). The historic and contemporary dominance of these species is attributed in part to congruence among their physiological characteristics and the regional natural disturbance regime. Specifically, upland oaks and hickories of the region are generally considered midtolerant of shade (Niinemets and Valladares 2006), fire tolerant, and have persistent reproductive strategies that rely on continuous establishment, development, and eventual release of advance reproduction (Johnson et al. 2019). As such, the frequent, low-severity disturbances across strata can be sufficient for shade midtolerant oak and hickory seedling establishment and development into advance reproduction, and more extensive canopy removals associated with intermediate-severity disturbances can release this advance reproduction from overstory competition and enable recruitment into canopy positions (Lorimer 1989).

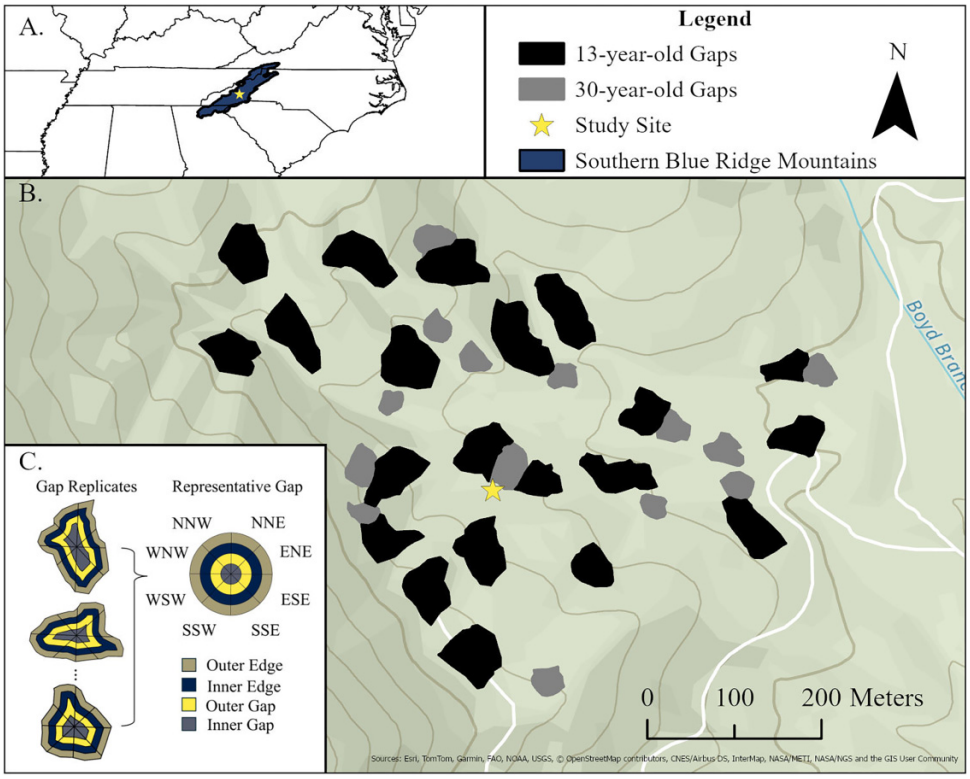
Group selection harvesting ("GSH") emulates canopy gap formation (Palik et al. 2020) by harvesting groups of overstory trees, functioning as a silvicultural analog to the mixed-severity gap-scale disturbance regime of the southern Appalachians. An appealing ecological characteristic of GSH is that it can promote tree species diversity by creating heterogeneity among resource gradients across the gap environment, whereby tree species with differing physiological characteristics may partition and coexist (i.e., the "gap partitioning hypothesis") (Ricklefs 1977; Denslow 1980). Long-term implementation of GSH can also lead to a structurally complex mosaic of even-aged cohorts that ultimately form multi-aged forest stands (Leak 1999; Halpin et al. 2017). The operational appeal of GSH is that it can be simple to implement relative to other multi-aged silvicultural harvest systems and can create fewer visual impacts relative to stand-level even- or two-aged regeneration approaches (Miller et al. 1995). Therefore, GSH may be both an effective and efficient approach for enhancing compositional and structural diversity, which are increasingly important forest management objectives given that they can enhance ecosystem function, resilience, and adaptability (Franklin et al. 2018).

Gap-based harvest systems such as GSH should theoretically be effective in regenerating upland oaks and hickories in contemporary mixed upland forests of the southern Appalachians (Forrester et al. 2023). However, studies formally testing GSH in mixed upland hardwoods have shown that it has been largely unsuccessful in recruiting high densities of oaks and hickories relative to mesophytic species (Weigel and Parker 1997; Jenkins and Parker 1998; Lorber 2003; Lhotka 2013; Phillips and Shure 2015; McNab and Oprean 2021). Unsuccessful recruitment following GSH is commonly attributed to shade tolerant red maple (*Acer rubrum* L.) suppressing the development of advance reproduction of oak and hickory and shade intolerant yellow-poplar (*Liriodendron tulipifera* L.) outcompeting oaks and hickories following overstory removal. Mesophytic species such as red maple and yellow-poplar have increased in dominance across the region over the last century (Nowacki and Abrams 2008; McEwan et al. 2011) and this "mesophication" is contributing to oak and hickory regeneration failures under nearly all regeneration harvest methods (Fei et al. 2011; Woodbridge et al. 2022). This is a concerning trend given that a decreased role of oaks and hickories will negatively impact wildlife (McShea et al. 2007), provisioning of ecosystem services (Caldwell et al. 2016), and local economies (Dhungel et al. 2023). Forests dominated by mesophytic species may also be less resilient to compounding stressors associated with climate change (Vose and Elliott 2016). Developing and testing silvicultural approaches to maintain an oak and hickory component in future forests is thus critical to the continued production of various cultural, provisioning, regulating, and supporting ecosystem services in southern Appalachian forests.

The largely unsuccessful oak and hickory regeneration outcomes from experiments testing traditional gap-based harvest systems like GSH have stimulated interest in alternative approaches, including locally adjusted expanding-gap or "femelschlag" systems (Forrester et al. 2023). Designing silvicultural prescriptions using these approaches would be aided by an improved understanding of how oaks and hickories partition within harvest gaps under novel levels of competition from mesophytic species. Yet the extent to which oaks and hickories partition across resource gradients within gaps in the southern Appalachians is still not well understood. Although some recent studies report that oak often regenerates in the periphery of gaps and into the intact forest edge (Lhotka and Stringer 2013; Berg et al. 2019; Greenler and Saunders 2019; McNab and Oprean 2021), finer-scale analyses are needed to clarify the extent and location of partitioning.

In this study, we evaluated the effectiveness of GSH to regenerate oaks and hickories in a typical dry-mesic southern Appalachian mixed upland hardwood forest. The objective was to leverage a field demonstration established in 1988 that applied GSH and monitored the tree regeneration response on near decadal intervals to answer the following questions: (1) What are the effects of GSH on density of oak and hickory regeneration in 13- and 30-year-old gaps?; (2) Do oak and hickory stems that regenerated following GSH exhibit spatial partitioning?; and (3) Is light a driver of spatial partitioning among oak and hickory regeneration? This research will provide insights into regeneration outcomes

Fig. 1. (A and B) Location of the Boyd Branch demonstration area within the Bent Creek Experimental Forest in western North Carolina, USA, and (C) figure of the representative gap polygon used for spatial analysis.



among oaks and hickories formed through GSH in the southern Appalachians, a region from which few similar experiments have been reported. These results will also complement the spatial trends among oak and hickory regeneration recently reported among these (McNab and Oprean 2021) and other forest gaps (Berg et al. 2019; Greenler and Saunders 2019) and identify potential causal mechanisms for these patterns. These collective results will be valuable for designing gap-based silvicultural treatments to promote structurally complex forests with an oak and hickory component among mixed upland hardwood forests of the southern Appalachians.

Materials and methods

Study area

The study area was in the Bent Creek Experimental Forest (BCEF) in the Pisgah National Forest in western North Carolina, USA, within the Southern Blue Ridge Physiographic Province of the southern Appalachian Mountains (Fig. 1A). BCEF has long, warm summers and short, cool winters with mean annual air temperatures ranging from 22.3 °C in July to 2.3 °C in January. Since the onset of this experiment, the frost-free growing season has averaged 193 days a year, typically beginning on 17 April and ending 27 October. Total annual precipitation averages 1220 mm, consists primarily of rainfall, and is evenly distributed throughout the year.

This study builds upon the Frothingham group selection study, which was installed within the Boyd Branch watershed of BCEF in 1988 (McNab and Oprean 2021). The study was developed to investigate GSH as an alternative to single tree selection, although here we have focused on regeneration within harvested gaps. Elevations within this shallow, east-facing cove range from 720 to 850 m. Ultisols of series Evard, Cowee, and Toecane dominate most of the gentler slopes across the site, whereas Inceptisols of the Tusquitee series are found on steeper slopes and along perennial streams. These generally deep (>100 cm) soils and the mountainous topography collectively contribute to a wide range of soil moisture conditions, ranging from submesic to subxeric. At the onset of the study in 1988, the site supported ~50–70-year-old second-growth upland hardwood forests with compositions typical of the southern Appalachian region. Pre-treatment tree (dbh > 10 cm) density was 478.9 trees per hectare (tph), which contributed to an overall basal area (BA) of 29.3 m^2/ha. The BA consisted mostly of large (dbh > 20 cm) upland oaks (black (*Quercus velutina* Lam.), chestnut (*Quercus montana* Willd.), scarlet (*Quercus coccinea* Muenchh.), white (*Quercus alba* L.), and northern red (*Quercus rubra* L.)), which collectively accounted for 36% of BA, and yellow-poplar, which accounted for another 31% of BA, especially in more mesic portions of the site. Hickory (*Carya tomentosa* Poir. Nutt. and *Carya glabra* Mill.) was only a minor (0.9%) overstory component. Midstory cohorts tended to be dominated by shade tolerant mesophytic hardwoods such as red maple (12% BA), sourwood (*Oxydendrum arboretum* L.), sassafras (*Sassafras albidum* Nutt.),

flowering dogwood (*Cornus florida* L.), and blackgum (*Nyssa sylvatica* N. biflora), which collectively accounted for another 14% of total stand BA. Evergreen shrubs, including rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.), also occurred periodically across the site. McNab and Oprean (2021) provided a more thorough account of pre-treatment forest conditions across the Frothingham group selection study site.

This study examined gaps (0.05–0.41 ha) that were commercially harvested over two separate entries. A 1988 entry created 14 gaps averaging 0.10 ha (0.05–0.14 ha) and a 2005 entry created 24 additional openings averaging 0.29 ha (0.13–0.41 ha) (Fig. 1B). Substantial portions of four gaps created during the 2005 entry were damaged during a subsequent entry in 2017 and were thus not included in this or later aspects of the experiment. All commercial timber and pulpwood products were hand-felled, skidded with wheeled equipment to the logging deck, and removed from the property during the harvest operation. Unmerchantable residuals, saplings, and sprout-origin regeneration of undesirable species (e.g., mesophytic hardwoods) were controlled shortly after each harvest using a combination of chemical and mechanical treatments. Oak and hickory species were also chemically released from competition within 3 years of each harvest (McNab and Oprean 2021). The design of this demonstration did not provide replication among gaps by aspect as all gaps could be characterized as east-facing coves with similar underlaying soil and other site factors. Gap sizes were generally within size ranges recommended in silvicultural guides for the central hardwood region (Dale et al. 1995; Miller et al. 1995; Cunningham 2014). The area, shapes, and distribution across the demonstration site also reflected local constraints on operability that would apply to others implementing GSH. As such, this collection of gaps provides an excellent demonstration of how to assess regeneration outcomes following GSH in the southern Appalachians.

Data collection and post-processing

Fixed-area plot data

In the summer of 2018, we collected tree data (dbh $\geq$ 0.05 cm) from the 30-year-old gaps ($N = 14$) created during the 1988 harvest entry and 13-year-old gaps created during the 2005 harvest entry ($N = 20$). We gathered regeneration data for all tree species within five circular 2.5 m fixed-area subplots in each gap. We established one plot at the gap center and placed the other four along the cardinal directions, halfway between the gap center and its edge. Tree species, diameter (dbh, cm), and height (m) were collected for each stem within these fixed-area plots. We classified species into four species groups: white oaks (white and chestnut oaks), red oaks (black, scarlet, and northern red oaks), hickories (all species), and other hardwoods. The other hardwoods group contained 23 tree species, but 89% of stem density within this group consisted of yellow-poplar (33%), red maple (30%), sweet birch (*Betula lenta* L.) (10%), sourwood (8%), and sassafras (8%). We used the fixed-area data to calculate mean density values for regeneration by species group in each gap.

Stem mapping oak and hickory regeneration

We mapped stems of all oak and hickory species with dominant, co-dominant, and intermediate crown classes by recording their distance (±4 cm) and azimuth (±0.5 degrees) from the gap center and noted species, diameter (cm), height (m), and crown class for each mapped stem. To simplify mapping in high-density clusters, we used a subsampling method, mapping the cluster centroid sapling and recording the number of similar conspecific stems within 1–2 m, following methods from Ziegler et al. (2017) and Schnake et al. (2023). We then randomly generated coordinates for unmapped stems within the cluster radius. This subsampling method accounted for approximately 15% of the 2137 mapped stems. Before spatial analysis, we grouped oak and hickory species into white oaks, red oaks, and hickories. Mapped saplings were also categorized by crown class within species groups. Dominant and co-dominant stems were combined into a single group, comprising 67%, 47%, and 38% of mapped white oaks, red oaks, and hickories in the 30-year-old gaps, and 58%, 55%, and 39% in the 13-year-old gaps. The remaining mapped stems had intermediate crown classes.

We analyzed spatial partitioning among oak and hickory regeneration within gaps using the mapped oak and hickory stems. We divided each gap into polygons by creating four concentric rings representing the inner and outer gap center and edge zones with widths equal to $\frac{1}{4}$ of the distance from the gap center to the nearest edge (radii of 17 and 28 m for 30-year-old and 13-year-old gaps, respectively). We further divided these rings along cardinal and sub-cardinal directions, creating 32 unique azimuth-zone sections (e.g., NNE outer gap edge) and summed saplings by species and crown class group. To account for irregular gap shapes, we averaged tree density for each species and crown class group across the 32 polygons by section to create a "representative gap" for each harvest entry (Fig. 1C). We used these representative gap polygons for spatial point pattern analyses.

Chestnut oaks comprised most mapped stems in the white oak group, accounting for 78% in the 30-year-old gaps and 88% in the 13-year-old gaps. Species densities in the red oak group were more evenly distributed, with 52% northern red oak, 33% black oak, and 15% scarlet oak in the 30-year-old gaps, and 51% black oak, 40% northern red oak, and 9% scarlet oak in the 13-year-old gaps. All hickory species were grouped due to the difficulty of differentiating between species in the field. The density values per species and species and crown class group by section for these representative gaps are included as supplementary material (Table S1).

Remotely sensed solar insolation within GSH gaps

Given that the light environment is notoriously difficult to accurately measure in the field, we derived remotely sensed estimates of the light environment within gaps to assess whether light levels in 2005 were a potential causal mecha-

Table 1. Categorical light groups incorporating mean solar insolation and diurnal variation in when solar insolation was received.

Light group	Light group criteria	Sections assigned
Low Light, Morning	<20% light, >55% received before solar noon	0
Low Light, Even	<20% light, 45%–55% received before solar noon	0
Low Light, Afternoon	<20% light, >55% received after solar noon	0
Medium-Low Light, Morning	20%–50% light, >55% received before solar noon	0
Medium-Low Light, Even	20%–50% light, 45%–55% received before solar noon	0
Medium-Low Light, Afternoon	20%–50% light, >55% received after solar noon	44
Medium-High Light, Morning	50%–75% light, >55% received before solar noon	1
Medium-High Light, Even	50%–75% light, 45%–55% received before solar noon	74
Medium-High Light, Afternoon	50%–75% light, >55% received after solar noon	90
High Light, Morning	>75% light, >55% light received before solar noon	246
High Light, Even	>75% light, 45%–55% received before solar noon	177
High Light, Afternoon	>75% light, >55% light received after solar noon	8

Table 2. Model parameters used for the generalized linear mixed models 1–3.

Model	Response variable	Family	Link function	Fixed effects	Random effects
1	Mean regeneration density (tph) in 30-year-old gaps	Tweedie	Log	Species group ($n = 4$)	Gap identifier
2	Mean regeneration density (tph) in 13-year-old gaps				
3	Density (tph) among mapped regeneration in 13-year-old gaps			Light group ($n = 5$)	Polygon section

nism for any patterns revealed in this study. We used lidar data (8 points/meter, North Carolina Department of Transportation) to create a 1 × 1 m resolution digital surface model (DSM) of a roughly 100 km^2 rectangular polygon bounding BCEF that included major topographic features that could influence insolation within the demonstration area. The DSM was then manipulated to represent near-immediate post-harvest forest conditions by eliminating canopy-height-valued raster cells from within the gaps and replacing them with cells representing the ground surface as derived from a digital elevation model (DEM) we created from the same lidar data. This approach achieved a condition within the DSM of bare ground within the gaps and tall vegetation surrounding the gaps. This solar insolation analysis was restricted to the 13-year-old gaps due to a lack of lidar data pre-dating 2005 from which to create high-resolution DSMs and DEMs as described here for the 30-year-old gaps.

We used the Raster Solar Radiation tool within the Spatial Analyst Toolkit of ArcGIS Pro V. 3.3.0 (ESRI 2024) to estimate solar insolation on the forest floor within the 13-year-old gaps, where we mapped sapling density. ESRI's Raster Solar Radiation tool uses hemispherical viewshed algorithms (Rich et al. 1994; Fu and Rich 1999, 2000; Rich and Fu 2000) to calculate insolation across a landscape while accounting for potential shadow casting by surrounding topographic features. Therefore, the DSM used for the solar analysis accounted for the potential effects of topography and surrounding vegetation on direct solar insolation within gaps. Solar insolation was estimated every 15 days between 15 April 2005 and 1 November 2005, which covers the first full growing season after the GSH treatments were implemented. Since diurnal light variation can influence partitioning among shade mid-tolerant species in temperate deciduous forests (Schnake et al. 2023), insolation was modeled separately before and after solar noon (NOAA Global Monitoring Laboratory).

Solar insolation models produced 1 m^2 resolution raster datasets of cells valued with combined direct and diffuse insolation (kWh/m^2) for each model period. All raster outputs were combined to create a single raster layer of mean solar insolation over the growing season (hereinafter, "light") within the demonstration area. We repeated this process for raster outputs from the light models conducted before solar noon to determine the percentage of mean light received before or after solar noon. We used zonal statistics to calculate the cell area-weighted mean percent of light and percent of light received before solar noon for each of the 32-polygon sections within the 20 gaps harvested in 2005 ($N = 640$). We used these values to classify sections into a categorical light group (Table 1) informed by research on oak species' light requirement (Gottschalk 1994; Guo et al. 2001; Dillaway et al. 2007). Light groups were later used as a response variable to test for relationships between mapped sapling densities and section-level light levels within the gaps harvested in 2005.

Analyses

Fixed-area plot data

We tested differences in tree regeneration density among species groups within the harvest gaps using generalized lin-

Table 3. Results from Global Moran's I tests for spatial autocorrelation among mapped sapling densities per section by species and crown class groups within our representative gap polygons.

Gaps	Species group	Crown class	Moran's index	*Z*-score	*P*-value	Spatial pattern
30-year-old	*Quercus alba*	All	−0.032	0.000	0.999	Random
		Dominant and co-dominant	−0.041	−0.163	0.870	Random
		Intermediate	−0.065	−0.665	0.506	Random
	Quercus rubra	All	0.016	0.944	0.345	Random
		Dominant and co-dominant	−0.001	0.638	0.524	Random
		Intermediate	0.000	0.629	0.530	Random
	Carya spp.	All	−0.035	−0.050	0.960	Random
		Dominant and co-dominant	0.010	0.874	0.382	Random
		Intermediate	−0.084	−1.127	0.260	Random
15-year-old	*Quercus alba*	All	0.339	7.446	<0.001	Clustered
		Dominant and co-dominant	0.256	5.774	<0.001	Clustered
		Intermediate	0.265	6.000	<0.001	Clustered
	Quercus rubra	All	0.257	5.763	<0.001	Clustered
		Dominant and co-dominant	0.213	4.926	<0.001	Clustered
		Intermediate	0.210	4.953	<0.001	Clustered
	Carya spp.	All	0.296	6.509	<0.001	Clustered
		Dominant and co-dominant	0.205	4.680	<0.001	Clustered
		Intermediate	0.199	4.619	<0.001	Clustered
	All Species	All	0.378	8.212	<0.001	Clustered

ear mixed models via the Laplace method (Raudenbush et al. 2000) of maximum likelihood estimation (Table 2). Analyses were completed using the *glmmTMB* package (Brooks et al. 2017) in R (R Core Team 2024) and were conducted separately for the 1988 (Model 1) and 2005 harvest gaps (Model 2) due to the temporal differences and differences in mean gap sizes between the two harvest entries. Mean stem density served as the response variable for both models. Species group ($N = 4$) was included as a categorical variable, and gap identifier was included as a categorical random effect to account for uncontrolled differences in slope, soil properties, and gap size across and within gaps.

Model diagnostics were completed using the *DHARMa* package (Hartig 2021) and informed selection of appropriate distributions and link functions to fit these models. We used the same package to test for overdispersion, zero-inflation, outliers, and spatial autocorrelation. The significance of the main effect of species group was assessed through Type III Analysis of Deviance using Wald χ^2-tests. Pairwise comparisons of estimated marginal means for main effects with *P*-values $\alpha \leq 0.05$ were conducted using the *emmeans* package (Length 2021), and we used the multivariate *t*-distribution method for *P*-value and confidence level adjustments.

Spatial point pattern analysis of oak and hickory regeneration

We calculated the Global Moran's I statistic to determine whether the spatial patterns among saplings for the species and crown class groups deviated from complete spatial randomness (CSR) and thus warranted additional investigation. If CSR was found, it would confirm no partitioning, eliminating the need for further spatial analysis. Fixed Euclidean distance bands of 11.3 and 18.6 m for the 30- and 13-year-old gaps were defined to ensure that each polygon was compared to at least eight neighbors and thus calculated a stable *Z*-score. This exploratory analysis provided evidence that mapped stems with dominant and co-dominant, and intermediate crown classes of both oak species groups, hickories, and all oaks and hickories and crown classes combined deviated from CSR toward clustering in the 13-year-old gaps (Table 3). Informed by these preliminary results, we conducted additional analysis suitable for clustered patterns to elucidate the characteristics of regeneration patterns within the harvest gaps. None of the species and crown class groups deviated from CSR within the 30-year-old gaps (Table 3), indicating regeneration was randomly distributed within these gaps and further spatial analysis was unnecessary.

We tested for evidence of significant clustering of high or low stem density using a "hot spot analysis" approach within the 13-year-old gaps by calculating the Local Getis-Ord Gi* (Getis and Ord 1992, 2010; Ord and Getis 1995) statistic for each section of the representative gap polygon. We again used a fixed distance band of 18.6 m to ensure comparison to eight neighbors and, therefore a valid *z*-score. The statistical significance of clusters was assessed using a false discovery rate correction, which ranks statistically significant *P*-values by strength and then uses estimates of the number of false positives for each confidence level to remove the weakest *P*-values. This approach potentially reduces the critical *P*-value thresholds for significance to account for multiple comparisons and potential spatial dependence in the data and has higher performance than other multiple testing procedures when applied to local statistics of spatial association (Caldas

Table 4. Pairwise comparisons of stem density among the four focal species groups from the fixed-area analyses of two harvest entries/time periods (models 1 and 2).

Species group	30-Year-old gap density (tph ± se)	15-Year-old gap density (tph ± se)
Other hardwoods*	3,361 ± 413[a]	6,886 ± 798[a]
Red oaks	432 ± 104[b]	1,118 ± 254[b]
White oaks	277 ± 79[b]	699 ± 175[b]
Hickories	223 ± 68[b]	184 ± 67[c]

Note: Values shown are mean number of stems ± standard error. Values not connected by the same letter are significantly different at an $\alpha = 0.05$ within each time period.
*Primarily species including yellow-poplar (33%), red maple (30%), sweet birch (10%), sourwood (8%), and sassafras (8%).

de Castro and Singer 2006). Hot spot analysis was conducted for each mapped species and crown class group and the combined oaks and hickories and crown class group for the 2005 gaps. ArcGIS Pro V 3.3.0 (ESRI 2024) was used for all spatial analyses.

Effects of modeled light on the patterns of oak and hickory regeneration

We used a generalized linear mixed model to test the effects of light on oak and hickory regeneration with at least intermediate crown classes (Model 3, Table 2). Initially, mapped sapling density per section for each species and crown class group was intended as the response as response variables. However, the imbalance of sections within each light group (Table 1), low sample sizes for some species groups within sections, and preliminary results showing similarities in spatial patterns across species and crown class groups led us to limit this analysis to a single model using the density of all oaks, hickories, and crown classes combined as the response variable. The single section assigned to the "Medium-High Light, Morning" group (Table 1) was also removed from the dataset prior to analysis due to the lack of replication within this group. This section was only 0.62% below the threshold for classification into the "Medium-High light, Even" group ($N = 74$), so we do not expect this removal to meaningfully influence the results. Light group ($N = 5$) was included as a categorical fixed effect. The gap section was included as a random effect to account for spatial autocorrelation and the same uncontrolled differences across gaps described for models 1 and 2. Selection of the appropriate model distribution and link function, as well as model diagnostics and post hoc tests, were conducted as described above for models 1 and 2. The significance of the main effect of light group was assessed through Type II Analysis of Deviance using Wald χ^2-tests given the imbalance of sections across light groups.

Results

Tree regeneration density in 30- and 13-year-old harvested gaps

Regeneration density differed among species groups in the 30- (χ^2 (df = 3, $N = 80$) = 158.2, $P < 0.001$) and 13-year-old harvest gaps (χ^2 (df = 3, $N = 80$) = 160.8, $P < 0.001$). Tph of white oak (432 tph), red oak (223 tph), and hickory (277 tph) species groups among the 30-year-old gaps were statistically similar ($P = 0.304$–0.951), although all were dominated by other hardwood species (3361 tph, $P < 0.001$) (Table 4). In 13-year-old gaps, tph of other hardwood species were greater (6886 tph, $P < 0.001$) than the red oak (1118 tph), white oak (699 tph), and hickory (184 tph) species groups (Table 4). The density of white and red oak regeneration was not different ($P = 0.378$) among 13-year-old gaps but both outnumbered hickory ($P < 0.003$).

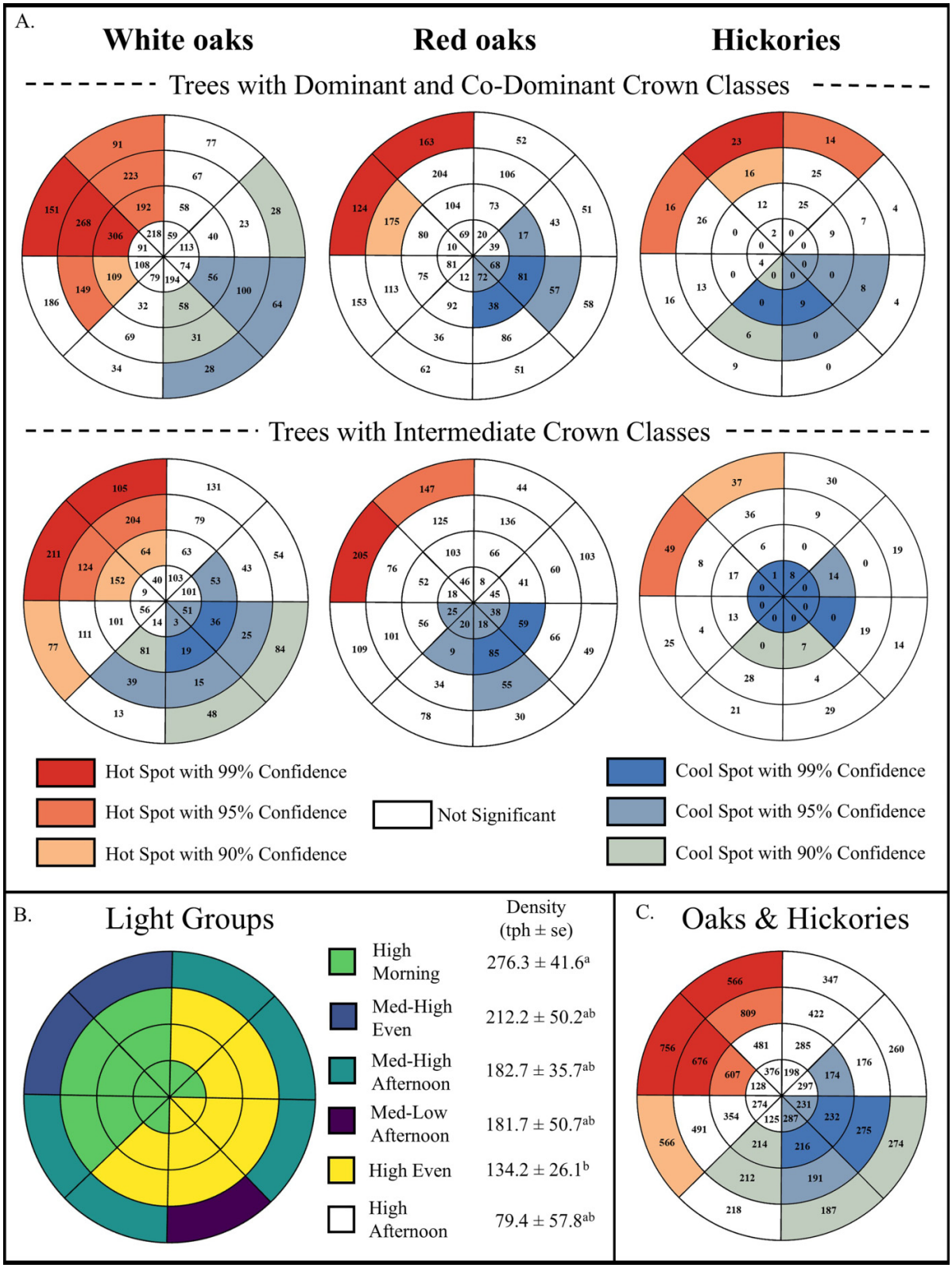
Spatial point pattern analysis of oak and hickory regeneration

The density of white oak, red oak, and hickory regeneration was randomly distributed within the 30-year-old gaps. Conversely, there was spatial clustering among gap sections for each of the species and crown class groups in the 13-year-old gaps (Fig. 2A). Across species and crown class groups, we documented high regeneration densities ("hot spots") in northwestern portions of the gaps, especially along the gap periphery. Conversely, we documented low regeneration densities ("cool spots") of white oaks, red oaks, and hickories in the eastern and southeastern portions of the gap environment (Fig. 2A). Most gap sections failed to fall within significant hot or cold spots but it is important to note that this non-significance does not indicate absence of oak and hickory regeneration. Rather, non-significance indicates that oak and hickory regeneration were generally present within these sections but not in higher or lower densities relative to the sections surrounding them.

Effects of modeled light on the patterns of oak and hickory regeneration in 13-year-old harvested gaps

The 13-year-old gaps, which ranged from 0.13 to 0.41 ha in area, received an average of 70% of the incoming light over the growing season, and light was received in nearly equal proportions before and after solar noon. However, when light levels from all sections were averaged, assigned to light groups (Table 1), and visualized using the representative polygon of the average of all 13-year-old gaps that was used for our hot spot analysis (Fig. 2B), it was apparent that a complex gradient of light formed within these gaps. Model 3 revealed that light significantly affected the combined densities of oak and hickory regeneration (χ^2 (df = 5, $N = 639$) = 17.62, $P = 0.004$), yet pairwise comparisons revealed only subtle and mostly non-significant differences in regeneration densities between

Fig. 2. (A and C) Significant hot spots and cool spots represent clusters of sections with high or low mapped regeneration of focal species, respectively. Non-significance indicates that these sections have and are generally surrounded by sections with average densities. Mean densities of regeneration that were used for the Global Moran's I and subsequent hot spot analysis are listed within each section. (B) Graphic representation of the spatial distribution of light levels and pairwise comparisons between densities of all oaks and hickories by light level group. Densities among light level groups not connected by the same letter are significantly different at an $\alpha = 0.05$.



light groups (Fig. 2B). Nonetheless, densities of regenerated oaks and hickories were highest in sections receiving high levels of light mostly in the morning, followed by medium-to-high levels throughout the day or in the afternoon, and medium-to-low levels in the afternoon. The "High Light, Afternoon" group was rare in the 13-year-old gaps (Table 1) and did not appear as an average light group in the representative gap shown in Fig. 2B. However, its sections overlapped with those in the "Medium-High, Afternoon," "Medium-Low, Afternoon," and "High Even" groups. Collectively, these sections had the lowest sapling densities.

Upon finding these relationships between light levels and regeneration density of all oaks and hickories combined (Fig. 2B), we noticed congruence with oak and hickory density patterns from the hot spot analyses (Fig. 2A). Based on this, we repeated the hot spot analysis as described previously using a representative polygon for the 13-year-old gaps with sections valued with densities of all oaks and hickories of both competitive and intermediate crown classes combined. We again found significant spatial clustering among gap sections (Table 3), with hot spots occurring west-northwest of gap center and cool spots in south-southeastern portions of gap center and outward toward the gap periphery (Fig. 2C).

Discussion

Tree regeneration density 30- and 13-years post-harvest

The density of the focal oak and hickory species groups was outnumbered by a factor of approximately 3.5 in both sets of gaps by the mostly mesophytic species comprising the "other hardwood" group. This result aligns with outcomes from other GSH experiments (Weigel and Parker 1997; Jenkins and Parker 1998; Lorber 2003; Lhotka 2013; Phillips and Shure 2015; McNab and Oprean 2021) and was not unexpected given the prevalence of fast-growing shade intolerant yellow-poplar and highly generalist red maple within the "other hardwood" species group. The ability of these two species to outcompete oak on productive cove sites such as those in this study is well-documented (Loftis 2004; Johnson et al. 2019), and data collected prior to the 1988 harvest entry showed that reproduction (height < 1.37 m) of red maple outnumbered the combined density of oaks and hickory reproduction by a factor of 3.75, and by a factor of nearly 16 among small midstory trees capable of regenerating via sprouting (1 cm $\leq$ dbh $\geq$ 10 cm) (McNab and Oprean 2021). Although we do not have understory data before the 2005 entry, we speculate that their location within the same stand translated to a similar level of pre-harvest competition from mesophytic species before the 2005 harvest. These results provide further evidence of the difficulty of regenerating upland oaks and hickories on productive sites relative to other species, especially yellow-poplar. These results also underscore the importance of abundant competitive advance reproduction of oaks being present before significant overstory removal if the desired outcome of the harvest is the regeneration of upland oaks (Loftis 2004; Johnson et al. 2019). While GSH may impose the canopy structure akin to the mixed-severity gap-scale disturbance regimes of the southern Appalachians, these results indicate that simply transitioning to natural disturbance-based silviculture is unlikely to overcome the deleterious effects of mesophication.

However, these results also suggest that additional post-harvest silvicultural treatments may improve the outcomes of GSH. The implementation of GSH in our study resulted in an average of 2000 oaks and hickories per hectare in the 13-year-old gaps, and nearly 1000 per hectare in the 30-year-old gaps. We recognize that approximately 20% of the relative density among regeneration being oaks and hickories in both sets of our gaps falls well short of commonly targeted relative densities that serve as thresholds indicating success, such as oaks accounting for at least 50% of the dominant and co-dominant stems on the onset of crown closure (Brose et al. 2008). Nonetheless, densities of oak and hickory regenerating within these gaps are a substantial increase over the pre-harvest densities of <100 tph of competitive (1 cm $\leq$ dbh $\geq$ 10 cm) oaks and hickories reported on this site prior to the 1988 GHS (McNab and Oprean 2021). They also exceed midstory oak and hickory densities reported in nearby mature and unharvested mixed upland hardwood stands (Elliott and Vose 2010). We therefore interpret our results from fixed-area plots as evidence that it is possible to increase regeneration of oak and hickory via GSH on productive sites, but that additional treatments such as crop tree release should be considered within the first ~30 years to increase the likelihood of their long-term recruitment into canopy positions (Lamson et al. 1990). The high average densities of oak regeneration in either set of gaps, many with dominant to co-dominant crowns (Fig. 2A; Table S1), would seemingly offer ample opportunities for more targeted release.

Alignment of light levels and oak and hickory regeneration

We documented significant evidence of partitioning of oak and hickory regeneration with dominant, co-dominant, and intermediate crown classes within the 13-year-old gaps (0.13–0.41 ha). Clustered sections of high sapling densities were more prevalent in northwestern positions of the gaps, especially along the periphery, and clusters of areas with lower densities were most prevalent in gap center and southeastern portions of the gaps (Figs. 2A and 2C). This finding aligns with other work from the region showing that high densities of these shade midtolerant species tend to occur along gap periphery (Lhotka and Stringer 2013; McNab and Oprean 2021) but refines the results to the specific direction and extent of these high- and low-density areas.

The lack of patterning among oak and hickory regeneration within the 30-year-old gaps aligns with studies showing that the spatial patterns among regenerating midtolerant tree species can shift from clustered during stand initiation (Poznanovic et al. 2014; Vilhar et al. 2015; Schnake et al. 2023) to more dispersed or regular patterns as forest stands mature. Competition-induced mortality within clusters can reduce density among conspecifics, leading to a more random distribution of overstory trees by species (Sharma et al. 2008;

Bragg 2013; Dimov et al. 2013; Gu et al. 2019). As oak and hickory were not mapped before age 30 in these gaps, we cannot quantitatively assess whether the patterns transitioned over 30 years. However, given the proximity and similar harvest methods and post-harvest treatments in the 30-year-old gaps and the 13-year-old gaps, and the lower tree densities in the 30-year-old gaps relative to the 13-year-old gaps, we view these results as evidence of competition-induced mortality and a transition to more random oak and hickory distribution.

Our spatial point pattern analyses revealed clear evidence of partitioning among oaks and hickories; however, oaks and hickories with at least intermediate crown classes successfully regenerated across most of the gap area (Figs. 2A and 2C). This conclusion is supported by three key findings. First, 6%–25% of sections were identified as hot spots, indicating high oak and hickory densities. Second, 44%–72% of sections showed no significant clustering, suggesting oak and hickory presence without notable density fluctuations relative to adjacent sections. Third, cool spots did not correspond to an absence of regeneration for either oak group, although hickory was absent in several of these areas. These findings reinforce the validity of our fixed-area analyses (Table 4), demonstrating that oak and hickory regeneration and recruitment is possible following GSH while providing an essential spatial context to the overall results.

When the results of the hot spot and modeled light level analyses are viewed in concert, light is apparently among the key drivers for the patterns among high and low densities of oak and hickory regeneration, at least among younger ($\leq$13 years old) regeneration pools. Specifically, there appears to be congruence between the spatial location of where hot and cool spots occurred and the spatial location of where these light levels and their corresponding higher or lower mean stem densities were located within the 13-year-old gaps (Fig. 2). These collective results also align with research on the light requirements for the regeneration and recruitment of oak and hickory (Gottschalk 1994; Guo et al. 2001; Dey et al. 2007; Dillaway et al. 2007). Densities were highest in areas receiving at least 50% light, which aligns with research showing that diameter and height growth among red oak seedlings can increase with increasing light levels up to 50%–70%. We also measured high sapling densities in areas receiving high levels of light, which aligns with research showing that oak grows well in full light if it is not being overtopped by competing vegetation. Finally, the fact that light levels were generally sufficient for oak throughout the gap helps clarify why there was at least some oak in every section of these gaps on average.

Unfortunately, we cannot definitively address the apparent divergence in oak and hickory densities in sections that both received similarly high amounts of light ($>$75%) and differed only slightly by when that light was received. Regeneration densities were highest with high levels of morning light, but lowest in sections receiving high levels of light received evenly throughout the day (Fig. 2B). We speculate that this may reflect light-influenced microclimatic variation in site conditions, with pre-noon light exposure associated with more moderate temperatures, humidity, and other factors. These patterns of microclimatic variation have been documented in other forest gaps and linked to physiological growth responses such as carbon fixation and photosynthetic rates in several temperate hardwood tree species (Canham et al. 1990; Wayne and Bazzaz 1993; Potter and Croft 2000; Guo et al. 2001; Schnake et al. 2023). Conversely, site conditions may have been hotter and drier in sections receiving high light levels in the afternoon. These results, along with the largely non-significant differences in oak and hickory densities across light groups (Fig. 2B), suggest that while light plays a key role in spatial partitioning, other factors also contribute. We speculate that interspecific competition between oaks and hickories and the high densities of red maple and yellow-poplar within these gaps (Table 4) could also influence the spatial patterns of competitive oak and hickory regeneration. We recommend that a valuable next step for researchers is to investigate light at a much finer scale than was possible in this experiment and explore the spatial patterns among focal species and their competitors.

Our findings show that GSH harvesting can be a viable option for regenerating upland oaks and hickories in the southern Appalachian Mountains. This supports continued implementation and assessment of GSH in the region. Our results also provide justification for continued development and testing of alternative gap-based harvest approaches like expanding-gap or “femelschlag” systems in which GSH is often an initial component (Forrester et al. 2023). The combined results of our analysis on spatial patterns of regeneration and light levels can also provide meaningful guidance for silviculturists and researchers developing gap-based harvest prescriptions. Specifically, the light modeling methodology could be replicated and used to inform gap shapes, sizes, and distribution of harvest gaps across sites that maximize area of the light levels where we documented higher densities of oak and hickory regeneration. A similar approach could also be used to inform the scale and direction of gap expansions in femelschlag systems, although this would ideally be preceded by research exploring spatial patterning and light levels in the forested environment surrounding gaps. However, high densities of competing mesophytic species in our gaps suggest that regardless of the gap-based harvest system used, intermediate stand treatments such as crop tree release will likely be necessary for regenerated oak and hickory to remain competitive and achieve canopy dominance or co-dominance in future forests. The spatial trends revealed through point pattern analyses may again be helpful when prescribing these release treatments by allowing field crews to focus on portions of the gaps where candidates for release may be more prevalent.

Our results also underscore the importance of establishing and maintaining long-term demonstration sites to study forest dynamics under different management approaches. Continuing to improve our understanding of regeneration processes under gap-based harvesting systems as we have done here will be fundamental to developing silvicultural approaches for managing resilient forests as global changes alter disturbance patterns and species pools. The availability of long-term demonstration and study sites facilitates these pursuits.

Acknowledgements

We thank K. Bakken, H. Brown, P. Menzies, and the Bent Creek Experimental Forest staff for their assistance in the field during various phases of this study. We appreciate thoughtful pre-submission comments and edits from J. Willis and C. Moorman, and feedback from our formal reviewers. This paper was written and prepared, in part, by U.S. Government employees on official time. This research was supported the U.S. Department of Agriculture, Forest Service. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or U.S. Government determination or policy.

Article information

History dates

Received: 11 March 2025
Accepted: 13 June 2025
Accepted manuscript online: 27 June 2025
Version of record online: 11 August 2025

Notes

This paper is one of a selection of papers from the North American Forest Ecology Workshop (NAFEW), Asheville, NC, June 24-27, 2024.

Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

David K. Schnake https://orcid.org/0000-0002-1974-7580
Jodi A. Forrester https://orcid.org/0000-0002-4606-0776
Andrew J. Sánchez Meador https://orcid.org/0000-0003-4238-8587

Author notes

Jodi A. Forrester and Tara L. Keyser served as Guest Editors at the time of manuscript review and acceptance; peer review and editorial decisions regarding this manuscript were handled by another editorial board member.

Author contributions

Conceptualization: DKS, JAF, TLK, ASM
Formal analysis: DKS
Investigation: DKS
Methodology: DKS, ASM
Project administration: JAF
Supervision: JAF
Writing – original draft: DKS
Writing – review & editing: DKS, JAF, TLK, ASM

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2025-0066.

References

Berg, E.C., Zarnoch, S.J., and McNab, W.H. 2019. Twenty-year survivorship of tree seedlings in wind-created gaps in an upland hardwood forest in the eastern US. New For. **50**(2): 323–344. doi:10.1007/s11056-018-9685-x.

Bragg, D.C. 2013. Composition, biomass, and overstory spatial patterns in a mature pine-hardwood stand in southeastern Arkansas. Castanea, **78**(1): 37–55. doi:10.2179/12-033.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. **9**(2): 378–400. doi:10.32614/rj-2017-066.

Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., et al. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic region. Gen. Tech. Rep. NRS-33. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. p. 100. doi:10.2737/NRS-GTR-33.

Caldas de Castro, M., and Singer, B.H. 2006. Controlling the false discovery rate: a new application to account for multiple and dependent tests in local statistics of spatial association. Geogr. Anal. **38**(2): 180–208. doi:10.1111/j.0016-7363.2006.00682.x.

Caldwell, P.V., Miniat, C.F., Elliott, K.J., Swank, W.T., Brantley, S.T., and Laseter, S.H. 2016. Declining water yield from forested mountain watersheds in response to climate change and forest mesophication. Global Change Biol. **22**(9): 2997–3012. doi:10.1111/gcb.13309. PMID: 27038309.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**: 620–631. doi:10.1139/x90-084.

Cunningham, R.A. 2014. Effects of regeneration opening size and simulated crop tree release on volume yields and economic value in oak-dominated stands.Master of Science Thesis, University of Kentucky, Kentucky. https://uknowledge.uky.edu/forestry_etds/19 [accessed January 2025].

Dale, M.E., Smith, H.C., and Pearcy, J.N. 1995. Size of clearcut opening affects species composition, growth rate, and stand characteristics. Res. Pap. NE-698. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. p. 21. doi:10.2737/NE-RP-698

Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. Biotropica, **12**(2): 47–55. doi:10.2307/2388156.

Dey, D.C., Miller, G.W., and Kabrick, J.M. 2007. Sustaining northern red oak forests: managing oak from regeneration to canopy dominance in mature stands. *In* Integrated Restoration of Forested Ecosystems to Achieve Multi-Resource Benefits: Proceedings of the 2007 National Silviculture Workshop. *Edited by* R.L. Deal. Gen. Tech. Rep. PNW-GTR-733. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, pp. 91–105.

Dhungel, G., Rossi, D., Henderson, J.D., Abt, R.C., Sheffield, R., and Baker, J. 2023. Critical market tipping points for high-grade white oak inventory decline in the Central Hardwood region of the United States. J. For. **121**(3): 224–234. doi:10.1093/jofore/fvad005.

Dillaway, D.N., Stringer, J.W., and Rieske, L.K. 2007. Light availability influences root carbohydrates, and potentially vigor, in white oak ad-

vance regeneration. For. Ecol. Manage. **250**(3): 227–233. doi:10.1016/j.foreco.2007.05.019.

Dimov, L.D., Chambers, J.L., and Lockhart, B.R. 2013. Tree species exhibit complex patterns of distribution in bottomland hardwood forests. Ann. For. Sci. **70**(8): 813–823. doi:10.1007/s13595-013-0322-8.

Elliott, K.J., and Vose, J.M. 2010. Short-term effects of prescribed fire on mixed oak forests in the southern Appalachians: vegetation response. J. Torrey Bot. Soc. **137**(1): 49–66. doi:10.3159/09-ra-014.1.

ESRI. 2024. ArcGIS Pro Version 3.3.0. Redlands, CA: Environmental Systems Research Institute.

Fei, S., Kong, N., Steiner, K.C., Moser, W.K., and Steiner, E.B. 2011. Change in oak abundance in the eastern United States from 1980 to 2008. For. Ecol. Manage. **262**(8): 1370–1377. doi:10.1016/j.foreco.2011.06.030.

Forrester, J.A., Keyser, T.L., and Schnake, D.K. 2023. Ecological silviculture for southern Appalachian hardwood forests. *In* Ecological silvicultural systems: exemplary models for sustainable forest management. *Edited by* B.J. Palik and A.W. D'Amato. John Wiley and Sons Ltd., Hoboken, NJ. USA. pp. 98–111.

Franklin, J.F., Johnson, K.N., and Johnson, D.L. 2018. Ecological forest management. Waveland Press, Long Grove, IL, USA. p. 646.

Fu, P., and Rich, P.M. 1999. The Solar Analyst 1.0 User Manual. Helios Environmental Modeling Institute (HEMI), USA.

Fu, P., and Rich, P.M. 2000. A geometric solar radiation model with applications in agriculture and forestry. Comput. Electron. Agric. **37**(1–3): 25–35. doi:10.1016/S0168-1699(02)00115-1.

Getis, A., and Ord, J.K. 1992. The analysis of spatial association by use of distance statistics. Geogr. Anal. **24**(3): 189–206. doi:10.1111/j.1538-4632.1992.tb00261.x.

Getis, A., and Ord, J.K. 2010. The analysis of spatial association by use of distance statistics. *In* Perspectives on spatial data analysis. *Edited by* L. Anselin and S. J. Rey. Springer Berlin Heidelberg. pp. 127–145. doi:10.1007/978-3-642-01976-0_10.

Gottschalk, K.W. 1994. Shade, leaf growth and crown development of *Quercus rubra*, *Q. velutina*, *Prunus serotina*, and *Acer rubrum* seedlings. Tree Physiol. **14**. 735–749. doi:10.1093/treephys/14.7-8-9.735. PMID: 14967644.

Greenberg, C.H., and McNab, W.H. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. For. Ecol. Manage. **104**(1–3): 179–191. doi:10.1016/S0378-1127(97)00246-6.

Greenberg, J.L., Collins, B.S., McNab, W.H., Miller, D.K., and Wein, G.R. 2016. Introduction to natural range of variation: type, frequency, severity, and post-disturbance structure in Central hardwood forests. *In* Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in Central hardwood forests, USA. Managing forest ecosystems. Vol. 32. *Edited by* C.A. Greenberg and B.C. Collins. Springer, Cham. pp. 1–32. doi:10.1007/978-3-319-21527-3_1.

Greenler, S.M., and Saunders, M.R. 2019. Short-term, spatial regeneration patterns following expanding group shelterwood harvests and prescribed fire in the Central Hardwood Region. For. Ecol. Manage. **432**(October 2018): 1053–1063. doi:10.1016/j.foreco.2018.10.043.

Gu, L., O'Hara, K.L., Li, W., and Gong, Z. 2019. Spatial patterns and interspecific associations among trees at different stand development stages in the natural secondary forests on the Loess Plateau, China. Ecol. Evol. **9**(11): 6410–6421. doi:10.1002/ece3.5216.

Guo, Y., Shelton, M.G., and Lockhart, B.R. 2001. Effects of light regimes on the growth of cherrybark oak seedlings. For. Sci. **47**(2): 270–277. doi:10.1093/forestscience/47.2.270.

Halpin, C.R., Lorimer, C.G., Hanson, J.J., and Palik, B.J. 2017. Predicted long-term effects of group selection on species composition and stand structure in northern hardwood forests. For. Ecol. Manage. **400**: 677–691. doi:10.1016/j.foreco.2017.06.037.

Hart, J.L. 2016. Gap scale disturbances in Central hardwood forests with implications for management. *In* Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in central hardwood forests, USA. Managing forest ecosystems. Vol. 32. *Edited by* C.A. Greenberg and B.C. Collins. Springer, Cham. pp. 33–47. doi:10.1007/978-3-319-21527-3_2.

Hartig, F. 2021. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models (R package version 0.4.4). Available from http://florianhartig.github.io/DHARMa/ [accessed January 2025].

Jenkins, M.A., and Parker, G.R. 1998. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. For. Ecol. Manage. **109**(1–3): 57–74. doi:10.1016/S0378-1127(98)00256-4.

Johnson, P.S., Shifley, S.R., Rogers, R., Dey, D.C., and Kabrick, J.M. 2019. The ecology and silviculture of oaks. 3rd ed. CABI, Wallingford, UK. p. 611. doi:10.1079/9781780647081.0000.

Lamson, N.I., Smith, H.C., Perkey, A.W., and Brock, S.M. 1990. Crown release increases growth of crop trees. Res. Pap. NE-635. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA. p. 8.

Leak, W.B. 1999. Species composition and structure of a northern hardwood stand after 61 years of group/patch selection. North. J. Appl. For. **16**(3): 151–153. doi:10.1093/njaf/16.3.151.

Length, R. 2021. emmeans: Estimated marginal means, aka least-squares means (R package version 1.7.0).

Lhotka, J.M. 2013. Effect of gap size on mid-rotation stand structure and species composition in a naturally regenerated mixed broadleaf forest. New For. **44**(3): 311–325. doi:10.1007/s11056-012-9319-7.

Lhotka, J.M., and Stringer, J.W. 2013. Forest edge effects on *Quercus* reproduction within naturally regenerated mixed broadleaf stands. Can. J. For. Res. **43**(10): 911–918. doi:10.1139/cjfr-2013-0231.

Loftis, D.L. 2004. Upland oak regeneration and management. *In* Upland oak ecology symposium: history, current conditions, and sustainability. *Edited by* M.A. Spetich. Gen. Tech. Rep. SRS-73. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. pp. 163–167. doi:10.2737/SRS-GTR-73.

Lorber, J.H. 2003. Effects of alternative silviculture practices on oak regeneration in the southern Appalachians. Master of Science thesis, Virginia Polytechnic Institute and State University, Virginia. Available from https://vtechworks.lib.vt.edu/handle/10919/35166 [accessed January 2025].

Lorimer, C.G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. Ecology, **70**(3): 565–567. doi:10.2307/1940207.

McEwan, R.W., Dyer, J.M., and Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. Ecography, **34**(2): 244–256. doi:10.1111/j.1600-0587.2010.06390.x.

McNab, W.H., and Oprean, T.M. 2021. Composition and structure of reproduction in group selection openings after 20 years in a southern Appalachian mixed-Hardwood forest. For. Sci. **67**(3): 335–346. doi:10.1093/forsci/fxab001.

McNab, W.H., Greenberg, C.H., and Berg, E.C. 2004. Landscape distribution and characteristics of large hurricane-related canopy gaps in a southern Appalachian watershed. For. Ecol. Manage. **196**(2–3): 435–447. doi:10.1016/j.foreco.2004.04.004.

McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., and Waldon, J. 2007. Forestry matters: decline of oaks will impact wildlife in Hardwood forests. J. Wildl. Manage. **71**(5): 1717–1728. doi:10.2193/2006-169.

Miller, G.W., Schuler, T.M., and Smith, H.C. 1995. Method for Applying Group Selection in Central Appalachian Hardwoods: Res. Pap. NE-696.

Niinemets, Ü., and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. **76**(4): 521–547. doi:10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.

Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience, **58**(2): 123–138. doi:10.1641/B580207.

Ord, J.K., and Getis, A. 1995. Local spatial autocorrelation statistics: distributional issues and an application. Geogr. Anal. **27**(4): 286–306. doi:10.1111/j.1538-4632.1995.tb00912.x.

Palik, B.J., D'Amato, A.W., Franklin, J.F., and Johnson, K.N. 2020. Ecological silviculture: foundations and applications. Waveland Press, Long grove, IL, USA. p. 343.

Phillips, D., and Shure, D. 2015. Patch-size effects on early succession in southern Appalachian forests. Ecology, **71**(1): 204–212. doi:10.2307/1940260.

Potter, B.E., and Croft, P.J. 2000. Spatial variation in growing season heat sums within northern hardwood forest canopy gaps. *In* Second Symposium on Environmental Applications. pp. 130–134.

Poznanovic, S.K., Poznanovic, A.J., Webster, C.R., and Bump, J.K. 2014. Spatial patterning of underrepresented tree species in canopy gaps 9 years after group selection cutting. For. Ecol. Manage. **331**: 1–11. doi:10.1016/j.foreco.2014.06.029.

R Core Team. 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Raudenbush, S.W., Yang, M.L., and Yosef, M. 2000. Maximum likelihood for generalized linear models with nested random effects via high-order, multivariate laplace approximation. J. Comput. Graph. Stat. **9**(1): 141–157. doi:10.1080/10618600.2000.10474870.

Rich, P.M., Dubayah, R., Hetrick, W.A., and and Saving, S.C. 1994. Using Viewshed Models to Calculate Intercepted Solar Radiation: Applications in Ecology. American Society for Photogrammetry and Remote Sensing Technical Papers, pp. 524–529.

Rich, P.M., and Fu, P. 2000. Topoclimatic habitat models. *In* Proceedings of the Fourth International Conference on Integrating GIS and Environmental Modeling (GIS/EM4): Problems, Prospects and Research Needs. *Edited by* B. Parks. Banff, Alberta, Canada.

Ricklefs, R.E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. Am. Nat. **111**(978): 376–381. doi:10.1086/283169.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. Ecology, **63**(5): 1533–1546. doi:10.2307/1938878.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press. pp. 17–33. doi:10.1016/B978-0-08-050495-7.50007-7.

Schnake, D.K., Forrester, J.A., Sánchez Meador, A.J., Mladenoff, D.J., and Lorimer, C.G. 2023. Tree regeneration and spatial patterning among midtolerant tree species following gap-based harvesting in a temperate hardwood forest. Front. For. Global Change, **6**. doi:10.3389/ffgc.2023.1144091. PMID: 38482191.

Sharma, B.D., Wang, J., and Miller, G. 2008. A GIS-based approach to stand visualization and spatial pattern analysis in a mixed hardwood forest in West Virginia. *In* Proceedings, 16th Central Hardwood Forest Conference, West Lafayette, IN. Gen. Tech. Rep. NRS-P-24. *Edited by* D.F. Jacobs and C.H. Michler. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. pp. 356–365.

Simon, S.A., Collins, T.K., Kauffman, G.L., McNab, W.H., and Ulrey, C.J. 2005. Ecological zones in the Southern Appalachians: first approximation. Res. Pap. SRS-41. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. p. 41. doi:10.2737/SRS-RP-41.

Vilhar, U., Roženbergar, D., Simončič, P., and Diaci, J. 2015. Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps. Ann. For. Sci. **72**(2): 253–266. doi:10.1007/s13595-014-0424-y.

Vose, J.M., and Elliott, K.J. 2016. Oak, fire, and global change in the eastern USA: what might the future hold? Fire Ecol. **12**(2): 160–179. doi:10.4996/fireecology.1202160.

Wayne, P.M., and Bazzaz, F.A. 1993. Morning vs afternoon sun patches in experimental forest gaps: consequences of temporal incongruency of resources to birch regeneration. Oecologia, **94**(2): 235–243. doi:10.1007/BF00341322. PMID: 28314037.

Weigel, D.R., and Parker, G.R. 1997. Tree regeneration response to the group selection method in Southern Indiana. North. J. Appl. For. **2**(14): 90–94. https://research.fs.usda.gov/treesearch/14831. doi:10.1093/njaf/14.2.90.

Woodbridge, M., Keyser, T.L., and Oswalt, C. 2022. Stand and environmental conditions drive functional shifts associated with mesophication in eastern US forests. Front. For. Global Change, **5**. doi:10.3389/ffgc.2022.991934. PMID: 36278245.

Yarnell, S.L. 1998. The southern Appalachians: a history of the landscape. Gen. Tech. Rep. SRS-18. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. p. 52.

Ziegler, J.P., Hoffman, C.M., Fornwalt, P.J., Sieg, C.H., Battaglia, M.A., Chambers, M.E., and Iniguez, J.M. 2017. Tree regeneration spatial patterns in ponderosa pine forests following stand-replacing fire: influence of topography and neighbors. Forests, **8**(10): 1–16. doi:10.3390/f8100391.