Maintaining mid-tolerant tree species with uneven-aged forest management: 9-year results from a novel group-selection experiment

Sarah Klingsporn Poznanovic, Christopher R. Webster* and Joseph K. Bump

School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931-1295, USA

*Corresponding author. E-mail: cwebster@mtu.edu

Received 25 January 2013

In forest ecosystems, disturbance intensity affects the ability of species with varying shade tolerances to successfully recruit into the overstory. Small openings (e.g. single treefall) perpetuate shade-tolerant species while larger openings (e.g. those created under group selection and other higher severity disturbances) enhance the abundance of shade-mid-tolerant and -intolerant species. Forty-nine modified group-selection openings in three size classes established during the winter of 2003/04 and 20 single-tree selection sites were re-evaluated in 2012 in order to determine: (1) how the densities of seedlings and saplings changed over time, (2) whether species composition differed between treatments and (3) whether the group-selection openings enhanced recruitment of underrepresented species, especially the mid-tolerant yellow birch (Betula alleghaniensis). Sugar and red maple (Acer saccharum and Acer rubrum) regeneration dominated at all sites and occurred in greater densities in the group-selection openings as compared with the single-tree selection sites. While yellow birch densities increased with opening size, survival and growth were likely inhibited by the drought conditions that have occurred since 2004. Ironwood (Ostrya virginiana) and black cherry (Prunus serotina) also benefited from opening creation. Consequently, while openings enhanced the representation of mid-tolerant species, they did not greatly alter the developmental trajectory of this forest type.

Introduction

In temperate and tropical forests, treefalls of varying intensity create openings that enable sunlight to reach the forest floor (Runkle, 1982; Lawton and Putz, 1988; McCarthy, 2001). These disturbances can largely determine the composition of the regenerating cohort in forest understories (Hébert and Huot, 2009; Richards and Hart, 2011). Small openings, created by the death of one to several trees, perpetuate shade-tolerant species that are able to survive and grow in low-light environments, whereas mid-tolerant and shade-intolerant species require larger forest openings, and thus a greater degree of disturbance, to survive and recruit into the overstory (Runkle, 1982; Stewart et al., 1991; McClure and Lee, 1993). Single-tree selection is an uneven-aged forest management technique used in temperate forests composed primarily of shade-tolerant hardwoods (O’Hara, 2001; Seymour et al., 2002; Schwartz et al., 2005; Neuendorff et al., 2007). This technique mimics in some ways natural single-tree death in old multi-cohort forests. However, in pre-European settlement forests, trees were larger in size compared with trees in managed forests today. Therefore, forest disturbances of the past produced a more heterogeneous landscape through variations in opening size, shape, and through the creation of biological legacies such as standing live and dead trees, tip-up mounds and coarse woody debris (CWD) (Clebsch and Busing, 1989; Beckage et al., 2000). Single-tree selection, on the other hand, simply removes the aboveground portion of smaller, narrow-crowned trees thus creating small (≏80 m²), relatively homogenous openings (Crow et al., 2002; Angers et al., 2005). Over time, single-tree selection has been found to reduce species richness and stand structural complexity, which can negatively impact ecosystem function and resilience (Jenkins and Parker, 1998; Neuendorff et al., 2007; Keyser and Loftis, 2013).

Group selection, another uneven-aged silvicultural practice, removes groups of trees (~100–2000 m²) creating larger openings that persist (inhibit closure from above by crown encroachment) for longer periods of time than those created through single-tree selection (Lamson and Leak, 2000; Webster and Lorimer, 2005). This alternative selection method has the potential to enhance mid-tolerant tree recruitment (Arbogast, 1957; Leak, 1999; Webster and Lorimer, 2005) and, when combined with other silvicultural practices such as biological-legacy retention, to more closely mimic natural disturbance regimes (Bolton and D’Amato, 2011; Hanson et al., 2012). Intermediate-to-large-sized gaps (>500 m²) can remain open long enough for mid-tolerant tree species to successfully recruit into the overstory (Webster and Lorimer, 2005; Kneeshaw and Prevost, 2007; Klingsporn et al., 2012). Nevertheless, other factors may prevent mid-tolerant trees from establishing and recruiting into the overstory despite the creation of light conditions amenable to establishment and...
growth (Godman and Krefting, 1960; Elie et al., 2009). Therefore, long-term studies are needed in order to determine the causal factors responsible for successes and failures in space and time (Tubbs, 1969; Lorenzetti et al., 2008; Arsenault et al., 2011). Yellow birch (Betula alleghaniensis Britt.), a shade-mid-tolerant tree, has been a management concern for decades due to overall declines in abundance and unreliability of regeneration (Godman and Krefting, 1960; Webster and Jensen, 2007; Lorenzetti et al., 2008). Studies designed to elucidate life history characteristics and successful regeneration techniques began in the mid-20th century and continue to this day (e.g. Zillgitt and Eyre, 1945; Webster and Jensen, 2007; Elie et al., 2009). Yellow birch is an important component of many forest types in eastern North America because of its wildlife value, contribution to forest structural and compositional complexity, and for its economic value as a timber product (Erdmann, 1990; Orrock and Pagels, 2003; Holloway and Malcolm, 2007). Factors thought to be responsible for difficulties regenerating yellow birch include lack of adequate sunlight, low competitive ability compared with other vegetation, lack of suitable substrates for germination and survival, herbivory, management practices that favour shade-tolerant species and inhospitable environmental conditions (Erdmann, 1990; Barras and Kellman, 1998; Gastaldello et al., 2007; Salk et al., 2011). Zillgitt and Eyre (1945) observed that, in the Lake States, group selection was the best method for regenerating yellow birch of the six methods they tested. Other studies recommend incomplete canopy removal to favour yellow birch regeneration (Arbogast, 1957; Godman and Krefting, 1960; Ward and Stephens, 1997). As group selection has not been widely practiced, long-term studies of regeneration dynamics using this silvicultural practice are important to chronicle (McDonald and Reynolds, 1999). Several studies report that group selection enhances recruitment of mid-tolerant species early in gap cohort development (Lorenzetti et al., 2008; Falk et al., 2010). However, since successful canopy recruitment requires decades, encouraging results at a single point in time, or even at several points early in development, may not ultimately lead to successful canopy recruitment of target species (Allison et al., 2003; Webster and Lorimer, 2005; Dornke et al., 2007). Studies that capture dynamics later in gap cohort development (>10 years) are available (e.g. McClure and Lee, 1993; McDonald and Reynolds, 1999; Bobiec, 2007). However, few studies continuously monitor change in regeneration dynamics over time. For example, after 61 years of group selection, Leak (1999) found that the mid-tolerant component of a northern hardwood forest in New Hampshire was maintained. Alternatively, Kern et al. (2012) observed that, over 12 growing seasons, competition with woody shrubs and herbivory counteracted the benefits of creating group-selection openings in a northern hardwood forest in northeastern Minnesota. These studies highlight the need for long-term results from various locations, as differences in soil type, herbivory, competition, climate and other environmental factors can affect canopy recruitment (Leak, 1999; Beckage et al., 2000; Falk et al., 2010).

We investigated the developmental trajectory of 49 group-selection openings ranging in size from 200 to 1460 m² and 20 reference sites (managed under single-tree selection) in the Great Lakes region, USA. The group-selection openings were modified so that a yellow birch legacy tree was retained in the centre of each opening, thus combining elements found to successfully regenerate yellow birch across its range (Zillgitt and Eyre, 1945; Wang, 1968; Ward and Stephens, 1997). More specifically, our objectives in this study were to determine how the densities of seedlings and saplings have changed over time, whether species composition differed between treatments, and ultimately, whether these treatments have the potential to lead to successful canopy recruitment of mid-tolerant trees, such as yellow birch.

Methods

Study area

The study site is located in the western Upper Peninsula of Michigan (section 30, T49N, R33W, 46° 37′ N, 88° 29′ W) at the Ford Center Research Forest, south of Alburtis, MI. The study area is categorized under the northern hardwood forest type within the Laurentian mixed forest province (Keys et al., 1995). The geology is characterized as glacial drift over Precambrian bedrock (Albert, 1995). Mean elevation at the study site is 430 m (Gesch et al., 2002; Gesch, 2007). Soils are predominantly Champion cobbly silt loam with smaller inclusions of Alstad silt loam, Amasa cobbly silt loam, Champion-Net complex, Kallio cobbly silt loam and Witbeck muck (Berndt, 1988, p. 15–49). All of the soil types are deep but vary from well-drained to somewhat poorly drained; slopes are mostly 0–15 per cent but extend up to 35 per cent (Berndt, 1988, p. 15–49). Temperatures range from an average of −9°C in January to 17°C in July (National Oceanic and Atmospheric Administration (NOAA), 2012a). Mean yearly precipitation is 84 cm and mean annual snowfall is 371 cm per year (Midwest Regional Climate Center (MRCC), 2012; NOAA, 2012a).

The primary habitat type of the study area is Acer saccharum-Tsuga canadensis/Dryopteris spinulosa (Burger and Kotar, 2003). Sugar maple (Acer saccharum Marsh.) and red maple (Acer rubrum L.) are the two dominant tree species. Yellow birch and eastern hemlock (Tsuga canadensis (L.) Carr) are co-dominants, but relative to the maples, their abundances are low. Black cherry (Prunus serotina Ehrh.), ironwood (Ostrya virginiana (P. Mill.) K. Kock), American basswood (Tilia americana L.), American elm (Ulmus americana L.), white spruce (Picea glauca (Moench) Voss), balsam fir (Abies balsamea (L.) Mill.), northern white cedar (Thuja occidentalis L.), serviceberry (Amelanchier spp. Medik.), trembling aspen (Populus tremuloides Michx.), black ash (Fraxinus nigra Marshall) and eastern white pine (Pinus strobus L.) also occur as minor species.

The study area was characterized as a pine–hardwood forest prior to the 1890s (Erickson et al., 1990). By the 1930s, most of the merchantable timber was harvested from the area (Erickson et al., 1990). Since the 1960s, single-tree selection has been the primary management technique used in northern hardwoods at the Ford Center with the goal of producing uneven-aged hardwood stands that yield high quality sawtimber and veneer (Michigan Technological University (MTU), 2010). Selection harvests are based on the BDq method (q factor of 1.3), and harvests usually occur on a 10- to 15-year cutting cycle (Schwartz et al., 2005). Residual basal area targets range from 16.1 to 20.7 m² ha⁻¹ (Schwartz et al., 2005). The 219-ha study area is composed of four adjacent management units that contain a mosaic of more than two dozen individual stands. Operational cruises are conducted prior to harvest, but detailed pre-harvest data at a scale and resolution suitable for comparison with our data are not available. Basal area across the four management units in 2003/04 was ~24 m² ha⁻¹ (Neuendorff et al., 2007).

Experimental design

This study is part of a long-term investigation into the ecological effects of group selection and legacy-tree retention on regeneration dynamics in northern hardwood forests. In the winter of 2003/04, 49 group-selection openings were created in three size classes based on ratios of the mean dominant and co-dominant tree canopy height (22 m) to opening diameter. Mean (±1 SE) treatment canopy gap areas were 267 ± 15 m² (small, n = 16), 642 ± 21 m² (medium, n = 17) and 1192 ± 39 m² (large, n = 16).
which correspond to opening diameters of 1, 1.5 and 2 times average oversoty tree height. Small, medium and large are relative terms used only to separate the three gap sizes evaluated in this study as other published studies have wide-ranging definitions of small, medium and large canopy gap opening sizes (White et al., 1985; Dickinson et al., 2000; Arseneault et al., 2011). To reduce interactions between treatments, a minimum distance of 60 m was maintained between all study sites (group-selection openings and references sites). All stems >10 cm dbh were removed from the openings except a single yellow birch tree that was retained in the centre of each opening to serve as a biological legacy, moderator of environmental extremes and as a seed tree. In addition, twenty single-tree selection reference sites from the uneven-aged closed canopy forest surrounding the treatments were also surveyed for comparison.

Reference sites were established to provide a baseline for stands with a long history (~50 years) of management using a BDG approach to single-tree selection. These sites were centred on randomly selected yellow birch canopy trees. Subplots were arrayed as if a mean size opening was created around the tree. The vast majority of stands containing these plots were harvested on the site maximum values to balance species with variable abundances (Gotelli and Ellison, 2004, p 257–259; Minitab Inc., 2010). Simple linear regression was used to evaluate the relationship between initial gap area and red raspberry per cent cover. Normal probability plots and plots of residuals versus fitted values were analysed to assess regression assumptions (Gotelli and Ellison, 2004, p 257–259; Minitab Inc., 2010).

Nonmetric multidimensional scaling (NMS) ordination as implemented in PC-ORD version 6.08 (McCune and Mefford, 2011) was used to examine compositional differences between treatment types along measured environmental gradients (McCune and Grace, 2002). Mean values for variables at each site and time period (2005 and 2012) were used for analysis. Sixty-nine sample units (gaps and single-tree selection sites), 10 species and 14 environmental variables were analysed. Sapling densities were relativized by column maximum values to balance species with variable abundances (McCune and Grace, 2002). Twelve environmental variables described initial conditions (2005) and included: group-selection opening area (m²), legacy-tree crown area (m²) and per cent cover of bare soil, CWD, ferns, graminoids, mosses, native forbs, red raspberry, eastern hemlock border trees, sugar maple border trees and yellow birch border trees. Change in crown area (m²) and gap area (m²) between 2004 and 2011 were also evaluated. The ordination was run using autoplot mode with a random starting configuration. The Sørensen (Bray–Curtis) distance measure was used with 250 runs of real data and 250 runs of random data with a maximum of 500 iterations possible. The dimensionality of the data was analysed using a Monte Carlo test. Pearson’s correlation coefficient was used to evaluate the relationship between species, environmental variables and NMS axes scores (Minitab Inc, 2010; McCune and Mefford, 2011). Significant Pearson’s correlations (P < 0.05) between axis scores and individual variables indicate which variables may be ecologically important; Pearson’s correlation values farthest away from zero (most positive or negative) describe variables that likely exert the strongest influence on community composition patterns (McCune and Grace, 2002).

Results

Seeding, sapling and understory attributes

Mean densities of ironwood (z-value = −3.11, P = 0.002), red maple (z-value = 7.97, P < 0.001) and sugar maple (z-value = 17.78, P < 0.001) seedlings displayed significant differences between 2005 and 2012 (Table 1; 2005 data not shown). Between treatments, only sugar maple and yellow birch seedling densities were significantly different (Table 1). Sugar maple seedlings densities were significantly less in the large (P < 0.001) and medium (P = 0.005) sized openings than in the single-tree selection sites (Table 1). Yellow birch seedlings densities were significantly greater in all group-selection openings than in the reference sites (P < 0.001) and also greater in the large openings than the small openings (P < 0.001; Table 1).

Sapling densities increased substantially especially for the maples but also for shade-mid-tolerant (yellow birch) and -intolerant (black cherry) species between 2005 and 2012 (Figure 1). Red maple (z-value = 8.63, P < 0.001), sugar maple (z-value = 13.56, P < 0.001), yellow birch (z-value = 5.09, P < 0.001) and black cherry (z-value = 4.77, P < 0.001) sapling densities were significantly greater in 2012. In 2005, 14 per cent of subplots contained yellow birch regeneration. By 2012, 12 per cent of the subplots contained
yellow birch. Of the subplots that contained yellow birch regeneration in 2005, only 32 per cent still contained yellow birch regeneration in 2012. Sugar maple dominated the sapling layer in 2012, surpassing all other species by 2 to over 300 times in the group-selection open-ings (Table 2). Sugar maple sapling densities were also 2 times greater in the group-selection openings than in the single-tree selection sites, although the differences between treatments were not significant (Table 2). Red maple was the second most abundant sapling layer species in both the openings and the single-tree selection sites in 2012. Black cherry abundances were greater in the openings than in the single-tree selection references sites, but no significant difference was found to occur between treatments. Yellow birch and ironwood sapling densities displayed significant differences between treatments. Ironwood sapling densities were significantly greater in the small openings than in single-tree selection sites (P = 0.005; Table 2). Yellow birch sapling densities were significantly greater in the large openings than in the single-tree selection sites (P = 0.004; Table 2).

Relative density of sugar maple saplings by treatment ranged from 56 to 82 per cent (large, small, STS, medium). Red maple relative density ranged from 9 to 35 per cent (medium, small, STS, large). The relative densities of all other species were below 5 per cent in all of the treatments except: small openings (ironwood 5%), medium openings (black cherry 6%) and large openings (yellow birch 5%). Over half of the sapling layer, in the group-selection openings (56–67%) and single-tree selection sites (67%), was comprised of saplings in the 0.5- to 1.5-m height class (Figure 2). Mean sapling density in the first height class ranged from 12 789 in the small to 9741 in the medium to 12 963 stems ha$^{-1}$ in the large group-selection openings, whereas at the single-tree selection sites density was 5314 stems ha$^{-1}$. The majority of the sapling layer within the group-selection openings (95%) and single-tree selection sites (86%) was <4.5 m tall.

Of the understory variables, only red raspberry cover increased noticeably between 2005 and 2012 (Table A2; 2005 data not shown but see Shields and Webster (2007)). Mean per cent red

Table 1 Mean densities (stems 100 m$^{-2} ± 1$ SE) of seedlings (stems <50 cm tall) in group-selection openings and single-tree selection reference sites 9 years following opening creation

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Small (n = 16)</th>
<th>Medium (n = 17)</th>
<th>Large (n = 16)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>NB</td>
<td>0.75 ± 0.54a</td>
<td>0.70 ± 0.70a</td>
<td>1.24 ± 0.79a</td>
<td>1.39 ± 1.20a</td>
</tr>
<tr>
<td>Black cherry</td>
<td>NB</td>
<td>8.95 ± 4.78a</td>
<td>6.32 ± 2.49a</td>
<td>1.24 ± 0.70a</td>
<td>9.75 ± 4.53a</td>
</tr>
<tr>
<td>Eastern hemlock</td>
<td>PS</td>
<td>0.75 ± 0.54a</td>
<td>0.94 ± 0.54a</td>
<td>0.50 ± 0.34a</td>
<td>1.99 ± 1.24a</td>
</tr>
<tr>
<td>Ironwood</td>
<td>PS</td>
<td>0.25 ± 0.25a</td>
<td>0.00 ± 0.00a</td>
<td>0.00 ± 0.00a</td>
<td>0.20 ± 0.20a</td>
</tr>
<tr>
<td>Red maple</td>
<td>NB</td>
<td>91.76 ± 32.75a</td>
<td>42.13 ± 14.97a</td>
<td>93.01 ± 21.93a</td>
<td>63.46 ± 18.20a</td>
</tr>
<tr>
<td>Sugar maple</td>
<td>NB</td>
<td>457.07 ± 120.14ab</td>
<td>194.73 ± 33.85a</td>
<td>133.54 ± 22.16a</td>
<td>650.35 ± 173.45b</td>
</tr>
<tr>
<td>Yellow birch</td>
<td>NB</td>
<td>5.97 ± 1.92b</td>
<td>12.87 ± 3.54bc</td>
<td>27.60 ± 8.37c</td>
<td>6.00 ± 0.00a</td>
</tr>
<tr>
<td>Other$^2$</td>
<td></td>
<td>1.99 ± 0.81</td>
<td>0.94 ± 0.54</td>
<td>0.50 ± 0.34</td>
<td>1.59 ± 1.06</td>
</tr>
</tbody>
</table>

Different letters across rows indicate significant differences between treatments (for 2005 and 2012 count data) using a generalized linear model and Tukey’s multiple comparisons of means (α = 0.05) with a Bonferroni correction (α′ = 0.007). Generalized linear model distribution types are Poisson (PS) or negative binomial (NB).

$^1$Reference sites have been managed using a q-factor approach (q = 1.3) on a 10-year cutting cycle with residual basal areas of between 16.1 and 20.7 m$^2$ ha$^{-1}$ since the 1960s.

$^2$Other includes: serviceberry, trembling aspen, northern white cedar, American elm, black ash, white spruce and pin cherry

Figure 1 Change in sapling density from 2005 to 2012 by treatment for (a) common tree species and (b) Acer spp. (stems ha$^{-1} ± 1$ SE). Note differences in scale between panels (a) and (b).
Table 2 Mean densities (stems ha\(^{-1}\) ± 1 SE) of saplings (stems ≥ 50 cm tall and < 12.7 cm dbh) in group-selection openings and single-tree selection reference sites 9 years following opening creation

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Group-selection openings</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small (n = 16)</td>
<td>Medium (n = 17)</td>
<td>Large (n = 16)</td>
</tr>
<tr>
<td>Balsam fir</td>
<td>NB</td>
<td>99.5 ± 77.1a</td>
<td>46.8 ± 32.1a</td>
</tr>
<tr>
<td>Black cherry</td>
<td>NB</td>
<td>622.0 ± 295.2a</td>
<td>983.5 ± 669.9a</td>
</tr>
<tr>
<td>Eastern hemlock</td>
<td>PS</td>
<td>74.6 ± 40.1a</td>
<td>0.00 ± 0.00a</td>
</tr>
<tr>
<td>Ironwood</td>
<td>NB</td>
<td>870.8 ± 491.9b</td>
<td>117.1 ± 74.5ab</td>
</tr>
<tr>
<td>Red maple</td>
<td>NB</td>
<td>3159.8 ± 1437.4a</td>
<td>1568.9 ± 498.7a</td>
</tr>
<tr>
<td>Sugar maple</td>
<td>NB</td>
<td>13 709.7 ± 2736.9a</td>
<td>14 331.2 ± 2309.4a</td>
</tr>
<tr>
<td>Yellow birch</td>
<td>NB</td>
<td>423.0 ± 245.0ab</td>
<td>327.8 ± 114.4ab</td>
</tr>
<tr>
<td>Other(^2)</td>
<td></td>
<td>99.5 ± 57.5</td>
<td>93.7 ± 54.3</td>
</tr>
</tbody>
</table>

Different letters across rows indicate significant differences between treatments (for 2005 and 2012 count data) using a generalized linear model and Tukey’s multiple comparisons of means (α = 0.05) with a Bonferroni correction (α’ = 0.007). Model types are Poisson (PS) or negative binomial (NB).\(^3\)Reference sites have been managed using a q-factor approach (q = 1.3) on a 10-year cutting cycle with residual basal areas of between 16.1 and 20.7 m\(^2\) ha\(^{-1}\) since the 1960s.\(^4\)Other includes: serviceberry, trembling aspen, northern white cedar, American elm, black ash, white spruce and pin cherry.

Figure 2 Relative density (%) of tree species juxtaposed with total stem density (stems ha\(^{-1}\)) by height class for (a) small, (b) medium, (c) large group-selection openings and (d) single-tree selection sites. The black line represents total stem density by 1-m height classes beginning with 1: (0.5 – 1.5 m). Note differences in scale between panels (a–c) and (d).
raspberry cover (±1 SE) increased by 9 ± 4 per cent in the small openings, 17 ± 4 per cent in the medium openings, 18 ± 3 per cent in the large openings and 0.5 ± 0.3 per cent in the single-tree selection sites between the two time periods. A simple linear regression of the change in red raspberry cover between time periods suggested that the magnitude of change was not significantly associated with initial opening area (P = 0.084). However, current red raspberry cover exhibited a significant positive relationship with initial opening area (R² = 0.10, y = 0.012x + 13.02, P = 0.029).

**Ordination**

The final NMS ordination was 3-dimensional with a stress of 13.51, instability of <0.0001 and cumulative R² of 0.802. Because axis 1 (R² = 0.326) and axis 2 (R² = 0.316) explained a greater amount of variability than axis 3 (R² = 0.160), joint plots of axes 1 and 2 are presented (Figures 3 and 4). Axis 1 was positively correlated with most of the species in the sapling layer, but the strongest correlations occurred with red maple (r = 0.46, P < 0.001), sugar maple (r = 0.64, P < 0.001) and yellow birch (r = 0.37, P < 0.001; Table 3; Figure 3). The environmental variables CWD and per cent of eastern hemlock border trees present were also positively correlated with axis 1, whereas sugar maple border trees displayed a negative correlation with axis 1 (Table 3; Figure 3). Sugar maple, which was positively correlated with axis 1, displayed a negative correlation with axis 2 (r = -0.39, P < 0.001; Table 3; Figure 3). Vector (arrow) length represents change in composition through time; longer vectors indicate greater compositional change than shorter vectors. Position and movement in the ordination space time; longer vectors indicate greater compositional change than shorter vectors. Position and movement in the ordination space reflected the increasing dominance of maples in the developing cohort. Less directionality was observed in reference sites. Several tree species were positively correlated with axis 1, which may be attributable, at least in part, to the abundance of eastern hemlock border trees. Higher abundances of eastern hemlock border trees could correlate with environmental conditions that may have been advantageous to a more diverse regenerating cohort. First, eastern hemlock usually occurs in relatively moist habitats (Godman and Lancaster, 1990), which was likely

**Discussion**

Canopy gaps initially increase light levels and reduce competition between plants for soil resources and water thus creating conditions where multiple species with a range of shade tolerances can regenerate (Minckler et al., 1973; Runke and Yetter, 1987). Even though species diversity has been shown to increase as gap size increases, other factors may override the effects of opening size in forest ecosystems leading to outcomes diverging from those anticipated (Bobiec, 2007; Bolton and D’Amato, 2011; Matonis et al., 2011; Kern et al., 2012). By assessing the understory composition of 49 group-selection openings and 20 single-tree selection sites 3 years after study implementation, our results document the difficulties in actively changing developmental trajectories to regenerate declining tree species. A lack of pre-harvest data limits the inferences we can make based on our dataset. However, since the study area has been managed using single-tree selection since the 1960s, the conditions present in the single-tree selection reference sites are very similar to pre-harvest conditions in the group-selection openings.

In general, seedling densities were lower in 2012 than during the initial survey. Of those seedlings showing significant differences between time periods, only red maple and sugar maple increased in abundance. Declines in seedling densities were likely attributable to recruitment into the sapling layer and high density-dependent mortality. Because tall saplings are better positioned at this phase of development to capture the gaps, changes in the seedling layer may be less consequential at this time.

Our sapling ordination results indicated that group-selection openings spanning a wide gradient in area increased in compositional similarity over time. Movement within the ordination space reflected the increasing dominance of maples in the developing gap cohort. Less directionality was observed in reference sites. Several tree species were positively correlated with axis 1, which may be attributable, at least in part, to the abundance of eastern hemlock border trees. Higher abundances of eastern hemlock border trees could correlate with environmental conditions that may have been advantageous to a more diverse regenerating cohort. First, eastern hemlock usually occurs in relatively moist habitats (Godman and Lancaster, 1990), which was likely
important given persistent growing season droughts during the course of our study. Second, eastern hemlock border trees are inversely proportional to hardwood border tree abundances and likely resulted in lower levels of broadleaf litter. Many small seeded trees, such as yellow birch and eastern hemlock, have difficulties establishing on thick matted layers of broadleaf litter (Erdmann, 1990; Barras and Kellman, 1998). Tubbs and Metzger (1969) also observed better growth of yellow birch in hemlock-hardwood sites as opposed to sites dominated by sugar maple.

The highest density of yellow birch in our study occurred within the largest group-selection openings (range = 886–1461 m²). Others have also reported that openings ≥800 m² are necessary for successful yellow birch recruitment (Leak, 1999; Hanson and Lorimer, 2007; Kneeshaw and Prevost, 2007). Nevertheless, all of the yellow birch regeneration in the large openings, in our study, resides within the shortest height class. This may be due to regeneration failures as only a third of the subplots that contained yellow birch regeneration in the initial survey still contained yellow birch regeneration in 2012. Subsequent re-establishment likely occurred since the total number of subplots containing yellow birch is similar between the two time periods. Weather patterns from 2004 to 2012 may have played a role in the yellow birch recruitment failures we observed. Yellow birch performs poorly under drought conditions and grows best in cool and moist environments (Tubbs, 1969; Erdmann, 1990; Perala and Alm, 1990), which have occurred only sporadically since this study was implemented. Retaining a centrally located yellow birch legacy tree may have contributed to continued establishment, since open-grown individuals more frequently produce heavy seed crops (Erdmann, 1990). Survival and growth of retained yellow birches has been excellent (98.8 per cent annual survival rate and threefold increase in diameter growth; Klingsporn et al., 2012). However, the yellow birch cohort that established sometime after 2005 is at a competitive disadvantage especially compared with sugar maple based on height.

Processes through which disturbances occur can be as important as the size of openings created in a forest matrix (Beckage et al., 2000). Many studies conclude that soil scarification is important for yellow birch regeneration (Godman and Krefting, 1960; Erdmann, 1990; Raymond et al., 2003; Prévost et al., 2010). Although active soil scarification was not applied to our sites, passive scarification did occur when the gaps were created. Incidental scarification caused by harvesting can be adequate to enhance yellow birch

Figure 4 NMS ordination plots illustrating sample plot movement through time; treatments are presented in separate panels: (a) small (n = 16), (b) medium (n = 17) and (c) large (n = 16) group-selection openings and (d) single-tree selection sites (n = 20). Each arrow represents the change in species composition of an individual study site from 2005 to 2012. Axes are represented by significantly correlated species (see Table 3).
regeneration (Lorenzetti et al., 2008; Prévost et al., 2010). However, in many of our sites where incidental scarification occurred, raspberry and/or red maple now dominate. Murray et al. (2012) also observed greater levels of red maple regeneration on scarified sites in a hemlock-hardwood forest in Wisconsin. In fact, the benefits of scarification may be eliminated under dry conditions (Winget and Kozlowski, 1965; Murray et al., 2012), particularly when raspberry dominates the understory layer (Prévost et al., 2010). Raspberry has been found to suppress tree regeneration in the northern Great Lakes region, especially within the first 10 years after disturbance, primarily through light attenuation and the effects of snow weighted raspberry canes suppressing young woody regeneration (Godman and Krefting, 1960; Archambault et al., 1998).

Sugar maple, the most prevalent species in our study, has been found to increase in abundance following gap creation and drought (Canham, 1988; Parshall, 1995; Bolton and D’Amato, 2011) through release of advance regeneration, sustained recruitment and high survivorship (Roberts and Dong, 1993). Nolet et al. (2008) also observed that sugar maple has a competitive advantage over yellow birch, based on stem growth, under high light conditions. Others have found greater abundances of yellow birch and red maple on more poorly drained sites, while sugar maple dominated on mesic sites (Metzger, 1980). Additionally, red maple, a species

![Figure 5](https://academic.oup.com/forestry/article-abstract/86/5/555/638331)
known to share environmental proclivities with yellow birch, has increased in abundance during the 20th century (Walters and Yawney, 1990; Abrams, 1998). Also, red maple, which is more shade tolerant and aggressive, is able to survive during both wet and dry periods, unlike yellow birch (Walters and Yawney, 1990; Leak and Smith, 1996). Therefore, sugar and red maple may ultimately be more competitive than yellow birch under current conditions.

One of the largest concentrations of yellow birch currently occurs in the Upper Peninsula of Michigan (Erdmann, 1990). However, yellow birch became established in the western Great Lakes region during a time of cooler and wetter climatic conditions than we are experiencing now (Jackson and Booth, 2002). While weather records from the period of yellow birch migration into the Great Lakes region are not available, the mean growing season PDSI value for the study area from 1895 to 2012 was nearly zero (−0.19) (NOAA, 2012b). Alternatively, the mean PDSI value from 2004 to 2012 was −2.09 and many more low PDSI values have occurred since 1986 (Figure 5; NOAA, 2012b). Climate predictions for the future indicate temperatures will be warmer, but precipitation regimes are much more uncertain (Environmental Protection Agency (EPA), 2013). Some models suggest that precipitation levels will slightly increase but that levels will be lower during the growing season months (EPA, 2013). If the future climate change predictions are reflective of conditions that have occurred over the duration of our experiment, then present environmental conditions may not be as favourable for yellow birch as they once were (Woods, 2004). Therefore, we suggest that future research consider the potential influence of changing climatic regimes on the efficacy of regeneration systems, especially those designed to enhance diversity or promote underrepresented tree species.

Conclusions

Past management practices and current environmental conditions necessitate a more concerted effort to regenerate declining tree species. Simply creating the most suitable light environment in time and space may not be adequate. In fact, Raymond et al. (2003) found that plant dynamics in canopy gaps are exceedingly controlled by prior stand conditions. In the group-selection openings we studied, sugar and red maple will likely be the predominant species to recruit into the overstory, with yellow birch, ironwood and black cherry recruiting as minor components in the openings. Corrective measures could potentially change the developmental trajectories of these openings. Many studies recommend release treatments for seedlings and saplings in order to increase opportunities for successful canopy recruitment (Arbogast, 1957; Wang, 1968; Tubbs and Metzger, 1969; Erdmann et al., 1975). Yellow birch, in particular, could benefit through release from competing vegetation since abundances are greater in the large openings, but heights are lower than the competing vegetation. Release would also benefit other underrepresented species especially at the sites where their abundances have increased relative to the single-tree selection reference sites. Nevertheless, the influence of historic and contemporary climatic conditions may complicate regeneration efforts and warrant additional study.

Acknowledgements

We thank the following individuals for their contributions to the establishment of the silvicultural trial: Joshua Shields, Linda Nagel, James Schmierer and Jon Neuendorff. We also thank Rachel Mason for her invaluable contributions to data collection and processing. Dr Philippe Nolet and three anonymous reviewers provided helpful comments on an earlier draft of this manuscript.

Conflict of interest statement

None declared.

Funding

Funding for this project was provided by the McIntire-Stennis Cooperative Forestry Research Program and School of Forest Resources and Environmental Science at Michigan Technological University.

References

Forestry


McCune, B. and Grace, J.B. 2002 Analysis of Ecological Communities. MJM Software Design, Gleneden Beach, OR, USA.


Minibit Inc., 2010 version Minibit® 16.1.1. In, State College, PA, USA.


### Appendix

**Table A1** Understory species list for the 2012 sampling period.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferns and fern allies</td>
<td></td>
</tr>
<tr>
<td>Athyrium filix-femina (L.) Roth</td>
<td>Lady fern</td>
</tr>
<tr>
<td>Dryopteris carthusiana (Vill.) H.P. Fuchs</td>
<td>Spinulose shield fern</td>
</tr>
<tr>
<td>Gymnocarpium dryopteris (L.) Newman</td>
<td>Oak fern</td>
</tr>
<tr>
<td>Matteuccia struthiopteris (L.) Todaro</td>
<td>Ostrich fern</td>
</tr>
<tr>
<td>Onoclea sensibilis L.</td>
<td>Sensitive fern</td>
</tr>
<tr>
<td>Osmunda cinnamomea L.</td>
<td>Cinnamon fern</td>
</tr>
<tr>
<td>Osmunda claytoniana L.</td>
<td>Interrupted fern</td>
</tr>
<tr>
<td>Phegopteris connectilis (Michx.) Watt</td>
<td>Long beech fern</td>
</tr>
<tr>
<td>Pteridium aquilinum (L.) Kuhn</td>
<td>Bracken fern</td>
</tr>
<tr>
<td>Equisetum sylvaticum (L.)</td>
<td>Woodland horsetail</td>
</tr>
<tr>
<td>Huperzia lucidula (Michx.) Trevisan</td>
<td>Shining clubmoss</td>
</tr>
<tr>
<td>Lycopodium annotinum L.</td>
<td>Stiff clubmoss</td>
</tr>
<tr>
<td>Phegopteris connectilis</td>
<td>Ground pine</td>
</tr>
<tr>
<td>Graminoids</td>
<td></td>
</tr>
<tr>
<td>Agrostis gigantea Roth</td>
<td>Redtop</td>
</tr>
<tr>
<td>Agrostis hyemalis (Walt.) Tucherman</td>
<td>Tickle-grass</td>
</tr>
<tr>
<td>Agrostis sp. L. Bent-grass</td>
<td></td>
</tr>
<tr>
<td>Brachyelytrum erectum (Schreb. ex Spreng.) P. Beauv.</td>
<td>Bearded short-husk</td>
</tr>
<tr>
<td>Carex arctata Boott ex Hook.</td>
<td></td>
</tr>
<tr>
<td>Carex gynandra Schwein.</td>
<td></td>
</tr>
<tr>
<td>Carex intumescens Rudge</td>
<td></td>
</tr>
<tr>
<td>Carex ormostachya Wieg.</td>
<td></td>
</tr>
<tr>
<td>Carex projecta Mackenzie</td>
<td></td>
</tr>
<tr>
<td>Carex sp. L.</td>
<td></td>
</tr>
<tr>
<td>Cinna latifolia (Trev. ex Goepp.) Griseb.</td>
<td>Drooping woodland sedge</td>
</tr>
<tr>
<td>Glyceria striata (Lam.) A.S. Hitchc.</td>
<td>Nodding sedge</td>
</tr>
<tr>
<td>Juncus effusus L.</td>
<td></td>
</tr>
<tr>
<td>Oryzopsis asperifolia Michx.</td>
<td></td>
</tr>
<tr>
<td>Scirpus atrovires Wild.</td>
<td></td>
</tr>
<tr>
<td>Scirpus cypereus (L.) Kunth</td>
<td></td>
</tr>
<tr>
<td>Native herbs/forbs</td>
<td></td>
</tr>
<tr>
<td>Allium tricoccum Aiton</td>
<td></td>
</tr>
<tr>
<td>Apocynum androsaemifolium L.</td>
<td></td>
</tr>
<tr>
<td>Aralia nudicaulis L.</td>
<td></td>
</tr>
<tr>
<td>Arisaema triphyllum (L.) Schott</td>
<td></td>
</tr>
<tr>
<td>Cardamine concatenata (Michx.) Sw.</td>
<td></td>
</tr>
<tr>
<td>Clintonia borealis (Ait.) Raf.</td>
<td></td>
</tr>
<tr>
<td>Captis trifolia (L.) Salisb.</td>
<td></td>
</tr>
<tr>
<td>Cornus canadensis L.</td>
<td></td>
</tr>
<tr>
<td>Epilobium ciliatum Raf.</td>
<td></td>
</tr>
<tr>
<td>Erythronium americanum Ker Gal.</td>
<td></td>
</tr>
<tr>
<td>Euthamia graminifolia (L.) Nutt.</td>
<td></td>
</tr>
<tr>
<td>Maianthemum canadense Desf.</td>
<td></td>
</tr>
<tr>
<td>Maianthemum racemosum (L.) Link</td>
<td></td>
</tr>
<tr>
<td>Mitella repens L.</td>
<td></td>
</tr>
<tr>
<td>Oxalis montana Raf.</td>
<td></td>
</tr>
<tr>
<td>Polygonatum pubescens (Willd.) Push</td>
<td></td>
</tr>
<tr>
<td>Polygonatum clinode Michx.</td>
<td></td>
</tr>
</tbody>
</table>

**Table A1** Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudognaphalium obtusifolium (L.) Hilliard &amp; Burt</td>
<td>Cat’s-foot</td>
</tr>
<tr>
<td>Rubus pubescens Raf.</td>
<td>Dwarf red raspberry</td>
</tr>
<tr>
<td>Scutellaria sp. L.</td>
<td>Skullcap</td>
</tr>
<tr>
<td>Solidago sp. L.</td>
<td>Goldenrod</td>
</tr>
<tr>
<td>Symphyotrichium lateriflorum (L.) Å.</td>
<td>Calico aster</td>
</tr>
<tr>
<td>Trientalis borealis Raf.</td>
<td>Starflower</td>
</tr>
<tr>
<td>Trillium cernuum L.</td>
<td>Nodding trillium</td>
</tr>
<tr>
<td>Viola spp. L.</td>
<td>Violet</td>
</tr>
<tr>
<td>Non-native herbs</td>
<td></td>
</tr>
<tr>
<td>Cirsium palustre (L.) Scop.</td>
<td>Marsh thistle</td>
</tr>
<tr>
<td>Galeopsis tetrahit L.</td>
<td>Hemp nettle</td>
</tr>
<tr>
<td>Hieracium aurantiacum L.</td>
<td>Orange hawkweed</td>
</tr>
<tr>
<td>Hieracium piloselloides VIII.</td>
<td>Tall hawkweed</td>
</tr>
<tr>
<td>Solanum dulcamara L.</td>
<td>Bittersweet nightshade</td>
</tr>
<tr>
<td>Veronica officinalis L.</td>
<td>Common gypsyweed</td>
</tr>
<tr>
<td>Acer spicatum Lam.</td>
<td>Mountain maple</td>
</tr>
<tr>
<td>Alnus incana (L.) Moench ssp. rugosa (Du Roi) Clausen</td>
<td>Speckled Alder</td>
</tr>
<tr>
<td>Clematis virginiana L.</td>
<td>Devil’s darning noodles</td>
</tr>
<tr>
<td>Cornus sp. L.</td>
<td>Dogwood</td>
</tr>
<tr>
<td>Corylus cornuta Marsh</td>
<td>Beaked hazelnut</td>
</tr>
<tr>
<td>Diervella ionica P. Mill.</td>
<td>Bush honeysuckle</td>
</tr>
<tr>
<td>Lonicerca canadensis Bartr. ex Marsh.</td>
<td>American fly honeysuckle</td>
</tr>
<tr>
<td>Prunus virginiana L.</td>
<td>Chokecherry</td>
</tr>
<tr>
<td>Ribes spp. L.</td>
<td>Currant</td>
</tr>
<tr>
<td>Rubus alleghaniensis Porter</td>
<td>Allegheny blackberry</td>
</tr>
<tr>
<td>Rubus idaeus L.</td>
<td>American red raspberry</td>
</tr>
<tr>
<td>Sambucus racemosa L.</td>
<td>Red elderberry</td>
</tr>
<tr>
<td>Salix spp. L.</td>
<td>Willow</td>
</tr>
<tr>
<td>Taxus canadensis Marsh.</td>
<td>Canada yew</td>
</tr>
<tr>
<td>Tree seedlings</td>
<td></td>
</tr>
<tr>
<td>Abies balsamea (L.) P. Mill.</td>
<td>Balsam fir</td>
</tr>
<tr>
<td>Acer rubrum L.</td>
<td>Red maple</td>
</tr>
<tr>
<td>Acer saccharum Marsh</td>
<td>Sugar maple</td>
</tr>
<tr>
<td>Amelanchier sp. Medik.</td>
<td>Serviceberry</td>
</tr>
<tr>
<td>Betula alleghaniensis Britt.</td>
<td>Yellow birch</td>
</tr>
<tr>
<td>Fraxinus nigra Marsh</td>
<td>Black ash</td>
</tr>
<tr>
<td>Ostrya virginiana (P. Mill.) K. Koch</td>
<td>Ironwood</td>
</tr>
<tr>
<td>Picea glauca (Moench) Voss</td>
<td>White spruce</td>
</tr>
<tr>
<td>Populus tremuloides Michx.</td>
<td>Trembling aspen</td>
</tr>
<tr>
<td>Prunus pensylvanica L.</td>
<td>Pin cherry</td>
</tr>
<tr>
<td>Prunus serotina Ehrh.</td>
<td>Black cherry</td>
</tr>
<tr>
<td>Thuja occidentalis L.</td>
<td>Northern white cedar</td>
</tr>
<tr>
<td>Tsuga canadensis (L.) Carr.</td>
<td>Eastern hemlock</td>
</tr>
<tr>
<td>Ulmus Americana L.</td>
<td>American elm</td>
</tr>
</tbody>
</table>

**Table A2** Mean understory cover (per cent ± 1 SE) in group-selection openings and single-tree selection reference sites during the summer of 2012.

<table>
<thead>
<tr>
<th></th>
<th>Group-selection openings</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small (n = 16)</td>
<td>Medium (n = 17)</td>
</tr>
<tr>
<td>Ferns</td>
<td>8.35 ± 2.23</td>
<td>5.90 ± 1.22</td>
</tr>
<tr>
<td>Graminoids</td>
<td>1.36 ± 0.36</td>
<td>1.83 ± 0.63</td>
</tr>
<tr>
<td>Moss</td>
<td>2.23 ± 0.49</td>
<td>1.54 ± 0.40</td>
</tr>
<tr>
<td>Native forbs</td>
<td>0.85 ± 0.36</td>
<td>0.34 ± 0.10</td>
</tr>
<tr>
<td>Non-native forbs</td>
<td>0.32 ± 0.16</td>
<td>0.24 ± 0.09</td>
</tr>
<tr>
<td>Raspberry</td>
<td>14.11 ± 3.81</td>
<td>26.46 ± 3.94</td>
</tr>
<tr>
<td>Other shrubs</td>
<td>0.61 ± 0.48</td>
<td>1.75 ± 0.51</td>
</tr>
<tr>
<td>Seedlings</td>
<td>5.29 ± 1.09</td>
<td>2.68 ± 0.45</td>
</tr>
<tr>
<td>CWD</td>
<td>4.34 ± 0.75</td>
<td>5.15 ± 1.04</td>
</tr>
<tr>
<td>Litter</td>
<td>59.51 ± 3.83</td>
<td>48.44 ± 3.67</td>
</tr>
<tr>
<td>Soil</td>
<td>1.00 ± 0.40</td>
<td>1.57 ± 0.61</td>
</tr>
</tbody>
</table>

See Table A1 for species list.