NRC Research Press

ARTICLE

Initial tree regeneration response to natural-disturbance-based silviculture in second-growth northern hardwood forests

Laura F. Reuling, Anthony W. D'Amato, Brian J. Palik, Karl J. Martin, and Dakota S.A. Fassnacht

Abstract: Northern hardwood stands in the Great Lakes region are often managed using single-tree selection, which generally favors regeneration of shade-tolerant species, especially sugar maple (*Acer saccharum* Marsh.) and may reduce regeneration of midtolerant and shade-intolerant species. These forests also tend to have lower microsite diversity than old-growth stands, which may negatively affect the regeneration of light-seeded species, including yellow birch (*Betula alleghaniensis* Britton). The objective of this research was to determine the initial effects of gap size and gap cleaning on tree regeneration in northern hardwood stands in northern Wisconsin, USA. The current study evaluated three gap sizes compared with a control. A gap-level cleaning treatment also examined effects of removal of advance regeneration and soil scarification. Postharvest seedling densities, especially shade-tolerant species, increased with increasing gap size. *Rubus* spp. increased significantly in the higher light conditions in these treatments. Density of yellow birch seedlings and saplings was low for all gap sizes but increased with removal of advance regeneration and soil scarification. These initial results underscore the challenges of using natural-disturbance-based treatments to increase the diversity of tree communities in second-growth forests and the importance of advance regeneration and seedbed conditions for increasing the abundance of historically important species.

Key words: northern hardwood, natural-disturbance-based management, yellow birch, sugar maple, canopy gaps.

Résumé : Les peuplements de feuillus nordiques de la région des Grands Lacs sont souvent aménagés à l'aide du jardinage par pied d'arbre qui favorise généralement la régénération d'espèces tolérantes à l'ombre, particulièrement l'érable à sucre (*Acer saccharum* Marsh.), et peut défavoriser la régénération d'espèces semi-tolérantes et intolérantes à l'ombre. Ces forêts ont aussi tendance à avoir une plus faible diversité de microsites que les vieux peuplements, ce qui peut influencer négativement la régénération d'espèces à graines légères, dont le bouleau jaune (*Betula alleghaniensis* Britton). L'objectif de cette étude était de déterminer les effets initiaux de la taille et du nettoiement des trouées sur la régénération des arbres dans des peuplements de feuillus nordiques du nord du Wisconsin, aux États-Unis. La présente étude a évalué trois tailles de trouées qui ont été comparées à un témoin. Nous avons aussi étudié les effets d'un traitement de nettoiement des trouées consistant à éliminer la régénération préétablie et à scarifier le sol. La densité des semis après la coupe, particulièrement les espèces tolérantes à l'ombre, a augmenté avec la taille des trouées. Dans ces traitements, la présence de *Rubus* spp. a significativement augmenté aux endroits les plus exposés à la lumière. La densité des semis et des gaules de bouleau jaune était faible peu importe la taille des trouées, mais a augmenté avec l'élimination de la régénération préétablie et le scarifiage du sol. Ces premiers résultats font ressortir les difficultés liées à l'utilisation de traitements fondés sur les perturbations naturelles pour accroître la diversité des communautés d'arbres dans les forêts de seconde venue. Ils mettent aussi en évidence l'importance de la régénération préétablie et des conditions des lits de germination pour augmenter l'abondance d'espèces historiquement importantes. [Traduit par la Rédaction]

Mots-clés : feuillus nordiques, aménagement fondé sur les perturbations naturelles, bouleau jaune, érable à sucre, trouées du couvert forestier.

Introduction

Old-growth, northern hardwood forests once made up approximately 40% of the forested landscape in the upper Great Lakes region of North America (Frelich 1995). Due in large part to the heavy logging of the late 1800s and early 1900s, little old-growth forest remains in this region (Frelich 1995). As the value of old-growth forests and their unique attributes and dynamics become more widely recognized (e.g., Humphrey 2005), researchers have begun to evaluate management alternatives that include restoring and sustaining old-growth characteristics among the objectives in forests managed for wood production (Bauhus et al. 2009).

Several major structural and compositional differences have been identified between old-growth and second-growth northern hardwood forests. Substantial differences can be found in tree diameter distributions (Hale et al. 1999), the number and size of cavity trees (Goodburn and Lorimer 1998), the amount and decay

---

Received 25 September 2018. Accepted 26 November 2018.

L.F. Reuling and A.W. D'Amato.* Department of Forest Resources, University of Minnesota, 115 Green Hall, 1530 Cleveland Avenue North, St. Paul, MN 55108, USA.
B.J. Palik. USDA Forest Service Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA.
K.J. Martin† and D.S.A. Fassnacht. Wisconsin Department of Natural Resources, 101 S. Webster St., Madison, WI 53703, USA.
Corresponding author: Laura F. Reuling (email: lreuling@umn.edu).
*Present address: Rubenstein School of Environment and Natural Resources, University of Vermont, 204e Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA.
†Present address: University of Wisconsin, Cooperative Extension, 625 Extension Building, 432 N. Lake Street, Madison, WI 53706, USA.

Can. J. For. Res. **49**: 628–639 (2019) dx.doi.org/10.1139/cjfr-2018-0406

class distribution of coarse woody material (CWM) (Goodburn and Lorimer 1998), and the size and distribution of canopy gaps (Dahir and Lorimer 1996). CWM and canopy-gap attributes are especially important for tree regeneration as they influence microsite conditions for seedling establishment (Gray and Spies 1997) and gradients of available light at the understory level (Canham et al. 1990), respectively. For example, downed, decaying logs are important in creating microsite conditions that favor the regeneration of several species historically important in old-growth northern hardwood forests, especially yellow birch (*Betula alleghaniensis* Britton) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Marx and Walters 2008). Similarly, gaps in old-growth stands are larger and more evenly distributed among size classes relative to gaps found in second-growth stands, ranging from 50 to >200 m^2 compared with less than 30 m^2 in second-growth stands (Dahir and Lorimer 1996). This range of gap sizes provides opportunities for species with different reproductive strategies and different levels of shade tolerance to coexist within the same stand (Vepakomma et al. 2011). The lack of larger gaps and less heterogeneity in gap size in second-growth forests has been suggested as a possible factor contributing to the loss of species of mid to low shade tolerance in various forest systems (Nuttle et al. 2013).

Northern hardwood stands in the upper Great Lakes region are often managed using single-tree selection, which creates small canopy gaps and generally favors the regeneration of shade-tolerant species, especially sugar maple (*Acer saccharum* Marsh.). The loss of midtolerant species and subsequent increase in shade-tolerant species with this type of management has been well documented in long-term studies (Jenkins and Parker 2001; Leak and Sendak 2002; Schuler 2004). Partially in response to these research findings, silviculture based on emulation of natural disturbance patterns that creates a greater range and diversity of gap sizes has been proposed as a way to maintain or increase diversity of shade tolerance classes in tree regeneration, particularly midtolerant species, as well as accelerate the development of old-growth structural characteristics (Bauhus et al. 2009).

One focus of a natural-disturbance-based approach for northern hardwood management includes greater use of larger canopy openings than single-tree selection generally accommodates. A rationale for this, stemming from the gap partitioning hypothesis, is that larger gaps will have increased diversity of seedlings and saplings due to microclimate differences within individual gaps (Denslow 1980). Light and moisture conditions are more variable in large gaps than in small gaps (Canham et al. 1990) and increased resource heterogeneity may increase species diversity as well (Denslow 1980). Several studies in northern hardwood systems have indicated that creating larger canopy gaps, similar in size to those found in old-growth forests, may increase the diversity of tree regeneration and allow trees of lower shade tolerance to regenerate (Leak 1999; Shields et al. 2007; Nuttle et al. 2013). However, in cases in which advance regeneration of shade-tolerant species is abundant or a well-developed shrub layer exists, canopy gaps may only serve to release species already present and accelerate succession to a forest with increased dominance of shade-tolerant species (Webb and Scanga 2001).

While small tree-fall gaps (one or two trees) are the most common disturbance in northern hardwood forests (Dahir and Lorimer 1996), mesoscale disturbances, especially wind disturbance, also occur on the landscape (Hanson and Lorimer 2007). Historically, the rotation period for disturbance that removed 30%–60% of the canopy in patches ranging from 10 to 5000 m^2 was 300–390 years in hardwood forests of upper Michigan (Frelich and Lorimer 1991). Most natural-disturbance-based approaches for management focus only on emulating tree-fall gaps and do not account for these mesoscale wind disturbances. However, these moderate-intensity disturbances, which on average may occur only once during the life-span of a cohort, can have important consequences for forest composition and structure by creating larger canopy openings, increasing solar radiation on the forest floor, and increasing heterogeneity in solar radiation when compared with single-tree and group selection (Hanson and Lorimer 2007). All these features have the potential to increase regeneration opportunities for midtolerant tree species.

The creation of favorable microsites in canopy gaps is also important for the regeneration of several northern hardwoods and associated species. Species such as yellow birch and eastern hemlock require decaying wood or exposed mineral soil seedbeds, features often associated with uprooted trees, while sugar maple seedlings are unlikely to be associated with decaying wood (Marx and Walters 2008). Site scarification and removal of advance regeneration have been suggested as ways to increase regeneration of yellow birch and other midtolerant species (Raymond et al. 2003; Gauthier et al. 2016), particularly on more nutrient-rich sites where dense understory layers of sugar maple seedlings have developed.

This study operationally examines silvicultural prescriptions commonly applied to second-growth northern hardwood stands (single-tree and group selection) and compares them with a silvicultural treatment designed to increase structural complexity and compositional diversity by emulating a wider range of historical disturbance severities. Harvesting and experimental treatments designed to create a range of canopy gap sizes, including small- to mid-sized gaps and small shelterwoods, augment CWM levels, and provide a diversity of microsites for regeneration were implemented at an operational scale across three sites in northern Wisconsin. We examined the initial (three-year) response of tree seedlings and saplings, as well as shrubs, to address the following questions. (*i*) How does gap size affect composition and diversity of trees and shrubs in the seedling and sapling layers? (*ii*) Does microsite condition within gaps affect the representation of midtolerant and shade-intolerant tree species and (or) have an effect on species diversity?

Materials and methods

Study sites

The current study is part of an ongoing operational-scale study in northern Wisconsin (Managed Old-growth Silvicultural Study (MOSS); Fassnacht et al. 2013). Sites were located at the Flambeau River State Forest (Flambeau or FLMB), the Northern Highland–American Legion State Forest (Northern Highland or NHAL), and the Argonne Experimental Forest within the Chequamegon–Nicolet National Forest (Argonne or ARGN). Four northern hardwood stands ~49 ha in size (ranging from 45 to 56 ha) were chosen at each site with selection criteria that stands be 70–90 years old, located on mesic, nutrient-rich sites, and have had no management inputs during the previous 10 years. Soils in these stands were silt loam or sandy loam, mesic, and nutrient rich to very nutrient rich (Table 1). The most common species in the overstory was sugar maple, which accounted for over 70% of the basal area of trees greater than 10 cm diameter at breast height (dbh) at the Argonne site (Table 1). Mean summer (June, July, August) temperatures ranged from 17 to 18 °C, and mean winter (December, January, February) temperatures ranged from –10 to –12 °C for this region. Mean annual precipitation was between 80 and 84 cm·$year^{-1}$, with 15%–20% falling as snow (1971–2000, Midwest Regional Climate Center, http://mcc.sws.uiuc.edu). More detailed site descriptions are available elsewhere (Fassnacht et al. 2013).

Silvicultural treatments

Three gap-size treatments and two CWM treatments were implemented at each site in the winter of 2007–2008 in an augmented split-plot design having three blocks (sites) (Piepho et al. 2006). An exception was the large gap – ambient CWM treatment (see description below) at Argonne, which was implemented one

Table 1. General site-level characteristics of the three study sites.

					Forest overstory composition by percentage of basal area§					
Site*	Stand age (years)	Habitat type†,‡	Soils†	Mean pretreatment basal area ($m^2 \cdot ha^{-1}$)	*Acer saccharum*	*Tilia americana*	*Fraxinus* spp.	*Tsuga canadensis*	*Acer rubrum*	*Betula alleghaniensis*
FLMB	75–83	AH–ATD	Silt loam over sandy loam	29.6	40.2	13.7	12.1	6.8	11.4	5.8
NHAL	89–91	ATD	Sandy loam	30.6	70.0	12.3	0.7	2.9	1.3	4.5
ARGN	79–92	AOCa–ATD	Sandy loam	32.9	71.6	6.0	4.4	7.3	4.0	3.1

*FLMB, Flambeau River State Forest; NHAL, Northern Highland–American Legion State Forest; ARGN, Argonne Experimental Forest.

†From Fassnacht et al. (2013).

‡Habitat type is defined by Kotar et al. (2002).

§Overstory composition is based on basal area of trees greater than 10 cm diameter at breast height (dbh).

year later in the winter of 2008–2009 due to operational limitations. Each stand (whole plot) was divided into two approximately 24 ha half-stands (split plots), with the entire stand receiving one gap-size treatment and each half-stand receiving a different CWM treatment. Each site also had an approximately 49 ha uncut control stand, which did not receive any gap size or CWM treatment.

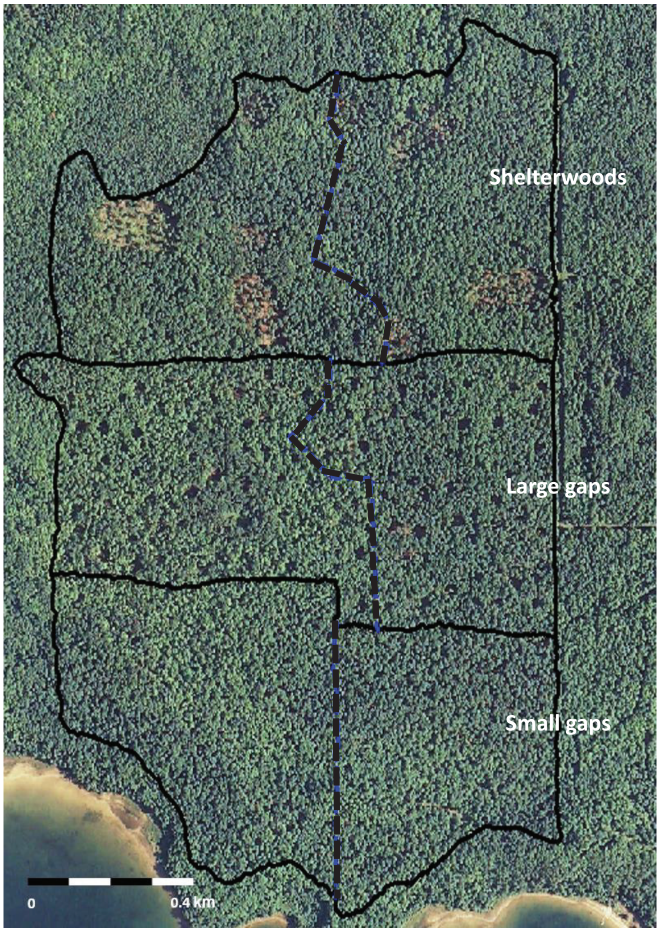
The gap-size treatments were as follows: (*i*) small gaps (10.7 m diameter, 90 m^2) plus matrix thinning, (*ii*) large gaps (18.3 m diameter (260 m^2) and 24.4 m diameter (470 m^2)) plus matrix thinning, and (*iii*) a treatment designed using shelterwoods to emulate a mesoscale wind disturbance based on the patterns of disturbance documented by Hanson and Lorimer (2007) (Fig. 1). Small and large gaps approximate the canopy opening sizes commonly created in operational harvests in the region using singe-tree selection and group selection, respectively. The three gap-size treatments were defined by the size of canopy gaps, number of gaps created per hectare, and additional thinning done to the matrix surrounding gap treatment areas. This study evaluates the effects of gap size (small, large, and shelterwood) and gap-level cleaning treatments on seedlings and saplings within gaps and shelterwoods. Seedlings and saplings in the thinned matrix between the gaps are not evaluated here.

For the small-gap treatment, approximately 10 gaps with a 10.7 m diameter were created per hectare and the rest of the stand was thinned to a residual basal area of 18.4–20.7 $m^2 \cdot ha^{-1}$. Additionally, during the harvest, these gaps were cleaned of all saplings greater than 2.54 cm dbh using a chainsaw. This treatment is widely practiced in this region to encourage the development of quality hardwood seedlings and saplings.

The large-gap treatment involved creating one gap per 0.4 ha, alternating sizes between 18.3 m and 24.4 m in diameter. Areas between gaps were thinned to achieve a residual basal area of 18.4–20.7 $m^2 \cdot ha^{-1}$. Within the large-gap treatment, a nested gap-level site preparation study was implemented with one of three treatments randomly assigned to each gap within a given gap-size and CWM treatment: (*i*) modified cleaning (hereafter referred to as "not cleaned") in which only saplings that were poorly formed or damaged prior to harvest were removed, (*ii*) cleaning (hereafter referred to as "cleaned") in which all saplings greater than 2.54 cm dbh were removed, and (*iii*) cleaned and scarified gaps (hereafter referred to as "scarified") in which gaps were cleaned of all saplings greater than 2.54 cm dbh and then scarified to expose 70%–90% mineral soil. Scarification was performed in September following harvest using a Salmon blade on a crawler bulldozer.

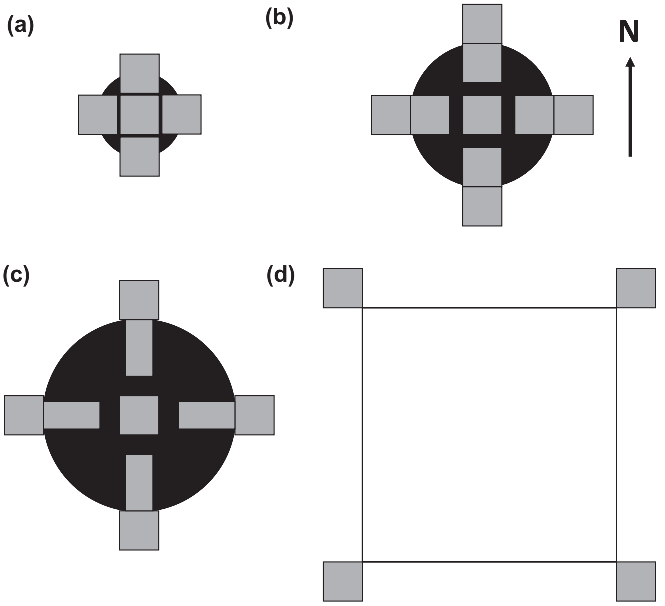
The mesoscale wind treatment included four small shelterwoods, a lightly thinned area, and a heavily thinned matrix in each half-stand (split plot). Of the four shelterwoods, two were 0.4 ha and two were 1.2 ha in size. Each shelterwood was cut to leave 60%–65% residual basal area. The lightly thinned area covered approximately 25% of the stand and the remaining portion of the stand was heavily thinned (approximately 65% of the stand). Target residual basal areas for the lightly and heavily thinned areas were 20.7–23.0 $m^2 \cdot ha^{-1}$ and 18.4–20.7 $m^2 \cdot ha^{-1}$, respectively, in the initial entry.

Fig. 1. Aerial photos of shelterwoods, large-gap treatment, and small-gap treatment stands at the Northern Highland site in 2008. Solid lines represent stand boundaries; dashed lines indicate split-plot divisions for ambient and high coarse woody material (CWM) treatments. [Colour online.]



CWM treatments were designated as ambient and high. In half-stands receiving the ambient CWM treatment, no additional CWM was deliberately created. In the stands receiving the high CWM treatment, the number of snags and amount of downed wood were deliberately increased during harvest to approximately 65% of the density and volume found in old-growth northern hardwood stands in the Sylvania Wilderness Area in Upper Michigan (Fassnacht et al. 2013), the nearest similar old-growth forests in the region. An additional 3.1–6.4 $m^3 \cdot ha^{-1}$ of downed woody material and 3.7–7.6 $snags \cdot ha^{-1}$ were created in the high CWM treatments (Fassnacht et al. 2013). Snags and CWM were created by double-girdling or felling, respectively, live canopy

Fig. 2. Potential locations of 25 m² regeneration plots in (*a*) 10.7 m diameter small gaps, (*b*) 18.3 m diameter large gaps, (*c*) 24.4 m diameter large gaps, and (*d*) shelterwood and control stand macroplots. Macroplots are 32 m × 32 m. Black circles indicate canopy gaps; gray boxes indicate potential locations of regeneration plots within gaps and macroplots. All locations were not sampled at each gap or macroplot.



trees greater than or equal to 25.4 cm dbh. Trees that were diseased or of poor form were targeted where possible.

Field methods

A series of 25 m² plots were established at each stand one year prior to treatment implementation for measuring forest understory, including tree regeneration. All regeneration plots were 5 m × 5 m except mid-distance plots in 24.4 m diameter gaps (Fig. 2). These were 7.19 m × 3.48 m to sample a similar portion of the variation in light environment from gap edge to gap center as was being sampled in the 18.3 m diameter gaps with the 5 m × 5 m plots (Fassnacht et al. 2013). Approximately 19% of the regeneration plots were fenced to exclude white-tailed deer (*Odocoileus virginianus* Zimmermann). This study focuses only on unfenced plots with impacts of deer browsing on the forest understory reported elsewhere (Reuling 2014). In treatment stands, regeneration plots were located within harvest gaps and shelterwoods, as described below. Regeneration plots in the control were located systematically throughout the stand, also described below.

Sampled small gaps (10.7 m diameter) each contained one regeneration plot randomly selected to be in one of five possible locations (Fig. 2*a*), but with gap centers sampled disproportionately (i.e., 45% of all sampled small gaps were sampled at the center). Thirty-six small gaps were sampled in each stand for a total of 108 small gaps sampled across the study.

Sampled large gaps (18.3 m and 24.4 m diameter) contained three or four plots per gap selected from nine possible locations to sample areas with different light levels within each gap (Figs. 2*b* and 2*c*). The center plot was included in all sampled large gaps, and two or three additional plots were randomly selected to be sampled, with certain constraints, e.g., plots could not be adjacent to another sampled plot, other than a plot at gap center (Figs. 2*b* and 2*c*). Measurements from the 25 m² regeneration plots were averaged within each large gap. In each stand, 24 gaps were sampled for each gap-level cleaning treatment (twelve 18.3 m diameter gaps and twelve 24.4 m diameter gaps) for a total of 72 large gaps sampled in each stand and 216 large gaps sampled across the study, divided equally across each gap-level cleaning treatment (not cleaned, cleaned, or scarified).

Small shelterwoods (0.4 ha) contained one 32 m × 32 m macroplot, while large shelterwoods (1.2 ha) contained two macroplots. Each macroplot had a sampled 25 m² regeneration plot located at three or four corners of the larger macroplot (Fig. 2*d*). Measurements from regeneration plots (three to four in small shelterwoods and six to eight in large shelterwoods) were averaged to the shelterwood level. Each stand in this study contained eight shelterwoods (four small and four large); therefore, a total of 24 shelterwoods were sampled across the study.

The control stands contained square 32 m × 32 m macroplots arranged in a grid pattern across the stand. The exact number of macroplots depended on the shape of the stand, as well as presence of wet areas, vernal ponds, and roads, which were not sampled. Sampled 25 m² regeneration plots were located randomly at one or two corners of each larger macroplot in the control stands (Fig. 2*d*). Measurements from regeneration plots were averaged for each macroplot. A total of 89 control stand macroplots were sampled across the study (27 at Flambeau, 29 at Northern Highland, and 33 at Argonne).

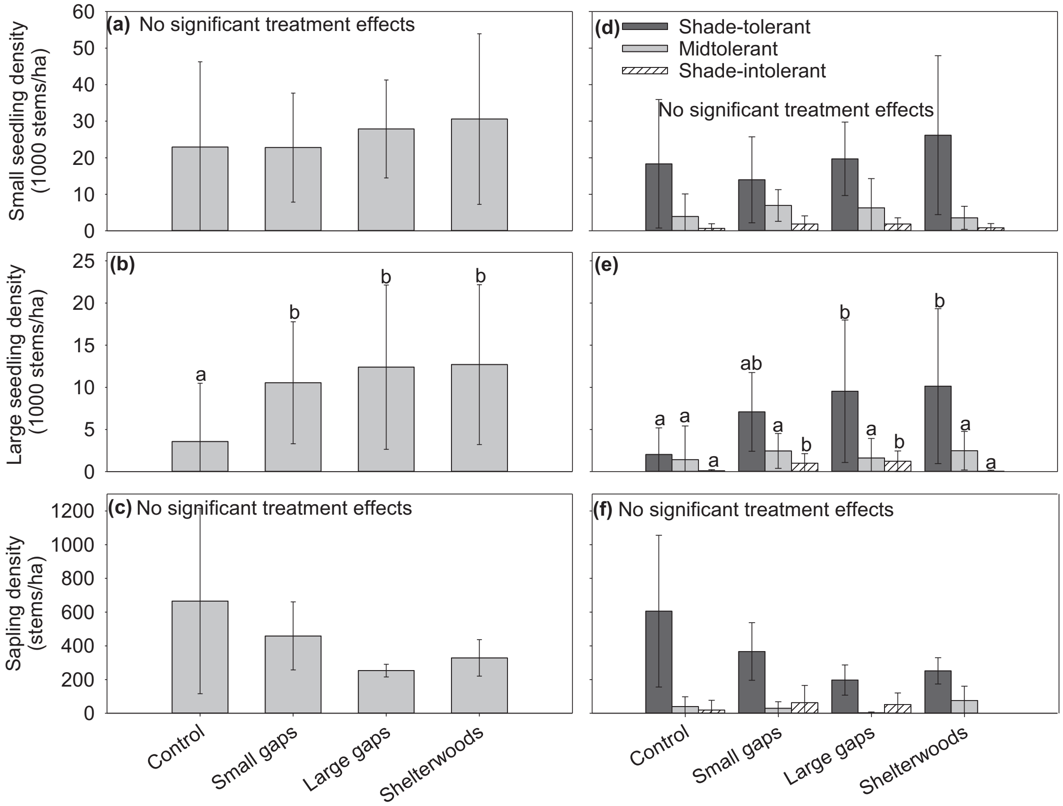
During the summer of 2007, the growing season prior to harvest, stem counts of woody species were tallied by species for seedlings and saplings in three size classes: small seedlings (0.1 m to <0.5 m tall), large seedlings (0.5 m tall to <2 cm dbh), and saplings (2 cm dbh to <10 cm dbh). Small seedlings were sampled in two 0.5 m × 1 m subplots within each regeneration plot (Fassnacht et al. 2013). Large seedlings were counted in a circular subplot with a 1.5 m radius (total area = 7 m²) that was centered in each regeneration plot. Saplings were counted in the entire 25 m² regeneration plot. Seedlings and saplings in these plots was again measured three years after treatment in June–August 2011, except the large gaps – ambient CWM treatment at Argonne, which was harvested one year after the other stands and so was sampled in June–August 2012. Seedbed conditions were not rigorously characterized after treatment; however, examinations of scarified areas indicated that exposed mineral soil seedbeds constituted >50% of the area in large gaps.

Statistical analyses

For analysis of gap-size effects, half-stands (i.e., the level at which CWM treatment was applied) were considered the unit of analysis, given the potential for the effect of CWM on seedlings and saplings. In contrast, for the gap-cleaning study, individual gaps were considered the unit of analysis because treatments (not cleaned, cleaned, scarified) were applied at the individual-gap level.

Mixed model analysis of variance (ANOVA) was used to determine the effects of gap size (control, small, large, shelterwood), gap-level cleaning treatments (not cleaned, cleaned, scarified), and CWM treatment (ambient and high) on species richness (number of species per plot), the Shannon–Wiener index (H'; Shannon and Weaver 1949)), and evenness (Pielou 1969) of tree regeneration. Mixed model analysis of covariance (ANCOVA) was used to determine effects of gap size and gap-level cleaning treatment on posttreatment densities of seedlings and saplings. The ANOVAs and ANCOVAs were performed using SAS statistical software (SAS Institute 2010). For ANCOVAs, pretreatment stem densities for the same size class were used as a covariate. When comparing gap size effects on seedlings and saplings, only the "cleaned" gaps were used for the large-gap treatment, because the other within-gap treatments were not applied to the small gaps or shelterwoods. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation or aligned rank transformation (Mansouri 1998). When significant main effects of fixed variables were found, Tukey's HSD was used to determine pairwise differences between treatments. Due to the

Fig. 3. Mean density (stems·ha^{-1}) of all tree species in three regeneration size classes: (*a*) small seedlings (0.1 m to <0.5 m tall), (*b*) large seedlings (0.5 m tall to <2 cm dbh), and (*c*) saplings (2 cm dbh to <10 cm dbh). Mean density of trees by shade-tolerance class in three size classes: (*d*) small seedlings, (*e*) large seedlings, and (*f*) saplings. Error bars represent 90% confidence intervals. Values for a given species group with different letters are significantly different at $p < 0.10$ with ANCOVA and Tukey's HSD.



large number and uncontrollable sources of variation in this study, there may be limited power to detect significant differences. For this reason, $p < 0.10$ was considered significant.

Results

Across all models, there was no significant effect of CWM on stem density of seedlings and saplings ($p > 0.2$). As such, the following sections focus primarily on the influence of gap size and gap-level cleaning treatments on patterns of regeneration.

Gap size

Pretreatment stem densities of seedlings and saplings are shown in Appendix A, Table A1. Overall densities of small tree seedlings and saplings were not significantly affected by gap size (Figs. 3*a* and 3*c*). Large seedling densities, however, were higher in all three gap sizes than in the controls (Fig. 3*b*). Gap size also affected the abundance of species of different shade-tolerance classes, but only in the large seedling size class (Figs. 3*d*–3*f*). Densities of shade-tolerant large seedlings were highest in the shelterwoods and the large gaps (Fig. 3*e*). Shade-tolerant seedlings and saplings included mostly sugar maple, with a significant component of ironwood (*Ostrya virginiana* (Mill.) K. Koch) and smaller proportions of basswood (*Tilia americana* L.) and red maple (*Acer rubrum* L.). Midtolerant seedlings and saplings were not significantly affected by gap size in any size class (Figs. 3*d*–3*f*). Midtolerant seedlings and saplings were largely composed of ash (*Fraxinus americana* L. and *Fraxinus nigra* Marshall), with some yellow birch, northern red oak (*Quercus rubra* L.), and elm (*Ulmus* spp.). Large shade-intolerant seedlings were at their highest densities in the small and large gaps and were at low densities in the shelterwoods and the controls; however, densities of shade-intolerant seedlings and saplings were low overall, making assessment of treatment effects difficult (Figs. 3*d*–3*f*). The most common species of shade-intolerant seedlings and saplings was black cherry (*Prunus serotina* Ehrh.), but bitternut hickory (*Carya cordiformis* Wangenh.), quaking aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Marsh.) were also present.

Sugar maple was the most commonly occurring species of seedlings and saplings in this study. Although gap size did not affect the density of small sugar maple seedlings or saplings (Figs. 4*a* and 4*c*), density of large sugar maple seedlings generally increased with increasing size of canopy gaps (Fig. 4*b*). Regeneration of ash was not affected as strongly by gap size, but the densities of small ash seedlings were highest in the large gaps (Fig. 4*a*). Ironwood seedlings and saplings were also common in the understory. Densities of large ironwood seedlings were higher in all gap sizes than in the controls, while densities of small seedlings and saplings of this species were not significantly affected by gap size (Fig. 4). Yellow birch was found in low densities in all stands. There were no large yellow birch seedlings in the small gaps or control treatments, while the large gaps had a mean of 43 yellow birch stems·ha^{-1} and the shelterwoods had a mean density of 20 yellow birch stems·ha^{-1} (Fig. 4*b*). *Rubus* spp. were at much higher densities in the shelterwoods and large gaps than in the small gaps or control. The control stands had little *Rubus* and no *Rubus* stems taller than 0.5 m (Figs. 4*a* and 4*b*).

Gap size had little effect on measures of plot-level tree diversity and only affected diversity measures in the large seedling and sapling size classes (Table 2). Species richness and evenness for large seedlings were significantly higher in the small gaps than in the controls; there was no difference among harvest treatments (Table 2). In the sapling size class, all diversity measures were

Fig. 4. Mean densities of (*a*) small seedlings, (*b*) large seedlings, and (*c*) saplings for common species in each gap size. Error bars represent 90% confidence intervals. Values for a given species with different letters are significantly different at $p < 0.10$ with ANCOVA and Tukey's HSD. See Fig. 3 for regeneration size class definitions.

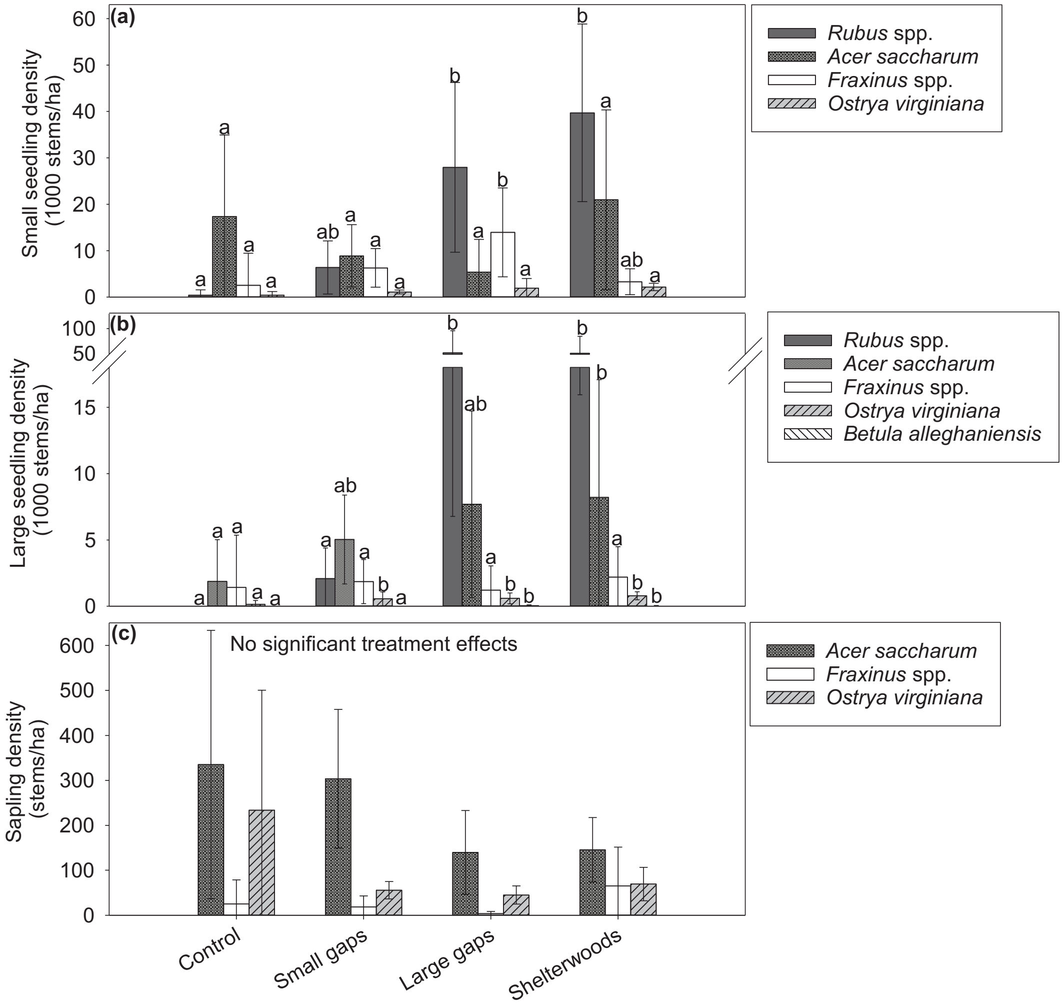


Table 2. Mean species richness (number of species per plot), evenness (Pielou 1969), and Shannon–Wiener diversity index (Shannon and Weaver 1949) in regeneration plots for all woody species by size class and gap size.

	Species richness	Species evenness	Shannon index
Small seedlings			
Control	0.9 (–0.1, 1.8)a	0.22 (–0.11, 0.56)a	0.17 (–0.01, 0.43)a
Small gaps	1.1 (0.6, 1.6)a	0.27 (0.01, 0.45)a	0.23 (0.07, 0.40)a
Large gaps	1.1 (0.7, 1.5)a	0.23 (0.12, 0.35)a	0.20 (0.09, 0.32)a
Shelterwoods	1.1 (0.6, 1.6)a	0.29 (0.16, 0.42)a	0.23 (0.12, 0.34)a
Large seedlings			
Control	0.7 (–0.3, 1.6)a	0.12 (–0.08, 0.33)a	0.10 (–0.07, 0.27)a
Small gaps	1.7 (0.7, 2.8)b	0.38 (0.12, 0.64)b	0.40 (0.10, 0.70)a
Large gaps	1.6 (0.7, 2.5)ab	0.34 (0.13, 0.56)ab	0.35 (0.12, 0.59)a
Shelterwoods	1.4 (0.7, 2.1)ab	0.31 (0.15, 0.47)ab	0.26 (0.12, 0.40)a
Saplings			
Control	0.8 (0.5, 1.2)a	0.15 (–0.04, 0.36)a	0.12 (–0.04, 0.28)a
Small gaps	0.6 (0.4, 0.8)ab	0.11 (0.03, 0.20)a	0.09 (0.02, 0.15)a
Large gaps	0.4 (0.3, 0.5)b	0.04 (0.02, 0.06)a	0.03 (0.01, 0.04)a
Shelterwoods	0.5 (0.3, 0.6)ab	0.06 (–0.01, 0.11)a	0.04 (–0.01, 0.09)a

Note: Plot sizes were 1 m^2 (small seedlings), 7 m^2 (large seedlings), and 25 m^2 (saplings). Values in parentheses are 90% confidence intervals. Different letters indicate significant differences between gap sizes within a size class at $p < 0.10$ using Tukey's HSD. See Fig. 3 for size class definitions.

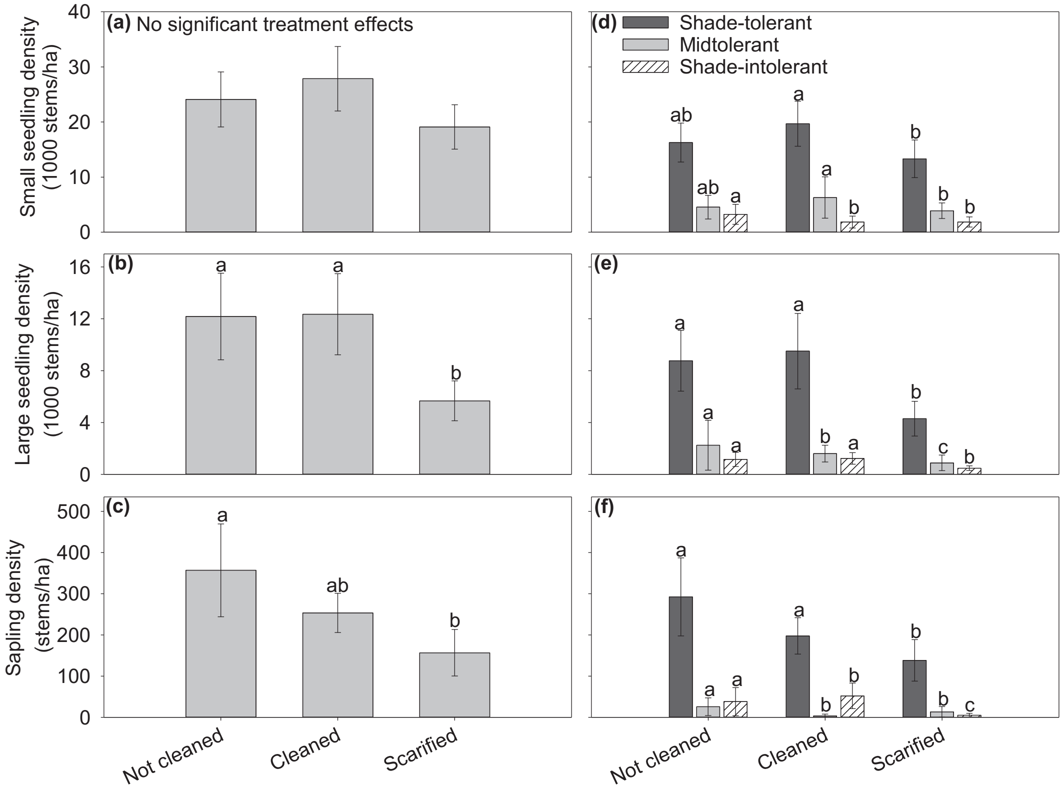
highest in the controls, although this difference was only significant for species richness between the controls and small gaps (Table 2). Shannon–Wiener index was not significantly affected by gap size for any size class (Table 2).

Gap-level cleaning treatments

Pretreatment stem densities of seedlings and saplings are shown in Appendix B, Table B1. Overall, scarification reduced stem density of most tree species but had less effect on seedlings in the smallest size class (Fig. 5). In the sapling size class, stem densities were generally highest in the gaps that had not been cleaned, likely because many of the saplings measured three years after treatment were also present prior to treatment but were not removed as they were in the cleaned and scarified gaps (Fig. 5*c*). Densities of shade-intolerant saplings were highest in the cleaned gaps (Fig. 5*f*).

Large seedlings of *Rubus* spp. had higher stem densities in the highly disturbed scarified and cleaned gaps relative to gaps that had not been cleaned, and the same pattern was true for small ironwood seedlings (Figs. 6*a* and 6*b*). Stem density of yellow birch seedlings and saplings was low in all treatments, but no yellow birch of any size was present in the gaps that had not been cleaned. Scarification had a positive effect on small yellow birch seedlings, but there was no difference in densities of large yellow birch seedlings between gaps that were cleaned and those that

Fig. 5. Mean density (stems·ha^{-1}) of all tree species in three regeneration size classes: (*a*) small seedlings, (*b*) large seedlings, and (*c*) saplings by gap-level cleaning treatment applied to large gaps (24.4 m diameter). Mean density of trees by shade-tolerance class in three regeneration size classes: (*d*) small seedlings, (*e*) large seedlings, and (*f*) saplings by gap-cleaning treatment applied to large gaps (24.4 m diameter). Error bars represent 90% confidence intervals; *n* = 48 for each gap-level cleaning treatment. Values for a given species group with different letters are significantly different at $p < 0.10$ with ANCOVA and Tukey's HSD. See Fig. 3 for regeneration size class definitions.



were scarified (Figs. 6*a* and 6*b*). Neither small nor large red maple seedlings were affected by gap-level cleaning treatments (Figs. 6*a* and 6*b*). Scarification had a significant negative impact on densities of sugar maple in all size classes (Fig. 6).

Scarification had a significantly negative effect on species richness of large seedlings and saplings (Table 3). Shannon–Wiener index was also significantly lower for large seedlings in scarified gaps compared with gaps receiving the other treatments (Table 3). Diversity of small seedlings was not affected by gap cleaning or scarification (Table 3).

Discussion

Our findings three years after treatment indicate that restoring the diversity of trees in second-growth northern hardwoods using canopy gaps of various sizes may prove challenging under contemporary forest conditions. While the creation of larger canopy gaps and shelterwoods to emulate meso-scale wind disturbance (Hanson and Lorimer 2007) did slightly increase the density of tree regeneration, these harvest treatments, at this early stage, served primarily to release advance regeneration of shade-tolerant species. For example, mean densities of sugar maple were at least 1.5 times higher, and sometimes more than six times higher, than mean densities of the next most common species (ash or ironwood) in all seedling and sapling size classes in all gap sizes. Microsite preparation through scarification, however, was successful in reducing stem density of shade-tolerant species and provided a slight benefit to the establishment of yellow birch, although it did not greatly benefit regeneration of other species. Scarification also had a small but slightly negative effect on diversity of seedlings and saplings at this early stage after treatment.

Gap size

Larger gaps allow more light to reach the forest floor, and this increase in resources can increase the density of seedlings and saplings (Bolton and D'Amato 2011). This study found higher densities of large seedlings in canopy gaps and shelterwoods but no significant effects of gap size on densities of small seedlings or saplings. Because these results are only three years after treatment, many of the large seedlings that we found were likely small seedlings present prior to harvesting that recruited to the large seedling class. Saplings present prior to treatments were likely damaged or intentionally removed during harvest, and it is probable that seedlings will grow into larger size classes, causing sapling densities in treatment stands to increase for a number of years. However, the effect of significantly higher densities of *Rubus* spp. found in the large gaps and shelterwoods on this dynamic is unclear. Findings from work examining long-term seedling and sapling development in northern hardwood forests in the northeastern United States suggest that tree seedlings can grow through *Rubus* patches and form a closed canopy above the shrub layer within 15 years, but only when advance regeneration is present (Donoso and Nyland 2006). In contrast, higher shrub densities, especially *Rubus* spp., were still inhibiting growth of seedlings 13 years after group selection harvests in northern Wisconsin (Kern et al. 2013). The stands studied by Kern et al. (2013) were slightly younger than those examined in our research and had little advance regeneration prior to harvest, but it is possible that the *Rubus* patches that we documented could impede growth of seedlings into larger size classes in the large gaps and shelterwoods, particularly when coupled with high levels of deer herbivory (Reuling 2014).

Fig. 6. Mean densities of (*a*) small seedlings, (*b*) large seedlings, and (*c*) saplings for common species by gap-level cleaning treatment. Error bars represent 90% confidence intervals; $n = 48$ for each gap-level cleaning treatment. Values for a given species with different letters are significantly different at $p < 0.10$ with ANCOVA and Tukey's HSD. See Fig. 3 for regeneration size class definitions.

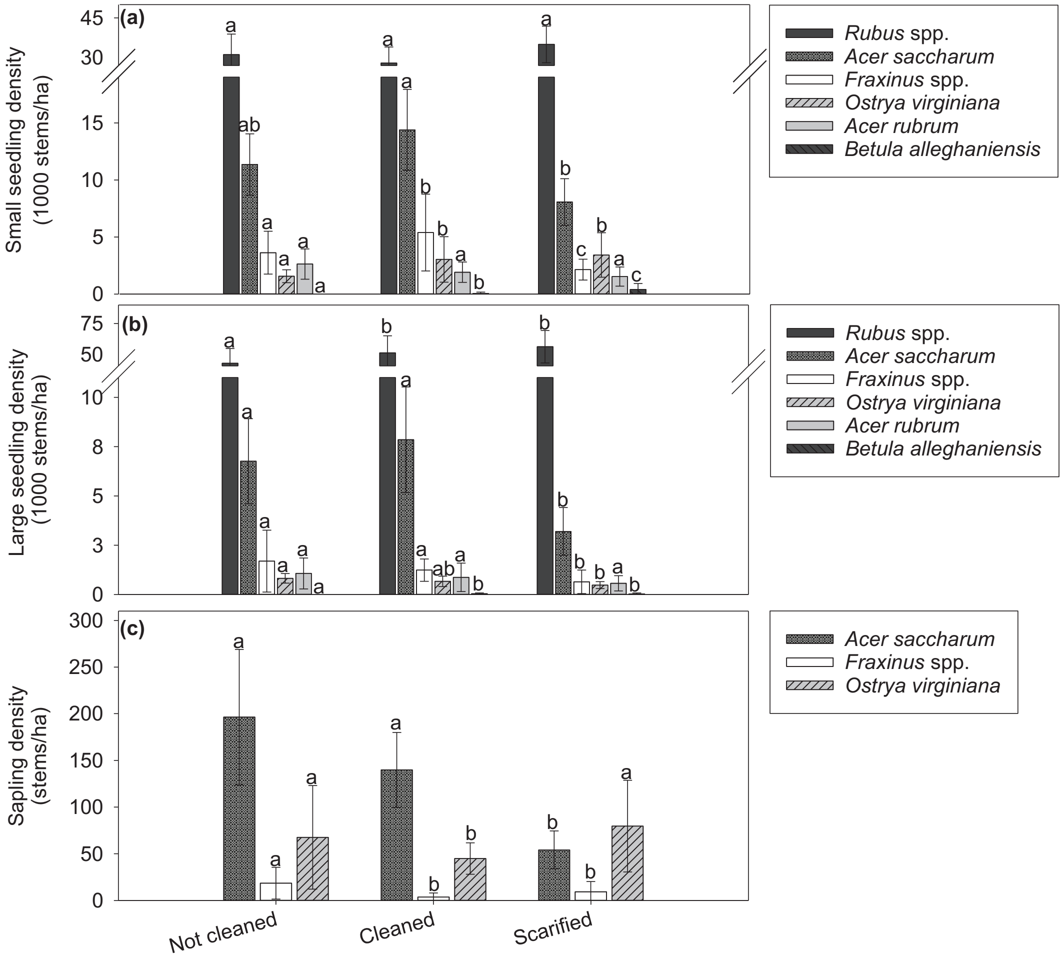


Table 3. Mean species richness (number of species per plot), evenness (Pielou 1969), and Shannon–Wiener index of diversity (Shannon and Weaver 1949) in regeneration plots for all woody species in large gaps by size class and gap-cleaning treatment.

	Species richness	Species evenness	Shannon index
Small seedlings			
Not cleaned	1.1 (0.9, 1.2)a	0.25 (0.20, 0.31)a	0.22 (0.17, 0.28)a
Cleaned	1.1 (0.9, 1.2)a	0.23 (0.18, 0.29)a	0.20 (0.15, 0.26)a
Scarified	0.9 (0.8, 1.1)a	0.22 (0.16, 0.27)a	0.18 (0.13, 0.23)a
Large seedlings			
Not cleaned	1.5 (1.2, 1.8)a	0.33 (0.27, 0.39)a	0.32 (0.26, 0.39)a
Cleaned	1.6 (1.3, 1.8)a	0.34 (0.28, 0.40)a	0.35 (0.28, 0.42)a
Scarified	1.0 (0.9, 1.2)b	0.25 (0.19, 0.31)a	0.22 (0.17, 0.28)b
Saplings			
Not cleaned	0.4 (0.3, 0.4)a	0.06 (0.03, 0.09)a	0.05 (0.02, 0.07)a
Cleaned	0.4 (0.3, 0.4)a	0.04 (0.02, 0.06)a	0.03 (0.01, 0.04)a
Scarified	0.2 (0.2, 0.3)b	0.03 (0.01, 0.05)a	0.02 (0.01, 0.03)a

Note: Values in parentheses are 90% confidence intervals; $n = 48$ for each gap-cleaning treatment. Different letters indicate significant differences between gap-cleaning treatments within a size class at $p < 0.10$ using Tukey's HSD. See Fig. 3 for regeneration size class definitions.

Creation of canopy gaps in hardwood systems has often been associated with increases in tree species diversity (Shields et al. 2007) and (or) the presence of species less tolerant of shade (Webster and Lorimer 2002). In contrast, some other studies have found that gaps had little effect on or decreased diversity, especially in the presence of high densities of advance regeneration or dense shrub layers (Shure et al. 2006). We found that gaps slightly increased diversity of seedlings and saplings by some measures, with species richness and evenness of large seedlings higher in small gaps than controls, but saw no additional effect of increasing gap size. Measures of sapling diversity were the same or lower in the harvest treatments compared with the controls, which may reflect the limited time frame of this study (three years after harvest).

Several studies have shown that larger gap sizes can lead to higher numbers of midtolerant and shade-intolerant seedlings and saplings (McClure and Lee 1993). We found a slight increase in the density of large shade-intolerant seedlings in gaps, compared with the controls, but no increase of shade-intolerant species in the shelterwoods and no significant effect of gap size on midtolerant species. Increased gap size seemed to only lead to the release of shade-tolerant species in the large-seedling size class.

Advance regeneration is an important replacement strategy for many shade-tolerant tree species. Sugar maple is tolerant of shade and can remain in the understory for many years before being released by a canopy-opening event (McClure et al. 2000). The majority of dominant sugar maple that establish in gaps are from advance regeneration, while most dominant yellow birch establish after gap creation (McClure et al. 2000). Because growth of sugar maple advance regeneration responds even to low light levels (Canham 1988), single-tree and group selection often lead to release of sugar maple seedlings and saplings and have little effect on other, less shade-tolerant species (Bolton and D'Amato 2011). In this study, all gap creation released sugar maple seedlings and saplings, and it was the most abundant species in all active treatments and across all seedling and sapling size classes.

Gap-level cleaning treatments

Given the ability of shade-tolerant species to dominate the seedling and sapling layer following gap formation in mesic forest systems, the removal or reduction of advance regeneration at the time of gap creation has often been suggested as a strategy for increasing diversity of seedlings and saplings in gaps (Kelty et al. 2003). In this study, scarification was successful in reducing densities of sugar maple and other shade-tolerant species, consistent with the findings of Raymond et al. (2003). However, neither cleaning nor the combination of cleaning and scarifying in large gaps had a positive effect on species richness or diversity. Scarification had a small negative effect on some measures of large seedling and sapling diversity. However, the stem density of small yellow birch seedlings was significantly higher in scarified gaps than the other gap-level cleaning treatments. Continued monitoring of this study will determine whether or not these small yellow birch seedlings can continue to compete with other species and grow into taller height classes.

Gap size, light availability, and favorable microsite conditions are likely all significant factors affecting yellow birch germination and establishment (Shields et al. 2007). While we saw little regeneration of yellow birch in any stands or treatments, no large yellow birch seedlings were present in the controls or small gaps. This is consistent with the findings of Webster and Lorimer (2005), who suggested a minimum gap opening size of 0.02 to 0.1 ha, a range in which the large gaps in this study fall. Shields et al. (2007) also found an increase in yellow birch seedlings in openings from 0.03 to 0.12 ha. Several other studies have also noted the importance of scarification and exposed mineral soil for the establishment of yellow birch (Godman and Krefting 1960; Raymond et al. 2003; Gauthier et al. 2016). In large gaps in this study, yellow birch was present only in gaps that had been cleaned or that had received a combination of cleaning and scarification. Some advance regeneration of yellow birch may have been present at the time of harvest, with cleaning alone serving to release those seedlings from competition (Shields et al. 2007). Although they are only midtolerant of shade, yellow birch seedlings establishing a few years before gap creation can survive in the understory and become dominant or codominant overstory trees after release (McClure et al. 2000). Scarification likely provided microsites for new yellow birch seedlings to establish, but seedbeds were not characterized after scarification to evaluate the effectiveness of this treatment in exposing mineral soil. It is possible that this treatment did not expose as much mineral soil as desired and a change in equipment or timing of scarification could lead to more successful yellow birch regeneration.

Additional factors affecting regeneration response

Regardless of treatment, densities of yellow birch seedlings and saplings were low, likely not high enough to sustain the 3%–6% of basal area of dominant yellow birch currently found in these stands. Additional factors that may have negatively impacted regeneration included drought, substrate height, seed crop, and browsing by white-tailed deer. During dry years, seedbed conditions in open, exposed microsites can be volatile, reducing germination and survival of yellow birch seedlings (Tubbs 1969). In this study, during the growing seasons following harvest (April–September 2008–2011), 58% of months had negative Palmer Drought Severity Index (PDSI) values, with values less than –2 (drought conditions) for 19% of growing season months (National Oceanic and Atmospheric Administration (NOAA) 2013). At all sites, yearly precipitation totals in 2008 and 2009 were more than 100 mm below the 1971–2000 averages and as much as 250 mm below average at the Argonne sites in 2009 (PRISM Climate Group 2013). Thus, drought may have had an inhibitory effect on yellow birch regeneration.

Substrate height may also influence yellow birch survival; after a natural disturbance, yellow birch seedlings often establish on tip-up mounds or downed wood, giving them a distinct height advantage over existing advance regeneration not afforded by mechanical scarification after harvest (Marx and Walters 2008). In this region, yellow birch have been found to produce a good or better seed crop every one to four years (Godman and Mattson 1976). The year 2009 was known to be a particularly good seed year for yellow birch in the study area, so seed crop was likely not a limiting factor for yellow birch regeneration in this study (Jeremiah Auer, Wisconsin Department of Natural Resources, personal communication, 2018). Finally, browsing by white-tailed deer can reduce regeneration success of sensitive species, including yellow birch (Kern et al. 2012). A companion study examining regeneration in deer exclosures indicates that browsing is influencing yellow birch recruitment at these sites (Reuling 2014).

In addition to its importance to yellow birch, decaying downed wood has also been shown to be important for germination of eastern hemlock (Marx and Walters 2008). In this study, we did not see any significant effect of increased CWM on regeneration; however, regeneration was evaluated at the gap and shelterwood levels, while CWM treatments were implemented at the stand level. Thus, some gaps and shelterwoods in the high CWM treatment stands did not necessarily contain augmented levels of CWM. Additionally, these data were collected only three years after treatment, and over 90% of trees that were cut and left as downed woody material were characterized as decay class 2. Only 5% of created downed wood was characterized as decay class 3, and none had reached decay classes 4 or 5, which tend to be most important for regeneration of these species (Marx and Walters 2008; decay classes based on Sollins et al. 1987). It is possible that the effect of CWM treatment will become significant in the future after harvested trees reach higher decay classes. These microsites will be particularly important in matrix areas where future gap harvests will likely coincide with areas containing well-decayed coarse wood substrates.

In addition to microsite characteristics and light availability, habitat type characteristics such as nutrient availability and soil moisture can influence composition and diversity of seedlings and saplings (Matonis et al. 2011). Most of the stands in this study were *Acer–Tsuga–Dryopteris* (ATD) habitat type, as well as some *Acer–Osmorhiza–Caulophyllum* (AOCa) and *Acer–Hydrophyllum* (AH), all of which are medium to very nutrient rich (Kotar et al. 2002). Other species might compete better with sugar maple on less productive sites such as the *Acer–Tsuga–Maianthemum* (ATM) habitat type, which is not as nutrient rich (Matonis et al. 2011). Matonis et al. (2011) found that mean seed production of species other than sugar maple and ironwood were 80% higher on ATM than on more nutrient-rich AOCa sites. ATD sites are often heavily dominated by sugar maple in all successional stages (Kotar et al. 2002). Had this study been performed on slightly less productive sites, it is possible that yellow birch and other hardwood species would have had stronger recruitment and competition with sugar maple.

Management implications

The canopy openings created by harvesting in this study generally did not increase diversity of tree regeneration. Instead, increasing canopy openness led to increased release of sugar maple advance regeneration, which may not be desirable when attempting to increase compositional diversity of a stand. In most plots, the second most common taxon of seedlings and saplings was ash, which is threatened by the spread of the introduced emerald ash borer (*Agrilus planipennis*) in this region. Yellow birch seedlings were only found in large gaps and shelterwoods. As has been suggested by other studies, this midtolerant species is unlikely to regenerate in small gaps (Webster and Lorimer 2005). Despite being present in low numbers in all stands, established yellow birch seedlings seemed to benefit from release from competition in cleaning treatments, and scarification slightly increased densities of small yellow birch seedlings. The different canopy gap sizes may have been more effective at increasing the abundance of this species if more deliberate measures such as scarification near mature yellow birch, retention of within-gap seed sources (Poznanovic et al. 2013), and gap-level cleaning and release treatments around established seedlings were applied.

The operational scale of this study reflects a common situation in the field in which there is little seed source of desired species, e.g., yellow birch, making the goal of increasing diversity of regeneration challenging. Given these findings, the use of more targeted restoration approaches including planting or seeding may be needed to increase the representation of less common species; however, these efforts will need to consider competition from advance regeneration present on site, coarse wood and microsite availability, pressure from herbivory (Reuling 2014), and habitat type.

Acknowledgements

We would like to thank C. Lorimer and T. Steele for the study design and implementation. We thank Teresa Pearson, Brian Werner, Susannah Rogers, Sara Reilly, and Joshua Waukau for assistance in the field. Support was provided by the Wisconsin Department of Natural Resources, a University of Minnesota Natural Resource Science and Management fellowship, and the Josephine and Waldemore Mohl fellowship.

References

Bauhus, J., Puettmann, K., and Messier, C. 2009. Silviculture for old-growth attributes. For. Ecol. Manage. **258**(4): 525–537. doi:10.1016/j.foreco.2009.01.053.

Bolton, N.W., and 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**(7): 1215–1222. doi:10.1016/j.foreco.2011.06.019.

Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology, **69**(3): 786–795. doi:10.2307/1941027.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**(5): 620–631. doi:10.1139/x90-084.

Dahir, S.E., and Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. Can. J. For. Res. **26**(10): 1875–1892. doi:10.1139/x26-212.

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

Donoso, P.J., and Nyland, R.D. 2006. Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* spp.) following clearcutting and shelterwood methods. North. J. Appl. For. **23**(4): 288–296.

Fassnacht, K.S., Padley, E.A., Steele, T.W., Lorimer, C.G., Palik, B.J., D'Amato, A.W., and Martin, K.J. 2013. Development and implementation of treatments in a long-term experiment to enhance forest structural and compositional complexity in second-growth northern hardwoods forests. Bureau of Science Services, Wisconsin Department of Natural Resources, Madison, Wis., Tech. Bull. 198.

Frelich, L.E. 1995. Old forest in the Lake States today and before European settlement. Nat. Areas J. **15**(2): 157–167.

Frelich, L.E., and Lorimer, C.G. 1991. Natural disturbance regimes in hemlock–hardwood forests of the upper Great Lakes region. Ecol. Monogr. **61**(2): 145–164. doi:10.2307/1943005.

Gauthier, M.M., Lambert, M.C., and Bédard, S. 2016. Effects of harvest gap size, soil scarification, and vegetation control on regeneration dynamics in sugar maple–yellow birch stands. For. Sci. **62**(2): 237–246. doi:10.5849/forsci.15-058.

Godman, R.M., and Krefting, L.W. 1960. Factors important to yellow birch establishment in Upper Michigan. Ecology, **41**(1): 18–28. doi:10.2307/1931935.

Godman, R.M., and Mattson, G.A. 1976. Seed crops and regeneration problems of 19 species in northeastern Wisconsin. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minn., Res. Pap. NC-123.

Goodburn, J.M., and Lorimer, C.G. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. Can. J. For. Res. **28**(3): 427–438. doi:10.1139/x98-014.

Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology, **78**(8): 2458–2473. doi:10.1890/0012-9658(1997)078[2458:MCOTSE]2.0.CO;2.

Hale, C.M., Pastor, J., and Rusterholz, K.A. 1999. Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, USA. Can. J. For. Res. **29**(10): 1479–1489. doi:10.1139/x99-076.

Hanson, J.J., and Lorimer, C.G. 2007. Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. Ecol. Appl. **17**(5): 1325–1340. doi:10.1890/06-1067.1. PMID:17708211.

Humphrey, J.W. 2005. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. Forestry, **78**(1): 33–53. doi:10.1093/forestry/cpi004.

Jenkins, M.A., and Parker, G.R. 2001. Woody species composition of disturbed forests in intermittent stream bottomlands of southern Indiana. J. Torrey Bot. Soc. **128**(2): 165–175. doi:10.2307/3088738.

Kelty, M.J., Kittredge, D.B., Jr., Kyker-Snowman, T., and Leighton, A.D. 2003. The conversion of even-aged stands to uneven-aged structure in southern New England. North. J. Appl. For. **20**(3): 109–116.

Kern, C.C., Reich, P.B., Montgomery, R.A., and 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. doi:10.1016/j.foreco.2011.12.002.

Kern, C.C., D'Amato, A.W., and Strong, T.F. 2013. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: what is the optimal gap size? For. Ecol. Manage. **304**: 110–120. doi:10.1016/j.foreco.2013.04.029.

Kotar, J., Kovach, J.A., and Burger, T.L. 2002. A guide to forest communities and habitat types of northern Wisconsin. 2nd ed. University of Wisconsin, Madison, Wis.

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

Leak, W.B., and Sendak, P.E. 2002. Changes in species, grade, and structure over 48 years in a managed New England northern hardwood stand. North. J. Appl. For. **19**(1): 25–27.

Mansouri, H. 1998. Multifactor analysis of variance based on the aligned rank transform technique. Comput. Stat. Data Anal. **29**: 177–189. doi:10.1016/S0167-9473(98)00077-2.

Marx, L., and Walters, M.B. 2008. Survival of tree seedlings on different species of decaying wood maintains tree distribution in Michigan hemlock–hardwood forests. J. Ecol. **96**(3): 505–513. doi:10.1111/j.1365-2745.2008.01360.x.

Matonis, M.S., Walters, M.B., and Millington, J.D.A. 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. For. Ecol. Manage. **262**(2): 286–298. doi:10.1016/j.foreco.2011.03.034.

McClure, J.W., and Lee, T.D. 1993. Small-scale disturbance in a northern hardwoods forest: effects on tree species abundance and distribution. Can. J. For. Res. **23**(7): 1347–1360. doi:10.1139/x93-172.

McClure, J.W., Lee, T.D., and Leak, W.B. 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manage. **127**(1–3): 181–189. doi:10.1016/S0378-1127(99)00129-2.

National Oceanic and Atmospheric Administration (NOAA). 2013. Wisconsin, Climate Divisions 1-3 Palmer Drought Severity Index (PDSI) 2008–2011 [online]. Available from https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/ [accessed 8 April 2013].

Nuttle, T., Royo, A.A., Adams, M.B., and Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. Ecol. Monogr. **83**(1): 3–17. doi:10.1890/11-2263.1.

Pielou, E.C. 1969. An introduction to mathematical ecology. John Wiley and Sons, New York.

Piepho, H.P., Williams, E.R., and Fleck, M. 2006. A note on the analysis of designed experiments with complex treatment structure. HortScience, **41**(2): 446–452. doi:10.21273/HORTSCI.41.2.446.

Poznanovic, S.K., Webster, C.R., and Bump, J.K. 2013. Maintaining mid-tolerant tree species with uneven-aged forest management: 9-year results from a novel group-selection experiment. Forestry, **86**(5): 555–567. doi:10.1093/forestry/cpt025.

PRISM Climate Group. 2013. 30-year normals [online]. Available from http://www.prism.oregonstate.edu/normals/ [accessed 21 August 2014].

Raymond, P., Munson, A.D., Ruel, J.C., and Nolet, P. 2003. Group and single-tree selection cutting in mixed tolerant hardwood–white pine stands: early establishment dynamics of white pine and associated species. For. Chron. **79**(6): 1093–1106. doi:10.5558/tfc791093-6.

Reuling, L.F. 2014. Effects of structural complexity restoration treatments and deer browsing on ground-layer community composition and tree regeneration in northern hardwood forests. M.Sc. thesis, University of Minnesota, St. Paul, Minn. doi:11299/163065.

SAS Institute. 2010. SAS Version 9.3. SAS Institute Inc., Cary, N.C.

Schuler, T.M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Can. J. For. Res. **34**(5): 985–997. doi:10.1139/x03-262.

Shannon, C.E., and Weaver, W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, Ill.

Shields, J.M., Webster, C.R., and Nagel, L.M. 2007. Factors influencing tree species diversity and *Betula alleghaniensis* establishment in silvicultural openings. Forestry, **80**(3): 293–307. doi:10.1093/forestry/cpm013.

Shure, D.J., Phillips, D.L., and Bostick, P.E. 2006. Gap size and succession in cutover southern Appalachian forests: an 18 year study of vegetation dynamics. Plant Ecol. **185**(2): 299–318. doi:10.1007/s11258-006-9105-8.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. **17**(12): 1585–1595. doi:10.1139/x87-243.

Tubbs, C.H. 1969. The influence of light, moisture, and seedbed on yellow birch regeneration. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minn., Res. Pap. NC-27.

Vepakomma, U., St-Onge, B., and Kneeshaw, D. 2011. Response of a boreal forest to canopy opening: assessing vertical and lateral tree growth with multitemporal lidar data. Ecol. Appl. **21**(1): 99–121. doi:10.1890/09-0896.1. PMID: 21516891.

Webb, S.L., and Scanga, S.E. 2001. Windstorm disturbance without patch dynamics: twelve years of change in a Minnesota forest. Ecology, **82**(3): 893–897. doi:10.1890/0012-9658(2001)082[0893:WDWPDT]2.0.CO;2.

Webster, C.R., and Lorimer, C.G. 2002. Single-tree versus group selection in hemlock–hardwood forests: are smaller openings less productive? Can. J. For. Res. **32**(4): 591–604. doi:10.1139/x02-003.

Webster, C.R., and Lorimer, C.G. 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a retrospective approach. Ecol. Appl. **15**(4): 1245–1262. doi:10.1890/04-0763.

Appendix A

Table A1. Mean pretreatment stem densities of seedlings and saplings by gap size.

	Small seedlings		Large seedlings		Saplings	
	Mean (stems·ha^{-1})	SE	Mean (stems·ha^{-1})	SE	Mean (stems·ha^{-1})	SE
Total trees						
Control	30 017	*13 473*	5632	*3647*	1000	*159*
Small gaps	27 424	*9448*	7436	*3415*	1079	*300*
Large gaps	52 674	*33 657*	6026	*4125*	806	*394*
Shelterwoods	30 625	*13 684*	6527	*4677*	801	*169*
Shade-tolerant trees						
Control	25 540	*12 173*	4053	*2494*	888	*69*
Small gaps	19 394	*8283*	5465	*2463*	967	*302*
Large gaps	47 546	*33 970*	5358	*3912*	791	*399*
Shelterwoods	29 306	*13 558*	5461	*3695*	654	*202*
Midtolerant trees						
Control	2921	*1872*	1257	*1185*	45	*25*
Small gaps	2727	*1765*	889	*636*	27	*19*
Large gaps	2905	*2362*	303	*265*	6	*4*
Shelterwoods	1111	*422*	1036	*978*	147	*127*
Shade-intolerant trees						
Control	1556	*1430*	322	*222*	67	*67*
Small gaps	5303	*4218*	1082	*926*	85	*85*
Large gaps	2222	*1123*	365	*271*	8	*8*
Shelterwoods	208	*208*	29	*29*	0	*0*
***Rubus* spp.**						
Control	98	*98*	0	*0*	0	*0*
Small gaps	0	*0*	0	*0*	0	*0*
Large gaps	278	*278*	72	*72*	0	*0*
Shelterwoods	278	*184*	20	*20*	0	*0*
Sugar maple						
Control	24 284	*12 031*	3693	*2410*	356	*99*
Small gaps	17 727	*6651*	4790	*2217*	545	*234*
Large gaps	46 123	*33 528*	4995	*3744*	430	*226*
Shelterwoods	28 438	*13 423*	5117	*3480*	338	*137*
Ash spp.						
Control	1801	*1728*	1245	*1173*	33	*17*
Small gaps	1667	*1116*	750	*582*	15	*15*
Large gaps	1227	*713*	185	*147*	4	*4*
Shelterwoods	972	*486*	913	*884*	128	*124*
Ironwood						
Control	269	*149*	298	*149*	464	*63*
Small gaps	152	*152*	557	*494*	352	*109*
Large gaps	671	*402*	327	*182*	329	*167*
Shelterwoods	556	*367*	255	*142*	278	*87*
Yellow birch						
Control	385	*385*	0	*0*	8	*8*
Small gaps	152	*152*	0	*0*	0	*0*
Large gaps	0	*0*	0	*0*	0	*0*
Shelterwoods	69	*69*	25	*13*	6	*6*

Note: Numbers in italics are one standard error. Small seedlings were 0.1 m to <0.5 m tall, large seedlings were 0.5 m tall to <2 cm dbh, and saplings were 2 cm dbh to <10 cm dbh.

Appendix B

Table B1. Mean pretreatment stem densities of seedlings and saplings by gap-cleaning treatment within large gaps.

	Small seedlings		Large seedlings		Saplings	
	Mean (stems·ha^{-1})	SE	Mean (stems·ha^{-1})	SE	Mean (stems·ha^{-1})	SE
Total trees						
Not cleaned	46 860	*26 001*	5822	*3265*	917	*441*
Cleaned	52 674	*33 657*	6026	*4125*	806	*394*
Scarified	36 115	*20 809*	5498	*3428*	914	*414*
Shade-tolerant trees						
Not cleaned	41 977	*25 878*	4844	*2743*	856	*449*
Cleaned	47 546	*33 970*	5358	*3912*	791	*399*
Scarified	33 337	*20 190*	4494	*2649*	884	*426*
Midtolerant trees						
Not cleaned	2762	*2309*	288	*256*	51	*41*
Cleaned	2905	*2362*	303	*265*	6	*4*
Scarified	1816	*1364*	550	*349*	10	*4*
Shade-intolerant trees						
Not cleaned	2121	*1069*	691	*541*	10	*6*
Cleaned	2222	*1123*	365	*271*	8	*8*
Scarified	962	*667*	453	*453*	21	*21*
***Rubus* spp.**						
Not cleaned	152	*152*	27	*19*	0	*0*
Cleaned	278	*278*	72	*72*	0	*0*
Scarified	203	*112*	6	*6*	0	*0*
Sugar maple						
Not cleaned	39 809	*24 916*	4113	*2384*	492	*281*
Cleaned	46 123	*33 528*	4995	*3744*	430	*226*
Scarified	32 142	*19 863*	3934	*2427*	388	*179*
Ash spp.						
Not cleaned	1853	*1410*	163	*155*	39	*33*
Cleaned	1227	*713*	185	*147*	4	*4*
Scarified	780	*519*	506	*345*	6	*1*
Ironwood						
Not cleaned	1086	*564*	697	*349*	321	*134*
Cleaned	671	*402*	327	*182*	329	*167*
Scarified	561	*185*	478	*192*	456	*234*
Yellow birch						
Not cleaned	0	*0*	11	*11*	6	*6*
Cleaned	0	*0*	0	*0*	0	*0*
Scarified	160	*116*	14	*8*	1	*1*

Note: Numbers in italics are one standard error. Small seedlings were 0.1 m to <0.5 m tall, large seedlings were 0.5 m tall to <2 cm dbh, and saplings were 2 cm dbh to <10 cm dbh.