Scarification and gap size have interacting effects on northern temperate seedling establishment

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ABSTRACT

After decades focused on promoting economically valuable species, management of northern temperate forests has increasingly become focused on promoting tree species diversity. Unfortunately, many formerly common species that could contribute to diversity including yellow birch (*Betula alleghaniensis* Britton.), paper birch (*Betula papyrifera* Marsh), eastern hemlock (*Tsuga canadensis* L.), and eastern white pine (*Pinus strobus* L.) are now uncommon in the seedling layer, raising concerns about our ability to use these species to increase diversity. In this study, two related seed addition experiments conducted in 45 variably-sized harvest gaps (107–3234 m^2) and four unharvested areas in Emmet County, Michigan, USA were used to investigate mechanisms potentially limiting seedling recruitment. The first experiment examined the influence of light (i.e. harvest gap size), competing vegetation, and deer browsing on seedling survival for three years in a 2×2 factorial, where subplots were unfenced or fenced to exclude deer, unclipped or clipped to control competing vegetation, and located across the gradient of gap sizes. The second experiment explored the influence of scarification, light, and competing vegetation on germination and subsequent survival for 2 years in a 2×2 factorial, in subplots that were unscarified or scarified to remove litter, unclipped or clipped to control competing vegetation, and located across the gradient of gap sizes. Eastern hemlock, paper birch, and yellow birch, all smaller-seeded species, were 12, 17, and 95 times more abundant in scarified plots compared to unscarified plots. In contrast, white pine, the largest-seeded species, was unaffected by scarification and had low overall germination. Shade tolerant hemlock and shade intolerant paper birch germinated at higher densities in lower light, smaller harvest gap environments, while both mid-tolerant species, white pine and yellow birch, were unaffected by light. Increasing light availability had a positive influence on each species' first year survival except white pine, and also improved second year survival for paper birch and eastern hemlock. Paper birch and hemlock third year survival also increased with increasing light. By the end of the third growing season, only paper birch survival was negatively impacted by competition from vegetation and no species were affected by exposure to deer browse pressure. At the conclusion of the study, large group selection gaps (24–50 m diameter) contained the highest density of each species except white pine, suggesting that large group selection gaps may provide the best opportunity for reestablishing this particular group of species in the seedling layer.

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1. Introduction

With the human population expected to surpass eight billion in the next decade (United Nations, 2013), demand for goods and services from already heavily exploited forest ecosystems will continue to increase. Unfortunately, due to changes in species composition including declining tree species diversity and evenness (Schuler and Gillespie, 2000; Lawrence, 2004; Amatangelo et al., 2011), the variety of goods and services some forest ecosystems can provide may soon decline (Chapin et al., 2000; Folke et al., 2004; Drever et al., 2006; Fischer et al., 2006). Complicating matters further, lower diversity may lead to declining resilience to novel disturbances, such as climate change and invasive pests and pathogens (Sturrock et al., 2011; Anderson-Teixeira et al., 2013; Duveneck et al., 2014).

The northern temperate forests of Eastern North America represent one such forest type where species composition shifts, including declining diversity, are occurring. Some of the most noticeable compositional changes include a decrease in overstory evenness (Zhang et al., 2000), an expansion of a few shade tolerant species (Schulte et al., 2007; Nowacki and Abrams, 2008; Amatangelo et al., 2011; Hanberry, 2013), a large decline in conifers (including hemlock and white pine) and less shade tolerant species (including paper birch and yellow birch), and seedling and sapling size classes dominated by a few shade tolerant species (Neuendorff et al., 2007; Matonis et al., 2011). Some of these demographic shifts (e.g. paper birch) cannot be considered unusual or unexpected, given that much of this land is second growth forest that is simply undergoing forest succession as it ages (Stearns, 1954; White and Mladenoff, 1994; Woods, 2000). Nevertheless, the loss of species diversity is an undesirable development for multiple-use management, which seeks to provide society with a variety of forest products and ecosystem services (Seymour and Hunter, 1999). Recognizing the problems associated with declining tree diversity, forest managers have begun investigating silvicultural means to increase tree species diversity within this forest type.

Emulating natural disturbance is one often suggested approach for promoting tree species diversity in northern temperate forests (Scheller and Mladenoff, 2002; Seymour et al., 2002; Bolton and D'Amato, 2011). Harvest disturbance using single-tree selection, a commonly used silvicultural system in northern hardwood forests for over 60 years, creates a series of environmentally similar small harvest gaps (<80 m^2 meters) (Crow et al., 2002; Angers et al., 2005; Klingsporn-Poznanovic et al., 2013). Unlike single-tree selection, a harvest regime patterned after natural disturbance regimes creates a variety of harvest gap sizes (Seymour et al., 2002). It is generally believed that the broader range of environmental conditions produced by a natural disturbance-patterned harvesting regime will promote more species diversity than a single-tree selection harvesting regime. This paradigm is based on the assumption that the lower light environments produced in smaller harvest gaps favor the establishment of shade tolerant species, while the higher light environments of larger harvest gaps promote the establishment of mid to shade intolerant species (Ricklefs, 1977; Denslow, 1980; McClure et al., 2000; Webster and Lorimer, 2005; Kneeshaw and Prèvost, 2007).

Nevertheless, recent evidence from gap regeneration studies suggests that gap dynamics are far less predictable, and may be influenced by several factors in addition to gap size (Shields et al., 2007; Falk et al., 2010; Gasser et al., 2010; Bolton and D'Amato, 2011; Matonis et al., 2011; Kern et al., 2012, 2013; Fahey and Lorimer, 2013; Klingsporn-Poznanovic et al., 2013). Consequently, management that manipulates gap size alone to regenerate a more diverse seedling cohort will likely fail. While current approaches have identified individual factors likely responsible for gap regeneration failure, a mechanistic understanding of how these factors interact to affect regeneration is currently lacking. This suggests that an experimental approach manipulating several potential inhibiting factors may be needed to identify the most critical bottlenecks inhibiting natural regeneration in northern harvest gaps.

Seedling establishment failure is one potential explanation for the variable patterns of tree recruitment within harvest gaps (Wright et al., 1998; Caspersen and Saprunoff, 2005). While harvest gap size can be manipulated to give individual species or groups of species a competitive advantage based on their shade tolerance, seed must be present and seedlings must be able to establish before any competitive advantage can be realized. As

such, manipulating factors to enhance the recruitment of young seedlings of declining tree species is an important prerequisite to manipulating factors that affect seedling growth and survival.

Similar to how tree species vary in their competitive abilities among light environments, tree species also vary in their abilities to germinate and establish on a variety of forest floor substrates (Perala and Alm, 1990; Shields et al., 2007; Marx and Walters, 2006, 2008). For instance, smaller-seeded species are more successful on easily-penetrable, moisture-holding substrates such as decaying coarse woody debris (hereafter referred to as CWD) compared to the undisturbed litter layer (McGee and Birmingham, 1997; Cornett et al., 2001; Caspersen and Saprunoff, 2005; Marx and Walters, 2008). In addition, smaller-seeded species also germinate and establish better on bare mineral soil compared to leaf litter (Raymond et al., 2003; Lorenzetti et al., 2008; Prèvost et al., 2010). By contrast, larger-seeded species, some of which are now dominating northern temperate forest understories (e.g., sugar maple, American beech) (Neuendorff et al., 2007; Matonis et al., 2011), are less constrained by substrate characteristics and thus can establish successfully on undisturbed leaf litter substrates (Caspersen and Saprunoff, 2005). Currently, in managed northern temperate forests, undisturbed leaf litter substrates dominate and CWD is becoming increasingly rare, as mortality of large trees has been greatly diminished by harvest removals (Hura and Crow, 2004). Furthermore, bare mineral soil substrates are likely becoming less common in selection-managed northern hardwood systems as timber harvests are often conducted in the winter over snowpack, which buffers the forest floor from mechanical disturbance (Shields et al., 2007). While conducting harvests over snow does not entirely eliminate the occurrence of forest floor disturbance, it likely does limit its extent to areas of the stand that are heavily traversed, such as skid trails or landings. As a result, the majority of the forest floor is left undisturbed (Personal observation). Collectively then, the lack of suitable seedling establishment substrates may contribute as much or more than low light availability to smaller-seeded species recruitment failures in managed northern temperate forests.

One apparent solution to this potential recruitment bottleneck is to increase the availability of favorable establishment sites. While CWD may take decades to develop naturally, and is prohibitively labor-intensive to restore artificially, bare mineral soil/humus establishment sites are relatively easy to create and may provide similar establishment opportunities. For example, the forest floor could be scarified, a silvicultural technique which disturbs the litter layer and understory vegetation by dragging chains or disks across the forest floor to increase bare mineral soil/humus availability. Indeed, scarification has been shown to be effective at promoting smaller-seeded species establishment (Godman and Krefting, 1960; Raymond et al., 2003; Lorenzetti et al., 2008; Prèvost et al., 2010). What remains unknown, however, is whether this observed increase in smaller-seeded species establishment following scarification is driven by greater seedling germination on bare mineral soil/humus microsites, or by greater subsequent survival of newly established seedlings. In addition, little is known about how gap size interacts with bare mineral soil/humus availability to influence patterns of seedling germination and subsequent survival for species of varying seed sizes. Given the movement toward a natural disturbance based harvest regime, quantifying these relationships is important if scarification is to be used effectively in the management of northern temperate forests.

Another potential explanation for inconsistent patterns of harvest gap recruitment is the interaction between harvest gap size

and non-tree vegetation (forbs, shrubs, ferns, and graminoids). By responding quickly to harvest, non-tree vegetation can compete strongly with newly established seedlings by decreasing light and other resources (Royo and Carson, 2006). Large gaps created by the removal of groups of trees (group selection or patch selection harvesting) may experience the greatest degree of resource diminishment, as highly competitive early successional species like raspberry (*Rubus idaeus*), blackberry (*Rubus occidentalis*), and sedge (*Carex* sp.) have been shown to increase in density in larger harvest gaps (Shields et al., 2007; Matonis et al., 2011; Kern et al., 2012). Consequently, intense competition for resources from non-tree vegetation may shift the competitive balance in large harvest gaps from resource-demanding shade intolerant species to more resource-conserving shade tolerant species that can withstand being overtopped and shaded by non-tree vegetation (Montgomery et al., 2010).

In addition to substrate limitations and competition from non-tree vegetation, browsing by white-tailed deer (*Odocoileus virginianus* (Zimmermann)) could also limit the efficacy of varying gap size to increase tree diversity. Indeed, browsing from elevated deer populations has been linked to altered regeneration patterns in several recent studies (Long et al., 2007; Witt and Webster, 2010; Kain et al., 2011; Randall and Walters, 2011; Matonis et al., 2011; Nuttle et al., 2014). Not all species, however, may be equally affected by browsing, as deer have been shown to browse certain species preferentially, while avoiding others (Horsley et al., 2003; Rooney and Waller, 2003; Long et al., 2007; Kain et al., 2011; Randall and Walters, 2011; Schumacher and Carson, 2013; Nuttle et al., 2014). Similarly, certain species of seedlings also show a greater tolerance to browsing compared to others (Augustine and McNaughton, 1998; Côtê et al., 2004). Therefore, even if silvicultural treatments are successful at overcoming establishment substrate and light/non-tree competition barriers to regeneration, outcomes in harvest gaps may still ultimately reflect local deer density (Millington et al., 2010).

In summary, the lack of predictable tree regeneration patterns in variably-sized harvest gaps may be due to interactions with other factors affecting the early stages of regeneration including substrate availability, competition with non-tree vegetation, and deer herbivory. Here, we examine the effects of these factors on germination, initial survival (1 year), and short-term survival (up to 3 years) of four species that are declining in northern temperate forests (eastern hemlock, white pine, paper birch, yellow birch) in a mesic northern hardwood stand. Specifically we predict: (1) smaller-seeded species will have greater germinant densities in scarified than unscarified subplots due to the dominance of leaf litter substrate in harvest gaps, (2) competition from non-tree vegetation will negatively affect seedling survival, especially for shade intolerant species in large group selection gaps, (3) browsing by deer in unfenced plots will lead to decreased seedling survival for all species compared to fenced plots, (4) in combination, sufficient resource availability and modest competition from non-tree vegetation will result in the highest seedling survivorship in medium-sized harvest gaps for all species.

To test these predictions we established two experiments that collectively tracked the germination and survival of eastern hemlock (*Tsuga canadensis* L.), yellow birch (*Betula alleghaniensis* Britton.), paper birch (*Betula papyrifera* Marsh), and eastern white pine (*Pinus strobus* L.) seedlings for up to three years in subplots established across 45 variably-sized harvest gaps and 4 unharvested areas in two adjacent, recently harvested northern hardwood stands. Subplots were either unscarified or scarified to create bare mineral soil/humus substrate, unclipped or clipped to control aboveground competition from non-tree vegetation, and unfenced or fenced to exclude deer. Collectively, this information will provide mechanistic insight into the causes of regeneration

failure for four tree species that are declining in the northern temperate forest and provide insight for the development of silvicultural prescriptions designed to increase tree species diversity.

2. Materials and methods

2.1. Study site

Our experimental sites were located in two adjacent northern hardwood stands in Emmet County, Michigan, USA (N45.574624–W85.074373). The stands feature post-glacial moraine topography and a mesic, rich to very rich habitat type (AFOca) (Burger and Kotar, 2003). Both stands were dominated by sugar maple (*Acer saccharum* (Marsh.) with white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), paper birch (*Betula papyrifera* (Marsh.)), black cherry (*Prunus serotina* (Ehrh.)), and American beech (*Fagus grandifolia* (Ehrh.)) as minor components of the overstories. In total, 45 harvest gaps ranging in size from 107 to 3234 m² and four unharvested areas were selected from the two stands (stand 1–40 harvest gaps + four unharvested areas; stand 2 – five harvest gaps). At least 50 m of unharvested forest separated harvest gaps from one another. Logging slash was removed from the interior of each gap and scattered along the borders.

2.2. Experiment one

The goal of this experiment was to identify the effects of light availability, non-tree vegetation, and deer herbivory on seedling survival. Beginning in the spring of 2011, we located main plots (13 × 13 m) in the center of each harvest gap and four unharvested areas. All existing advanced regeneration (seedlings and saplings) was then removed with a brush saw from each main plot. Main plots were then either fenced to exclude deer (30) or left unfenced (15). To ensure our fencing/non-fencing treatments were evenly distributed across the full range of gap sizes, an equal number of fenced and unfenced plots were chosen within four gap size categories; unharvested (0 m diameter), single-tree gaps (<23 m diameter), large group gaps (24–50 m diameter), and patch cut gaps (PC) (>50 m diameter). Gap size was determined by measuring the distance between boles of gap edge trees (Runkle, 1981). Four subplots (4 m²) were established within each main plot. Each subplot was randomly assigned one of four treatments: control, surface scarification, non-tree vegetation (forb, graminoids, ferns, shrubs) control, and surface scarification with vegetation control. Scarification was conducted in late-May and was accomplished by raking away the litter layer to create a bare mineral soil/humus seedbed. Vegetation removal was accomplished by clipping all non-tree vegetation to the ground once per month throughout the growing season. After scarification, 500 cold-stratified seeds each of eastern hemlock (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan), yellow birch (Pennsylvania source, Sheffield's seeds, Locke, New York), and paper birch (Michigan source, Sheffield's seeds Locke, New York) were sown in late-May in each subplot. These species were chosen due to their declining status in northern temperate forests, their rareness in the overstory at our site (seed dispersal control), and for the variation that exists in their seed weight and shade tolerance (Table 1). Prior to sowing, we conducted germination tests on each species to ensure seed viability. Despite yellow birch demonstrating adequate germination in the test, poor germination was observed in the field, prompting us to remove yellow birch results from this report.

For each subplot, we assessed non-tree vegetation cover and height, light availability above non-tree vegetation, and light availability at the forest floor (beneath non-tree vegetation). Non-tree

Table 1
Average seed weight of a cleaned seed and shade tolerance rating for each investigated species.

Species	Seed size (Mg)	Shade tolerance
Hemlock	2.43	4.83
Paper birch	0.33	1.54
Yellow birch	1.01	3.17
White pine	17.24	3.21

Note: Seed weight information obtained from Bonner and Karrfalt (2008), while shade tolerance is based on the continuous index of Niinemets and Valladares (2006).

vegetation density was determined by visually estimating subplot coverage to the nearest five percent (looking down) and by measuring its height (cm) at nine pre-determined locations in September annually. Canopy openness, total light availability, and diffuse light availability were estimated from analyses of hemispherical photographs taken in July 2011 at a height of 1.5 m (which was above the non-tree vegetation layer) using Gap Light Analyzer v 2.0 (Frazer et al., 1999) with an automatic threshold value determined for each photo from Sidelook v. 1.1.01 (Nobis and Hunziker, 2005). Diffuse light was ultimately chosen as our light availability metric, as it consistently explained higher amounts of variation in preliminary models of seedling germination and survival compared to total light or canopy openness. To quantify the impact of competing non-tree vegetation on light availability to developing seedlings, we estimated the light environment at 1 cm height (below non-tree competing vegetation) relative to the light environment at 1.5 m height (above competing vegetation in mid-July 2012) as diffuse non-interceptance (DIFN) with an LAI 2000 plant canopy analyzer (LI-COR Incorporated, Lincoln, Nebraska). This value as a proportion of non-intercepted diffuse light was then multiplied by the diffuse light value (as a proportion of open sky light reaching 1.5 m height) obtained with canopy photos to estimate light availability to seedlings established on the forest floor (i.e. 1 cm height). Each seedling was given a colored tag denoting its cohort year at the time of its germination. Seedling survivorship for sown species was then monitored within subplots at the end of September for three years.

2.3. Experiment two

The goals of this experiment were to (a) acquire higher resolution information than in Experiment One on how light, substrate availability, and non-tree vegetation affect the germination and survival via more frequent censusing, and (b) assess the effects of these factors on a greater number of species than those that successfully germinated in Experiment One (i.e. paper birch and eastern hemlock). In spring 2012, we established four additional subplots adjacent to the main plot in 13 of the 40 harvest gaps and two understory locations. Gaps were selected from gap size strata in order to assure we captured the entire range of gap sizes. Subplots were also established in five additional single-tree gaps, located in an adjacent recently harvested stand (summer 2011), as a lack of available gap space prevented us from locating subplots outside of the main plot in the single-tree gaps used in Experiment One. Each of the four new subplots were randomly assigned one of the treatment options described above in Experiment One. After scarification, 500 cold-stratified seeds of eastern hemlock (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan), yellow birch (Pennsylvania source, Sheffield's seeds, Locke, New York), paper birch (Michigan source, Sheffield's seeds Locke, New York), and white pine (Michigan source, Michigan Department of Natural Resources, Wyman Nursery, Manistique Michigan) were spread evenly throughout each subplot. Due to a shortage in seed, white

pine was only added to subplots in 10 of the 18 harvest gaps and two understory locations.

In each subplot in each location, we assessed non-tree vegetation cover and height, light availability above non-tree vegetation, and light availability below non-tree vegetation using the same protocol described in Experiment One. Germination was surveyed within each subplot on a bi-weekly basis from early-May through September. We increased the sampling intensity in this experiment to get a more accurate measurement of germination and early survival, as high seedling mortality was observed in Experiment One prior to our lone September census. A seed was considered successfully germinated and established once its first true leaves expanded. Each established seedling was then tagged and monitored for survival over the next two years.

2.4. Statistical analysis

For statistical analysis, we kept the results of each experiment separate. This was done to exclude potential confounding factors including differences in cohort age, sampling intensity and variation in climate between years. As such, we used the cohort from Experiment One (less intense sampling, smaller species pool, but longer duration) to compare third year survival, while the cohort established in Experiment Two (greater sampling intensity and larger species pool) was used to compare germination, first year survival, and second year survival of individual species. We examined the effects of scarified/unscarified, light availability, species, and their interactions on seed germination for each of the four species (Experiment Two) with Generalized Linear Mixed Models (GLMM) assuming a Poisson distribution with a logarithmic link function. This method was adopted because our data were heavily right skewed due to the large number of plots with few or no germinants. Clipping was not considered as a factor for germination, as the competing non-tree vegetation was already altered in subplots receiving scarification treatments.

To examine seedling first, second, and third year survival we used Generalized Logistic Mixed Models assuming a binomial distribution. For first and second year survival of each of the four species, we considered the effects of clipping/unclipped, light availability, species, and their interactions. Fencing was not included as a factor at these intervals because seedling establishment and second year survival were only evaluated in unfenced subplots (Experiment Two). Fencing was, however, considered along with each previously mentioned factor in third year survival of paper birch and hemlock, as seedling survivorship was evaluated in subplots which had been either fenced or left unfenced (Experiment One).

Prior to model construction we tested for co-linearity between the predictors with Pearson's correlations. All Pearson's correlation coefficients were <0.7 indicating that co-linearity would not have severe effects on model estimation and prediction, thus justifying our co-consideration of all predictors in modeling (Dormann et al., 2013). Model selection was accomplished through backwards elimination. If the results of our modeling produced an interaction term exceeding the suggested threshold for pooling variances ($p > 0.25$, Bancroft, 1964), we eliminated the highest order interaction term with the highest P value and re-ran the model. This protocol was repeated until all interactions fell below the pooling threshold. Main effects and interactions $p < 0.05$ were considered significant. Significant species interactions were investigated by examining the response of each individual species to the significant interacting factor. Once we arrived at a final model, we checked the model for dispersion of the distribution, goodness of fit, and the existence of potential outliers. Model dispersion was estimated by calculating an over-dispersion factor ($\hat{c}$ = chi-square/df). Models whose dispersion factors exceeded

one were considered over-dispersed. In such cases, parameter estimates were obtained using a *quasi-likelihood* approach which inflated the standard errors of each factor estimate by $\sqrt{\hat{c}}$. The model was then re-run and checked for significance. Model fit and potential outlier detection was accomplished by examining plots of studentized deviance residuals. Model fit was evaluated by visually inspecting how evenly the residuals were distributed around zero. Points on the plot exceeding two standard deviations of the mean were identified as potential outliers. To evaluate the influence of such points, we used Cook's distance statistic. Distance statistics exceeding one were identified as potentially having strong leverage effects on the model. To investigate these effects, we removed the potential outlier from the data set and re-ran the model. If all parameters in the model remained significant, the potential outlier was kept as part of the data set. However, if changes in parameter significance occurred without the outlier, the point was then removed (Ramsey and Schafer, 1997). All analyses were performed in JMP 9.0 (SAS Institute, Cary, NC).

3. Results

3.1. Germination

Scarification dramatically increased bare mineral soil/humus availability compared to unscarified plots (Table 2) and had strong

Table 2
Mean percent cover of mineral soil/humus, hardwood litter, and non-tree vegetation (shrubs, forbs, ferns, graminoids) in scarified and unscarified subplots at the time of sowing.

Treatment	Mineral soil/humus (mean% cover)	Hardwood litter (mean% cover)	Non-tree vegetation (mean% cover)
Scarified	90	5	5
Unscarified	5	55	40

Table 3
Results of a generalized linear mixed model for the effects of scarification, light, species, and their interactions on germination for hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three way interactions in the original model. All interactions with Prob ChiSq > 0.25 were pooled with the error term and the models rerun. Effects and interactions with Prob ChiSq < 0.05 were considered significant.

	Factor	L-R ChiSquare	Prob > ChiSq
Germination	Scarification	37.91	<.0001
	Species	3.42	0.1304
	Scarification × species	11.05	0.0115
	Light	13.11	0.0003
	Species × light	10.98	0.0118
	R^2 = .43		

overall effects on germination, but significant species and scarification interactions indicate that species responded differently to scarification (Table 3). Smaller seeded hemlock, paper birch, and yellow birch (Table 1) were, on average, 12, 17, and 95 times more abundant in scarified plots compared to unscarified plots (Table 4). In contrast, white pine, the largest seeded species (Table 1), which had lower overall germination than the other species, was unaffected by scarification (Table 4). Light availability, which increased along with harvest gap size, also affected germination, but a significant interaction with species indicated that species also responded differently to light (Fig. 1) (Tables 3 and 5). Shade tolerant hemlock and shade intolerant paper birch both germinated at greater densities in lower light environments, while both mid-tolerant species, white pine and yellow birch, were unaffected by light (Fig. 1).

3.2. Seedling survival

First and second year survival were strongly affected by the main effects of species and light availability and modestly affected by their interaction (Table 6). With the exception of white pine, all species' first year survival increased with light; however, the strength of response varied among species, with hemlock showing the most dramatic increase in survival with increased light (Fig. 2). Similar increases in second year survival with light were observed for hemlock and paper birch, but white pine and yellow birch second year survival did not respond significantly to light (Fig. 3). In the third year, seedling survival was most strongly influenced by clipping, light, and species (only hemlock and paper birch tested) (Table 7). Clipping (Table 8) and light (data not shown) both had positive effects on each species (Table 7); however, only the survival of paper birch was significantly improved by clipping (Table 8). In addition, the effect of clipping was independent of light availability, indicating that clipping was equally effective across the range of gap sizes. Overall, paper birch exhibited higher third year survivorship (65%) compared to hemlock (21%). Clipping did not affect first or second year survival and fencing (deer exclusion) was not a significant factor in establishment or survival in any year for any species (data not shown).

3.3. Temporal changes in seedling density in harvest gaps

Across gap sizes, seedling density in scarified subplots was a function of germination and subsequent survival. In integrating these effects, we found that the optimal gap size for maximizing seedling density changed over time for most species. Maximum seedling density for white pine and hemlock, for example, shifted from unharvested areas where they germinated best (Fig. 4) to higher light environments where they survived better (Fig. 4). Paper birch followed a similar pattern, as it germinated best in single-tree gaps but survived best in larger group harvest gaps after

Table 4
Observed germination response of paper birch, yellow birch, hemlock, and white pine in scarified and unscarified subplots.

Species	Treatment	Sub-plots	Mean seedlings/4 m²	Median	Range	SD
Paper birch	Scarified***	40	17.15	7.5	0–128	24.97
Yellow birch	Scarified***	40	9.53	1	0–113	20.38
Hemlock	Scarified***	40	10.98	2	0–59	16.02
White pine	Scarified	24	2.04	1	0–13	2.84
Paper birch	Unscarified	40	0.98	0	0–16	2.65
Yellow birch	Unscarified	40	0.1	0	0–1	0.3
Hemlock	Unscarified	40	0.88	0	0–18	2.93
White pine	Unscarified	24	2	1	0–8	2.19

Note: White pine was seeded in fewer subplots due to seed shortages.
*** Represent statistically significant differences (Prob > |Z| < 0.0001, Wilcoxon/Kruskal–Wallis test).
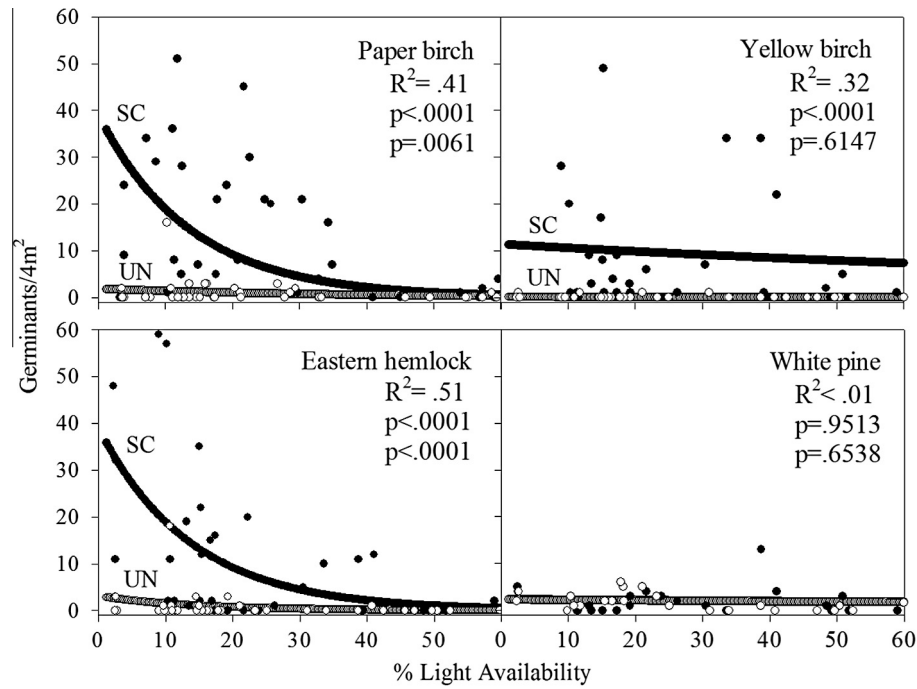
Fig. 1. The effects of scarification (SC) and light on paper birch, yellow birch, eastern hemlock, and white pine germination. Black circles represent germination in scarified plots, while white circles reflect germination in unscarified plots. R^2 applies to the whole model including the main effects of scarification and light availability. Partial P values are displayed for scarification and light in that order.

Table 5
Summary of environmental conditions across different gap size classes. With the exception of the first row, values represent mean values.

Variable	Understory (0 m dia)	Single tree (<23 m dia)	Large group (24–50 m dia)	Patch cut (>50 m dia)
Gaps/understory (n = 49)	4	13	24	8
Gap light (%)	4.2	9.2	26.4	52.1
Non-tree vegetation cover (%)	10	12	66	76
Non-tree vegetation height (cm)	3	4	27	44
Rubus spp. cover (%)	0	1	15	50
Forest floor light (%)	4.0	8.8	16.3	20.3

Table 6
Results of a generalized logistic mixed model for the effects of clipping, light, species, and their interactions on first year survival and second year survival for hemlock, yellow birch, paper birch, and white pine. Each combination of factors was considered up to three-way interactions in the original model. All interactions with Prob ChiSq > 0.25 were pooled with the error term and the models rerun. Effects and interactions with Prob ChiSq < 0.05 were considered significant.

	Factor	L-R ChiSquare	Prob > ChiSq
Survival (first year)	Species	92.01	<.0001
	Light	35.94	<.0001
	Species × light	12.5	0.0059
	R^2 = .44		
Survival (second year)	Species	78.9	<.0001
	Light	22.43	<.0001
	Species × light	10.19	0.017
	R^2 = .37		

three years (Fig. 4). In contrast to these species, yellow birch showed no change in environmental preference, as it germinated and survived at its greatest density in larger group harvest gaps (Fig. 4).

4. Discussion

4.1. Germination

Since the seed to seedling transition is one of the earliest steps in the natural regeneration process, factors affecting germination have the potential to strongly influence forest stand dynamics. Small-seeded species (yellow birch, paper birch, and hemlock) germinants were overwhelmingly more abundant in scarified compared to unscarified subplots, demonstrating the strong influence of bare mineral soil/humus on seedling layer composition. These results support our initial hypothesis of substrate limitation for smaller seeded species, and are consistent with germination patterns found in other forest types (Valkonen and Maguire, 2005), seedling substrate associations found in northern hardwood forests (Godman and Krefting, 1960; Caspersen and Saprunoff, 2005;Bolton and D'Amato, 2011; Bèland and Chicoine, 2013), and post scarification seedling layer composition from other forest types (Raymond et al., 2003; Lorenzetti et al., 2008; Beguin et al., 2009; Prèvost et al., 2010). Collectively, these findings suggest that substrate-related germination failures are likely contributing to the scarcity of smaller seeded species seedlings in mesic northern temperate forests (Neuendorff et al., 2007; Matonis et al., 2011).
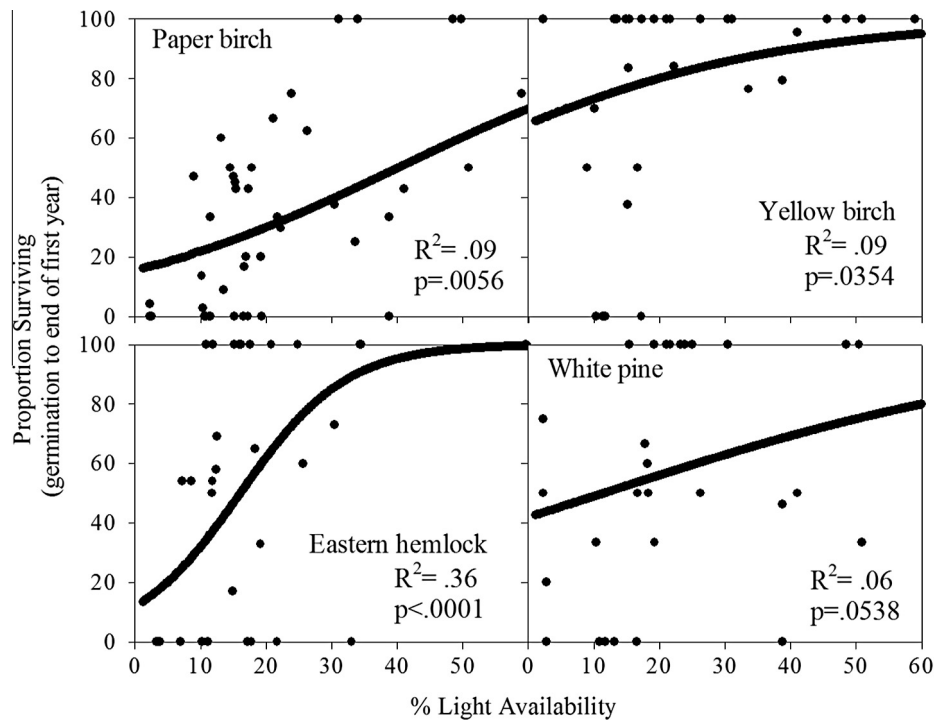
Fig. 2. The effect of light availability on paper birch, yellow birch, eastern hemlock, and white pine first year survival. R^2 and partial P values represent the effect of light on first year survival.
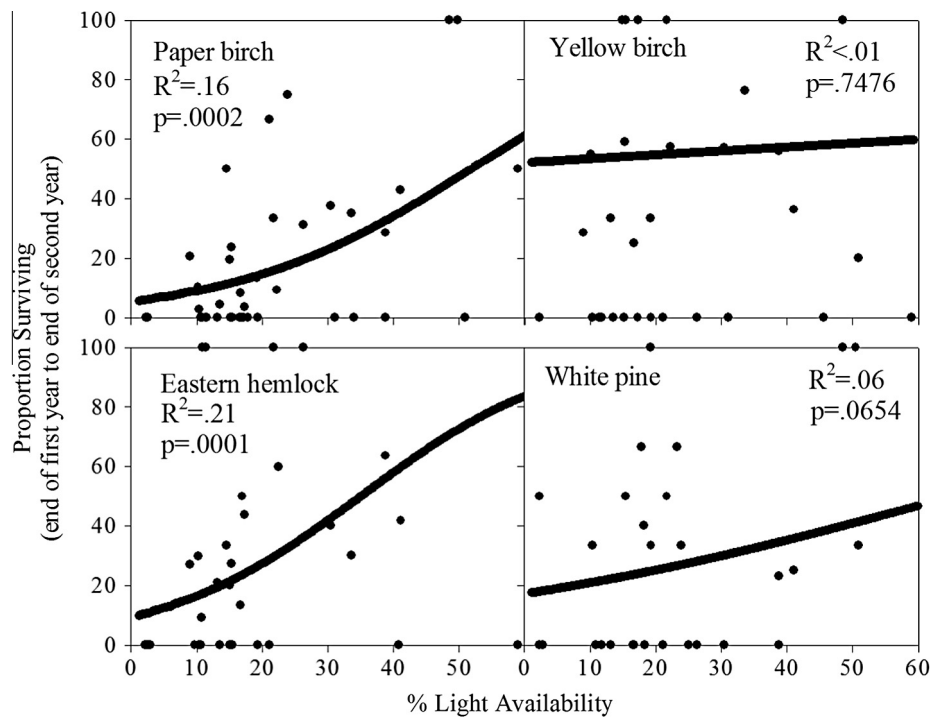
Fig. 3. The effect of light availability on paper birch, yellow birch, eastern hemlock, and white pine seedling second year survival. R^2 and partial P values represent the effect of light on seedling survival.

However, it should also be noted that a reduction in local seed sources may also factor into natural regeneration failures, and were not considered in this seed addition study.

In contrast to the germination response of smaller seeded species, white pine was unaffected by the scarification treatment. While limited to just one species, this finding supports our non-substrate limitation hypothesis for larger-seeded species and the

findings of Cornett et al. (1998), who also found white pine emergence to be insensitive to forest floor disturbance, but differs with the findings of Raymond et al. (2003) who found white pine germination was improved by scarification.

There are several potential biological explanations for this discrepancy, though before any of these possibilities are considered, it should be noted that in this study white pine was seeded in

Table 7
Results of a generalized logistic mixed model for the effects of clipping, light, species, fencing, and their interactions on third year hemlock and paper birch survival. Each combination of factors was considered up to three-way interactions in the original model. All interactions with Prob ChiSq > 0.25 were pooled with the error term and the models rerun. Effects and interactions with Prob ChiSq < 0.05 were considered significant.

	Factor	L-R ChiSquare	Prob > ChiSq
Survival (third year)	Clipping	15.81	<.0001
	Light	17.76	<.0001
	Species	2.9	0.0886
	Clipping × species	4.24	0.0394
	R^2 = .40		

fewer harvest gaps than the other species, and also germinated at a lower density. Given this preface, one potential explanation for lower white pine germination may come from a difference in leaf litter depth between studies. The overstory at our site is dominated by sugar maple and other mesic hardwoods which produce relatively nutrient rich, quickly decomposing litter resulting in relatively thin litter layers (Melillo et al., 1982). In contrast, the dominant overstory species in Raymond et al. (2003) was white pine (38% volume) which produces a more recalcitrant litter layer (Melillo et al., 1982; Rustad and Cronan, 1988), and, thus, could be characterized by a thicker litter layer that may have imposed a larger impediment to white pine germination. Temperature differences may also have contributed to differences in litter layer depth, as Raymond et al. (2003) was conducted in a colder, subboreal climate which likely would have had slower decomposition rates than those which likely exist at our more temperate field site. Consequently, scarification may have had a larger effect on forest floor conditions at the site used by Raymond et al. (2003).

Another factor which may have minimized influence of scarification on white pine germination is seed predation. White pine seeds are a preferred food for small mammals (Abbott, 1961; Martell, 1979), and studies have demonstrated greater germination when seed predators are excluded (Cornett et al., 1998; Raymond et al., 2003). In this study, no attempts were made to exclude seed predators, and white pine germinant density was the lowest among our experimental species. Thus, we cannot eliminate the possibility that seed predation may have confounded positive scarification effects if there was greater seed loss to predators in scarified than unscarifed plots. This is plausible if seeds are more apparent in scarified than unscarified areas, but is contrary to the finding that a continuous non-tree vegetation layer, which scarification disrupts, encourages small mammal seed predation (Royo and Carson, 2008).
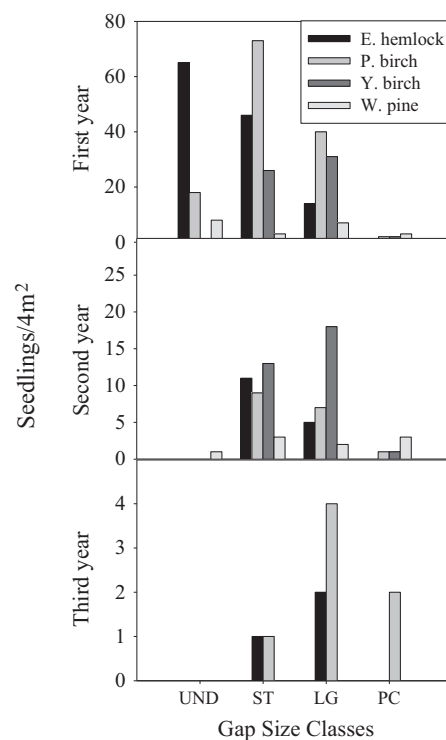
The presence of earthworms (Lumbricus spp.) may also have contributed to a thinner litter layer at our site. Several studies have reported a large decrease in litter layer depth in areas occupied by invasive earthworms (Hale et al., 2005; Frelich et al., 2006; Suárez et al., 2006). While no attempts were made to detect earthworms at our site, we do not believe that earthworms are having strong effects on litter layer depth, as each of our light seeded species germinated at significantly lower densities in unscarified plots.

Fig. 4. Average germination and number of second and third year surviving seedlings in unharvested areas (UND) (0 m diameter), single tree gaps (ST) (<23 m diameter), large group gaps (LG) (24–50 m diameter), and patch cut gaps (PC) (>50 m diameter). *Third year cohorts were only tracked for eastern hemlock and paper birch.

In addition to scarification, species responded differently to light availability. While the decline in hemlock germination in higher light environments was consistent with its reputation as a shade specialist, the preference for lower light environments by paper birch was unexpected given its collection of early successional life history traits (Burns and Honkala, 1990). Nevertheless, this finding is consistent with earlier studies which found greater hemlock and paper birch germination in shade (Hough, 1960; Goerlich and Nyland, 2000).

One potential explanation for this pattern may be related to microclimatic differences between lower light environments (unharvested/single-tree harvest gaps) and higher light environments (large group selection gaps/patch cuts), as lower light forest understories have lower temperature fluctuations and higher humidity compared to understories in higher light environments (Phillips and Shure, 1990; Strong et al., 1997). These climatic differences may have led to greater seed and/or germinating seedling desiccation in higher light environments than lower light environments. Germination substrate moisture may have been a particularly important factor in this study, as although hemlock and yellow birch prefer warm, moist conditions for germination and can germinate as late as July in the northern portion of their range

Table 8
The effect of clipping on paper birch and hemlock third year survival. SD = standard deviation.

Species	Cohort age	Treatment	Subplots	Mean (%)	Median	Range	SD
Paper birch	3	Clipped*	26	68	82	0–100	39
Paper birch	3	Unclipped	19	33	0	0–100	46
Hemlock	3	Clipped	32	27	6	0–100	37
Hemlock	3	Unclipped	28	15	0	0–100	32

* Represent statistically significant differences (Prob > |Z| = 0.05 Wilcoxon/Kruskal–Wallis test).

(Burns and Honkala, 1990; Goerlich and Nyland, 2000), their window for germinating in open, more drought susceptible locations may have been truncated given our May seed sowing. Consistent with our findings, Jordan and Sharpe (1967) witnessed little hemlock germination on south facing aspects and/or open canopy areas following a May seeding, and speculated that had they seeded just after snow-melt in late-March to early-April they might have increased germination in more exposed locations.

In contrast to hemlock and paper birch, light availability had no effect on white pine and yellow birch germination. As previously mentioned, seed predation may account for the overall low germination observed for white pine; however, the insignificant response of yellow birch to light availability is surprising considering that light has been shown to lessen the effect of a water-soluble germination inhibitor present on its seed-coat (Redmond and Robinson, 1954). Nevertheless, this finding is consistent with previous work which also found yellow birch germinant density did not increase with increasing light availability (Houle, 1992). While the exact mechanism remains unclear, the gentle decline in germination with increasing light availability does, however, suggest that moisture stress is likely a stronger constraint on yellow birch germination than its seed coat germination inhibitor. The high overall variability in its germination also suggests that microenvironment differences between subplots may be highly influential, as germination tended to be higher in subplots where clay was a more prominent component of the soil (Personal observation). The importance of clay would also support the notion that soil moisture is critical for yellow birch germination reported by Godman and Krefting (1960).

While the limited range of species investigated in this study restricts our ability to comment on general trends among species, these results do suggest that lower light availability (associated with single-tree gaps) is not a strong constraint on germination for this particular group of species. Thus, moving away from single-tree selection toward a natural disturbance based silvicultural system is unlikely to increase these species' initial representation in harvest gaps. This underscores the importance of considering factors that affect not just seedling survivorship, but also germination when natural regeneration is the goal.

4.2. Seedling survival

Within harvest gaps, increasing light availability (larger harvest gaps) had a positive influence on first year survival of each species except white pine. Higher survival was also observed during the second growing season in higher light environments for hemlock and paper birch. This finding is unsurprising considering that previous work, including on some of the same species, has shown light to be positively related to seedling survival over the range we examined (Walters and Reich, 2000). It also supports the notion that larger canopy harvest gaps provide important regeneration opportunities for less tolerant species in forest systems where large scale disturbances are uncommon (Runkle, 1982; McCarthy, 2001). In contrast to the light-dependent survival response of shade intolerant paper birch, the combination of a mid-tolerance of shade and a short survival census period (two years) may account for the unresponsiveness of yellow birch and white pine survival to light (Burns and Honkala, 1990; Kobe et al., 1995). Nevertheless hemlock, a species of higher shade tolerance, responded positively to increasing light availability, suggesting that another unmeasured factor(s) may be obscuring the influence of light availability on the survival of white pine and yellow birch.

Consistent with our expectations, seedlings that established in unclipped subplots were quickly overtopped by non-tree vegetation in larger canopy openings, which reduced light environments and survival by the third year when compared to seedlings established in clipped subplots. While limited to just two species (hemlock and paper birch), and only statistically significant for paper birch, this finding suggests that competition from non-tree vegetation can influence seeding layer composition even at the earliest stages of seedling development. In our opinion, the insignificant response of yellow birch, white pine, and hemlock to clipping was likely due to their greater shade tolerance and the short duration of this experiment, rather than an indicator of the potential influence of non-tree vegetation over seedling layer composition, as previous work has shown non-tree vegetation to have negative effects on each species' survival (George and Bazzaz, 1999; Saunders and Puettmann, 1999; Gasser et al., 2010; Kern et al., 2012).

Browsing was not shown to be a significant factor affecting seedling survival for any species. While this finding runs contrary to our initial hypothesis, we urge caution in its interpretation, as severe browsing effects have been observed on larger seedlings planted in neighboring (<2 m away) subplots (unpublished data). These observations suggest that slash is having little to no influence on browse pressure since larger, planted seedlings are being selectively browsed. We attribute the insignificance of browsing to the availability of more palatable food that is easier to find than our smaller seedlings. Consequently, we do not believe the results of this study should be taken as evidence that deer are an inconsequential factor influencing natural regeneration in northern temperate forests, as our separate observations and the findings of several other investigators support the opposite (Millington et al., 2010; Witt and Webster, 2010; Matonis et al., 2011; Kern et al., 2012).

5. Conclusion and management recommendations

The collective findings from the two manipulative experiments comprising this study provide several important insights for the development of natural disturbance-patterned harvest regimes in managed northern temperate forests. Central among these is the importance of bare mineral soil/humus for smaller-seeded species germination. While we cannot predict whether seedlings established in scarified plots will successfully pass through the series of filters that exist between seedling establishment and canopy ascension, scarification at least gives smaller-seeded species the opportunity to complete this transition by allowing them to germinate. Without the opportunity to bypass this critical early filter, species traits that may otherwise facilitate gap capture including shade tolerance, browse tolerance, drought tolerance, and competitive ability would be rendered effectively moot. Thus, our findings support the notion put forth by Bolton and D'Amato (2011) suggesting that germination substrate may override the influence of harvest gap size for smaller-seeded species, and demonstrate the importance of incorporating surface disturbance into silvicultural prescriptions (e.g., harvesting in the absence of snow or scarification). However, it should be emphasized again that seed supply issues may override the influence of substrate under natural regeneration conditions.

Variation in harvest gap size also affected seedling demographics. Although no harvest gap size provided the optimal environment for seed germination, large group harvest gaps supported the highest density of seedlings for all species except white pine, which germinated at low initial densities. Taken together, our results suggest that large group selection harvest gaps may represent the best management option for establishing a new seedling cohort for this particular group of species, as they provide generally favorable environments for seed germination and encourage greater seedling establishment and survival. This pattern also provides initial support for adopting an expanding gap harvesting system where harvest gaps are expanded once advanced regeneration

has been achieved (Raymond et al., 2009). Nevertheless, our results also indicate that non-tree vegetation had a negative effect on seedling survival. As such, management efforts may need to consider vegetation control options if they are attempting to regenerate this collection of species in harvest gaps on high quality sites.

Acknowledgements

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