Tree Regeneration Response to Variable-Sized Group Selection Harvest Gaps in Northern Wisconsin

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Abstract.—We established a field experiment in an even-aged, second-growth northern hardwood forest in north-central Wisconsin, testing the response of tree regeneration to deer exclusion and group-selection harvesting where small (50 m^2), medium (200 m^2), and large (380 m^2) gaps were created. We measured occurrence and height of saplings 9 years post-treatment and modeled incoming solar radiation in gaps to assess light distribution across the gap environments.

Densities of tolerant and midtolerant saplings were similar in medium and large gaps but tolerant saplings outnumbered midtolerants approximately four to one in small gaps. However, tolerant saplings averaged two meters taller than midtolerants across gap sizes. Deer exclusion increased midtolerant-sapling density but did not influence tolerant-sapling density. Modeled light levels decreased with gap size and varied by position within gaps. We attribute the increases in tree diversity in gaps over 200 m^2 to higher light levels across medium and large gaps.

INTRODUCTION

Long-term implementation of group selection harvesting (GSH), a gap-scale silvicultural system in which groups of overstory trees are harvested to emulate canopy-gap formation following natural disturbances of low-to-moderate severity, can create complex mosaics of differing even-aged conditions at the stand scale (Palik et al. 2020). Although not widely implemented in the Great Lakes region, GSH can increase structural and compositional diversity in northern hardwood forests. These attributes are particularly important as both can improve ecosystem function and may increase ecosystem resilience and adaptability (Ehbrecht et al. 2017, LaRue et al. 2019, Messier et al. 2013, Peuttmann et al. 2012).

Prior research from The Flambeau Experiment has already demonstrated sapling densities and species diversity are higher in gaps relative to controls (Forrester et al. 2014, Sabo et al. 2019). Here we use the infrastructure of the Flambeau Experiment to test the effect of three different GSH gap sizes and deer-exclusion fencing on sapling (d.b.h. ≥0.5 cm, height ≥1.37 m) density and total height of shade-tolerant and midtolerant tree regeneration 9 years post-treatment. We also model incoming solar radiation to test the assumption of resource heterogeneity within and between our GSH gaps, which approximately span the range of gap sizes that form naturally in northern hardwood forests of the Great Lakes region (LS-NH) following frequent disturbances of low to moderate severity (Bolton and D'Amato 2012, Frelich and Lorimer 1991, Palik et al. 2020, Schliemann and Bockheim 2011, Woods 2004). Studies which quantify the density and height variation among saplings of different shade-tolerance classes nearly a decade after harvest—and characterize light availability across several gap sizes—will help inform future implementation of gap-based regeneration methods in LS-NH.

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MATERIALS AND METHODS

This study was conducted in an even-aged, northern hardwood stand in the Flambeau River State Forest of north-central Wisconsin, United States (45.617778, -90.785556), that regenerated following clearcut harvesting in the mid-1920s. The rich site supports a stand dominated (>50 percent basal area) in all cohorts by *Acer saccharum*, with other associates of LS-NH occupying less than 16 percent of the basal area each (Forrester et al. 2014). Deer density averaged 8–12 deer km^{-2} (Robert Rolley, Wisconsin Department of Natural Resources as cited in Sabo et al. 2019). Fifteen 80×80 m plots randomly placed throughout the stand contain three nested and randomly situated but nonoverlapping-circular subplots in which small (50 m^2), medium (200 m^2), and large (380 m^2) canopy gaps were harvested in January 2007. Deer exclosures were installed around the perimeter of five plots creating categorical treatments of subplot size (hereafter "gap size") and deer exclusion.

In summer 2016, species and d.b.h. (cm) were recorded for all saplings within the subplots. Sapling heights (m) were subsampled by dividing the subplots into cardinal-direction-oriented quadrants and recording the height of the three tallest saplings of each species within each quadrant. Ground-level percent solar radiation was estimated within the gaps using the Voxel Octree Solar Toolkit (VOSTOK; Bechtold and Höfle 2020). We accounted for the potential effects of shadow casting from surrounding vegetation by converting vegetation points of an airborne light detection and ranging (LiDAR) point cloud of the study area into cubic voxels with dimensions of 0.85 m. Solar radiation was estimated at LiDAR ground points by ray-casting modeled solar radiation across the study area as influenced by solar angle at the study location over the growing season.

We used nested generalized linear mixed models (GLMMs) with linear negative binomial (Hardin and Hilbe 2007) and Gaussian distributions with log and identify link functions to test effects gap size, deer exclusion, and shade tolerance on sapling density (tph) and height (m), respectively. Although sapling data were recorded by cardinal-direction-oriented quadrants, our sample of only 15 replicates of each gap size, coupled with an absence of midtolerant saplings from over 25 percent of quadrants, prevented incorporating quadrant as a fixed effect in the density of height models. We therefore simplified our models by combining the values for quadrants in each gap to calculate our response variables of subplot-mean sapling density and height. To test for differences in percent-solar radiation (hereafter "light") within and across gap sizes, we subdivided subplots into five section locations: Center, North, South, East, and West. These section locations were selected based on gradients of light reported in other gap studies from similar latitudes (Canham et al. 1990, Kneeshaw and Bergeron 1999, Gendreau-Berthiaume and Kneeshaw 2009, Marquis 1965). Scalar values of solar radiation associated with the point cloud of ground points within each section were averaged and converted to percentage of maximum in the study area. These values were used as a response variable in a GLMM with a beta distribution and logit link function to test the effects of gap size and section location on light.

RESULTS

A significant ($p < 0.001$) interaction between gap size and shade tolerance showed that midtolerant sapling regeneration, dominated by *Fraxinus* spp. (65 percent), was less frequent in small subplots than in either medium or large subplots ($p \leq 0.002$) but the densities of midtolerants in medium and large subplots were similar ($p > 0.9$; Figure 1). Densities of tolerant saplings, predominately *Acer saccharum* (66 percent), were similar ($p \geq 0.63$) across the three subplot sizes (Fig. 1). Though tolerant saplings outnumbered ($p = 0.003$) midtolerants in small subplots, densities of both tolerance classes were more variable among large and medium gaps and did not differ significantly between tolerance classes ($p > 0.8$ for all). Deer exclusion influenced ($p = 0.054$) density patterns, with fewer midtolerant than tolerant saplings occurring in unfenced plots ($p \leq 0.004$). Mean height

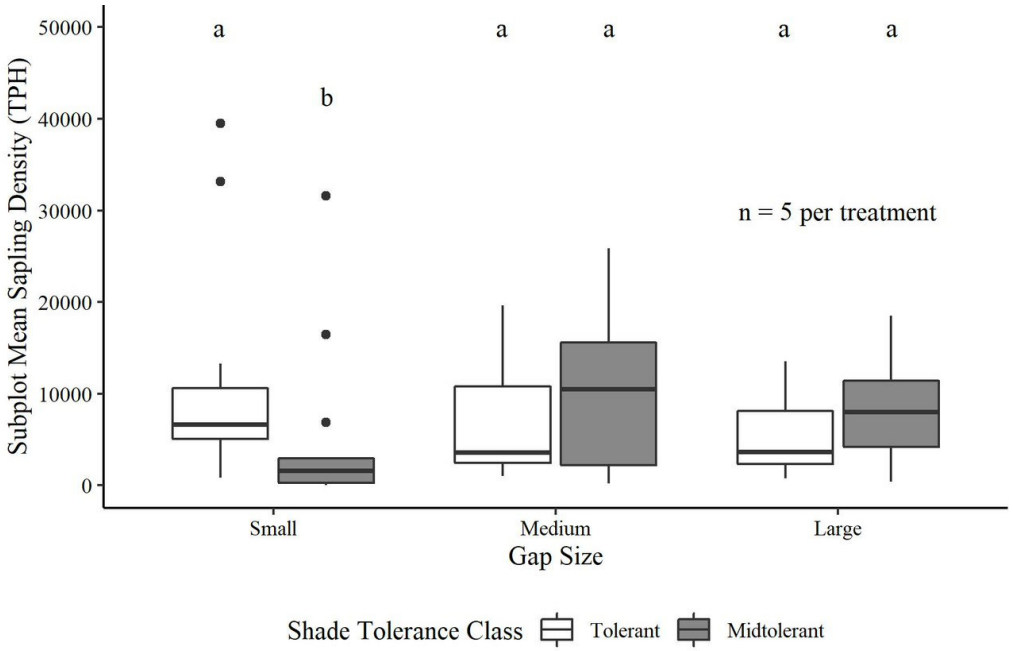

Figure 1.—Pairwise comparisons of the gap size × shade tolerance class interaction on subplot-level estimated marginal mean sapling density (TPH). Boxes not connected by the same letter are significantly different at an α = 0.05.

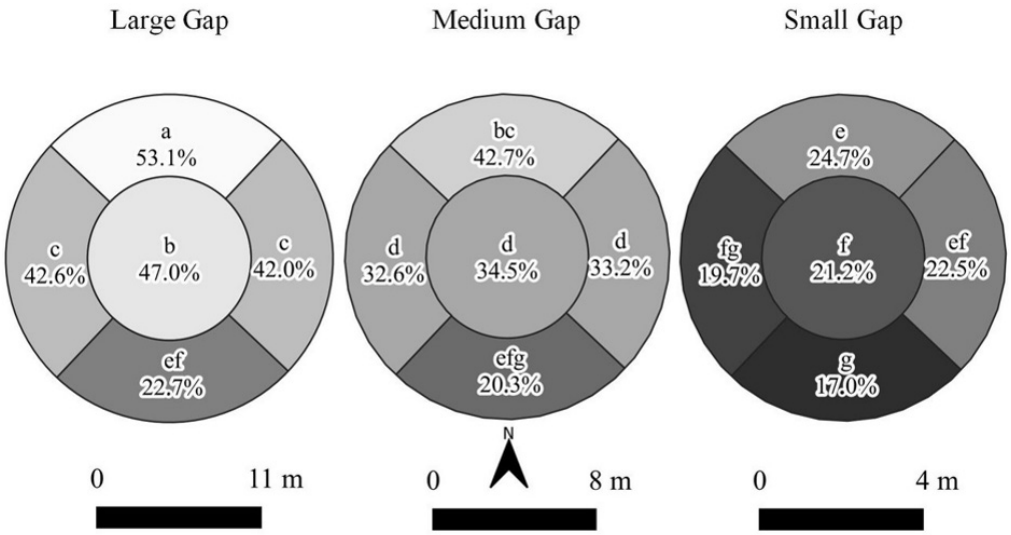

Figure 2.—Pairwise comparisons of percent direct solar radiation by gap size and section. Polygons of different colors and not connected by the same letters are significantly different at an α = 0.05. Note the differences in scales among gap sizes.

differed between the two tolerance classes ($p < 0.0001$), with mean height among tolerant saplings (6.8 m) averaging over 2 meters taller than midtolerant saplings (4.6 m) ($p < 0.0001$), but height was not significantly impacted by gap size for either tolerance class ($p \geq 0.21$).

A significant interaction between gap size and subplot-section location ($p < 0.0001$) revealed greater light intensity with increasing gap size ($p < 0.0001$) and from north to south, regardless of gap size ($p < 0.0001$; Fig. 2). Light levels in eastern and western sections were often different than northern or southern sections, although the significance of differences dissipated with gap size (Fig. 2). The range of light values also declined with gap size from a range of approximately 30 percent in large gaps to less than 8 percent in small gaps. The patterns are interesting and complex,

yet considerable overlap in light levels occurred within and across gap sizes depending on the sections being considered. For example, light in the center of large gaps was equivalent to light in the northern portions of medium gaps ($p = 0.8$) and light in the southern sections of large gaps was similar to light in the northern section of small subplots ($p > 0.9$).

DISCUSSION AND CONCLUSIONS

Our results generally agree with some (Forrester et al. 2014, Kern et al. 2013, Knapp et al. 2019a, Knapp et al. 2019b, Knapp et al. 2021, Sabo et al. 2019) but differ from several other gap-based silviculture experiments in LS-NH (Bolton and D'Amato 2012, Reuling et al. 2019) in that we found that GSH can be a viable regeneration approach to meet objectives related to increased tree-species diversity. Indeed, our approximately balanced ratio of tolerant and midtolerant sapling regeneration in GSH gaps ≥200 m^2 may rightfully provide some managers confidence in this regeneration approach. However, another similarity between our results and those reported by others (Bolton and D'Amato 2012, Kern et al. 2013, Knapp et al. 2019a, Knapp et al. 2019b, Knapp et al. 2021, Reuling et al. 2019) is that advance regeneration of tolerant species was released by GSH and is contributing to a 2-meter height advantage among tolerant species. Continued monitoring of regeneration in these gaps will be necessary to determine whether midtolerant species ultimately ascend to canopy positions given their current height disadvantage. Interestingly, previous research from this experiment reported that tolerant and midtolerant saplings had similar height growth rates following GSH (Forrester et al. 2014). We believe these collective findings accentuate the importance of additional research on whether implementing stand-tending practices in conjunction with GSH—such as pre- or post-harvest control of advance regeneration of tolerant species—can lead to long-term diversification in species composition.

We attribute our density-related findings to the higher light levels in gaps of at least 200 m^2. After accounting for shadowing from surrounding vegetation, approximately 41 and 33 percent of incoming light reached the forest floor in large and medium gaps, respectively, compared to only 21 percent in small gaps. This trend, as well as our findings in support of a significant north-south gradient, was expected and agrees with trends reported in other studies of light in gaps in northern hardwood systems (Canham et al. 1990, Gendreau-Berthiaume and Kneeshaw 2009, Marquis 1965). As such, we interpreted our results as evidence that the wider ranges of higher-light levels found in medium and large gaps is more conducive to regenerating mixtures of tolerant and midtolerant saplings than the narrower range of lower-light values associated with gaps less than 50 m^2.

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CITATION: Schnake, David K.; Forrester, Jodi A.; Sanchez-Meador, Andrew J.; Mladenoff, David J.; Lorimer, Craig. 2023. **Tree Regeneration Response to Variable-Sized Group Selection Harvest Gaps in Northern Wisconsin.** In: Kern, Christel C.; Dickinson, Yvette L., eds. Proceedings of the first biennial Northern Hardwood Conference 2021: Bridging science and management for the future. Gen. Tech. Rep. NRS-P-211. Madison, WI: U.S. Department of Agriculture, Forest Service, Northern Research Station: 32–37. https://doi.org/10.2737/NRS-GTR-P-211-paper8.