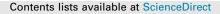
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Scarification and gap size have interacting effects on northern temperate seedling establishment



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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 m²) 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 largestseeded 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).



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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 m² 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.

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