Forest Ecology and Management 262 (2011) 1215–1222

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA

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ARTICLE INFO

Article history:
Received 6 May 2011
Received in revised form 9 June 2011
Accepted 12 June 2011
Available online 6 July 2011

Keywords:
Acer saccharum
Betula alleghaniensis
Natural disturbance-based forest management
Downed coarse woody debris
Seedling recruitment patterns

ABSTRACT

The use of silvicultural systems based on the natural disturbance patterns for a given region has been suggested as an approach for promoting late-successional forest characteristics and maintaining native biodiversity in managed forests. To this end, we examined the effectiveness of natural disturbance-based harvest gaps in maintaining and restoring native tree species diversity within second-growth northern hardwood systems in northeastern Minnesota, USA. In particular, tree regeneration and downed coarse woody debris (CWD) were measured 6- and 7-years post-treatment in 46 gaps that emulated the historic range of natural canopy opening sizes for northern hardwood forests in the upper Great Lakes region. Measurements were compared across gap size-classes (>0–0.02, >0.02–0.04, >0.04 ha) and with closed canopy portions of these systems. In addition, the factors affecting the recruitment of *Betula alleghaniensis* across gaps and within closed canopy were investigated due to the historical importance of this species in these forests.

Seedling and sapling densities increased in harvest gaps; however, results indicated that these gaps did little to increase tree diversity, including the recruitment of shade mid-tolerant species, such as *B. alleghaniensis*. Gaps were dominated primarily by *Acer saccharum* and age distributions of dominant saplings within gaps indicated that most individuals established 10–40 years prior to gap formation. Establishment of *B. alleghaniensis* was strongly related to highly decayed, large coniferous pieces of CWD with little recruitment occurring on the undisturbed forest floor. Age distributions of *B. alleghaniensis* established on CWD suggest this species can persist on this substrate for at least a decade. Levels of CWD increased with increasing gap size; however, all gaps had lower levels of CWD compared to the surrounding intact forest. Our results suggest that management regimes based on natural canopy gap sizes within northern hardwood systems will do little to restore native tree diversity if provisions for creating the suitable seedling microsites historically generated by natural disturbance (e.g., exposed mineral soil, highly decayed wood) are not included within management prescriptions.

1. Introduction

There is increasing global concern regarding the loss of native biodiversity from forest systems (Klenner et al., 2009), particularly within managed forests (Hunter, 1999). In many cases, past management practices have led to a simplification of forest structure, resulting in a loss of habitat for a diversity of organisms (Latty et al., 2006). One proposed management approach for restoring and maintaining native biodiversity and accelerating forest succession toward old-growth characteristics within managed forests is natural disturbance-based silviculture (Fries et al., 1997; Seymour et al., 2002). This approach bases the intensity and patterns of harvest entries upon natural disturbances occurring throughout the landscape (Perera et al., 2004). Despite the endorsement of this approach as a means to accomplish biodiversity-related goals in managed forests (Long, 2009), there have been few formal tests of the response of forest systems to harvesting regimes patterned after natural disturbances relative to more traditional approaches.

Natural disturbances within northern hardwood systems in the north temperate region of North America are primarily driven by wind, insects, and disease (Frelich and Lorimer, 1991; Frelich, 2002). These disturbances create canopy gaps, ranging from small to large in size (0.0004–0.1 ha; Seymour et al., 2002) that typically close by border tree encroachment and understory tree ascension (Hibbs, 1982; Runkle, 1982). Generally, small canopy gaps maintain shade tolerant species, such as *Acer saccharum* Marshall (sugar maple) (Canham, 1988), whereas large canopy gaps allow for the recruitment of shade mid-tolerant species (hereafter "mid-tolerant"), including *Betula alleghaniensis* Britton (yellow birch)

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doi:10.1016/j.foreco.2011.06.019

(McClure et al., 2000; Webster and Lorimer, 2005), due to higher light availability within larger canopy gaps.

Historically, a variety of gap sizes have been created by natural disturbances in the region. In contrast, management of northern hardwood forests in the upper Great Lakes region has emphasized single-tree selection (Arbogast, 1957; Crow et al., 2002; Angers et al., 2005). Canopy openings created through this approach generally favor the ascension of shade tolerant species, such as *A. saccharum*, to the canopy (Neuendorff et al., 2007). As a result, *B. alleghaniensis* and other mid-tolerant species have declined throughout the region while shade tolerant species are increasingly abundant (Webster and Lorimer, 2005; Shields et al., 2007; Webster and Jensen, 2007). Similar increases in shade tolerant species at the expense of more mid-tolerant components have been documented in other regions of the globe in which single-tree selection systems are employed (Yoshida et al., 2006). The use of natural disturbance-based systems that create a diversity of gap sizes, including larger canopy gaps, may provide one potential means to restore this mid-tolerant component. Nonetheless, several studies in other regions of the globe have indicated that even larger gap sizes are often dominated by shade-tolerant species when pre-disturbance communities contain high levels of advance regeneration (Kwit and Platt, 2003; Nagel et al., 2006; Collet et al., 2008; Madsen and Hahn, 2008).

Beyond gap size, other factors, including the presence of suitable microhabitat conditions, such as downed coarse woody debris (CWD), tip-up mounds, and exposed mineral soil, strongly influence the recruitment of a given species within gaps (Grubb, 1977; Nakashizuka, 1989; Gray and Spies, 1998). Within northern hardwood systems, several genera primarily establish on CWD or exposed mineral soil seedbeds relative to the undisturbed forest floor (e.g., *Betula*, *Picea*, and *Thuja*) (Cornett et al., 2001; Caspersen and Saprunoff, 2005; Shields et al., 2007; Marx and Walters, 2008). These species generally have small wind-dispersed seeds with low nutrient reserves for germination and establishment (McGee and Birmingham, 1997) and large-diameter CWD and exposed mineral soil represent microhabitats with relatively stable moisture environments and less competition for early establishment (Harmon et al., 1986; Franklin et al., 1987; Nakashizuka, 1989).

Much of the timber harvesting within northern hardwood systems occurs during winter months under snow-covered, frozen soil conditions, thus limiting the levels of exposed mineral soil within harvest gaps (Shields et al., 2007). As such, CWD may represent the only suitable microhabitat for several species within gap-based silvicultural prescriptions that do not include provisions for deliberate soil scarification. Numerous studies have demonstrated that the abundance of CWD is lower in managed northern hardwood forests relative to old-growth systems (Goodburn and Lorimer, 1998; Hura and Crow, 2004; Vanderwel et al., 2008). Lower levels of CWD in managed forest systems result primarily from the removal of larger trees for timber products that otherwise would have served as inputs of CWD (Fridman and Walheim, 2000; Siitonen et al., 2000; Lorimer et al., 2001). As a result, there is often a lower availability of suitable microhabitats for species, such as *B. alleghaniensis*, within managed northern hardwood forests compared to pre-European settlement conditions.

This study investigated the influence of harvest techniques that emulate some aspects of natural canopy gap openings, namely size, on tree composition and stand structure 6- and 7-years post-harvest within second-growth northern hardwood systems in the upper Great Lakes region. The objective for this work was to develop an understanding of how effectively natural disturbance-based harvest gaps maintained and restored tree species diversity within second-growth northern hardwood forests in the region. To achieve this objective, we examined the response of tree regeneration and forest structure (e.g., seedling densities, CWD) to a range of gap sizes patterned after natural disturbances for the region. We hypothesized that (i) large harvest gaps will enhance seedling diversity, including the presence of mid-tolerant species, relative to smaller canopy gaps; (ii) advance regeneration will dominate small gap succession; and (iii) *B. alleghaniensis* establishment will be strongly correlated with the availability of CWD substrates.

2. Methods

2.1. Study sites

Study sites were located along the northern shore of Lake Superior in northeastern Minnesota, USA (Table 1). Elevations within this area range from 381 to 472 m and soils are loams derived from glacial tills (Hobbs and Goebel, 1982). Mean annual precipitation is 739 mm and mean annual temperatures range from −8.5 °C in January to 18.7 °C in July. Forests within the study area are dominated by *A. saccharum*, with lesser amounts of *B. alleghaniensis*, *Fraxinus nigra* Marshall (black ash), *Betula papyrifera* Marshall (paper birch), and *Thuja occidentalis* L. (northern white cedar).

2.2. Study design

A total of 46 gaps ranging from 0.008 to 0.07 ha were created within each site and replicated across four blocks (Big Pine (BP), Birch Cut (BC), Power Line (PL), and Schoolhouse (SH)) in a completely randomized block design (Fig. 1). Gaps were designed to emulate the historic range of canopy gap sizes occurring within old-growth northern hardwood forests of the upper Great Lakes region (Frelich and Lorimer, 1991; Schliemann and Bockheim, 2011), with a target structure of 56%, 22%, and 22% of a site occupied by gaps $\leqslant 0.02$, >0.02–0.4, and >0.04 ha in area, respectively. It is important to note that larger natural canopy gaps (0.1–0.5 ha) generated by moderate intensity disturbances also occasionally occur in these systems (rotation periods of 300–390 years; Frelich and Lorimer, 1991; Hanson and Lorimer, 2007); however, the study design focused on the prevailing natural disturbance regime for these areas. The range of gap sizes examined included gap areas shown to be sufficient in size for the successful establishment and recruitment of *B. alleghaniensis* in northern hardwood forests (Webster and Lorimer, 2005). Gaps were created by fully mechanized cut-to-length harvesting systems composed of a harvester and forwarder during the winters of 2002 and 2003. Distance between gaps was $\geqslant 30$ m and gaps had hard edges (i.e., intact) and elliptical to circular shapes. Gap area was determined based on stem maps generated from the location of border trees.

2.3. Field procedures

Harvest gaps were measured in the summer of 2009 to assess the 6- and 7-year vegetation responses of these communities to harvesting treatments. To ensure adequate representation of gap environments, transects were laid across each gap oriented in subcardinal directions (NE, NW, SE, and SW) and extended to the gap edge. Along each transect, 1-m^2 plots were systematically located and used for measuring tree regeneration and understory plant communities. Spacing between plots along each transect was adjusted according to gap size to provide an even distribution across transects. To ensure consistent sampling intensities, each transect contained enough plots to represent a sampling of 5% of each gap area (e.g., eight, 1-m^2 sampling plots for a 0.016 ha gap). The density and species of tree seedlings (stems $\leqslant 1.34$ m in height) were recorded for each meter square census. Additionally, saplings (>1.34 m in height and <10 cm diameter at breast height [DBH]) were tallied by species for the entire gap area.

Table 1
Physiographic and compositional characteristics of the second-growth northern hardwood systems examined in northeastern Minnesota, USA.

Site	Lat/long	Harvest year	Elevation (m)	Aspect (°)	Slope (%)	Canopy Composition[a] (% basal area)
Big Pine (BP)	(47.47, −91.1496)	2003	487	162	8	*Acer saccharum:* 84% *Betula alleghaniensis:* 3% *Betula papyrifera:* 3% *Thuja occidentalis:* 9%
Birch Cut (BC)	(47.45, −91.1885)	2002	455	119	6	*Acer saccharum:* 89% *Betula alleghaniensis:* 3% *Acer rubrum:* 3% *Picea glauca:* 3% *Thuja occidentalis:* 3%
Power Line (PL)	(47.34, −91.2037)	2003	385	142	10	*Acer saccharum:* 74% *Fraxinus nigra:* 24% *Populus grandidentata:* 2%
Schoolhouse (SH)	(47.46, −91.1977)	2002	478	327	2	*Acer saccharum:* 63% *Betula alleghaniensis:* 15% *Picea glauca:* 15% *Thuja occidentalis:* 7%

[a] Canopy composition based upon unharvested portions of study area.

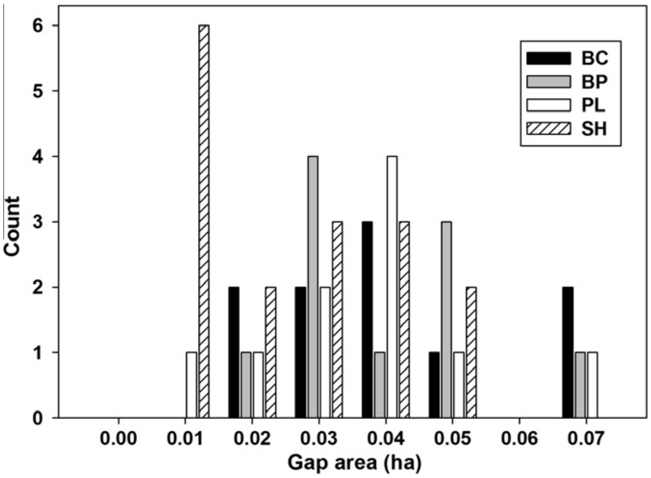

Fig. 1. Distribution of gap sizes examined in the Birch Cut (BC), Big Pine (BP), Power Line (PL) and Schoolhouse (SH) study areas in northeastern Minnesota, USA.

The abundance of downed coarse woody debris (CWD) was measured within gaps using the line intersect method (van Wagner, 1968). Volume (V) was calculated with the following formula:

$$V = (\pi^2 \Sigma d^2 / 8L) \times 10,000\ \mathrm{m}^2/\mathrm{ha} \tag{a}$$

where d is the diameter of the log where the transect intersects the log and L is the total length of the transect. Decay class, species, and diameter were recorded for all CWD ($\geqslant$10 cm) encountered. Decay classes were defined according to Fraver et al. (2002) as: class I (wood is sound, bark intact, smaller to medium sized branches present); class II (wood is sound to partially rotten, branch stubs firmly attached with only larger stubs present, some bark slippage); class III (wood is substantially rotten, branch stubs easily pulled from softwood species, wood texture is soft and compacts when wet); or decay class IV (wood is mostly rotten, branch stubs rotted down to log surface, bark no longer attached or absent [except *Betula* spp.], log is oval or flattened in shape. Additionally, all CWD intercepted was surveyed for the presence of tree seedlings in an effort to examine the importance of this substrate for the establishment of different tree species. If seedlings were found, a paired plot equal in surface area to the log and located one meter away on the forest floor was surveyed for tree seedlings following the methods outlined in Marx and Walters (2008). Based on this sampling design, we assumed that nurse logs and forest floor areas within each pair received the same seed rain allowing us to characterize the importance of these substrates for the establishment of a given canopy species. Surface area (SA) was calculated for each piece of CWD and was based on log decay class and type (i.e., stump or log). Boles and stumps were calculated as half-cylinders (b) and flat areas (c), respectively, using the following formulas:

$$\mathrm{SA} = (2(\pi r^2) + (2\pi r) \times L)/2 \tag{b}$$

$$\mathrm{SA} = L \times W \tag{c}$$

where r is the radius of a log, L is the length and W is the diameter of the stump or log. In cases in which large (>0.5 m in height) *B. alleghaniensis* seedlings were encountered on a log they were harvested for aging to characterize the age structure of regeneration for this species on deadwood substrates.

A pool of saplings within gaps most likely to recruit into the canopy (i.e., "potential gap winners" (PGW)) were identified and harvested to examine the age structure of gap winning saplings and evaluate the relative importance of advance regeneration versus gap-origin recruitment within these systems. PGW are saplings within a gap that are assumed to have a high probability of ascending into the canopy layer based on two criteria: height relative to other saplings and gap position (Lee Frelich, personal communication). In particular, saplings with greater heights, irrespective of species, and located within the center of the gap and not directly under bordering tree crowns were assumed to have a greater likelihood of ascending into the canopy layer (cf. Cole and Lorimer, 2005). Given the greater juvenile growth rates of more light-demanding species, this approach could bias sampling towards these individuals; however, we felt this was less of an issue in the systems we examined given the dominance of shade tolerant species throughout these areas. The number of PGW destructively sampled was proportional to gap size with greater numbers being removed from larger gaps (four, six, eight, or ten saplings within >0–0.02, >0.02–0.04, >0.04). Stem cross sections were taken from each sapling as close to the forest floor as possible to determine date of establishment.

Light availability within each gap was measured using an LAI-2000 Plant Canopy Analyzer (Li-Cor, 2000). Three readings were taken at breast height (1.34 m) along a 180° azimuth at the center of the gap and averaged per gap. Measurements were taken during cloudy conditions with a reference measurement in an open area >1,000 m^2. The outer rings of the LAI-2000 were removed from analysis to remove the influence of the nearby saplings and shrub species close to the sensor.

A series of 400 m^2 control plots were randomly placed in unharvested, intact forest portions of each site to approximate pre-harvest vegetation conditions. Plots were placed at least 60 m from gap treatments to reduce edge effects (Fraver, 1994). For all control plots ($n = 14$) measurements were performed in the same manner as study gaps. With the exception of PL, each site contained three plots that were randomly located within unharvested portions of each stand. Due to a greater degree of variation in canopy composition at the PL site, an additional two plots were included within the intact forest portions of this site for a total of five control plots. In addition to within-plot CWD measurements, half of the total length of CWD transects laid in gaps were established and measured outside of plots throughout the intact forest portions of each site for comparisons of CWD abundance. Although the use of relatively short transects (178–246 m, sensu Harmon and Sexton, 1996) may have limited our ability to fully capture the variation in downed CWD in control areas, the average coefficient of variation for within-site downed CWD abundance was 41.3%, which is within acceptable levels of accuracy for sampling coarse woody debris (cf. Woldendorp et al., 2004). Comparisons of regeneration densities and CWD abundance within the control plots to those collected from these areas prior to harvest (Burton et al., 2009) indicated that control plots served as an accurate representation of pre-harvest conditions.

2.4. Statistical analysis

Analysis of variance (ANOVA) was used to compare substrate affinity between *B. alleghaniensis* and *A. saccharum* seedlings. ANOVAs tested the effect of substrate (CWD or forest floor) on the density of *B. alleghaniensis* and *A. saccharum*. For tree species demographics throughout gaps, sapling tallies per hectare and seedling abundance per hectare were averaged across gap size classes within a study site and ANOVAs used to examine the effect of gap size class on seedling and sapling densities. In addition, ANOVA was also used to examine the effect of nurse log surface area, decay class, and wood type (hardwood or conifer) on the density of *B. alleghaniensis* established on CWD. Tukey–Kramer multiple comparisons were used in cases in which a significant main effect was detected. Kolomogrov–Smirnov tests were conducted to compare the distribution of CWD among decay classes across harvest gap size classes and the intact forest. Pearson's correlation analyses were used to examine the relationship between the observed densities of *B. allegheniensis* and measured variables likely related to establishment, such as CWD type and gap size. Data on tree regeneration was used from all four sites; however, the PL site was not included in analyses of *B. alleghaniensis* establishment due to the absence of this species from this site. All statistical analyses were done with SAS statistical software (SAS Institute, 2008).

3. Results

3.1. Seedling and sapling response to gap treatments

A total of nine tree species were encountered in both regeneration layers across the study sites (Table 2). Of these species, eight were found in both the seedling and sapling layers. *A. saccharum* dominated seedling and sapling layers, with the highest relative density among the combined stem densities across all sites (37% and 82%, respectively). Densities generally increased as gap size increased (Fig. 2). In particular, density of seedlings and saplings was greater in large gaps (>0.02 ha) compared to small gaps and the intact forest (Fig. 2). For seedlings (Fig. 2a), large gaps had over twice as many individuals as small gaps and four times as many as the intact forest. Medium (not large) gaps had over twice as many saplings as in small gaps and over four times as many saplings as the intact forest (Fig. 2b). Age distributions based on harvested potential gap winners (PGW) indicated that most of these individuals were present as advance regeneration prior to gap creation (Fig. 3a). In particular, PGW ages ranged from 7 to 57 years and the average age was 7 years greater than the date of gap creation (14 ± 0.49 years). Most PGW were *A. saccharum*. A few other species were present, including shade tolerant conifers (*Abies balsamea* and *Picea glauca*) and one *Fraxinus nigra* stump sprout. Although not statistically significant, the average heights of PGW were generally greater in large gaps (>0.02 ha; Fig. 2c).

3.2. Coarse woody debris abundance

The average abundance of CWD across study sites was 60.5 ± 14.5 m^3/ha. Overall, the abundance of CWD was greater in the intact forest than within gaps (Table 3). CWD volume distributions across harvested gap size classes differed significantly (based on Kolomogrov–Smirnov tests). In particular, small and medium size gaps (<0.04 ha) had lower amounts of CWD within decay classes I and II compared to the intact forest (Table 3).

3.3. Patterns of seedling establishment on coarse woody debris

A total of 116 wood pieces were intercepted across the three sites examined for seedling recruitment on nurse logs (BC, BP, and SH). Of those 116 wood pieces, 68 contained tree seedlings and were used for paired plot forest floor surveys (see Section 2). Substrate significantly affected *B. alleghaniensis* establishment ($F = 32.37$, $P = 0.0301$), as nurse logs averaged 8.1 ± 1.7 seedlings/m^2 whereas no seedlings occurred on the forest floor throughout the sampled area. The age range (4–22 years) and median age (6 years) of *B. alleghaniensis* harvested from CWD ($n = 64$) is presented in Fig. 3b. Substrate also significantly affected *A. saccharum* establishment ($F = 17.32$, $P = 0.0551$) with densities of *A. saccharum* seedlings on the forest floor being over 13 times as great as those found on nurse logs (32.9 ± 4.3 versus 2.5 ± 0.5 seedlings/m^2).

Overall, the highest proportion of *B. alleghaniensis* seedlings was found on larger pieces of highly decayed (decay classes IV and V) conifer CWD (Fig. 4). Correspondingly, the site with the greatest abundance of *B. alleghaniensis* seedlings (SH) also had the greatest volume of highly decayed conifer CWD (decay classes IV and V; Table 3). In addition, this site also had the greatest abundance of *B. alleghaniensis* in the canopy. Measured factors significantly related to *B. alleghaniensis* establishment on CWD were wood type, decay class, surface area, and available light (Table 4). In particular, establishment rates were greater on large, highly decayed coniferous logs (Table 4). In addition, the positive correlation with higher leaf area suggested that more *B. alleghaniensis* seedlings occurred on wood pieces within the intact forest or small gaps compared to larger gaps.

4. Discussion

4.1. Tree response to natural disturbance-based harvest gaps

The findings of this work suggest that solely applying harvest gaps approximating the natural range of gap sizes documented for the upper Great Lakes region may not be sufficient for increasing the diversity of tree species within second-growth stands. In the present study, size-class diversity increased following silvicultural treatments through the release of existing advance regeneration; however, few changes in tree species composition were detected within the regeneration layer. Despite larger gaps (>0.02 ha) having higher densities of seedlings and saplings,

Table 2
Average seedling (#/m^2) and sapling (#/ha) densities in harvest gaps and intact forest areas. Percentage of a gap size with no seedlings or saplings for a given species are in parentheses. Seedlings were stems $\leqslant$1.34 m in height and saplings were stems >1.34 m in height and <10 cm DBH.

Species	Seedlings/m^2 Gap size class (ha)				Saplings/ha Gap size class (ha)			
	Intact forest	>0–0.02	>0.02–0.04	>0.04	Intact forest	>0–0.02	>0.02–0.04	>0.04
Abies balsamea	–	3.9 (88)	0.3 (91)	0.1 (93)	2.1 (50)	30.5 (38)	25.5 (70)	1.0 (93)
Acer rubrum	–	–	0.1 (96)	–	–	7.9 (88)	–	–
Acer saccharum	5.8 (25)	3.2 (13)	13.3 (0)	13.1 (0)	67.7 (0)	255.9 (0)	825.1 (0)	659.8 (0)
Acer spicatum	1.4 (50)	2.7 (63)	5.3 (65)	8.4 (27)	2.2 (25)	–	5.5 (83)	20.7 (47)
Betula alleghaniensis	–	–	1.0 (74)	0.2 (93)	0.2 (75)	–	1.9 (87)	–
Betula papyrifera	–	–	–	–	0.2 (75)	–	–	–
Fraxinus nigra	–	1.1 (88)	1.5 (87)	3.3 (73)	–	–	1.5 (96)	0.7 (93)
Picea glauca	–	–	0.4 (96)	–	0.2 (75)	3.1 (88)	5.0 (74)	1.0 (87)
Prunus virginiana	1.3 (50)	0.9 (75)	9.0 (39)	5.9 (40)	0.8 (50)	7.2 (75)	20.6 (52)	14.9 (53)

regeneration densities consisted mainly of *A. saccharum*. Regardless of gap size, the regeneration of mid-tolerant *B. alleghaniensis* occurred exclusively on CWD that existed in the stand prior to gap creation. These findings are consistent with those found in other forest types around the globe in which pre-disturbance advance regeneration of tolerant species has dominated gap succession, regardless of gap size (Batista et al., 1998; Kwit and Platt, 2003; Nagel et al., 2006; Collet et al., 2008; Madsen and Hahn, 2008). Based on these results, provisions for creating suitable microsite conditions, such as exposed mineral soil and coarse woody debris, and the removal of pre-harvest advance regeneration may be necessary to fully restore tree species diversity using the natural disturbance-based silviculture systems we examined.

Gap size is recognized as an important control over the density of tree seedlings and saplings within forest systems (Brokaw and Busing, 2000). Consistent with other work examining northern hardwood systems, larger gaps (>0.02 ha) in the present study had higher densities of seedlings and saplings compared to small gaps and intact forest (Prevost et al., 2010). Although tree seedling and sapling abundance increased with gap size, compositional diversity was minimally impacted by gap size. In particular, *A. saccharum* can live in the understory for many years to decades until released (Canham, 1985, 1988) and the created canopy gaps in this study served to release existing *A. saccharum* excluding other species from the seedling and sapling layer. These findings underscore the importance of treatments that remove existing shade-tolerant advance regeneration when objectives include the restoration of more light-demanding species within harvest gaps (Tubbs and Metzger, 1969; Kelty et al., 2003; Collet et al., 2008). By mimicking only canopy openness with little disturbance to the forest floor or advance regeneration, the experimental harvest released advance regeneration and may have accelerated stand development pushing the future canopy towards increasing *A. saccharum* dominance (McClure et al., 2000; Webster and Lorimer, 2002). In contrast, natural canopy gaps generated by wind disturbances often contain exposed mineral soil seedbeds in the form of tip-up mounds that are free of advance regeneration and have been shown to be important for the establishment of species with small, wind-dispersed seeds, including *B. alleghaniensis* (Beatty, 1984; Nakashizuka, 1989; Peterson et al., 1990).

4.2. *Betula alleghaniensis* regeneration

The importance of CWD as a substrate for tree establishment is widely recognized (Harmon et al., 1986; McGee and Birmingham, 1997; Marx and Walters, 2008). Within the systems we examined, CWD was critical to *B. alleghaniensis* establishment, as all *B. alleghaniensis* encountered occurred on CWD. This finding is consistent with other work examining the establishment of this species within the upper Great Lakes region (Marx and Walters, 2008). Specifically, Marx and Walters (2008) found that the establishment of *B. alleghaniensis* was dependent on *Tsuga canadensis* (L.) logs and we found a similar affinity to conifer wood with *B. alleghaniensis* establishing primarily on *Thuja occidentalis* logs within our study. This dependence on *T. occidentalis* CWD creates a challenge in relation to the maintenance of *B. alleghaniensis* on the landscape due to the declining presence of *T. occidentalis* across the upper Great Lakes region; a decline linked to over-browsing of *T. occidentalis* by herbivores, mainly white-tailed deer (*Odocoileus virginianus*) (Cornett et al., 2000). Concomitantly, this decline reduces the future availability of suitable seedbeds for *B. alleghaniensis* establishment.

Although recruitment of *B. alleghaniensis* in northern hardwood forests is often linked with gap formation (Lorimer and Frelich, 1989; McClure et al., 2000), retrospective work examining the recruitment dynamics of this species has highlighted that it may also successfully establish as advance regeneration (Webster and Lorimer, 2005). The age distribution of *B. alleghaniensis* on CWD we documented support this assertion as numerous seedlings established prior to gap creation (Fig. 3b). Nonetheless, the vast majority of seedlings encountered established within a few years of gap formation, which is consistent with the findings of McClure et al. (2000) in their examination of *B. alleghaniensis* age structures within northern hardwood systems in New Hampshire, USA.

4.3. Coarse-woody debris

The abundance of CWD within forest systems is dependent upon the severity and frequency of disturbance (Franklin et al., 1987). Managed systems generally have less CWD compared to old-growth systems (Goodburn and Lorimer, 1998; Siitonen et al., 2000), but tremendous variation may also exist within a given forest due to differences in disturbance or management history (Kirby et al., 1998; D'Amato et al., 2008). In particular, there were vast differences among gap size classes in terms of the amount of CWD on the forest floor with smaller gaps containing lower amounts of CWD than larger gaps and the intact forest containing higher volumes than all gaps. The differences between intact forest areas and gaps may be due to the mechanical breakage of CWD through logging disturbance, which may have reduced the amount of CWD within the harvested areas (Freedman et al., 1996). Observed differences between gap size classes, particularly the higher volumes of CWD in larger versus smaller gaps, may have been due to the higher volume of timber removed from the larger gap treatments, which resulted in greater slash levels.

5. Management implications

Forest management goals increasingly incorporate biodiversity objectives in response to global concerns regarding the ecological

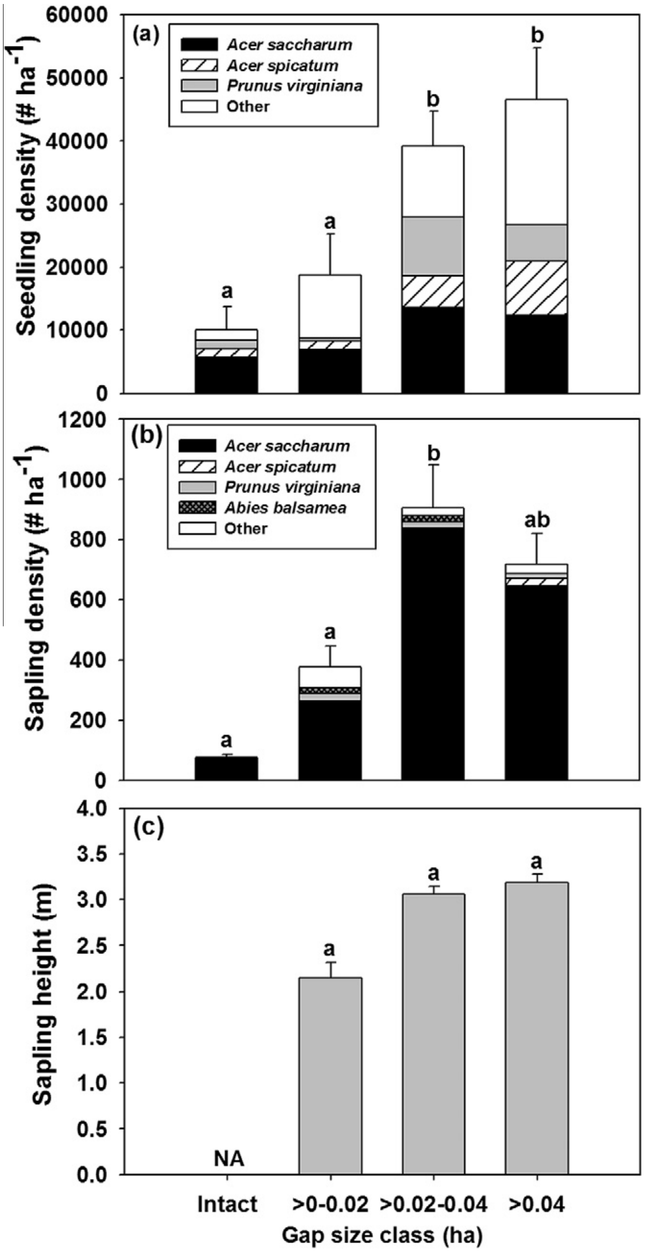

Fig. 2. (a) Seedling and (b) sapling densities and (c) average height for potential gap winning saplings by harvest gap size class. Potential gap winners are defined as saplings most likely to ascend into the canopy based on height and location within gap. Error bars represent one standard error and correspond to densities and heights across species and statistically significant differences ($P < 0.05$) between gap size classes and intact forest are denoted with different letters. Species within the "Other" category included *Acer rubrum*, *Betula alleghaniensis*, *Fraxinus nigra*, and *Picea glauca*.

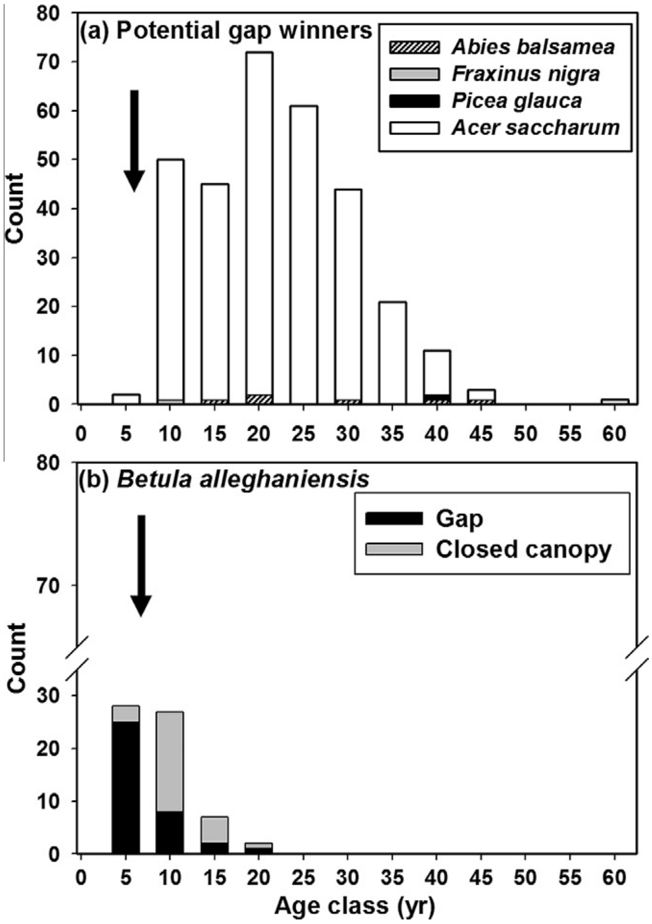

Fig. 3. Age distributions of (a) potential gap winners harvested from study gaps across all sites ($n = 310$) and (b) *Betula alleghaniensis* located on nurse logs within gaps and the intact forest ($n = 64$). Arrows indicate year of harvest (6- or 7-years).

Table 3

Average downed coarse woody debris (CWD) volume and standard errors (in parentheses for gap size class) across harvest gap size and decay class. Note the absence of CWD in decay class I within gaps is likely due the minimum size threshold used for measuring CWD (i.e., 10 cm in diameter). Gap size classes with different letters have significantly different distributions (Kolomogrov–Smirnov test; $P < 0.05$). Decay class is based on Fraver et al. (2002).

Gap size class (ha)	Total volume (m^3 ha^{-1})	Decay class volume (m^3 ha^{-1})			
		I	II	III	IV
Intact forest[a]	77.75 (35.45)	16.84	19.44	28.51	10.37
>0–0.02[b]	4.86 (0.82)	0	0	2.43	2.44
>0.02–0.04[b]	8.44 (2.68)	0	4.79	2.74	0.92
>0.04[ab]	19.15 (8.07)	0	5.47	5.47	8.2

sustainability of traditional forest management regimes. Approaches based on natural disturbance patterns provide significant opportunities to harvest wood products, while also achieving biodiversity-related goals. Nevertheless, these approaches are currently in their experimental phases and the findings of this work highlight that simply creating harvest openings representative of the historic range of variability is insufficient for restoring and maintaining underrepresented tree species in northern hardwood forests. Although these treatments served to accelerate stand development by releasing shade tolerant advance regeneration (e.g., *A. saccharum*) these harvests did not provide opportunities for species requiring microhabitats, such as coarse woody debris or exposed mineral soil. Relatedly, minimizing soil disturbance during harvesting is an important aspect of best management practices for maintaining site productivity; however, the application of these guidelines should also be considered within the context of the silvicultural objectives for a given site, particularly where soil conditions allow for harvests under non-frozen conditions. Given the importance of microsite factors, such as exposed mineral soil and decayed wood, as "safe sites" for the germination and establishment of *B. alleghaniensis* (Shields et al., 2007), restoration efforts for this species will need to go beyond creating the large canopy openings historically maintaining this species on the landbase (Webster and Lorimer, 2005). Based on the findings of this and other studies, prescriptions that couple site scarification with

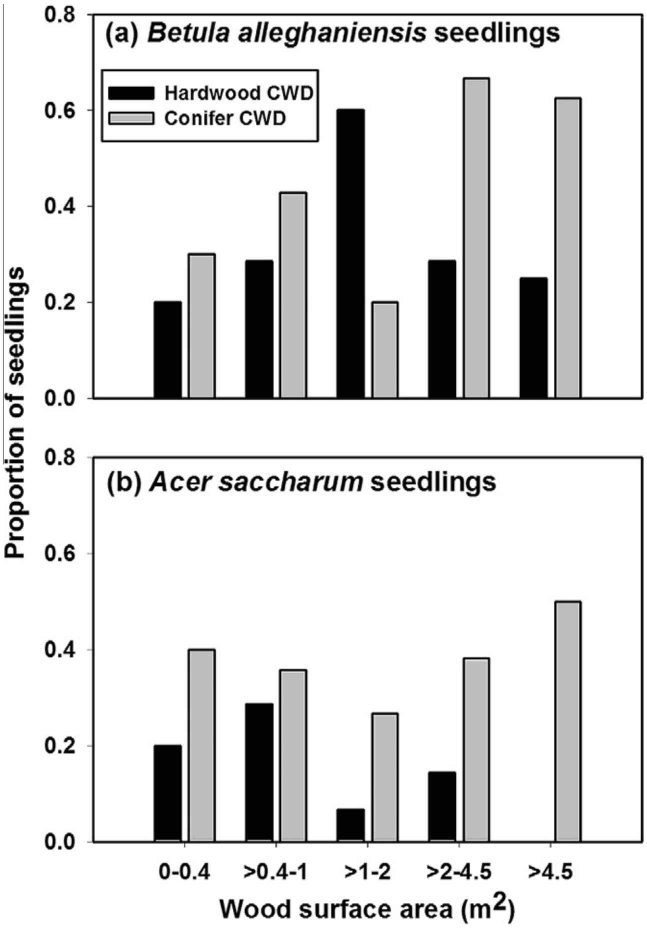

Fig. 4. Proportion of *Betula alleghaniensis* and *Acer saccharum* established on nurse logs across all encountered decay classes, surface area size class, and wood type (hardwood species versus conifer species). Proportion is based on wood pieces with at least one established seedling.

Table 4
Pearson's correlations between *Betula alleghaniensis* occurrence on nurse logs and downed coarse woody debris (CWD) characteristics and measured environmental factors. Significant correlations are bolded ($P < 0.05$).

CWD characteristic/environmental factor	Pearson correlation coefficient
CWD type (hardwood/softwood)	−**0.3887**
CWD surface area (m^2)	**0.3533**
Leaf area index	**0.3168**
CWD decay class	**0.2933**
Gap size (m^2)	−0.2647
Density of overstory yellow birch (#/ha)	0.1619

mechanical removal of *A. saccharum* saplings will be needed to increase the recruitment opportunities for *B. alleghaniensis* and other mid-tolerant species in these systems. The demonstrated affinity of *B. alleghaniensis* for coniferous CWD also suggests that increasing the abundance of this structural element may serve to promote the recruitment of this and other deadwood-dependent species within second-growth systems.

Acknowledgements

We are grateful to The Nature Conservancy in Minnesota, Lake County Land Department, and the Manitou Collaborative for initiating the project. Funding for the project was provided by the Cox Family Fund for Science and Research and the Minnesota Agricultural Experiment Station. We thank Eric Zenner, Meredith Cornett, Julia Burton, Chris Dunham, Lee Frelich and Mark White for their efforts in designing and overseeing treatment implementation. In addition, we acknowledge Matt Tyler, John Segari, Chad Roy, Joseph Shannon, and Allison Esper for their assistance with field and laboratory measurements.

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