



Diversifying the composition and structure of managed, late-successional forests with harvest gaps: What is the optimal gap size?

Christel C. Kern^{a,*}, Anthony W. D'Amato^b, Terry F. Strong^{a,1}

^a US Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA

^b Department of Forest Resources, University of Minnesota, 1530 North Cleveland Avenue, Saint Paul, MN 55108, USA

ARTICLE INFO

Article history:

Received 4 March 2013

Received in revised form 17 April 2013

Accepted 18 April 2013

Keywords:

Uneven-aged management

Selection system

Tree recruitment

Shrub interference

Microclimatic extremes

Sugar maple

ABSTRACT

Managing forests for resilience is crucial in the face of uncertain future environmental conditions. Because harvest gap size alters the species diversity and vertical and horizontal structural heterogeneity, there may be an optimum range of gap sizes for conferring resilience to environmental uncertainty. We examined the impacts of different harvest gap sizes on structure and composition in northern hardwood forests of the upper Great Lakes region, USA using a robustly-designed experiment consisting of six harvest gap sizes replicated 12 times with over a decade of repeated measurements. We found that germinant (trees < 0.15 m tall) densities were greatest in year 2 (71.6 stems m⁻²) but were present in all measurement years (0, 2, 6, and 12 years post-harvest), suggesting a continuous influx of tree seedlings on site. Sapling (> 0.6 m tall) densities were greatest (3.9 stems m⁻²) at the end of the study period (year 12) and were composed primarily of three species (*Acer saccharum*, *Fraxinus americana*, *Ostrya virginiana*) already present on site. The 6 and 10 m diameter (dia.) harvest gaps had, on average, the minimum number of saplings (~2 stems m⁻²) needed to fill dominant positions in small canopy openings, but, by year 12, small gaps were closed by crown extension of mature edge trees. Medium (20 m dia.) to large harvest gaps (30 and 46 m dia.) had fewer saplings than small gaps. The understory layer of medium and large gaps were dominated by shrubs (*Rubus* sp.) that dampened growth of species such as *F. americana*. Consequently, gap-filling from the sapling layer would not occur in the near future, and, from a management perspective, would be considered a regeneration failure within larger gaps. Our study suggests that the optimum gap size does not exist and using harvest gaps to create resilient forests with structural and compositional diversity alone is challenging on productive habitats. In particular, medium to large gaps will likely require microsite specific placement of desired advance regeneration or additional treatments (e.g., vegetation control) to cultivate a dense sapling layer in an acceptable timeframe after harvest.

Published by Elsevier B.V.

1. Introduction

Managing forests for resilience is crucial in the face of uncertain future environmental conditions (Millar et al., 2007). Resilient forests maintain essential functions and sustain a range of ecosystem goods and services despite changing climate and disturbances. For instance, variation in species and within-stand structural complexity provides a range of species traits and growing conditions that enhances the capacity of an ecosystem to respond to a natural disturbance. Thus, in managed forests, ecosystem resilience can be achieved through creative harvest prescriptions and reforestation practices that influence the variation of species composition and stand structure (Drever et al., 2006).

One example of a management practice that can be utilized to restore or maintain resilience is harvest-created canopy gaps. Harvest gaps create vertical and horizontal heterogeneity in stand structure and diversity through recruitment of less abundant species (Gray and Spies, 1996). Harvest gaps have been proposed as a component of natural disturbance-based management by emulating the frequency, distribution, and size of canopy gaps that result from natural disturbance at various stages of stand development (Coates and Burton, 1997; Franklin et al., 2007). Harvest gaps are also inherent outcomes from previous partial harvests (Eyre and Zillgitt, 1953), especially in uneven-aged management where the goal is to maintain multiple age classes within one stand. For example, in selection system silviculture, individual or group removal of dominant and co-dominant trees creates growing space for new age class recruitment and development among older age classes (Smith et al., 1997).

* Corresponding author. Tel.: +1 218 326 7134; fax: +1 218 326 7123.

E-mail address: cckern@fs.fed.us (C.C. Kern).

¹ Retired.

Ideally, the size of harvest gaps can be manipulated to influence tree diversity within a given management approach. Larger gaps facilitate establishment of more trees intolerant to shade than smaller openings (Ricklefs, 1977; Denslow, 1980). This was the premise for the development of selection system silviculture. Single-tree selection was developed in shade tolerant European silver fir (*Abies alba*) forests to perpetuate this species in multi-aged stands, and group selection was developed to maintain a component of Norway spruce (*Picea abies*) and diversify this forest type (Puettmann et al., 2009). Today, harvest gaps are a key component of close-to-nature approaches in other forest types, such as European beech (*Fagus sylvatica* L.) (Naaf and Wulf, 2007; Madsen and Hahn, 2008). In North American forests, harvest gap size has been important to tree recruitment, diversity, and productivity of managed mixed species, multi-aged forests (Gray and Spies, 1996; Webster and Lorimer, 2002; Holladay et al., 2006). However, outcomes of various harvest gap sizes are not simple to predict because tree recruitment is influenced by more factors than gap size alone (Brokaw and Busing, 2000), including proximity to seed source, suitability of microsite, presence of advanced or pre-gap regeneration, intensity of local browsing pressure, and abundance of competing vegetation (Schutz, 1997; Dietze and Clark, 2008; Falk et al., 2010; Bolton and D'Amato, 2011). Thus, the long-term efficacy of using harvest gap size to influence tree diversity remains unclear.

The northern hardwood forests of the US and Canada are an example of a forest type in which managers often desire to maintain tree diversity and structural heterogeneity while sustaining a variety of forest goods and services. The predominant management approach for this forest type is the single-tree selection system (Jacobs, 1987), which, after decades of application, has led to declines in tree species diversity (Niese and Strong, 1992; Neuendorff et al., 2007) and regional homogenization of forest conditions (Schulte et al., 2007). As a result, in the northeastern US, group and patch selection has been developed to maintain a component of shade intolerant trees in this forest type (Leak and Filip, 1977; Leak, 1999; Kelty et al., 2003). In the western Great Lakes region, a single-tree/group selection hybrid approach has emerged to recruit trees mid-tolerant to shade, such as yellow birch (*Betula alleghaniensis*), into the predominately shade tolerant sugar maple (*Acer saccharum*) stands (Erdmann, 1986; Nyland, 1987). Specifically, single-tree removals are interspersed with group removals that create small gaps for release and thinning and medium gaps for new age class development, respectively. Although, in northern hardwoods in the northeastern US, long-term studies have indicated that mid-tolerant trees occupy at least one-third of the basal area 40–60 years after large gap creation (Leak, 1999; McClure et al., 2000). Recent observations in northern hardwood forests of western Great Lakes suggest that seedlings may not recruit in larger gaps because of elevated deer browsing (Matonis et al., 2011). In light of these findings and the suite of emerging objectives related to increasing forest adaptation potential, there is great need for long-term evaluations of the effectiveness of different harvest gap sizes at restoring and maintaining forest resilience in mixed species, multi-aged forests.

In this study, we asked the following questions: How does gap size influence tree seedling recruitment over time? Once seedlings are established, how does gap size influence tree sapling composition and diversity over time? And, more broadly, how does gap size influence mode of gap-filling and future canopy composition? We addressed these questions with a robustly-designed experiment with a decade of repeated measurements of regenerating trees across six harvest gap sizes replicated 12 times. We hypothesized that tree recruitment would occur shortly after harvest and would include a combination of pre-harvest advance regeneration and post-harvest recruits. We also hypothesized that shade tolerant

trees would dominate small and large gaps, because these trees would tolerate the low resource conditions under close proximity of mature edge trees in small gaps and under the thick shrub layers anticipated to develop in the large gaps. Therefore, we hypothesized that medium gaps would harbor a dense, diverse sapling layer with greatest potential of all gap sizes to diversify the future forest canopy.

2. Materials and methods

2.1. Study site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located on the Chequamegon-Nicolet National Forest in northern Wisconsin, USA (N45°56', W88°59'). Similar to many forests in the region, the study ecosystem regenerated after exploitive timber harvesting during the early twentieth century. Before study installation (1994), the forest had no recent management and was estimated to be 60 years old and in the stem exclusion stage of stand development (Oliver and Larson, 1996).

In 1993, an initial field reconnaissance was conducted to determine the homogeneity of composition, structure, and physiography of the study area. The inventory resulted in delineation of seven uniform areas of which four were selected randomly for study. The inventory also described the initial site conditions. Sugar maple (*A. saccharum*) dominated the site but 12 other trees species were identified. Tree (≥ 4 cm diameter at breast height [DBH]) basal area ranged from 20 to 39 m² ha⁻¹ and tree density ranged from 89 to 285 trees ha⁻¹. The forest canopy was closed with an occasional small canopy gap created by recent single-tree blowdown. The topography is a hummocky kame-kettle complex with some cradles and knolls created from tip-up mounds (resulting from past canopy tree blowdowns). Soils are primarily Padus sandy loam (coarse-loamy, mixed, frigid Alfic Haplorthods) with inclusions of Padus-Pence sandy loam (sandy, mixed, frigid Entic Haplorthods) (USDA Natural Resource Conservation Service, 2005). There was a thick forest floor layer across most of the study site suggesting little presence or impact of invasive earthworms on these areas, as has been documented in other northern hardwood forests in the region (Loss et al., 2013).

The habitat type is considered nutrient rich, mesic and well suited for sugar maple growth and classified as *Acer-Tsuga/Dryopteris* (ATD) according to a habitat type classification system by Kotar et al. (2002). ATD is one of several mesic habitat types (e.g., *Acer-Tsuga/Maianthemum* [ATM] and *Acer/Osmorhiza-Caulophyllum* [AOCa]) supporting northern hardwood forests of the western Great Lakes region. ATM and AOca habitat types typically are more species rich, have more species less tolerant to shade, and pose more management options to influence species composition than ATD habitat types, which are heavily dominated by sugar maple (Kotar et al., 2002).

2.2. Study design

The experimental design was a randomized complete block with sub-sampling. There were two levels of replication, block and replicate within block. Three replicates of each of six circular gap sizes (0 [reference area], 6, 10, 20, 30, and 46 m diameter gaps) were randomly assigned in each of four adjacent blocks. Experimental gaps were created by dormant-season timber harvesting in 1994 (two blocks) and 1995 (two blocks). The resulting design included 12 reference areas (0.4047 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). Openings were measured in 1997 and 2008 from gap center to dripline in cardinal and sub-cardinal directions (eight total radii) (Table 1).

Table 1
Number of treatment replicates and their mean size (mean [standard error]) at two and 12 years after harvest at the Divide Canopy Gap Study located in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

Gap size (diameter)		0 m	6 m	10 m	20 m	30 m	46 m
No. of replicates		12	11	11	10	12	12
Diameter (m)	Year 2	–	4.7 (0.2)	8.2 (0.6)	17.8 (0.7)	28.8 (0.6)	45.2 (0.7)
	Year 12	–	3.5 (0.7)	5.0 (0.6)	15.7 (0.7)	25.9 (1.5)	45.0 (0.6)
Area (m ²)	Year 2	–	21.9 (3.9)	62.8 (9.6)	268.6 (25.9)	699.3 (30.1)	1729.3 (54.0)
	Year 12	–	13.9 (8.7)	25.9 (10.0)	203.4 (24.1)	592.3 (65.0)	1708.6 (36.2)
Diameter: Height	Year 2	–	0.2 (0.0)	0.3 (0.1)	0.7 (0.1)	1.2 (0.1)	1.9 (0.1)
	Year 12	–	0.1 (0.1)	0.2 (0.1)	0.6 (0.1)	1.0 (0.1)	1.9 (0.1)

In 1997, gap area ranged from 9.9 m² to 1986 m² (gap diameter to tree height ratio 0.1 to 2.2). By 2008 (hereafter “year 13”), most small gap openings were closed and similar to the forest matrix conditions, while large gaps remained open.

In addition to gap creation, the four blocks were also thinned (except for the reference areas) in 1994–1995 following first harvest entry guidelines in Erdmann (1986), a Lake States management publication for converting even-aged northern hardwood forests to uneven-aged stand conditions. To improve residual stand vigor, this first thinning entry (an “improvement cut”) removes trees anticipated to die from self-thinning, disease, or damage or that have minimal potential to gain economic value before the next harvest entry (approximately 20 years). The thinning reduced the forest matrix density to a mean basal area of 23 m² ha⁻¹ (range: 15–33 m² ha⁻¹), while reference areas remained uncut at 31.1 m² ha⁻¹ (range: 27–37 m² ha⁻¹).

In 1997, deer exclosures were added to the study design on a subset of the experimental units (one reference area, 20 m gap and 46 m gap per block; 12 total exclosures) and were maintained for 4 years. The exclosures were constructed with 1-m tall rabbit guard fence. The resulting exclosure enclosed vegetation in the shape of a ‘+’ sign with 3.6-m wide arms in each cardinal direction. The exclosures were designed to reduce costs and were believed to

deter deer from dwelling in a confined area. The deer exclosures were not a significant factor in any of our analyses. In particular, we were not able to determine if the exclosures were effective at reducing browse and browsing effects were insignificant outside the exclosure or if the exclosures were ineffective and browsing effects were ubiquitous inside and outside the exclosures. Thus, these results are not presented.

2.3. Field sampling

Permanent sample points were arrayed in four transects radiating in cardinal directions from gap centers to 5–10 m into the adjacent forest matrix (the “forest-gap transect”; see Fig. 1 in Janowiak et al. (2008)). Number and spacing of sampling points per transect varied by gap size. In the control, 30 m, and 46 m gaps, there were 24, 17, and 24 sample points, respectively, each spaced 5.5 m apart. In the 6 m, 10 m, and 20 m gaps, there were 9, 13, and 17 points, respectively, each spaced 3.7 m apart.

Two plot sizes were used to estimate density and size of woody species at each permanent sampling point. A quadrat (1 × 1 m) plot was used to collect data on tree seedlings ≤0.6 m tall and all shrubs, and a circular (1.8-m radius) plot was used to collect tree sapling (>0.6 m tall) data. Individual species were tallied by height

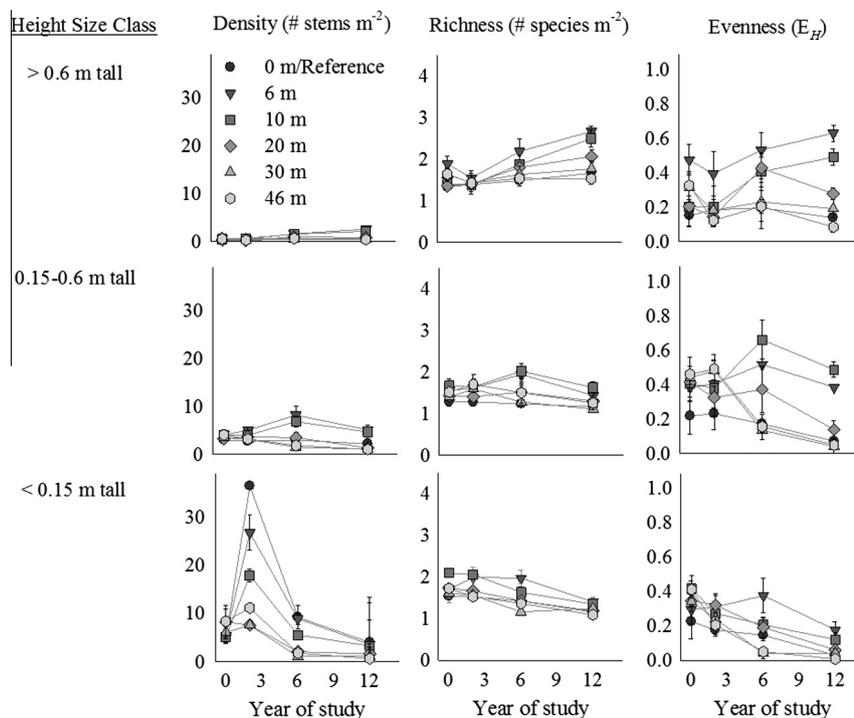


Fig. 1. Mean density, richness, and evenness of woody stems by gap size over time for three height size classes in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Y-axis labels are located at the top of each column of graphs and each row of graphs represents a different height size class (labeled at the far left).

class (<0.15 m and 0.15–0.6 m tall in quadrats and >0.6–2.1 m tall, >2.1 m tall–4 cm diameter at breast height (DBH), and >4–12 cm DBH in circular plots). In addition, the tallest sapling or “dominant” individual of each tree species was identified in each circular plot and then measured for DBH and total height. Nomenclature follows PLANTS Database (2009). Measurements were made during mid-summer (late June–early August) over four survey periods: pre-harvest (1994 [two blocks]–1995 [two blocks]; “year 0” hereafter) and post-harvest in 1997 (“year 2” hereafter), 2000 (two blocks) or 2001 (two blocks) (“year 6” hereafter), and 2007 (“year 12” hereafter) with one exception. Raspberry (*Rubus idaeus*) densities were only collected in year 12.

2.4. Data analysis

Generalized linear mixed models were used to examine the influence of gap size on tree seedling recruitment and sapling development. Gap size was treated as a fixed effect and subset to include only permanent sample points within the reference areas and within opening driplines as measured in 1997. Replicate (e.g., an individual gap or reference area within a block) means were considered random subsamples within each block and were weighted by the number of permanent sample points. Models were checked for normality, residual variation, and outliers. Analyses were performed using the PROC MIXED and the PROC GLIMMIX procedures in SAS Institute Inc. (2008).

A few species (*A. saccharum*, *Fraxinus americana*, *Ostrya virginiana*, and *R. idaeus*) dominated the understory. As such, infrequent species were classified as “Other trees” or “Other shrubs.” Similarly, the majority of individual stem heights were noted in the two smallest height size classes, <0.15 m and 0.15–0.6 m tall; thus, all stems >0.6 m tall were combined into one size class. The analysis approach for each component of the tree seedling and sapling community examined is described below.

2.4.1. Tree reproduction

Size of dominant saplings across gap sizes were analyzed by species (*A. saccharum*, *F. americana*, *O. virginiana*) using repeated measures. Serial correlation was modeled with compound symmetry structure after comparing various repeated measure models with Akaike's Information Criterion (AIC). Repeated measures were also used to analyze the effect of density and diversity of all tree species by height size class. Diversity responses included species richness and evenness (see calculations in Magurran (1988)) and were transformed (lognormal or square-root) to meet model assumptions. Because survey year and survey year*treatment were significant in all models of density and diversity by height size class, models were also run by survey year to isolate treatment effects at each time step. Post-hoc pair-wise comparisons (Bonferroni correction $P < 0.003$) were made when group differences were detected ($P < 0.05$).

To test for tree (>0.6 m tall) compositional differences among gap sizes and survey years, we used multi-response permutation procedure (MRPP) and indicator species analysis (ISA) in PC-Ord v5.31 (McCune and Medford, 2006) using both abundance and presence/absence data. MRPP is a nonparametric test for group differences that are greater than expected by chance and accommodated our unbalanced design. Post Hoc pair-wise comparisons (with Bonferroni correction $P < 0.003$) were made when group differences were detected ($P < 0.05$). Group differences were then analyzed with ISA for species associations using indicator values that ranged from no indication (0) to perfect group indication (100). Species were considered significant indicators of a group when $P < 0.05$ based on a Monte Carlo test using 1000 permutations (McCune and Grace, 2002).

2.4.2. Relationships between trees and shrubs

The effect of shrub abundance, gap size, and their interaction on tree growth was analyzed using an ANCOVA. Growth responses of dominant saplings were the absolute difference of replicate means between years 2 and 12 in DBH (log-transformed), height, and height:DBH (hereafter Ht:Dia). Year 2 growth responses were used as covariates and means of raspberry cover in years 2, 6, and 12 (log-transformed) represented the effects of dominant shrubs. Gap size was represented with actual mean gap diameters in year 2. Growth models were compared among full- and sub-models (gap size and raspberry abundance, gap size alone, or raspberry alone) then selected based on the corrected AIC. All models within two delta units of the best approximating model (lowest AIC) were interpreted. Parameter coefficients and fit (R^2) were used to interpret model effects and suitability.

The relationship between the density of trees and shrubs were analyzed by including life form (tree or shrub) in the model. The data were subset to year 12, because raspberry densities were only available that year. Post-hoc pair-wise comparisons (with Tukey's HSD) were made when group differences were detected ($P < 0.05$).

3. Results

3.1. Tree density, diversity, and composition over time

Tree reproduction changed significantly in density, richness, and evenness over time (Fig. 1 and Table 2). Maximum mean densities followed a temporal dynamic reflective of regeneration development with maximum densities of shorter height classes occurring in early years and maximum mean densities of taller height classes occurring in later years (Fig. 1 and Table 2). For example, shorter stature ‘germinants’ (trees < 0.15 m tall) maximized mean density in year 2 at 71.6 stems m^{-2} , while slightly taller ‘seedlings’ (trees 0.15–0.6 m tall) maximized mean density in year 6 at 14.2 stems m^{-2} and even taller ‘saplings’ (trees > 0.6 m tall) maximized at 3.9 stems m^{-2} in year 12. Richness followed a similar height class by time pattern. Generally, germinants (<0.15 m tall) had greater densities, but lower evenness, than taller height classes.

Gap size significantly influenced density and diversity in earlier years for shorter height classes and in later years for taller height classes (Fig. 1 and Table 3). Germinants (<0.15 m tall) were denser and richer with greater evenness in smaller gaps (6 m and 10 m) than larger gaps or reference areas in years 6 and 12 ($P \leq 0.041$ pair-wise comparison; Fig. 2). Saplings (>0.6 m tall) were few, even in year 12, but were also generally found in greater numbers, richness, and evenness in smaller gaps ($P \leq 0.049$ pair-wise comparisons).

The composition of tree reproduction changed significantly over time based on both abundances and presence/absence for each

Table 2

P-values from full model analysis for tree density, richness, and evenness by height size class of saplings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Significant values (<0.05) are in bold.

Height Size Class	Effect	Density	Richness	Evenness
<0.15 m	Year	<0.001	<0.001	<0.001
	Gap size	0.000	0.024	0.611
	Year × gap size	<0.001	0.002	<0.001
0.15–0.6 m	Year	0.007	<0.001	<0.001
	Gap size	0.026	0.040	0.010
	Year × gap size	0.001	0.000	<0.001
>0.6 m	Year	<0.001	<0.001	0.001
	Gap size	0.019	0.037	0.018
	Year × gap size	<0.001	0.001	<0.001

Table 3
P-values from treatment-only (Gap size) sub-model analysis and overall means (standard error [se]) for tree density (stems m^{-2}), richness (species m^{-2}), and evenness by survey year and height size class of saplings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Significant values (<0.05) are in bold.

Height size class	Survey year	Density		Richness		Evenness	
		P-value	Mean (se)	P-value	Mean (se)	P-value	Mean (se)
<0.15 m	0	0.597	6.3 (0.6)	0.168	1.7 (0.1)	0.338	0.34 (0.03)
	2	<0.001	17.9 (4.8)	0.104	1.7 (0.1)	0.832	0.25 (0.02)
	6	<0.001	4.7 (1.5)	<0.001	1.5 (0.1)	0.001	0.17 (0.05)
	12	0.014	2.3 (0.6)	0.450	1.2 (0.0)	0.153	0.07 (0.03)
0.15–0.6 m	0	0.954	3.6 (0.2)	0.200	1.5 (0.1)	0.148	0.39 (0.04)
	2	0.932	3.6 (0.3)	0.024	1.5 (0.1)	0.093	0.38 (0.04)
	6	<0.001	4.1 (1.1)	<0.001	1.6 (0.1)	<0.001	0.33 (0.09)
	12	<0.001	2.5 (0.8)	0.016	1.3 (0.1)	<0.001	0.19 (0.08)
>0.6 m	0	0.751	0.5 (0.1)	0.022	0.5 (0.1)	0.139	0.28 (0.05)
	2	0.239	0.4 (0.1)	0.905	1.4 (0.0)	0.397	0.20 (0.04)
	6	0.109	1.0 (0.2)	0.097	1.8 (0.1)	0.015	0.33 (0.06)
	12	<0.001	1.2 (0.4)	<0.001	2.0 (0.2)	<0.001	0.30 (0.09)

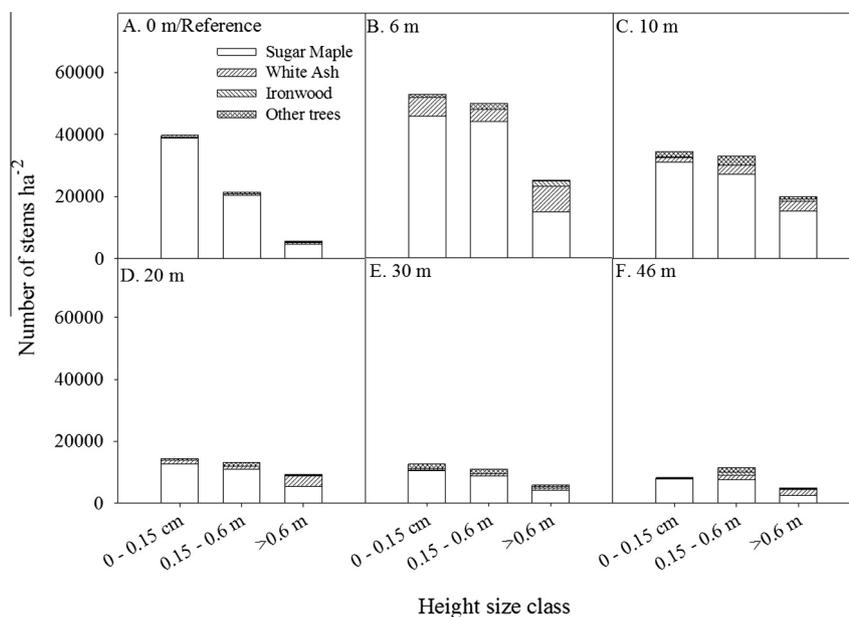


Fig. 2. Mean density of woody stems by species and height size class 12 years post-harvest in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Panels are labeled by gap size (diameter) treatment.

height class (MRPP, $P < 0.001$). By year 12, composition of tree reproduction was significantly different than years 0 and 2 ($P \leq 0.011$, pair-wise comparisons) and gap size was an important factor explaining composition for all height classes (Fig. 2 and Table 4). In all years post-harvest, composition of germinants (<0.15 m tall) was significantly different (MRPP, $P \leq 0.046$) among references, small gaps (6 and 10 m), and larger gaps when based on abundance, but was not different in any year when composition was measured by presence/absence. Indicator species analysis (ISA) found that reference areas had significant indicator values (IV) for sugar maple in years 2 (IV = 22.9) and 6 (IV = 27.9) and for ironwood in year 2 (IV = 22.3). In years 6 and 12, composition of seedlings (0.15–0.6 m tall) were generally different among references, small gaps (6 and 10 m), and larger gaps based on abundance and presence/absence. ISA of seedlings (0.15–0.6 m tall) did not detect a strong affinity between any species and gap size in any year. By year 12, composition of saplings (>0.6 m tall) were also different among references, small gaps, and large gaps, but were also different when based on presence/absence. ISA of saplings (>0.6 m tall) in year 12 found white ash (IV = 39) and ironwood (IV = 42.8) significantly related to 6 m gaps and sugar maple (IV = 30.4) significantly related to 10 m gaps.

3.2. Size of dominant saplings

Dominant saplings of sugar maple, white ash, and ironwood grew in diameter and height over time ($P < 0.001$) as expected. Gap size was important to some but not all dominants' size (Fig. 3). Sugar maple DBH differentiated among harvest gaps and references only in year 12 ($P = 0.033$), because uncut saplings in the references were larger than ingrowth saplings of 6, 10, and 20 m gaps ($P \leq 0.22$ pair-wise comparisons). Heights of sugar maple dominants were not different across the gap sizes in any year ($P \geq 0.098$). Moreover, gap size was not a significant factor in the diameter ($P \geq 0.215$) or height ($P \geq 0.333$) of white ash dominants in any year, although, by year 12, they were nominally larger in the larger gap sizes. Size of ironwood dominants were significantly affected by gap size in year 12 only ($P < 0.001$). Ironwood was taller ($P \leq 0.013$) with a larger DBH ($P \leq 0.002$) in harvest gaps versus references.

3.3. Effect of shrub competition

In year 12, gap size ($P \leq 0.040$) and lifeform ($P < 0.001$) were significant factors affecting woody stem density across all height

Table 4

Relative density (mean ± standard error) by survey year and species (sugar maple, white ash, ironwood, and other tree species) for saplings (stems > 0.6 m tall) in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

Survey year	Gap size	Sugar maple	White ash	Ironwood	Other trees
0	0	0.68 (0.15)	0.04 (0.03)	0.28 (0.16)	0 (0)
	6	0.5 (0.06)	0.13 (0.06)	0.36 (0.06)	0 (0)
	10	0.56 (0.15)	0.21 (0.11)	0.23 (0.18)	0.01 (0.01)
	20	0.59 (0.18)	0.13 (0.05)	0.27 (0.14)	0.01 (0.01)
	30	0.71 (0.07)	0.14 (0.05)	0.11 (0.05)	0.03 (0.03)
2	0	0.67 (0.14)	0.06 (0.05)	0.26 (0.15)	0 (0)
	6	0.41 (0.07)	0.3 (0.15)	0.28 (0.12)	0.01 (0.01)
	10	0.54 (0.21)	0.11 (0.1)	0.35 (0.22)	0 (0)
	20	0.35 (0.13)	0.42 (0.2)	0.2 (0.12)	0.02 (0.01)
	30	0.52 (0.17)	0.24 (0.07)	0.14 (0.07)	0.1 (0.08)
6	0	0.59 (0.13)	0.11 (0.08)	0.29 (0.15)	0.01 (0)
	6	0.32 (0.11)	0.44 (0.18)	0.23 (0.09)	0 (0)
	10	0.62 (0.09)	0.17 (0.08)	0.21 (0.12)	0.01 (0.01)
	20	0.53 (0.13)	0.4 (0.14)	0.07 (0.03)	0 (0)
	30	0.59 (0.1)	0.28 (0.06)	0.11 (0.07)	0.02 (0.01)
12	0	0.82 (0.03)	0.08 (0.06)	0.1 (0.03)	0 (0)
	6	0.51 (0.13)	0.34 (0.14)	0.12 (0.04)	0.03 (0.03)
	10	0.76 (0.05)	0.11 (0.07)	0.11 (0.06)	0.02 (0.01)
	20	0.55 (0.13)	0.37 (0.13)	0.02 (0.01)	0.06 (0.02)
	30	0.5 (0.05)	0.11 (0.03)	0.06 (0.02)	0.33 (0.06)
	46	0.32 (0.09)	0.21 (0.11)	0.06 (0.01)	0.4 (0.05)

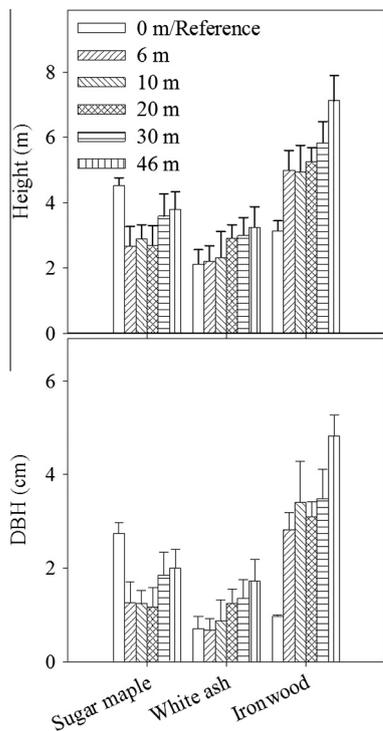


Fig. 3. Weighted mean size (+standard error) of dominant saplings (tallest stem species⁻¹ plot⁻¹) across gap size treatments 12 years after harvest in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

classes. In references and small gaps, tree density was nearly double the density of shrubs, while, in large gaps, the opposite was true (Fig. 4). Tree density sharply declined between 10 and 20 m gaps and remained low in the larger gap sizes, while shrub density increased linearly as gap size increased.

The effects of shrubs on tree growth from years 2 to 12 were evident in dominant saplings (Table 5). For sugar maple, a full model with gap size and raspberry was important to Ht:Dia growth, although these models largely did not explain height

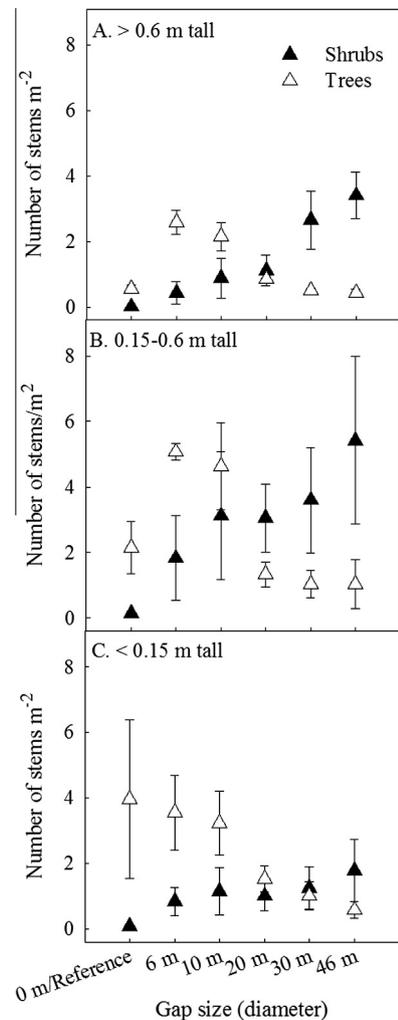


Fig. 4. Mean (±standard error) density of woody stems by height size class and lifeform across a gap size treatment 12 years after harvest in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

Table 5
Parameter coefficients (mean [standard error]) and fit (R^2) of selected models (lowest AICc) describing the effects of treatment, average shrub competition, and initial size (2 years post-harvest) on species and growth response (absolute change in response from years 2 to 12) of dominant saplings in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA.

Response	Sugar maple			White ash			Ironwood		
	Selected model	Coefficient	R^2	Selected model	Coefficient	R^2	Selected model	Coefficient	R^2
Height	Intercept	233.6 (44.5)	0.03	Intercept	27.1 (57.7)	0.39	Intercept	247.3 (69.7)	0.54
	Gap size	0.8 (5.9)		Gap size	26.8 (7.3)		Gap size	24.1 (9.5)	
	Raspberry	-6.6 (22.2)		Raspberry	-17 (29.3)		Raspberry	34 (35.2)	
	Gap size*Raspberry	0 (1.7)		Gap size*Raspberry	-5.9 (2.1)		Gap size*Raspberry	-5.8 (2.6)	
	Year 2 height	-0.1 (0.2)		Year 2 height	1 (0.5)		Year 2 height	-0.6 (0.2)	
DBH	Intercept	0.91 (0.06)	0.00	Intercept	0.34 (0.08)	0.38	Intercept	0.64 (0.14)	0.43
	Gap size			Gap size	0.02 (0.01)		Raspberry	0.27 (0.05)	
	Year 2 DBH			Year 2 DBH	1.71 (0.48)		Year 2 DBH	-0.12 (0.1)	
				Intercept	311.5 (15.8)		Intercept	217.3 (23.1)	
Ht:Dia	Intercept	240.6 (20)	0.89	Intercept	311.5 (15.8)	0.91	Intercept	217.3 (23.1)	0.90
	Gap size	3.4 (3)		Gap size	-2.8 (2.7)		Gap size	-6.5 (3.6)	
	Raspberry	9.5 (11.4)		Raspberry	2.7 (10.9)		Raspberry	31.6 (14.2)	
	Gap size*Raspberry	-1.5 (0.9)		Gap size*Raspberry	0.1 (0.8)		Gap size*Raspberry	0.9 (1)	
	Year 2 Ht:Dia	-1.1 (0.1)		Year 2 Ht:Dia	-1.2 (0.1)		Year 2 Ht:Dia	-1 (0.1)	

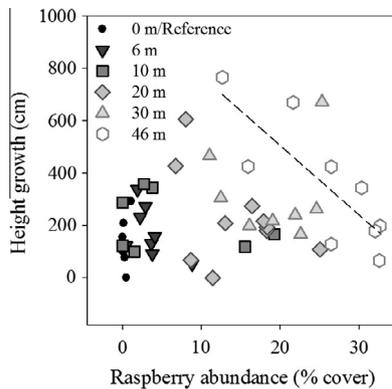


Fig. 5. The relationship of mean height growth between 2 and 12 years after harvest of white ash saplings and year 2 raspberry abundance by gap size in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. The dashed line represents the linear relationship in 46 m gaps only.

growth and DBH growth. For white ash, a full model with gap size and raspberry explained height growth and Ht:Dia growth. Gap size had a positive effect on height growth, while raspberry had a negative effect. For example, in 46 m gaps, white ash dominants grew taller when raspberry abundance was low, but not when raspberry abundance was high (Fig. 5). For ironwood, height growth and Ht:Dia growth was also explained by full models, where greater raspberry abundance was related to more growth.

4. Discussion

Developing management approaches that can restore or maintain resilience is crucial in the face of uncertain change. Here, we tested the efficacy of harvest gaps to create structural and compositional diversity over a decade in a mesic northern hardwood forest. Broadly, we found that small gaps maintain an understory layer dominated by shade-tolerant tree species, but regenerating species contributed little to diversifying the future forest composition. Medium to large gaps structurally were open with a thick shrub layer and very few saplings 12 years after harvest, which, by management standards would be considered a regeneration failure. Thus, using medium to large gaps to establish a new cohort of trees and diversify tree composition through the recruitment of less abundant species was not feasible with harvest gaps alone. Our study suggests that using harvest gaps on productive sites for sugar maple like ours (an ATD habitat type) is challenging and will likely require additional treatments to perpetuate tree

dominance and diversify tree composition. We discuss these ideas in the following subsections.

4.1. How did gap size influence tree recruitment over time?

We found that gap size mattered to tree recruitment and likely reflected the interaction between gap size and shrub abundance. Overall, more trees recruited into smaller gaps (6 and 10 m) than larger gaps (≥ 20 m), where shrub density was high. Furthermore, sapling (>0.6 m tall) densities at our site appear too low and too sparse to eventually fill larger gaps at 12 years after harvest. The larger gaps were regeneration failures by some standards, (<0.1 stems/ m^2 of trees >2.1 m tall (*sensu* Matonis et al., 2011); <0.25 stems/ m^2 of trees >0.6 m tall (*sensu* Gasser et al., 2010)). Regeneration failures have been noted in harvest gaps in productive sites with dense understories (Eyre and Zillgitt, 1953; Tubbs, 1968; Gasser et al., 2010) and in areas of high deer populations (Matonis et al., 2011). Our study did not test vegetation removal effects directly; however, the negative association between tree density and growth with increasing raspberry abundance suggests raspberry was a significant factor to tree recruitment in larger gaps at this site. While previous work has suggested that tree seedlings will grow through *Rubus* patches within 5–7 years and form a closed canopy shading out raspberry in 10–15 years (Donoso and Nyland, 2006), our results indicate an alternative developmental pathway in which there is little tree regeneration above or below the shrub layer 13 years after harvest. Given these findings, the early removal of competing vegetation within large harvest gaps is necessary for improving sugar maple regeneration densities on sites such as those examined in this study (Gasser et al., 2010).

Tree recruitment may have been influenced also by microclimatic variation among the gap sizes. Specifically, shortly after harvest, extreme weather events were recorded for this site. Micrometeorological measurements indicated that spring frosts and excessive summer heat events occurred in larger gaps, whereas these extreme conditions did not occur in references or were moderated in the smaller gaps. In addition, the larger gaps on average tended to be warmer in the summer and cooler in the winter than the other treatments (Strong et al., 1997). Extreme microclimatic variation has been indicated as a factor limiting tree seedling germination and survival in large harvest gaps within other forest types (Wright et al., 1998; Gray et al., 2002; Raymond et al., 2006) and may partially explain the lower regeneration densities we observed in the larger gaps.

Beyond shrub competition and microclimate conditions, other unmeasured factors may have influenced tree recruitment among

the gap sizes. For example, deer herbivory may have limited recruitment into larger gaps at our site. According to Wisconsin Department of Natural Resources, local landscape unit deer populations were above historical levels (>4 deer/km² (McCaffery, 1986; Alverson et al., 1988)) most of the study period. Matonis et al. (2011) found sugar maple sapling (1–2 m tall) densities inversely related to stand-level deer populations and elevated deer populations have been shown to inhibit gap-filling through excessive browsing of saplings (Pedersen and Wallis, 2004). At our site, deer exclosures were installed around a subset of the treatments during the first few years of the study; however, we found no statistical differences in tree regeneration inside or outside of exclosures in those first few years. Herbivores may have affected recruitment in years after the exclosure treatments, especially in the larger gaps where *Rubus* patches may have attracted deer (Horsley et al., 2003). However, we speculate that this is not entirely true, because we observed regenerating trees more often along edges rather than gap centers. If deer were a significant factor in the large gap recruitment, edge browsing by deer would have created the opposite phenomenon: more saplings in gap centers and less in gap edges. Thus, we feel deer browsing did influence some aspects of tree regeneration on site, such as growth (Kern et al., 2012), but likely played a limited role in tree recruitment differences among the gaps sizes.

Damage from harvesting may have influenced tree recruitment patterns among the gap sizes. Greater machinery traffic significantly reduced potential fine-root growth of sugar maple one year after harvest at another site (Malo and Messier, 2011), while another site with rocky loam soils showed no compaction effects after six harvests at 10-year intervals (Tarpey et al., 2008). At our site, compaction within gaps was limited by restricting machinery traffic to the forest matrix around gaps during the dormant season. However, felling and extracting trees from gaps likely damage advanced regeneration, especially in large gaps where more trees were removed than in small gaps. Logging damage was greatest in the smaller diameter classes in other forests (Lamson et al., 1985; Seablom and Reed, 2005). Although our harvest gaps were cleaned of trees ≥ 2.5 cm DBH, we suspect the residual advance regeneration (< 2.5 cm DBH) were damaged, because the few saplings observed in year 13 were of poor form (*personal observation*). Thus, we speculate that logging damage may have influenced tree recruitment patterns among the gap sizes.

Tree recruitment is usually abundant in northern hardwood stands (Eyre and Zillgitt, 1953) and failure has generally not been an issue such that regeneration research has focused on species composition and not seedling numbers per se. Our results lend support to a growing body of studies documenting potential problems with new age class establishment through larger gaps on productive sites. While our results support our hypothesis that tree recruitment would begin shortly after harvest, this initial recruitment event did not lead to full stocking in larger gaps. These findings have important implications as managers seek sustainable management strategies for addressing global environmental change and suggest that the creation of large harvest gaps run the risk of regeneration failures without provisions for competition control and regeneration protection.

4.2. How does gap size influence tree sapling composition and diversity over time?

We found that gap size impacted the relative abundances of different tree species; however, the constituent species comprising a given gap size were unaffected. In particular, tree composition across gaps was similar: primarily dominated by sugar maple with fewer amounts of white ash and ironwood seedlings. Gap size

influenced the abundance at which these dominant species occurred; it did not influence tree species assemblage such that tree characteristics or traits were discretely different by gap size. The same was true for diversity measures. Gap size influenced diversity starting in year 2 in germinants (< 0.15 m tall) through year 12 in saplings (> 0.6 m tall). However, richness differences were less than one species between gap sizes. Thus, our hypothesis that medium gaps would foster a unique tree composition of species of a wide range of shade tolerances making it the most diverse gap size was not supported. These results support the notion that gaps have little effect on species diversity on ATD habitat types, or sites well-suited for and dominated by long-lived, shade-tolerant species such as sugar maple.

Worldwide, the influence of shrubs on tree regeneration is a recognized concern in managed forests. Pervasive shrub layers limit tree species regeneration through resource competition, allelopathy, and physical impediment of seedling germination and growth, or indirectly through modifications of interspecific interactions (Royo and Carson, 2006). For example, shrubs in mixed oak forests reduced light, soil moisture, and seed rain and increased litter biomass. Consequently, tree seedling densities were low beneath canopy gaps with dense *Rhododendron* (Beckage et al., 2000). Moreover, in another study, dense fern understories were shown to interfere with the emergence of trees species by reducing available resources and substrate variability (George and Bazzaz, 1999). We anticipated more regeneration of yellow birch, red oak (*Quercus rubra*), and white pine (*Pinus strobus*) or mid-tolerant species that would have added diversity to the larger gap sizes. We observed reduced light availability ($< 1.6\%$ of light above canopy [unpublished data]) and uniformly thick leaf litter at ground level below raspberry patches in large gaps (*personal observation*). As such, we speculate that shrubs at our site limited establishment opportunities for less shade tolerant tree species to regenerate from seed.

In similar forests to ours, gap size did not affect tree diversity (Shields et al., 2007; Bolton and D'Amato, 2011), while, in other forest types, it has (Runkle, 1982; Phillips and Shure, 1990; Busing and White, 1997). The association between larger gaps and higher tree species diversity in the latter studies is often attributed to an influx of less shade tolerant species in the larger gaps in addition to advance regeneration of shade tolerant species (Poulson and Platt, 1989; McClure and Lee, 1993). In northern hardwood forests, gap effects on species diversity vary with habitat type. For example, yellow birch shared dominance with sugar maple on ATM sites, and, as a result, increasing gap size increased species diversity (Webster and Lorimer, 2003). ATD sites like those examined in this study are known for their sugar maple dominance (Kotar et al., 2002; Shields et al., 2007). Diverse seed sources were present in the overstory with $\sim 25\%$ of the residual forest matrix basal area in species other than sugar maple, including red oak, yellow birch, hemlock (*Tsuga canadensis*), ironwood, white ash, black cherry (*Prunus serotina*), and butternut (*Juglans cinerea*), but this overstory tree diversity did not result in understory tree diversity. Seed rain was not measured on site and, in the years shortly after harvest, may not have been significant enough to contribute to gap level diversity. However, the yellow birch seed crop appeared abundant after harvest (*personal observation*). In northern Wisconsin, droughts shortly after harvest (Palmer Drought Severity Index - 1.4 – -4.0, State of Wisconsin Climatology Office) may have prohibited establishment of seedlings, because yellow birch seedlings are sensitive to low moisture (Raymond et al., 2006). In addition, recent studies have shown yellow birch seedling survival increases with higher amounts of coarse woody debris (Shields et al., 2007; Marx and Walters, 2008; Bolton and D'Amato, 2011), which was largely unavailable on our site. This highlights the synchrony of several key events, including available seed, suitable microsite,

conductive growing conditions, and minimal effects from damaging agents, coinciding with harvest gap creation.

4.3. How does gap size influence mode of gap-filling and future canopy composition?

We found that gap size was important to sapling layer height development and subsequent potential mode of gap-filling and future composition. A sapling layer developed in smaller gaps; however, these gaps were closed after the 12 year period, inhibiting ascension of the regenerating trees into the overstory. This suggests that the mode of gap-filling will likely be through edge tree crown extension and not by the sapling layer. In another study, saplings in small harvest gaps (<11 m dia.) required 52 years to reach the main canopy due to gap closure by crown extension of mature edge trees and subsequent declining height growth rates (Webster and Lorimer, 2005). Another disturbance, such as another harvest entry, would be necessary to release this cohort of trees (Canham, 1985; Webster and Jensen, 2007). Thus, single-tree selection, which typically creates gaps <11 m dia., require short cutting cycles (10–15 years) (Tubbs, 1977; Erdmann, 1986).

On the other hand, sapling layer development in the larger gaps was sparse with trees mainly located at the edges of gaps. Recovery of this ecosystem to tree dominance will likely occur over time with gap-filling by saplings from gap edge to center as noted in another study (Metzger and Tubbs, 1971). Furthermore, the larger gaps represent within-stand locations where the successional trajectory has been set back to shrub dominance. The dominance of raspberry on site appears stable in the short-term with raspberry abundant across a range of size classes.

Based on current understory tree composition, the future forest composition in harvest gaps appears simpler and less diverse than the existing overstory. The three dominant species were sugar maple, ironwood, and white ash. Gap size had a minimal influence on sugar maple growth. Because sugar maple is a shade tolerant species and can germinate through thick duff, it will likely be a key species in recovery of tree cover in larger gaps, further increasing its abundance over time. Sugar maple is typically an abundant and valuable component in managed and unmanaged second-growth northern hardwood forests of the western Great Lakes (Crow et al., 2002; Neuendorff et al., 2007; Gronewold et al., 2010). Moreover, increasing gap size increased height growth of ironwood. Ironwood is considered a species of wide amplitude or ability to regenerate across a range of conditions irrespective of habitat types, available light conditions, deer densities, or competing vegetation (Matonis et al., 2011). Based on our observations, most ironwood saplings were of stump sprout origin. Along with not being a browse preferred species, the prolific sprouting ability of this species will aid in recovery of larger gaps by eventually shading out raspberry and allowing other species such as sugar maple to establish. Finally, white ash saplings also responded positively to increasing gap size but negatively to raspberry competition as found in another study (Matonis et al., 2011). Continued dominance of raspberry patches on site may limit growth and survival of this species' potential to reach a canopy position. In addition, white ash is a browse preferred species, of which we did observe excessive browsing of this species on site. In addition, white ash is a host species of Emerald ash borer (*Agrilus planipennis*), whose infestations kill understory saplings to vigorous dominant white ash trees, diminishing its potential as a future canopy dominant. Thus, our study highlights that some of the broader diversity issues across the range of northern hardwood forests manifest themselves at the gap-level, especially at productive sites like ours.

4.4. Are medium gaps the appropriate gap size to increase compositional diversity of mixed species, multi-aged stands managed under a single-tree/group selection hybrid approach?

In theory, saplings with contrasting life history strategies perform differentially or partition among gap sizes such that greater growth and survival occur in smaller gaps for shade tolerant trees and in larger gaps for shade intolerant species (Ricklefs, 1977; Denslow, 1980). We hypothesized that medium gaps would increase tree species diversity, because a mix of shade tolerant and intolerant species could co-exist. Thus, adding a medium gap size to single-tree selection was a hybrid approach to diversifying composition in managed multi-aged stands. However, increasing gap size did not significantly change composition or add tree diversity to the stand. Thus, medium gaps as a component of a hybrid selection approach did not function as intended and were not niches for mid-tolerant tree recruitment over 13 years. In fact, tree diversity and recruitment was higher in small gaps. This highlights that the importance of small gaps and their location from one harvest entry to the next. Small gap monumentation would improve opportunities for tree release and delineate areas to be avoided by machinery with future harvest entries. Further, use of a group selection approach will be challenging with competing vegetation without additional silvicultural practices such as scarification, tree release with herbicides or brush cutting, and/or within-gap seed tree retention of midtolerant seed sources (Shields et al., 2007; Gasser et al., 2010). Incorporating substrate structure such as coarse woody debris or tipup mounds will increase opportunity to regenerate less tolerant species as well (Shields et al., 2007; Bolton and D'Amato, 2011). However, for northern hardwood forests of the western Great Lakes region, these management options may be more successful in other mesic habitat types, such as ATM and AOCa.

Tree recruitment and diversity within harvest gaps may respond differently on other sites, different from ours. For instance, at sites with lower productivity, which are less favorable for sugar maple growth and potentially for competing vegetation, the success of using gap size to influence tree regeneration density and diversity may prove more fruitful. In addition, at the study's initiation, the stands were about 60 years old and in late stages of stem exclusion (Oliver and Larson, 1996) resulting in very little advance regeneration across the site. As such, we suspect that applying harvest gaps or group selection to older stands in later stages of stand development (e.g., understory re-initiation or old growth stage according to Oliver and Larson (1996)) could result in greater recruitment into larger gaps due to the higher levels of advance regeneration found in these stages of development.

In selection silviculture, regular cutting cycles are key to establishing new age classes among the older classes to sustain merchantable harvests over time. For sites similar to ours, selection is challenging, because new age classes in small gaps must be continuously released with a regular cutting cycle (Webster and Lorimer, 2005), which is not feasible for some landowners. In addition, fully-stocked age classes were not obtained in larger gaps. Poor age class development compromises feasibility of future harvests to meet economic goals and maintain and restore ecosystem goods and services. At the current point in time, the larger gaps appear as gap-level regeneration failures, while, in practice, regeneration success is judged at a stand-level. If most of the new age class establishment is developed with smaller gaps and larger gaps represent a small proportion of new age class establishment, then stands may still meet regeneration standards with few persistent gaps of early successional habitat. In some regions, a mix of early and late-successional habitat might be desirable (Swanson et al., 2010).

Finally, our results indicate that the opportunities to diversify these forests through larger harvest gaps appear limited on sites

like ours, as tree recruitment and diversity was greater with smaller rather than larger harvest gaps. Unfortunately, these smaller gaps have low functional diversity (Kern et al., 2013) and contribute to the broad issues of species homogenization that has been documented in northern hardwood systems over the past couple of decades (Neuendorff et al., 2007; Schulte et al., 2007). Furthermore, some work suggests that even those management regimes that use only smaller harvest gaps may be unsustainable in areas with high deer densities indicating that what was once viewed as a reliable management regime may no longer be sustainable into the future (Matonis et al., 2011).

5. Conclusions

In conclusion, our study suggests that (1) gap size is inversely related to tree regeneration on ATD habitat types (high site quality) for northern hardwood stands in the upper Great Lakes region; (2) applying group selection methods with medium to large gaps (≥ 20 m) alone will not ensure successful northern hardwood regeneration nor will it increase the diversity of these forests compared to applying single-tree or group selection with small groups (< 20 m); and (3) post-harvest release treatments may be required on these sites to facilitate recruitment and gap-filling by saplings in larger gaps. Currently, these untreated large gaps provide small patches of early successional habitat in mature forests, which may be desirable for achieving certain habitat objectives, but pose considerable challenges to the long-term sustainability of tree cover and associated benefits on these sites.

Acknowledgements

This study was supported by the US Forest Service: the Northern Research Station (and former North Central Research Station) funded research staff to design, collect and analyze data and the Chequamegon-Nicolet National Forest (and former Nicolet National Forest) provided logistical support of the timber harvest to implement study design. The research could not have been completed without the additional mentoring and leadership of Brian Palik, Peter Reich, Rebecca Montgomery, and John Zasada. We greatly appreciated the technical assistance from Adam Weise, Maggie (Haas) Lorenz, Kris Gray, and Ben Gosack, and many others. John Kabrick, Michael Walters, and two anonymous reviewers provided valuable feedback on an earlier version of the manuscript.

References

- Alverson, W.S., Waller, D.M., Solheim, S.L., 1988. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2, 348–358.
- Beckage, B., Clark, J.S., Clinton, B.D., Haines, B.L., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Can. J. For. Res.* 30, 1617–1631.
- Bolton, N.W., D'Amato, A.W., 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *For. Ecol. Manage.* 262, 1215–1222.
- Brokaw, N.V.L., Busing, R.T., 2000. Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15, 183–188.
- Busing, R.T., White, P.S., 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* 78, 562–568.
- Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torrey Botanical Club* 112, 145.
- Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For. Ecol. Manage.* 99, 337–354.
- Crow, T.R., Buckley, D.S., Nauertz, E.A., Zasada, J.C., 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. *For. Sci.* 48, 129–145.
- Denslow, J.S., 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12, 47–55.
- Dietze, M.C., Clark, J.S., 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecol. Monogr.* 78, 331–347.
- Donoso, P.J., Nyland, R.D., 2006. Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* sp.) following clearcutting and shelterwood methods. *N. J. Appl. For.* 23, 288–296.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., Flannigan, M., 2006. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* 36, 2285–2299.
- Erdmann, G.G., 1986. Developing quality in second-growth stands. In: Mroz, G.D., Reed, D.D. (Eds.), *The Northern Hardwood Resource: Management and Potential*. Michigan Technological University, Houghton, MI, pp. 206–222.
- Eyre, F.H., Zillgitt, W.M., 1953. Partial cuttings in northern hardwoods of the Lake States: Twenty-year experimental results, USDA Forest Service Lake States Forest Experiment Station Broomall PA. Technical Bulletin LS-1076, pp. 124.
- Falk, K.J., Elliott, K.A., Burke, D.M., Nol, E., 2010. Early seedling response to group selection harvesting in a northern hardwood forest. *Forestry Chron.* 86, 100–109.
- Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural disturbance and stand development principles for ecological forestry. USDA Forest Service, Northern Research Station, Newtown Square, PA. General Technical, Report NRS-19, pp. 44.
- Gasser, D., Messier, C., Beaudet, M., Lechowicz, M.J., 2010. Sugar maple and yellow birch regeneration in response to canopy opening, liming and vegetation control in a temperate deciduous forest of Quebec. *For. Ecol. Manage.* 259, 2006–2014.
- George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80, 833–845.
- Gray, A.N., Spies, T.A., 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84, 635.
- Gray, A.N., Spies, T.A., Easter, M.J., 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. For. Res.* 32, 332.
- Gronewold, C.A., D'Amato, A.W., Palik, B.J., 2010. The influence of cutting cycle and stocking level on the structure and composition of managed old-growth northern hardwoods. *For. Ecol. Manage.* 259, 1151.
- Holladay, C.-A., Kwit, C., Collins, B., 2006. Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size. *For. Ecol. Manage.* 223, 218–225.
- Horsley, S.B., Stout, S.L., DeCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.
- Jacobs, R.D., 1987. Silvicultural systems for northern hardwoods in the Midwest and Lake States. In: *Proceedings of the symposium on managing northern hardwoods*. SUNY College of Environmental Resources and Forestry, Syracuse, NY, pp. 383–388.
- Janowiak, M.K., Nagel, L.M., Webster, C.R., 2008. Spatial scale and stand structure in northern hardwood forests: implications for quantifying diameter distributions. *For. Sci.* 54, 497–506.
- Kelty, M.J., Kittredge, D.B., Kyker-Snowman, T., Leighton, A.D., 2003. The conversion of even-aged stands to uneven-aged structure in southern New England. *N. J. Appl. For.* 20, 109–116.
- Kern, C.C., Reich, P.B., Montgomery, R.A., Strong, T.F., 2012. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? *For. Ecol. Manage.* 267, 134–143.
- Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. *J. Plant Ecol.* 6, 101–112.
- Kotar, J., Kovach, J.A., Burger, T.L., 2002. *A guide to Forest Communities and Habitat Types of Northern Wisconsin*. University of Wisconsin, Madison, WI, USA.
- Lamson, N.I., Smith, H.C., Miller, G.W., 1985. Logging damage using an individual-tree selection practice in Appalachian hardwood stands. *N. J. Appl. For.* 2, 117–120.
- Leak, W.B., 1999. Species composition and structure of a northern hardwood stand after 61 years of group/patch selection. *N. J. Appl. For.* 16, 151–153.
- Leak, W.B., Filip, S.M., 1977. 38 Years of group selection in New England northern hardwoods. *J. For.* 75, 641–643.
- Loss, S.R., Hueffmeier, R.M., Hale, C.M., Host, G.E., Sjerven, G., Frelich, L.E., 2013. Earthworm invasions in northern hardwood forests: a rapid assessment method. *Nat. Areas J.* 33, 21–30.
- Madsen, P., Hahn, K., 2008. Natural regeneration in a beech-dominated forest managed by close-to-nature principles - a gap cutting based experiment. *Can. J. For. Res.-Rev. Can. Rech. For.* 38, 1716–1729.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, New Jersey, USA.
- Malo, C., Messier, C., 2011. Impact of primary and secondary machinery tracks on fine root growth of sugar maple after selection cutting. *Can. J. For. Res.* 41, 892–897.
- Marx, L., Walters, M.B., 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock-hardwood forests. *Ecology* 96, 505–513.
- Matonis, M.S., Walters, M.B., Millington, J.D.A., 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. *For. Ecol. Manage.* 262, 286–298.
- McCaffery, K., 1986. On deer carrying capacity in northern Wisconsin. In: *Transactions of the twenty-second Northeast deer technical committee*. Vermont Fish and Wildlife Department, Waterbury VT.
- McClure, J.W., Lee, T.D., 1993. Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. *Can. J. For. Res.* 23, 1347–1360.

- McClure, J.W., Lee, T.D., Leak, W.B., 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. *For. Ecol. Manage.* 127, 181–189.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Designs, Gleneden Beach, OR, USA.
- McCune, B., Medford, M.J., 2006. PC-ORD, multivariate analysis of ecological data, Version 5. In: MjM Software, Gleneden Beach, Oregon, USA.
- Metzger, F.T., Tubbs, C.H., 1971. Influence of cutting methods on regeneration of second-growth northern hardwoods. *J. For.* 69, 559–564.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Naaf, T., Wulf, M., 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. *For. Ecol. Manage.* 244, 141–149.
- Neuendorff, J.K., Nagel, L.M., Webster, C.R., Janowiak, M.K., 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. *N. J. Appl. For.* 24, 197–202.
- Niese, J.N., Strong, T.F., 1992. Economic and tree diversity trade-offs in managed northern hardwoods. *Can. J. For. Res.* 22, 1807–1813.
- Nyland, R.D., 1987. Selection system and its application to uneven-aged northern hardwoods. In: Nyland, R.D. (Ed.), *Managing Northern Hardwoods*. SUNY College of Environmental Science and Forestry, Syracuse, NY.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*, update ed. John Wiley, New York.
- Pedersen, B.S., Wallis, A.M., 2004. Effects of white-tailed deer herbivory on forest gap dynamics in a wildlife preserve, Pennsylvania, USA. *Nat. Areas J.* 24, 82–94.
- Phillips, D.L., Shure, D.J., 1990. Patch-size effects on early succession in southern Appalachian forests. *Ecology* 71, 204–212.
- Poulson, T.L., Platt, W.J., 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70, 553–555.
- Puettmann, K.J., Coates, K.D., Messier, C., 2009. *A Critique of Silviculture: Managing for Complexity*. Island Press, Washington, D.C.
- Raymond, P., Munson, A.D., Ruel, J.-C., Coates, K.D., 2006. Spatial patterns of soil microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood–white pine stands. *Can. J. For. Res.* 36, 639–651.
- Ricklefs, R.E., 1977. Environmental heterogeneity and plant species diversity: a hypothesis. *Am. Nat.* 111, 376–381.
- Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* 36, 1345–1362.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 64, 623.
- SAS Institute Inc., 2008. SAS version 9.2. Cary, NC, USA.
- Schulte, L., Mladenoff, D., Crow, T., Merrick, L., Cleland, D., 2007. Homogenization of northern US Great Lakes forests due to land use. *Landsc. Ecol.* 22, 1089–1103.
- Schutz, J.P., 1997. Selection forests—a concept for sustainable use: 90 years of experience of growth and yield research in selection forestry in Switzerland. In: Emmingham, W.H. (Ed.), *Proceedings of the IUFRO Interdisciplinary Uneven-aged management symposium*. Oregon State University, Corvallis, OR.
- Seablom, T.J., Reed, D.D., 2005. Assessment of factors contributing to residual tree damage from mechanized harvesting in northern hardwoods. *N. J. Appl. For.* 22, 124–131.
- Shields, J.M., Webster, C.R., Nagel, L.M., 2007. Factors influencing tree species diversity and *Betula alleghaniensis* establishment in silvicultural openings. *Forestry* 80, 293–307.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. *The Practice of Silviculture: Applied Forest Ecology*, ninth ed. John Wiley & Sons, Inc., New York, USA.
- Strong, T.F., Teclaw, R.M., Zasada, J.C., 1997. Monitoring the effects of partial cutting and gap size on microclimate and vegetation responses in northern hardwood forests in Wisconsin. In: *Proceedings of the National Silviculture Workshop*. USDA Forest Service, Warren, PA, pp. 42–47.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2010. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9, 117–125.
- Tarper, R.A., Jurgensen, M.F., Palik, B.J., Kolka, R.K., 2008. The long-term effects of silvicultural thinning and partial cutting on soil compaction in red pine (*Pinus resinosa* Ait.) and northern hardwood stands in the northern Great Lakes Region of the United States. *Can. J. Soil Sci.* 88, 849–857.
- Tubbs, C.H., 1968. The influence of residual stand densities on regeneration in sugar maple stands. USDA Forest Service North Central Forest Experiment Station, Saint Paul, Minnesota. Research Note NC-47.
- Tubbs, C.H., 1977. *Manager's handbook for northern hardwoods in the North Central States*. USDA Forest Service North Central Forest Experiment Station, Saint Paul, Minnesota. General Technical Report NC-39, pp. 29.
- USDA Natural Resource Conservation Service, 2005. *Soil Survey of Forest County, Wisconsin*. National Cooperative Soil Survey.
- USDA NRCS, 2009. The PLANTS Database (<<http://plants.usda.gov>>). In: USDA NRCS, National Plant Data Center, Baton Rouge, LA USA.
- Webster, C.R., Jensen, N.R., 2007. A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Can. J. For. Res.* 37, 682–689.
- Webster, C.R., Lorimer, C.G., 2002. Single-tree versus group selection in hemlock-hardwood forests: are smaller openings less productive? *Can. J. For. Res.* 32, 591.
- Webster, C.R., Lorimer, C.G., 2003. Manipulating group-selection size to promote tree species diversity in hemlock-hardwood forests. In: *Proceedings of Society of American Foresters National Convention*, Buffalo, NY, pp. 299–309.
- Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. *Ecol. Appl.* 15, 1245–1262.
- Wright, E.F., Coates, K.D., Bartemucci, P., 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. *Can. J. For. Res.* 28, 1352–1364.