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Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings?

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A B S T R A C T

Innovative forestry practices that use natural disturbance and stand developmental processes as models to increase forest complexity are now being considered as a way to conserve biodiversity while managing for a range of objectives. We evaluated the influence of harvest-created gap size (6, 10, 20, 30, and 46 m diameter gaps and uncut references) over 12 growing seasons on planted tree seedling growth and survival for four tree species that tend to experience poor recruitment in both managed and unmanaged northern hardwood forests in eastern North America. We expected, based on silvics, that the three mid-tolerant species (yellow birch [*Betula alleghaniensis*], red oak [*Quercus rubra*], and white pine [*Pinus strobus*]) would perform best in intermediate-sized gaps, and the one shade tolerant species (hemlock [*Tsuga canadensis*]) would perform best in small gaps. However, all four of the species grew taller with increasing gap size, while survival was highest in intermediate gap sizes. Although gap size had statistically significant effects on growth and survival, the magnitude of the effects were modest. With the exception of a small portion of white pine individuals (35% of survivors were >150 cm tall), trees were short (<1 m) and few survived (<30%) 12 years after planting. Evidence from deer exclosures and individual gaps with high shrub (*Rubus idaeus*) densities suggest that browsing and shrub competition resulted in poor tree growth and survival, and may have constrained the magnitude of many potential tree seedling responses to gap size. Our study highlights the management challenges of using gap size as a tool to influence future forest composition in forests with overly abundant deer and pervasive shrub layers and underscores the importance of silvicultural prescriptions that include measures for reducing these impacts.

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1. Introduction

Innovative forestry practices that use natural disturbance and stand developmental processes as models to increase forest complexity are now being considered as a way to conserve biodiversity while managing for a range of objectives (Swanson and Franklin, 1992; Franklin et al., 2007). For instance, harvest-created canopy gaps within group or patch selection systems create spatial heterogeneity within closed forests and can be manipulated in size and frequency to correspond to regional, small-scale natural disturbance regimes (Coates and Burton, 1997; Seymour et al., 2002). Detailed information on silvicultural components such as gap size are needed to provide flexibility in future management options (Smith et al., 1997).

Manipulating gap size in closed forests affects the distribution of understory resources and microsites and, thus in theory, favors species of varying shade tolerance. This idea is a basic premise behind alternate forms of the selection system (Hawley, 1937). The small gaps that result from single-tree selection perpetuate shade tolerant species (e.g., Schwartz et al., 2005), while the larger gaps created in group selection regenerate trees less tolerant to shade (e.g., Leak and Filip, 1977). This idea is also supported by an underlying concept in forest ecology, the Gap Partitioning Hypothesis (GPH) (Ricklefs, 1977; Denslow, 1980). According to this theory, shade intolerant species perform best in large gap sizes by outcompeting tolerant species there. Large gaps increase soil temperature and light availability, while in small gaps, microclimate and light availability are moderated by overstory trees. Small gaps and intact forest provide conditions more conducive for germination and growth of shade tolerant species than for shade intolerant species. Even within a gap, variability in the microenvironment can favor species of different shade tolerances, where less tolerant species perform better than shade tolerant species in gap centers than in

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gap edges. The Gap Partitioning Hypothesis suggests that saplings with contrasting life history strategies coexist along resource gradients between closed forest and open gap centers; thus, in a forested landscape, larger canopy gaps increase tree diversity. Ideally, a forest manager could prescribe, based on silvics, gap sizes targeted towards life history traits of desired species and thereby influence future forest composition (Messier et al., 1999).

Although shade tolerance traits may make trees more suitable for one gap size over another, other factors can override canopy gap effects on understory tree regeneration. A review by Brokaw and Busing (2000) found that recruitment limitation, resilient pre-gap vegetation, and broad species traits undermine gap partitioning. Deer browsing could negate the positive effects of increased light within canopy gaps as well. White-tailed deer (*Odocoileus virginianus*) are regarded as keystone herbivores in forest ecosystems affecting composition, succession, and function (see reviews Russell et al., 2001; Cote et al., 2004), and some research has shown that tree growth and survival, based on shade tolerance rankings, were obscured across light gradients when deer were present (Tripler et al., 2005; Krueger et al., 2009). Moreover, dense forest understories diminish resource availability to tree seedlings (Beckage and Clark, 2003). In a recent review, Royo and Carson (2006) reported that formation of recalcitrant understory layers influence forest dynamics worldwide. Montgomery et al. (2010) found that shrub layers differentially influenced planted tree seedling growth and survival in closed canopy versus gap conditions because of a mix of competitive and facilitative impacts involving aboveground and belowground resources. The efficacy of using harvest-created gaps as a tool for tree regeneration is unclear when other factors, such as deer browsing and dense shrub layers, are present.

In this study, our main objective was to study the efficacy of different harvest gap sizes at regenerating four targeted tree species that have declined in abundance in managed northern temperate forests (Goodburn and Lorimer, 1999; Crow et al., 2002). We did this by establishing harvest-created, experimental gaps that differed in area by two orders of magnitude and by measuring the growth and survival of planted trees over a 12-year period. Secondarily, we tested the effect of high deer and shrub populations on tree growth and survival within the experimental gaps. Deer browsing was quantified with deer exclosure treatments and shrub competition was quantified from data collected in a companion study measuring ground-layer composition at the same site (Kern, 2011). This design allowed us to test several hypotheses. We hypothesized, based on silvics, that our three mid tolerant study species (yellow birch [*Betula alleghaniensis*], red oak [*Quercus rubra*], and white pine [*Pinus strobus*]) would perform best in intermediate gaps and more central within-gap locations, while one shade tolerant study species (hemlock [*Tsuga canadensis*]) would perform best in small gaps and gap edge locations. In addition, we expected tree growth and survival to increase in the absence of deer and in low densities of shrubs.

2. Methods

2.1. Study site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located in the Chequamegon-Nicolet National Forest in northern Wisconsin, USA (T40°N R12E). The natural disturbance regime of northern hardwood forests is primarily characterized by canopy gap disturbances (Frelich and Lorimer, 1991). Similar to many forests in the region, the study ecosystem regenerated after exploitive timber harvesting during the early twentieth century. Before study installation in 1994, the forest had had no recent management and was estimated to be 60 years old. The topography of the study areas is a hummocky kame-kettle complex with some cradles and knolls created from tip-up mounds (resulting from past canopy tree blowdowns). Soils are Stambaugh silt loam loess, overlying stratified sand and gravel. The habitat type is considered nutrient rich, mesic and well suited for sugar maple growth and classified as *Acer–Tsuga/Dryopteris* (ATD) according to a regional habitat type classification system (Kotar et al., 2002). Sugar maple (*Acer saccharum*) dominates the site but 12 other species of trees are present.

2.2. Study species

Four species, hemlock, white pine, yellow birch, and red oak, were selected for study. Regionally, these tree species have declined in abundance over the past century (Schulte et al., 2007). In this forest type, common management practices, such as single-tree selection, have facilitated regeneration of shade tolerant sugar maple (*A. saccharum*) at the expense of these study species (Schwartz et al., 2005), when compared to tree composition of old-growth forests (Goodburn and Lorimer, 1999; Crow et al., 2002). The small, dispersed openings created from single-tree cutting do not emulate the range of variability in natural disturbance such that canopy openings are too small and ephemeral in managed forests for mid-tolerant species' survival (Webster and Jensen, 2007). Hemlock, a shade-tolerant species, has declined in abundance as well, due to browsing by abundant deer populations and limited light for regeneration (Rooney et al., 2000; Witt and Webster, 2010). Moreover, microsite availability for yellow birch and hemlock establishment is often limited in managed stands, further complicating their regeneration (Tubbs, 1969; Rooney et al., 2000; Marx and Walters, 2008). Consequently, a better understanding of these species' growth and survival as related to potential management tools, such as gap size, are important to understanding how to perpetuate these species.

2.3. Study design

2.3.1. Treatments

The experimental treatment was harvest gap size, which had six levels: 0 (reference area), 6, 10, 20, 30, and 46 m diameter gaps (Fig. 1). The gap size treatments were intended to represent the range of openings in selection cuttings, which are often described by gap diameter in Lake State silvicultural guides (e.g., Wisconsin Department of Natural Resources, 2008, chap. 40). The smallest gap size, 6 m, represented the crown width and removal of one mature tree and the 6 and 10 m represented the range of gap sizes in single-tree selection harvests typical in second-growth northern hardwood forests in the Lake States (Erdmann, 1986). The larger gap sizes represented group selection openings intended to regenerate less tolerant tree species, sizes often used in eastern northern hardwood forests (e.g., Leak and Filip, 1977) but largely untested in the Lake States region (but see Eyre and Zillgitt, 1953; Shields et al., 2007).

The gap size treatments were randomly assigned through two levels of randomization within the study site. Four relatively uniform blocks (16–24 ha) among seven were selected and subdivided into 0.4-ha sections. Within each block, each gap size treatment was randomly assigned to a 0.4-ha section thrice (three replicates of gap size per block). The resulting design consisted of 12 reference areas (0.4 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). Experimental gaps were created through dormant-season timber harvesting in 1994 (two blocks) and 1995 (two blocks). Openings were measured in 1997 and 2008 from gap center to dripline in cardinal and sub-cardinal directions (eight total radii). The 1997 measurements were used to