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Effects of experimental partial harvesting regimes on forest canopy structure and complexity

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ABSTRACT

The physical structure of forest canopies regulates numerous ecological processes and functions, and management strategies to promote specific structural features, such as high structural complexity, are increasingly desired. Partial disturbances — including partial harvests — can modify forest canopy structure, but their specific effects may be influenced by differences in characteristics such as intensity and frequency. Understanding the variable effects of silvicultural treatments on canopy structure will be essential to designing silvicultural regimes that can promote canopy structural complexity. We evaluated the effect of partial harvesting regimes on canopy structure (i.e., density, cover, height, arrangement, and heterogeneity) and complexity (as rugosity), quantified using a suite of metrics derived from portable canopy lidar, across three levels of harvesting intensity in three multi-decadal silvicultural experiments. We specifically assessed: 1) how repeated partial harvesting disturbance affected canopy structure and complexity relative to unmanipulated controls, 2) whether effects of partial harvesting differed among harvesting intensities or 3) between old- and second-growth stands, and 4) if canopy light interception differed among stands with different histories of partial harvesting disturbance. Findings indicated that canopy structure development under partial harvesting regimes differed from that of control stands, reducing vertical and canopy structural complexity at a fine (i.e., 1–6 ha treatment unit) scale, but increasing among-unit variability in canopy structure relative to controls. Variation in intensity among treatments produced relatively little distinction in fine-scale canopy structural outcomes, but the higher intensity selection harvesting regime in particular differed significantly from controls across all metrics of canopy structure. Partial harvesting affected the developmental trajectories of both old-growth and maturing, secondary forest stands, where selection-based management seemed to decrease structural features associated with old forests. Our findings suggest management regimes developed for timber goals could accommodate alternative goals that promote multi-scale canopy structural complexity across managed northern hardwood forest landscapes by adapting the timing (e.g., extending cutting intervals) and intensity (e.g., low intensity harvests) of partial harvesting to retain or develop elements of canopy complexity.

1. Introduction

Disturbances are a key driver of heterogeneity in forest ecosystem structure and function across a range of spatial and temporal scales (Frolking et al., 2009; Turner, 2010). Characteristics of disturbances, including factors such as spatial extent, frequency, and severity interact with forest attributes (e.g. vegetation composition, density, and spatial arrangement) to shape structural and functional outcomes (Turner et al., 1998; Turner, 2010; Seidl et al., 2011; Johnstone et al., 2016). Partial disturbances modify forest and canopy structure without resulting in complete stand replacement (Oliver and Larson, 1996; Cowden et al., 2014; Hart and Kleinman, 2018), leaving material and spatial legacies that can influence ecosystem recovery and resulting forest structure and function over long timescales (Turner, 2010; Johnstone et al., 2016). A range of partial disturbance severities and patterns have been an important component of disturbance regimes in temperate mixed northern hardwood forests of North America, where wind, pest outbreaks, and fire were prominent agents of disturbance historically (Frelich and Lorimer, 1991; Schulte and Mladenoff, 2005; Stueve et al., 2011). Moderate severity partial disturbances (i.e., those resulting in

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more than single-tree gap formation) can have considerable effects on forest structure and complexity (Hanson and Lorimer, 2007; Atkins et al., 2020), help maintain species diversity (Woods, 2004), and strongly influence forest productivity and carbon dynamics (Hicke et al., 2012). However, the effects of moderate partial disturbances on forests are less understood compared to low severity gap-scale or catastrophic stand-replacing disturbances (Hart and Kleinman, 2018), and variation among partial disturbances in severity, spatial patterning, and frequency can result in a wide range of structural and functional outcomes (Hart and Kleinman, 2018; Aszalós et al., 2022; Alveshere, 2023).

In the modern northern hardwood forest landscape, anthropogenic disturbance — primarily in the form of partial harvesting systems — dominates the contemporary disturbance regime (Stueve et al., 2011; Canham et al., 2013). Partial harvests in this region are typically applied using selection systems, which are uneven-aged approaches that loosely mimic natural gap dynamics through patchy removal of 20–30 % of stand basal area on a 10–15 year interval (Tubbs, 1977a; Hanson and Lorimer, 2007). Selection systems were introduced during the early-to-mid-20th century as a "more natural" harvesting approach in response to concerns around the sustainability of exploitative logging practices and have been widely adopted in northern hardwood silviculture, in part because they favor regeneration and dominance of late-successional, shade-tolerant species with high commercial value (Eyre and Zillgett, 1953; Kern et al., 2014; Pond et al., 2014). However, selection systems also produce relatively homogenous structural conditions because openings are formed synchronously and are largely uniform in size (Angers et al., 2005; Hanson and Lorimer, 2007). This contrasts with the natural disturbance regime, where "gap-phase" dynamics are superimposed on less frequent moderate-severity events, creating canopy openings of varying size and promoting structural heterogeneity (Runkle, 1982; Hanson and Lorimer, 2007). Prior studies have illustrated simplified species composition (Leak and Sendak, 2002; Neuendorff et al., 2007; Gronewold et al., 2010) and reductions in structural elements nominally associated with structural complexity (e.g., defective trees, large snags, and large living trees) in northern hardwood stands following selection-based management (Angers et al., 2005; Gronewold et al., 2010; Straus et al., 2011; Yoshida et al., 2017).

Partial disturbance, whether associated with natural or anthropogenic sources, alters canopy structure including both the quantity and spatial distribution of canopy vegetation (e.g., Atkins et al., 2020; Fahey et al., 2020; Gough et al., 2022), factors which affect the forest resource environment and ecosystem functioning (Walcroft et al., 2005; Reich, 2012; Atkins et al., 2018b). Vegetation quantity, often estimated with measures such as Leaf Area Index (LAI; one-sided leaf area per unit ground area) or Vegetation Area Index (VAI; area of all vegetative tissues — as inferred from lidar return density — per unit ground area), influences forest light environments and related processes; for example, canopies with higher vegetation area/density intercept more light, thereby facilitating greater canopy photosynthetic rates and net primary productivity (NPP) (Reich, 2012; Atkins et al., 2018b). Canopy structural complexity describes the physical arrangement of canopy vegetation and is often quantified as canopy rugosity (i.e., spatial variation in the positioning of canopy elements), which has been mechanistically linked to productivity through positive relationships with canopy light interception and light-use efficiency (LUE) (Hardiman et al., 2011, 2013b; Atkins et al., 2018b; Gough et al., 2019). Shifts in canopy structural complexity following moderate disturbance can continue to manifest over time with longer-term implications for ecosystem structure and function (Gough et al., 2016, 2022; Atkins et al., 2020). Understanding the effects of selection harvesting — the preeminent disturbance agent in northern temperate hardwood forests — on the physical structure and complexity of forest canopies is therefore a crucial step toward more sustainably managing northern hardwood forests.

The overarching goal of this study was to evaluate how selection-based partial harvesting regimes have influenced forest canopy structure and complexity in northern hardwood forests. Several long-term experimental silvicultural trials emphasizing selection cutting systems were initiated in the upper Great Lakes region in the mid-20th century to evaluate sustainable-yield partial harvesting strategies in the region's northern hardwood forests (D'Amato et al., 2011; Kern et al., 2014). These trials offer an experimental framework in which to test how partial disturbances in the form of variants of partial harvesting over multi-decadal time scales influence forest canopy structure. To address our overall research goal, we assessed the following specific research questions: 1) How does repeated partial harvesting disturbance affect canopy structure and complexity relative to unmanipulated controls?; 2) How does varying intensity of partial harvesting differentially affect canopy structure?; 3) Does the effect of partial harvesting on canopy structure differ between old- and second-growth stands?; and 4) Does canopy light interception differ among stands with different histories of partial harvesting disturbance? We hypothesized that canopy structure would be simplified by partial harvesting, this effect would be greatest in higher intensity treatments and second-growth forests, and that canopy light interception would be greatest in controls and decline with increasing treatment intensity. In addition to evaluating the consequences of widespread utilization of selection systems on the ecology of northern hardwood forests, our results are also discussed in relation to the general effects of variable disturbance patterns on forest canopy structure and complexity.

2. Methods

2.1. Study ecosystem

The influence of partial harvesting regimes on forest canopy structure was evaluated in three long-term silvicultural experiments situated in the Laurentian Mixed Forest Province of the North Central United States' Great Lakes region (Table 1; Fig. 1; additional details below). Climate in the region is continental with cold winters and warm summers. Average temperatures range from 17.4 °C in summer to − 9.8 °C in winter (Berndt, 1988). Mean annual precipitation ranges from 813 to 874 mm across the three sites (Berndt, 1988; Adams et al., 2008). The three study sites are situated in northern hardwood forests. Composition and soil variation among the sites are described below. The study design at each site included a control (reference condition, untreated) and

Table 1
Summary of silvicultural trials and field plots (i.e. treatment units) used for this study. Intensity corresponds (inversely) to the residual stocking, or target basal area retained following treatments during repeated partial harvest cutting.

Trial	Location	Forest condition at initiation of trial[a]	No. units surveyed	Unit area (ha)	Intensity (residual stocking [m^2 ha^{-1}])
Cutting Cycles and Stocking Levels Study	Dukes EF *, MI	Old-growth, uneven-aged	29	4–6	High (11.5)
			8		Moderate (16.1)
			9		Low (20.7)
			3		Control
Cutting Methods Study	Argonne EF*, WI	Second-growth, even-aged	12	1	High (13.8)
			3		Moderate (17.2)
			3		Low (20.7)
			3		Control
Cutting Methods Study	Ford Forest, MI	Second-growth, uneven-aged	4	2–6	High (11)
			1		Moderate (16)
			1		Low (21)
			1		Control

* EF: Experimental Forest.
[a] Old-growth condition: stands not cleared or intensely cut during European settlement in the late 19th and early 20th centuries. Second-growth condition: stands that were cutover during the same period.

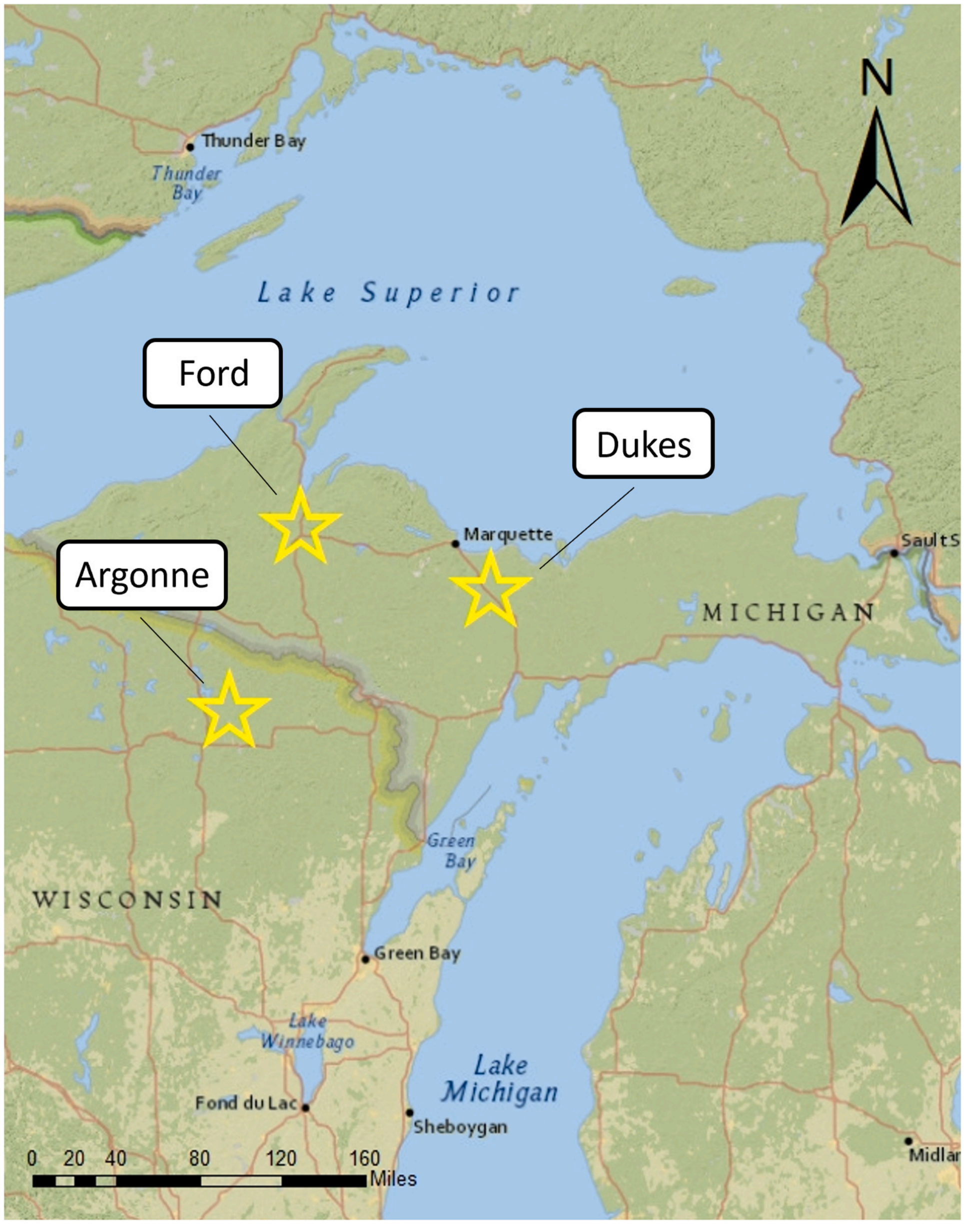

Fig. 1. Locations of three multi-decadal silvicultural trials in the North Central United States.

treatments that test variations of partial harvesting, representing a gradient of disturbance intensity.

The Cutting Cycles and Stocking Levels Study (CCSLS) at Dukes Experimental Forest, Hiawatha National Forest, in the Upper Peninsula of Michigan (46.364138, − 87.135231) was established by the USDA Forest Service in 1952 (Crow et al., 1981). The study was established in an uneven-aged, old-growth northern hardwood forest dominated by sugar maple (*Acer saccharum* Marsh.) with minor salvage cutting prior to study establishment (Tubbs 1977b). Soils include Munising sandy loam, Skanee sandy loam, Angelica sandy loam, and Linwood muck (Adams et al., 2008). The experiment tested effects of selection harvesting residual basal areas and cutting cycles on growth rates (Crow et al., 1981). Treated (experimental) units are 4–6 ha in area and arranged in a randomized complete block (RCB) design with three blocks (replicates). The experiment was actively treated between 1952 and 1972, treated in part in 1985, and again 2007–2008. A preliminary analysis indicated that, for our study, the CCSLS cutting cycle effects were not significant, but stocking treatments were (see Appendix A). Therefore, data were collected from experimental units representing three stocking levels or residual basal areas (and ignoring cutting cycle; Table 1). Because an uncut control was not explicitly included in the study design, we instead sampled sugar maple-dominated stands in the Dukes Research Natural Area, a 94-ha unmanaged area adjacent to treated units but within the same forest that has served as a reference unit for nearby silviculture studies (Woods, 2000). The Dukes RNA and CCSLS share similar soils, disturbance history, and forest composition (Adams et al., 2008; additional details at https://www.fs.usda.gov/research/nrs/rnas/locations/dukes).

The Cutting Methods Study at Argonne Experimental Forest, Chequamegon-Nicolet National Forest, in northern Wisconsin (45.753575, − 88.969119) was established by the USDA Forest Service in 1951. At establishment, the site was an even-aged, second-growth northern hardwood forest that regenerated after a cutover in 1905 (Erdmann and Oberg, 1973). The dominant vegetation includes sugar maple, yellow birch (*Betula alleghaniensis* Britton), and eastern hemlock (*Tsuga canadensis* [L] Carr), which occur primarily on Iron River Loam soils (Adams et al., 2008). The study is a RCB design with four levels of stocking (including a control) and three blocks. Experimental units are

1-ha in size and were harvested using single tree selection-like treatments at 10-year cutting cycle intervals from 1952 to 2012.

The Cutting Methods Study at Ford Forest, Michigan Technological University, in the Upper Peninsula of Michigan (46.646828, −88.483525) was established in 1956 (Bourdo and Johnson, 1957). The study site is an uneven-aged northern hardwood forest primarily composed of sugar maple and red maple (*Acer rubrum* L.), but the area once supported pine-hardwood forest. The primary soil type is Allouez gravelly course sandy loam (Berndt, 1988). Prior to study establishment the stands were selectively cut in the early 1900s, leaving approx. 30 % of the merchantable volume (Bourdo and Johnson, 1957). Only one block was created, and treatment and control units were assigned non-randomly in a sequence of increasing management intensity. For our study, three stocking levels and a control experimental unit at the Ford Forest were used. Experimental units ranged from approx. 2–6 ha in area and were treated with partial harvesting (single-tree selection) on 10-year cutting cycles to prescribed stocking levels (Table 1).

2.2. Sampling methods

In summer of 2018, three 50-m transects were established to collect canopy structure and light transmittance data within each experimental unit. Transect length was determined based on prior work showing 50 m is adequate to characterize canopy structure and its variability using the methodology we employed (details below; Hardiman et al., 2018). Transects were randomly distributed across units but were always sampled perpendicularly to the stand edge. At each of the experimental units, a portable canopy LiDAR (PCL) system was used to measure forest canopy structure (Parker et al., 2004). The PCL system is a user mounted apparatus that holds an upward facing laser (LD90-3100VHS-FLP, 2000 Hz; RIEGL Laser Measurement Systems; Horn, Austria); pulses are emitted vertically towards the canopy and points are generated along the walked transect at each height at which the pulse is occluded by vegetation. Pulse hits are registered to create a 2-dimensional point cloud representing canopy structure along the length of the transect (mean pulse density across transects = 496 pulses m^{-1}). Photosynthetically active radiation (PAR) was measured for every 1 m segment along the same transects from a height of 1 m using a digital ceptometer (AccuPAR LP-80, Decagon Devices, Inc, Pullman, WA) under uniform, clear sky conditions. Above canopy PAR was estimated by measuring PAR in fully illuminated areas under nearby canopy openings.

2.3. Data processing

Raw PCL data were processed in R 4.2.1 (R Core Team, 2022) using the process_multi_pcl() function in the *forestr* package (Atkins et al., 2018a). Points from each cloud were segregated into 1 m by 1 m bins to create a 2-dimensional grid characterizing vegetation area and density (assessed as VAI) for each X, Z bin in the transect (Fig. 2). A suite of 23 metrics of canopy structural characteristics that describe traits of the canopy were then calculated from the gridded data (Table 2; Fahey et al., 2019). Treatment unit-level means were calculated for each metric by averaging results from the three transects in each unit. For a more detailed description of processing with the *forestr* package, see Atkins et al. (2018a). The fraction of PAR intercepted by the canopy (fPAR) was calculated as $(PAR_{above\ canopy} - PAR_{below\ canopy})/PAR_{above\ canopy}$. For

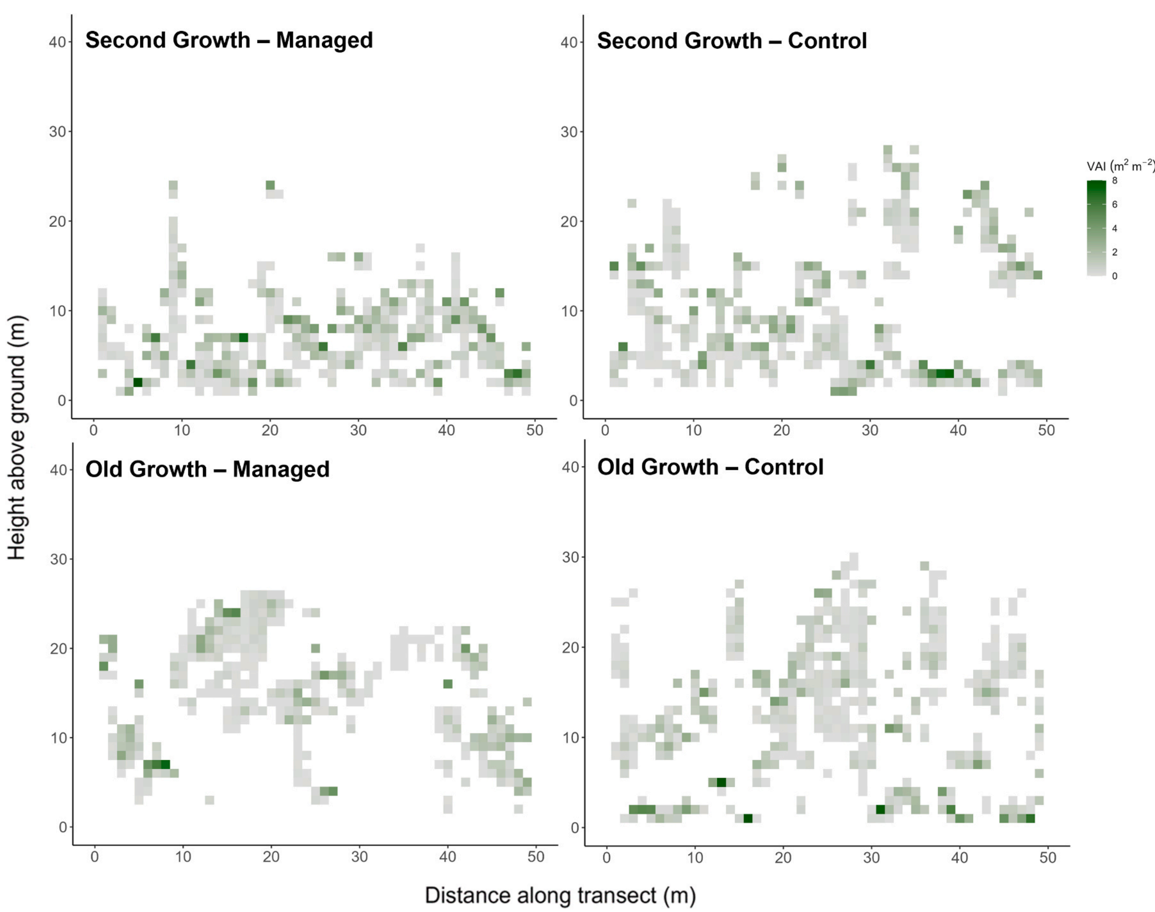

Fig. 2. Portable canopy lidar (PCL) hit grids depicting vegetation area index (VAI) and its distribution throughout the canopy profile in four northern hardwood stands in the North Central United States. Each panel represents a single 50-m transect, or 2-dimensional "slice" of the canopy. Each grid cell corresponds to a 1 m × 1 m (X, Z) data bin, with darker colors indicating greater vegetation area and density.

Table 2
Description of canopy structure metrics computed from lidar data using the *forestr* R package (Atkins et al., 2018a).

Metric	Data name	Description
Area and density		
Mean VAI	mean.vai	Mean column sum of vegetation area index (VAI) – ratio of lidar returns in each 1 m^2 (x, z) bin to total no. returns in column (i.e., ratio of one-sided canopy vegetation area to ground area).
Maximum VAI (VAI_{max})	max.el	VAI of the densest 1 m^2 (x, z bin) within the canopy
Mean height of VAI_{max}	mode.el	Mean height of VAI_{max} across all columns in transect
Mean peak VAI	mean.peak.vai	Mean of VAI_{max} across all columns in transect
SD of height of max VAI	mode.2	Standard deviation of height of VAI_{max} for each column
Height		
Mean leaf height	mean.height	Mean of density-adjusted* average lidar return (i.e, vegetation) heights for each column across a transect
$Height^2$	height.2	Standard deviation of column mean leaf height
Variance in mean height	mean.height.var	Variance of column mean leaf height
Root mean square height	mean.height.rms	Root mean square of column mean leaf height
Mean outer canopy height	mean.max.height	Mean of maximum canopy height across all columns in transect
Maximum canopy height	max.can.height	Maximum height of canopy (raw lidar returns)
Mean return height	mean.return.ht	Mean height of raw lidar returns
SD of height of max VAI	sd.return.ht	Standard deviation of the height of VAI_{max} for each column
Arrangement		
Clumping index	clumping.index	Degree of foliar clumping (see Hardiman et al., 2013a for derivation)
Canopy porosity	porosity	Ratio of 1 m^2 (x, z) bins with no lidar returns to total number of bins
Cover/Openness		
Deep gap fraction	deep.gap	Number of columns with no lidar returns divided by transect length
Cover fraction	cover.fraction	Ratio of the number of lidar returns to the number of lidar pulses emitted
Gap fraction	sky.fraction	1 - the ratio of the number of lidar returns to the number of lidar pulses emitted
Heterogeneity/ Complexity		
Mean *SD* of leaf height	mean.std	Transect mean of column variability of mean leaf height
SD of vertical *SD*	std.std	Standard deviation of column variability of mean leaf height
Effective number of layers (ENL)	enl	Measure of vertical structure based on space occupied by vegetation within 1 m thick vertical layers relative to total space occupied in a stand
Rumple	rumple	Ratio of outer canopy surface area —interpolated from maximum canopy height of each column along a transect — to ground surface area (transect length)
Top rugosity	top.rugosity	Standard deviation of column maximum canopy heights across a transect
Canopy rugosity	rugosity	Horizontal (transect-wise) variance of vertical (column) variance in density-adjusted[a] mean leaf heights (i.e., horizontal and vertical spatial heterogeneity of vegetation density and its distribution)

Note: Table adapted from Atkins et al. (2018a); column footprint is 1 m.
[a] Density-adjusted: measure is adjusted to account for occlusion following methodology of MacArthur and Horn (1969); see Atkins et al. (2018a) for computational derivation.

each transect, $PAR_{below\ canopy}$ was calculated by averaging below-canopy PAR measurements (n = 50 per transect). Treatment unit-level means were calculated by averaging fPAR from the three transects in each unit.

2.4. Univariate analyses

Effects of treatment intensity on canopy structure and light attenuation were evaluated through analysis of variance (ANOVA) in R 4.2.1 (R Core Team, 2022). Relationships between specific canopy structural traits and light attenuation were further explored through correlation analysis. Treatment effects were evaluated for six response variables selected from the overall set of canopy structural metrics (Table 2) that describe different aspects of canopy structure (Atkins et al., 2018a): mean outer canopy height (MOCH) – a measure of canopy height, vegetation area index (VAI) – a measure of canopy vegetation area and density, cover fraction (CF) – a measure of cover, clumping index (Ω) – a measure of leaf arrangement, mean standard deviation of leaf height (meanStd) – a measure of vertical heterogeneity, and canopy rugosity (R_C) – a measure of canopy structural complexity. Effects on light attenuation were evaluated based on fPAR as a response variable.

Observations from Dukes, Argonne, and Ford sites were combined into a single dataset (n = 45) for analyses. For each response variable of interest, we fit a linear mixed-effects model using restricted maximum likelihood estimation via the 'lmerTest' package (Kuznetsova et al., 2017). Responses of interest were modeled with treatment intensity as a fixed effect and replicate nested within site as a random effect. Canopy rugosity data were log transformed to meet parametric requirements. Type III ANOVAs were used to evaluate differences among treatment intensities. Where differences were detected at alpha < 0.05, multivariate *t* distribution "mvt" - corrected pairwise comparisons were made among unweighted estimated marginal means for each intensity using the 'emmeans' package in R (Lenth, 2022). The same package and correction were used to contrast the estimated marginal mean from each intensity to the estimated marginal mean over the other treatment levels.

2.5. Multivariate analyses

Effects of treatment intensity and site on the full suite of canopy structural metrics were evaluated using Non-metric Multi-dimensional Scaling (NMDS) and Multi-response Permutation Procedure (MRPP) in PC-ORD v.7.09 (Wild Blueberry Media LLC, Corvallis, OR, USA). NMDS was conducted on a matrix of 23 structural response variables (factors; Table 2) and 45 plots using Sorensen's (Bray-Curtis) distance measure. Responses were relativized to their respective maximum values prior to analysis so that all variables were scaled equivalently (Fahey et al., 2019). NMDS was conducted with the "Slow and Thorough" autopilot setting, and the robustness of each solution evaluated from 250 runs each of real and randomized data (McCune and Grace, 2002). MRPP with Sorensen's (Bray-Curtis) distance measure was then used to test for significant differences in multivariate suites of traits among treatments and sites, and to make pairwise comparisons when main effects were significant (McCune and Grace, 2002).

3. Results

3.1. Univariate analyses

Across all three sites, all six evaluated structural response variables differed significantly among treatment intensity groups (all $P \leq 0.05$; Table 3). Mean outer canopy height (MOCH) differed significantly between only the High intensity treatment and controls based on individual pairwise comparisons ($P = 0.037$; Fig. 3A). A linear contrast of all three treatments against the control indicated that MOCH was lower in treatments compared to controls ($P = 0.023$). High intensity treatments had significantly lower vegetation area index (VAI) relative to controls

Table 3
Analysis of variance results for six structural response variables compared among treated and unmanipulated (control) stands from three silvicultural experiments in the north-central United States. High, moderate, and low treatments reflect treatment intensity and correspond with levels of basal area retention (Table 1).

Metric/Treatment	Mean (SE)	*F*	*df*	*P*
Mean vegetation area index (VAI)		3.645	3,35.628	0.022
Control	7.36 (0.453)			
High	6.23 (0.423)			
Moderate	6.65 (0.420)			
Low	6.51 (0.420)			
Mean outer canopy height (m)		2.919	3,35.961	0.047
Control	16.70 (1.047)			
High	13.50 (0.884)			
Moderate	13.90 (0.865)			
Low	14.00 (0.865)			
Clumping index		4.132	3,36.617	0.013
Control	0.91 (0.016)			
High	0.87 (0.014)			
Moderate	0.89 (0.014)			
Low	0.90 (0.014)			
Cover fraction		3.795	3,35.983	0.018
Control	97.00 (4.33)			
High	85.10 (3.97)			
Moderate	90.00 (3.93)			
Low	87.60 (3.93)			
Mean *SD* of leaf height		19.259	3,36.196	< 0.001
Control	22.11 (1.87)			
High	9.85 (1.70)			
Moderate	12.31 (1.68)			
Low	12.47 (1.68)			
Canopy rugosity (m)		9.017	3,36.953	< 0.001
Control	24.50 (3.90)			
High	12.00 (1.74)			
Moderate	14.80 (2.13)			
Low	15.20 (2.18)			

Note: Mean values are estimated marginal means, followed by standard errors (SE). Numerator degrees of freedom (*df*) are listed first, denominator degrees of freedom are listed second.

($P = 0.013$; Fig. 3B), and mean VAI across all treatments was lower than that of controls based on a linear contrast ($P = 0.019$). High intensity treatments also resulted in lower cover fraction (CF) compared to controls ($P = 0.012$; Fig. 3C), and CF across all treatments was also lower than that of controls based on a linear contrast ($P = 0.019$). High intensity treatments had a lower clumping index than the Low intensity regime ($P = 0.039$) and controls ($P = 0.017$) based on pairwise comparisons (Fig. 3D). All treatments resulted in a lower standard deviation of leaf height (meanStd) compared to controls ($P < 0.001$; Fig. 3E). All three treatments reduced canopy rugosity (R_C) relative to controls based on pairwise comparisons ($P \leq 0.006$; Fig. 3F). There was no significant variation in fraction of PAR intercepted by the canopy (fPAR) among treatments ($F = 0.369$; $P = 0.776$; Fig. 4). Relationships between fPAR and various aspects of canopy structure were moderately positive for vegetation area (VAI; $r = 0.63$) and cover (CF; $r = 0.65$) and weakly negative for vertical heterogeneity (meanStd; $r = -0.11$) and canopy structural complexity (R_C; $r = -0.09$).

3.2. Multivariate analyses

Results from the ordination analysis generally supported treatment-level findings from ANOVA. The NMDS resulted in a 3-dimensional solution, with a final stress of 5.530 and final instability of < 0.001 after 80 iterations. The proportion of randomized runs with stress ≤ the selected solution was 0.004. Axis 1 explained 60.2 % of the variance in the original data matrix and was most strongly related to height and vertical heterogeneity (e.g. maximum canopy height, H_{max}, $r = 0.724$; height^2 or the standard deviation of mean leaf height, σ_H, $r = 0.941$; correlations for all metrics provided in Table S1). Axis 2 explained an additional 27.3 % of the variance and was strongly related to vegetation area/density and cover (e.g., mean VAI, $r = -0.716$; gap fraction, $r = 0.692$). Axis 3 (not illustrated) explained a small additional amount of variance (10.0 %) and was most closely related to foliage height and outer canopy heterogeneity (e.g., mean return height, $r = -0.720$; rumple, $r = 0.699$). Controls clearly separated from treated units in ordination space (Fig. 5A); observations from controls generally had higher values along axis 1 and lower values along axis 2 compared to the three treatments, illustrating the greater height, heterogeneity, vegetation density, and cover generally observed in controls. The multi-dimensional separation of the control group from each treatment group was supported by MRPP ($P = 0.003$), which indicated differences between each treatment (aggregated across sites) and the controls ($P \leq 0.003$).

Site-level differences were detected through NMDS and MRPP ($P = 0.001$). Pairwise comparisons showed differences between the Dukes (old-growth) and Argonne (second-growth) sites ($P < 0.001$). Observations from Argonne were generally lower along axes 1 and 2 compared to Dukes, indicating lower canopy height and heterogeneity and greater vegetation density and cover at the younger Argonne stands (Fig. 5B). Canopy structure of control units appeared to converge across sites and was similar among second-growth stands at Argonne and Ford and old-growth stands at Dukes. However, treatment effects on structure differed between second-growth and old-growth stands. Treated old-growth stands at Dukes exhibited less cover and vegetation area than controls. Treated second-growth stands at Argonne and Ford had shorter canopies and were less structurally complex than controls, as well as in comparison to treated old-growth stands at Dukes.

4. Discussion

Our evaluation of how partial harvesting regimes have influenced canopy structure and complexity in long-term silvicultural trials illustrated that widespread utilization of selection systems has several potential consequences for canopy structural development in northern hardwood forests. We specifically assessed: 1) how repeated partial harvesting disturbance affected canopy structure and complexity relative to unmanipulated controls, 2) whether effects of partial harvesting differed among harvesting intensities or 3) between old- and second-growth stands, and 4) if canopy light interception differed among stands with different histories of partial harvesting disturbance. We found that repeated partial harvesting disturbance tended to reduce stand-scale vertical and canopy structural complexity relative to unmanipulated controls (obj. 1), consistent with our hypothesis. Partial harvesting seemed to limit the development and retention of structural features associated with old forests in both old-growth and maturing, secondary stands, with more pronounced effects on second-growth stands as predicted (obj. 3). However, counter to expectation, variation in intensity among treatments produced relatively little distinction in canopy structural outcomes (obj. 2), and light interception was similar among stands with different histories of partial harvesting disturbance (obj. 4).

Our findings indicated that canopy structure development under partial harvesting regimes differed from that under the background or natural disturbance regime (i.e., unmanipulated controls). In the northern hardwood forests studied here, wind and pest/disease mortality are the primary agents of natural disturbance (Frelich, 2002). Susceptibility to both these agents and natural senescence (more likely in the later-successional forests at Dukes) generally increases with tree size, age, and canopy position (Foster, 1988; Canham et al., 2001; Seidl et al., 2011), often resulting in primarily top-down directional effects on the forest canopy (Abrams and Scott, 1989; Meigs and Keeton, 2018). Less frequent moderate severity disturbance events are also a component of the natural disturbance regime and have more spatially variable effects and often result in patchy and heterogenous structure (Woods, 2004; Hanson and Lorimer, 2007; Fahey et al., 2015). This natural

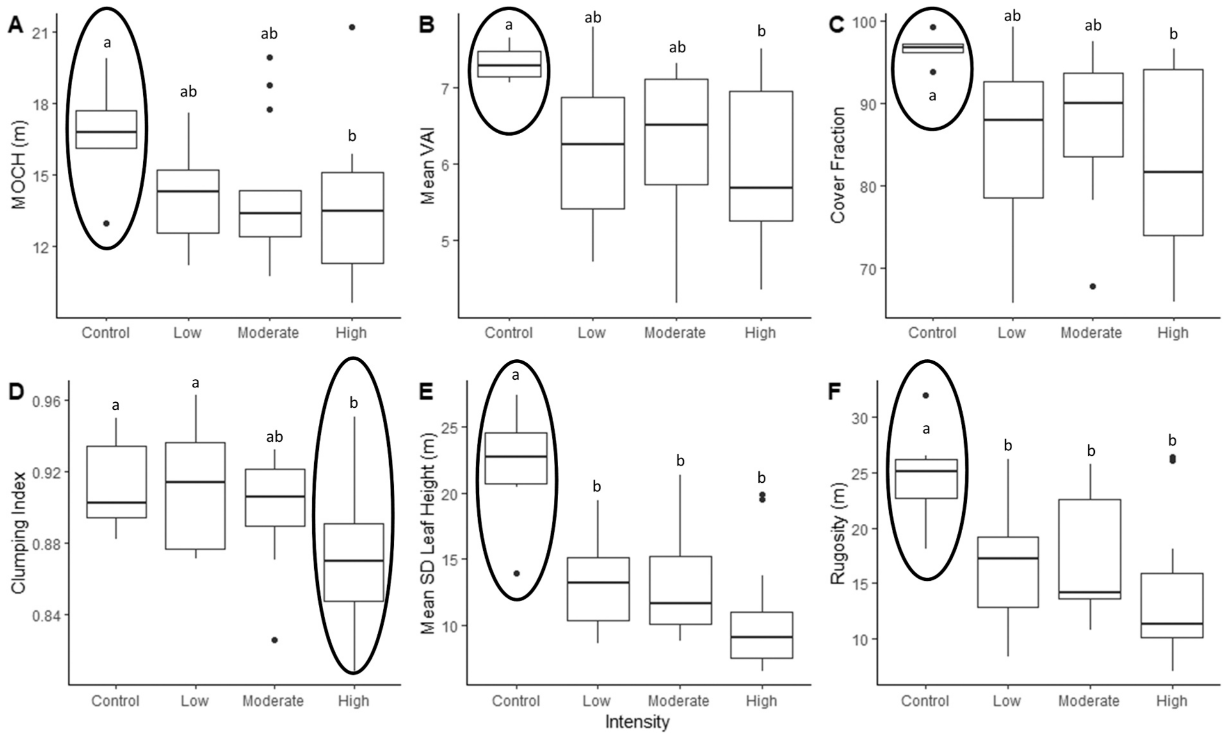

Fig. 3. Results of pairwise comparisons for six structural response variables compared among treated and unmanipulated (control) stands from three silvicultural experiments in the North Central United States. High, moderate, and low treatments reflect treatment intensity and correspond with levels of basal area retention (Table 1). Evaluated response variables include: A) mean outer canopy height (MOCH), B) vegetation area index (VAI), C) cover fraction (CF), D) clumping index (Ω), E) mean standard deviation of leaf height (meanStd), and F) canopy rugosity (R_C) (Table 2; see Atkins et al., 2018a for further details on computation). Solid bars indicate medians, hinges indicate 25th and 75th percentiles, and points denote outliers. Different letters indicate significant differences between estimated marginal means at *alpha* = 0.05 (mvt correction). Ellipses indicate significant contrasts for circled treatments compared to averages across all other treatments at *alpha* = 0.05 (mvt correction). For panels E and F, controls were excluded in linear contrasts for low, moderate, and high treatments.

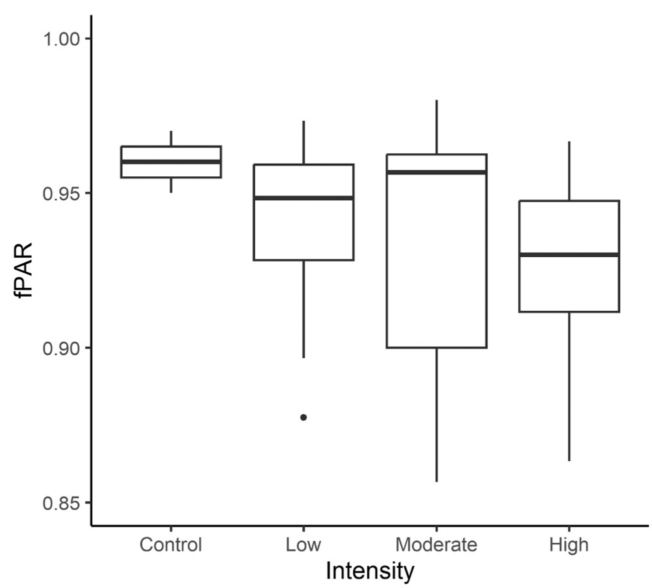

Fig. 4. Illustration of variation in the fraction of photosynthetically active radiation intercepted by the canopy (fPAR) among treated and unmanipulated (control) stands from three silvicultural experiments in the North Central United States. High, moderate, and low treatments reflect treatment intensity and correspond with levels of basal area retention (Table 1). Solid bars indicate medians, hinges indicate 25th and 75th percentiles, and points denote outliers.

disturbance regime combining "gap-phase" dynamics and periodic moderate disturbance appears to broadly promote development of multi-layered, structurally complex forests (Hanson and Lorimer, 2007; Gough et al., 2010, 2013, 2016; Halpin and Lorimer, 2016). In contrast, traditional selection harvesting systems loosely mimic only the gap-scale processes of the natural regime (e.g. see Hanson and Lorimer, 2007) and have been shown to reduce canopy height and forest complexity (Gronewold et al., 2010; Alveshere, 2023). We found that stands exposed to repeated partial harvests exhibited low vertical and overall canopy structural complexity relative to unmanipulated controls, which were likely affected primarily by background levels of mostly gap-scale disturbance but may also have been influenced by moderate severity disturbances (Woods, 2004; Fahey et al., 2015). However, there was greater openness and lower canopy density (VAI) in treated stands relative to controls, which also will likely have implications for future stand development trajectories. We suggest that low complexity in these partially harvested stands likely resulted largely from the top-down directionality of the treatments (Alveshere, 2023). Another possible driver of this pattern is synchronicity of gap formation and low variation in gap size associated with selection harvesting, which have also been implicated as factors in homogenization (e.g., see Angers et al., 2005; Hanson and Lorimer, 2007). However, we found higher canopy openness and variance in openness in managed stands, which suggests against a strong role for this characteristic of selection systems in reducing canopy complexity.

Variation in intensity among the selection treatments implemented in these experimental silvicultural systems produced relatively little distinction in fine-scale canopy structural outcomes. Selection harvesting treatments, and the low severity gap-scale disturbances they best approximate, often have somewhat localized and consistent effects on forest structure and development (Halpin and Lorimer, 2016; Meigs

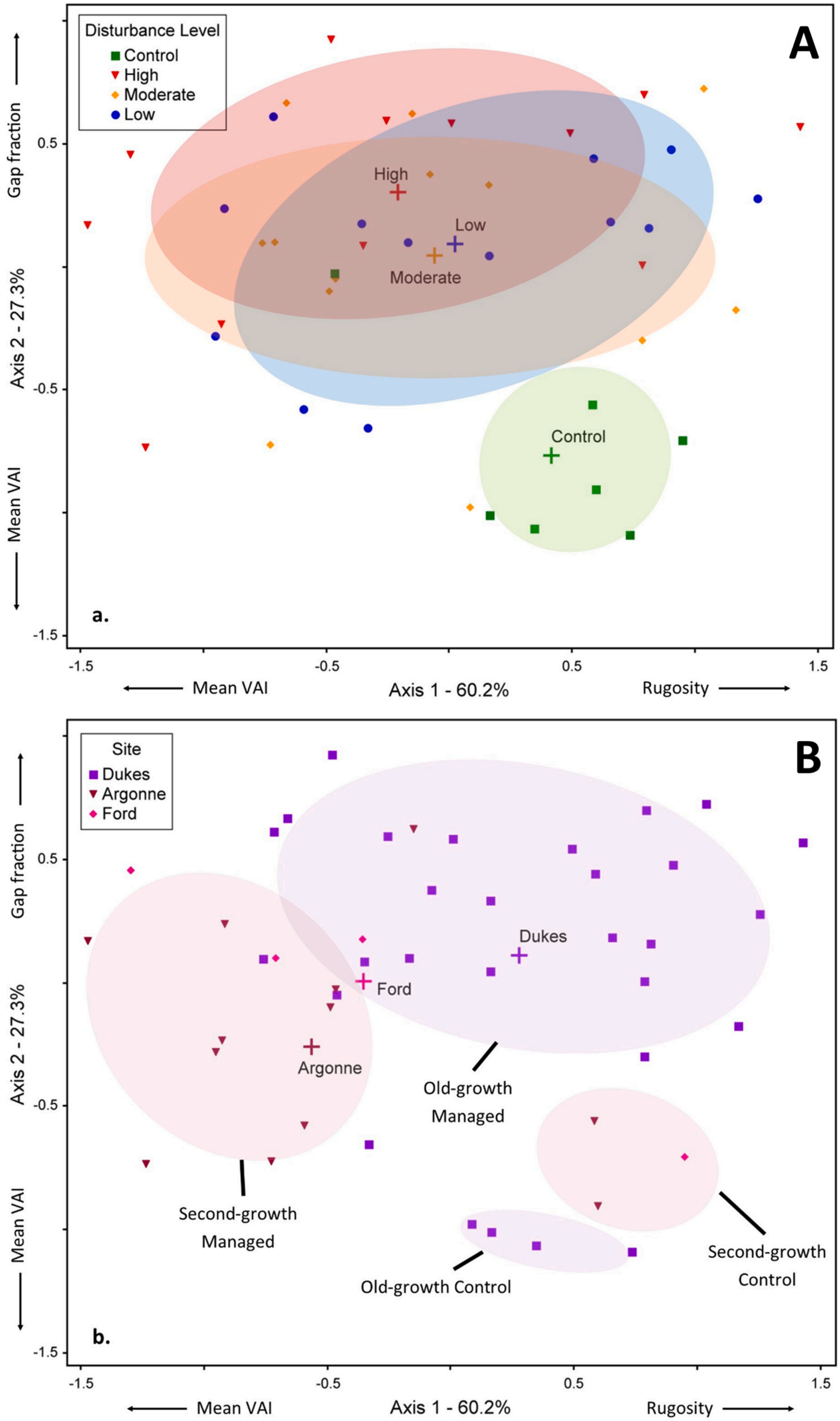

Fig. 5. Multivariate structural trends indicated by non-metric multi-dimensional scaling ordination of matrices of structural metrics across 45 plots (i.e. treatment units), which were arrayed in treated and unmanipulated (control) stands across three silvicultural experiments in the North Central United States. Panel A) illustrates plots coded by treatment category with high, moderate, and low intensity treatments corresponding to levels of basal area retention (Table 1). Panel B) illustrates plots coded by site and initial age structure (see methods).

et al., 2017; Aszalós et al., 2022; Gough et al., 2022). In mixed northern hardwood forests, frequent low severity disturbance events typically affect one to several canopy trees and result in small gap formation that promotes fine-scale canopy reorganization through lateral in-growth and localized release and recruitment of shade tolerant, suppressed trees (Frelich and Lorimer, 1991; Woods, 2004). At the regime level, this pattern of gap-phase disturbance and recovery has been alternatively implicated in maintaining or simplifying stand-scale structure as well as maintaining late-successional species composition (Woods, 2004; Reyes et al., 2010; Halpin and Lorimer, 2016; Fahey et al., 2020). In contrast, higher intensity moderate partial disturbance produces a wider range of residual structure (Meigs et al., 2017; Hart and Kleinman, 2018; Atkins et al., 2020; Aszalós et al., 2022) and light conditions (Hanson and Lorimer, 2007; Cowden et al., 2014). In this study the higher intensity selection harvesting regime was associated with canopy simplification, characterized by lower vertical heterogeneity and overall complexity, while the lower intensity regimes resulted in canopy structure somewhat intermediate with respect to higher intensity and control units (Fig. 3). This finding suggests that the range of intensity associated with selection harvesting treatments was not substantial enough to mimic variation associated with low-moderate severity disturbance regimes and their variable impacts on canopy structure (Fahey et al., 2015, 2019; Atkins et al., 2020). Our findings on canopy structural outcomes tracked those of prior studies focused on other aspects of forest structure. For example, Gronewold et al. (2010) found that low intensity selection harvesting maintained structural conditions (e.g., large trees, snags, and downed woody debris) approximating reference structure, while these features were reduced under higher intensity treatments.

Variation in severity within a disturbance or management regime is an important source of among-stand heterogeneity in forest structure and resource availability that may help maintain species diversity and promote structural complexity at stand and landscape scales over time (Hanson and Lorimer, 2007; Reyes et al., 2010; Turner, 2010; Halpin and Lorimer, 2016). In our study, partial harvest regimes were associated with reduced vertical and canopy structural complexity at a fine (i.e., 1–6 ha treatment unit) scale, but also generally increased among-unit variability in canopy structure relative to the range of conditions present across controls (Fig. 5). This finding suggests that implementation of partial harvesting alongside retention of unmanipulated stands may have the potential to promote some degree of among-stand, landscape-scale heterogeneity in canopy structural conditions. Our findings are generally in line with evidence from the literature on disturbance and management effects on heterogeneity and structural complexity in northern forests (Kuuluvainen, 2009; Halpin and Lorimer, 2016; Meigs et al., 2017; Aszalós et al., 2022). Notably, simulation experiments based in the same study region found repeated disturbances of uniform severity often caused stands to structurally retrogress to less complex stages, while mixed-severity regimes promoted spatially heterogenous structural conditions (Halpin and Lorimer, 2016). Although the selection treatments implemented here produced some degree of variability in canopy structure relative to unmanipulated controls, the fine-scale simplification and lack of differentiation among the treatments suggests that more variability in treatment intensity and spatial patterning is likely needed to effectively promote stand–landscape scale heterogeneity in canopy structure.

Our results indicate that application of partial harvesting regimes has affected the structural development of both maturing, secondary and old-growth forest stands, and that selection-based management may affect the development and retention of structural features associated with old forests. Control stands from the old-growth (Dukes) and second-growth (Argonne, Ford) forests exhibited similar canopy structure and complexity (Fig. 5B), suggesting that unmanipulated second-growth stands converged on structure similar to uneven-aged, old-growth forests despite substantial differences in initial age structure and stand conditions. This convergence of canopy structure is likely related to increasing complexity in younger, second-growth stands due to the influence of natural stand development processes (e.g., self-thinning) and resulting increase in canopy height and the number of large trees with age (D'Amato et al., 2011). In contrast, both managed secondary and old-growth stands differed in canopy structure from unmanaged controls, and generally had lower complexity and more open canopy conditions. Prior research suggests that stands in different development stages may respond differently to partial disturbances and regimes of comparable intensity and pattern (D'Amato et al., 2011; Halpin and Lorimer, 2016; Hart and Cox, 2017). Our results provide limited evidence in support of this notion, as the managed old-growth stands had more open canopies but retained vertical canopy structural complexity more similar to controls. In contrast, managed second-growth stands exhibited much lower vertical and overall canopy structural complexity than controls, and were also less complex than managed old-growth stands. These results suggest that the initially uneven-aged old-growth stands at Dukes largely retained vertical and overall structural complexity under partial harvesting, while these management regimes appeared to limit the development of vertical complexity in the younger stands at Argonne and Ford. These observed differences may reflect resistance and resilience (i.e. propensity to persist and/or recover following perturbation) of canopy structure in late-successional, old-growth stands to low- to moderate-severity disturbances (Halpin and Lorimer, 2016) that is related to the presence of higher densities of large trees (e.g., McRoberts et al., 2008; Meigs et al., 2017; Bassil et al., 2019; Seidel et al., 2019). These results also suggest that delaying application of selection-focused management until later in stand development could reduce negative impacts treatments may have on canopy structure and complexity.

In contrast to other studies that have illustrated strong linkages between canopy structure and light interception (e.g., Hardiman et al., 2013b; Atkins et al., 2018b; Fahey et al., 2020), we found little variation and no significant relationships in the fraction of photosynthetically active radiation intercepted by the canopy (fPAR) across different treatments and study sites. Relatively fine differences in canopy structure and complexity and similarities in composition and associated shade tolerance among treated stands may explain the lack of significant variation in light interception among treatments. Atkins et al. (2018b) found strong correlations between various measures of canopy structure and fPAR across forest types in eastern North America. However, variation in vegetation area/density, canopy structural complexity, and fPAR were much greater across different forest types and ecoclimatic domains than among northern hardwood stands in the Great Lakes region. We suggest that the relatively high vegetation area and cover maintained by even the highest intensity regime in this study was sufficient to intercept most incoming solar radiation (fPAR: 0.86–0.98). Prior work indicates that leaf area plateaus (LAI $\sim$ 4.5 m^2/m^2) early in stand development in northern Great Lakes region forests (Gough et al., 2007; Hardiman et al., 2011), and the lowest VAI (a surrogate of LAI) measured at our study sites was 4.18 m^2/m^2, suggesting leaf area was near or at the saturation point across treated stands.

5. Conclusion

Our findings build on growing understanding of the effect of forest management on canopy structure and complexity (Ehbrecht et al., 2017; Stiers et al., 2018; Willim et al., 2022; Alveshere et al., 2024) and have a variety of implications for management of northern hardwood forests. Similar to recommendations by Gronewold et al. (2010), our findings suggest applying partial harvests, such as selection systems, at lower intensities (i.e., with higher retention) may help retain structural features commonly associated with late-successional forests, including high canopy structural complexity. Differences in treatment effects on complexity between old- and second-growth stands suggest that complexity was conserved following partial harvests in old-growth stands, which were putatively more structurally complex when trials were initiated. In contrast, partial harvesting may have inhibited the development of complex structure in second-growth stands, which, when unmanipulated, developed complex structure similar to old-growth over the multi-decadal time frame of these studies. Findings from simulation experiments support this notion; for example, simulated partial harvest regimes in an initially mature second-growth northern hardwood stand largely maintained mature structure over a 300-year period, while the same stand attained old-growth size structure within 15 years in the absence of harvesting (Hanson et al., 2012). Our results suggest that management regimes that have historically focused on sustaining dominance of late-successional species with high commercial value can be adapted to support goals to develop or maintain ecologically important structural features. Adapting partial harvest systems for alternative goals in these ecosystems such as promoting multi-scale canopy structural complexity would require alternative application, such as: 1) allowing second-growth forests to progress to later stages of development prior to partial harvesting, 2) harvesting at relatively low intensities, particularly when canopy complexity exists, to maintain ecologically important canopy characteristics while meeting other economic or restoration goals, 3) leaving some second-growth stands unmanaged to promote natural development of canopy complexity, and 4) strategically producing a mosaic of managed and unmanaged stands.

CRediT authorship contribution statement

Brandon C. Alveshere: Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Robert T. Fahey:** Writing – review & editing, Visualization, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Christel C. Kern:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Robert T. Fahey reports financial support was provided by United States Department of Agriculture National Institute of Food and Agriculture (McIntire-Stennis). 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. . Preliminary analysis to test the effect of cutting cycle in the Cutting Cycles and Stocking Levels Study (CCSLS) at Dukes Experimental Forest

Analysis method

To evaluate whether treatments of the same intensity but differing cutting cycle (a proxy for return interval) constituted distinct treatment groups, we fit an initial set of models using data from only the Cutting Cycles and Stocking Levels Experiment at Dukes Experimental Forest (n = 29). Fitted models for each response included intensity, return interval, and their interaction as fixed effects and replicate as a random effect. Type III ANOVA was used to test for differences in effects of return interval or its interaction with intensity while accounting for effects of intensity.

Result

The main effects of cutting cycle were not significant for any of the six structural response variables evaluated ($F \leq 1.378$; $P \geq 0.279$). There was a marginally significant interaction between intensity and cutting cycle for clumping index (Ω) ($F = 3.015$; $P = 0.047$). Treatment units of a given intensity level, but differing cutting cycle, were therefore treated as equivalent in subsequent analyses (e.g., moderate intensity treatments at intervals of 5, 10, 15 years were all treated together as "Moderate").

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122347.

Data availability

Data will be made available on request.

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