



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?

Christel C. Kern^{a,b,*}, Peter B. Reich^b, Rebecca A. Montgomery^b, Terry F. Strong^{a,1}

^a US Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA

^b Department of Forest Resources, University of Minnesota–Twin Cities, 1530 North Cleveland Avenue, Saint Paul, MN 55108, USA

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ABSTRACT

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 overstorey 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

* Corresponding author at: US Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA. Tel.: +1 218 326 7134; fax: +1 218 326 7123.

E-mail address: cckern@fs.fed.us (C.C. Kern).

¹ Retired.

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. Secondly, 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

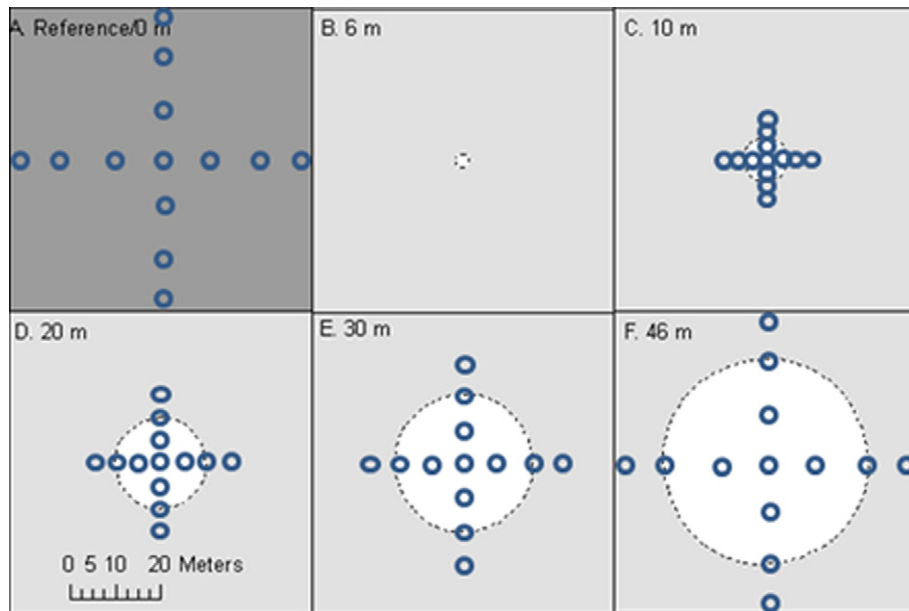


Fig. 1. Gap sizes and tree planting layout. Each panel represents a 0.4 ha square, the size of the reference area. (A) Uncut reference area (0.4 ha). (B–F) Experimental gaps embedded in a thinned forest matrix (gap diameters are labeled in each panel). Circles with dotted line perimeters represent ideal experimental gap driplines, but, in reality, opening shape, diameter, and proximity to planting locations varied. Circles with solid line perimeters represent approximate tree planting group (4 trees; 1 species⁻¹) locations. To aid interpretation, tree planting in the 6 m (B) was not illustrated but followed the same planting layout as the other gap sizes (center, mid center to edge, edge, and forest locations in four cardinal directions).

confirm gap size treatment levels and ranged from 9.9 to 1986 m² (gap diameter to tree height ratio 0.1–2.2). In 2008, the measurements determined gap opening status and denoted that most small gaps were closed and similar to the forest matrix conditions, while large gaps remained open.

In addition to gap creation, the four blocks were also thinned (except for the reference areas) in 1994–1995 following first harvest entry guidelines in Erdmann (1986), a Lake States management publication for converting even-aged northern hardwood forests to uneven-aged stand conditions. To improve residual stand vigor, this first thinning entry (an “improvement cut”) removes trees anticipated to die from self-thinning, disease, damage or that have minimal potential to gain economic value before the next harvest entry (approximately 20 years). The thinning reduced the forest matrix density by ~25% to a mean basal area of 23 m² ha⁻¹ (±1.8 SE).

2.3.2. Planting layout of the sample population

In May 1997, we planted containerized seedlings of yellow birch (average 25–30 cm tall) and hemlock (15–20 cm tall) and bare-root (3–0) red oak (25–35 cm tall) and white pine (15–30 cm tall). Seedlings were planted in groups of four individuals (one individual per species). Spacing between individuals within a group ranged from 0.5 to 2 m. One group was planted within 2 m of gap centers. Three groups were planted equidistantly along each of four transects that radiated in cardinal directions from gap centers to ~7 m into the adjacent forest (the “forest-gap transect”). In total, thirteen groups were planted in each experimental gap and reference area (Fig. 1).

2.3.3. Deer fence sub-design

Over the last century, the regional deer populations in northern Wisconsin varied between 5 and 12 deer km⁻², an elevated density from pre-settlement times (<4 deer km⁻²) (McCaffery, 1986; Alverson et al., 1988). To isolate the effect of the gaps from the effect of browsing, deer fences (exclosures) were installed on a subset of the experimental units (one reference area, 20 m gap and 46 m gap per block; 12 total exclosures) in 1997. Due to funding limitations, the

exclosures were maintained for only four years. The exclosures were constructed with 1-m tall rabbit guard fence along all four of the forest-gap transects of a gap or reference area. The resulting exclosures were shaped in similar fashion to a plus sign (+) with four segments 1.8-m wide extending in each cardinal direction from gap center to ~7 m into the adjacent forest. Although deer can jump over this height easily, it was expected that the combination of a 1-m height fence with a narrow opening (1.8-m wide) would reduce, but not eliminate deer entry. We chose this design to reduce costs and to deter deer from dwelling in the confined fenced-in areas.

2.4. Data collection

2.4.1. Growth and survival

We measured the growth and survival of planted trees in fall after the 1st, 2nd, 4th, and 12th growing seasons. Growth responses included total height in growing seasons 1, 2, 4, and 12; current height increment of the tree’s leader in growing seasons 1, 2, and 4; and diameter (at 15 cm aboveground) in growing season 12. Trees were considered dead when all leaves/needles were desiccated or missing. Lifespan was calculated in months and right-censored if the individual was still alive in growing season 12.

2.4.2. Browsing

To quantify browsing pressure on site, we created a binary variable indicating whether or not an individual was noted as “browsed” at the time of planted seedling growth measurements. Gap-level browse was calculated by dividing the number of trees browsed by the number of trees alive within a gap or reference area. Rigorous browsing data procedures were not an explicit part of the planted seedlings’ measurement protocol and, therefore, our analysis should be considered a low estimate of browsing pressure on the study site. In addition, we also gathered annual forest-wide estimates of deer density for the study duration from the Wisconsin Department of Natural Resources Deer Management Unit 39 (~1065 km² of deer habitat).

2.4.3. Shrub competition

Ground-layer vegetation was assessed within the study site to examine native plant community composition among gap sizes (Kern, 2011). Permanent sample plots (1 m²) were arrayed along the forest-gap transects. These plots were adjacent to, but did not include, the planted seedlings. Individual species abundance was visually assessed and placed into one of eight cover classes (0; 1 or 2 individuals and <1% cover; 2–20 individuals and <1% cover; >20 individuals and/or 1–5%; 5–25%; 26–50%; 51–75%; 76–100%). Field data were collected during mid-summer (late June–early August) over four survey periods: pre-harvest (1994 [two blocks]–1995 [two blocks]) and post harvest in 1997, 2000 (two blocks)–2001 (two blocks), and 2008. For the current study, we tested for effects of raspberry abundance on planted tree performance, since raspberry has been identified as a major competitor to northern hardwood tree regeneration in the Lake States region (Metzger and Tubbs, 1971) and it was one of the most abundant species in the ground and shrub layer vegetation.

2.5. Data analysis

2.5.1. Gap size and location

We used all gap size treatment levels as fixed effects. However, to isolate the effect of gap size, we subset the analysis to include only trees planted within reference areas and within opening driplines as measured in 1997. Means of experimental unit (i.e., an individual gap or reference area) were used in growth analyses. Because six gaps were not planted, 62 experimental units (gaps and reference areas) were used in analysis such that sample size was 12, 9, 8, 9, 12, and 12 experimental unit means in the 0, 6, 10, 20, 30, and 46 m gap size treatments, respectively.

We used 46 m gaps to examine the effects of within-gap location. The 46 m gaps were the largest gap size treatment and it was in those gaps that we expected to find the most dramatic responses from gap edges to center and from south to north edges. Means of planting location were treated as fixed effects and categorized by cardinal direction (N, E, S, W) and gap proximity (“Forest”, “Gap Edge”, “Mid Gap”, or “Gap Center”, which were 0–8 m into the adjacent forest matrix or 0–8 m, 8.1–16 m, and 16.1+ m into the gap opening, respectively). Because our site is located in northern latitudes, we expected greater growth in northern within-gap locations where light levels are greater than southern within-gap locations (Canham et al., 1990; Gray et al., 2002). Therefore, we further subset the within-gap analysis to north–south locations.

2.5.2. Statistical approach

The first step in analysis tested the growth and survival responses by species in a randomized complete block with subsampling. The design was split into two separate generalized linear mixed models: (1) among gap sizes (fixed effect) and (2) among locations within 46 m gaps (fixed effect). Gap size replicates were random subsamples within each block. Models of height over time were also analyzed with repeated measures using heterogeneous autoregressive-1 error structure. When gap size was significant, polynomial contrasts were used to test for linear, quadratic, and cubic trends across increasing gap size (0–46 m) by growing season. Analyses were conducted with the GLIMMIX Procedure in SAS (SAS Institute Inc., 2008) using the gamma distribution for height and initial height increment (except for hemlock which used the lognormal distribution), the lognormal distribution for diameter, and the negative binomial distribution for lifespan. Seedling survival was also tested with nonparametric estimates of survivor function with the product-limit (Kaplan–Meier) method. Log-rank tests were used to test for differences in survival curves by

gap size or location. Analyses were conducted with the LIFETEST Procedure in SAS (SAS Institute Inc., 2008).

As a second step, we tested for effects of browse on planted tree performance. To do this, tree growth and survival responses were subset to gap sizes with deer exclosures, i.e., the 0, 20, and 46 m gap sizes. Exclosure effects were evaluated on planted tree seedlings' growth and survival and gap-level browse as described in the first step of analysis but with the addition of a binary variable, the presence or absence of a deer exclosure.

Lastly, previous research on site showed that gap size and raspberry cover were similarly correlated to a major gradient of ordination analysis ($\tau = 0.48$ and $\tau = 0.64$, respectively) such that increasing gap size was associated with increasing raspberry cover (Kern, 2011). Based on this, we subset the data to isolate the effects of raspberry competition from gap size. Only plots located within opening driplines and within a reference area were used to calculate gap-level means of raspberry (*Rubus idaeus*) abundance in 1997, 2000–01, and 2008, which corresponds to growing seasons 1, 4, and 12 of the planted seedling measurements (no data collected for growing season 2). For growth and lifespan responses, we subset the data to the 46 m gaps and tested mean raspberry abundance effects by species and growing season. For survival analysis, we subset the data to 20–46 m gaps to capture a range of lifespans and categorized raspberry abundance to produce survival curves. We created raspberry abundance categories by (1) relativizing raspberry cover to the maximum cover value in each growing season to detrend temporal changes (gap replicate raspberry cover mean/current growing season's maximum raspberry cover mean) and then (2) classing it into one of three cover codes (0–25%, 25–60%, and 60–100% relative raspberry cover), roughly representing low, intermediate, and high levels of raspberry cover.

3. Results

3.1. Survival

Gap size influenced survival functions over time (Fig. 2). Overall, the probability of survival was higher in gaps than in reference conditions (Pair-wise comparisons, $P < 0.05$) for red oak and white pine. In contrast, probability of survival for hemlock was initially highest in reference areas (Pair-wise comparisons, $P < 0.01$), but by growing season 12 was highest in 10 m gaps. In general, after 12 growing seasons, overall planted tree survival was <30% (Fig. 3a). Mean lifespan was approximately three years (34.4 ± 2.4 , 33.7 ± 3.7 , 39.1 ± 3.5 , and 35.9 ± 6.3 months for yellow birch, red oak, white pine, and red oak, respectively). Tree longevity was related to gap sizes usually with linear trends, as trees lived longer in larger gaps (Table 1). However, pair-wise comparison suggested more complicated patterns (Fig. 3b). For example, lifespan was greater in 10 m than references for red oak and white pine, but not for hemlock whose lifespan was similar between 10 m and references.

Surprisingly, small effects of within-gap location were seen. Probability of survival ($\chi^2 \leq 8.22$, $P \geq 0.08$) and lifespan (Table 2) were similar from north to south within 46 m gaps by species. Further, among species, survival functions ($\chi^2 \leq 5.61$, $P \geq 0.13$) and lifespan ($F = 0.87$, $P = 0.46$) were similar from north to south within 46 m gaps.

3.2. Growth

Most trees grew taller with time, as expected, although growing season 12 heights were similar to growing season 4 heights for yellow birch and hemlock (Fig. 4). Within growing seasons, taller trees were typically associated with larger gaps (linear trend of height with gap size) in the early growing seasons (1–4) for all species

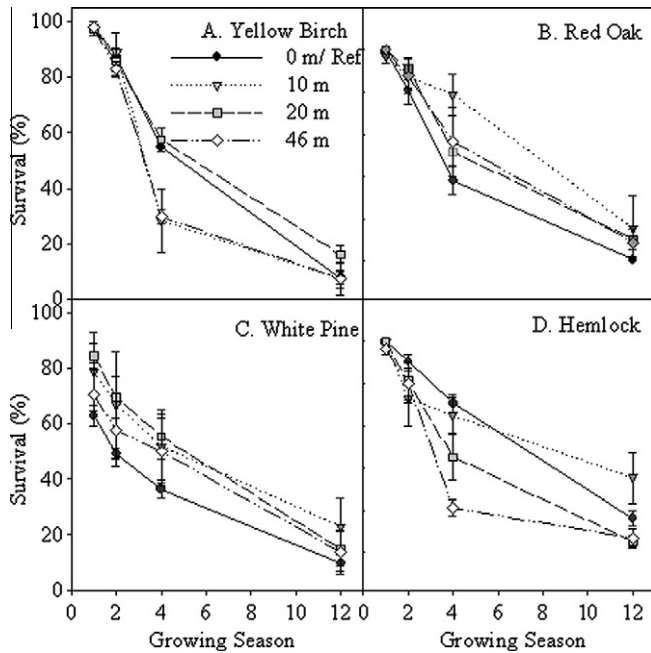


Fig. 2. Planted tree species' survival by gap size treatment in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Log-rank test of equality over strata (gap size) results are noted for each species. For ease of interpretation, the 6 and 30 m survival curves are not shown. (Growing season 12 survival is also illustrated in Fig. 3a for all gap sizes).

(Table 1). By growing season 12, white pine was the tallest of the planted species, with an average height of 181.7 ± 49.1 cm in the largest gap size (Fig. 3c). Within 46 m gaps, yellow birch and white pine were taller in southern mid-gap locations than southern edge locations (Fig. 5, Table 2).

In addition, initial height increment (growing seasons 1–4) increased with gap size (Table 1, Fig. 3d) with yellow birch having the greatest initial height increment, 13.9 ± 1.0 cm y^{-1} , of the planted species. Diameter in the 12th growing season was similar among the gap sizes for yellow birch, red oak, and hemlock. White pine diameter increased with increasing gap size (Table 1, Fig. 3e) and had the largest overall mean diameter (28.2 ± 9.2 mm) of the planted species in the 46 m gap. Diameter and height increment responses examined from north to south within 46 m gaps were not significantly different for any species (Table 2).

3.3. Deer herbivory

In growing seasons 1–4, probability of survival was marginally higher when white pine ($\chi^2 = 3.52$, $P = 0.06$) and hemlock ($\chi^2 = 2.70$, $P = 0.10$) were protected from deer. Furthermore, mean height was greater in enclosures for yellow birch ($F = 5.58$, $P = 0.02$) and hemlock ($F = 4.42$, $P = 0.04$), regardless of gap size (0, 20, or 46 m). For example, in growing season 2, yellow birch and hemlock were 11.5 ± 3.0 and 4.0 ± 1.5 cm, respectively, taller in enclosures. Presence or absence of a deer enclosure did not affect initial height increment, diameter or lifespan for any species.

Percent of trees noted for browse ($F = 37.07$, $P < 0.01$) and forest-wide deer density (data not shown) showed similar temporal variations over the study period. Regional deer density ranged from 3 to 12 deer km^{-2} during the study. The least amount of browsing ($3.0 \pm 0.5\%$) was noted in the first growing season when deer densities were estimated at 5.4 deer km^{-2} and the most browsing ($22.0 \pm 1.2\%$) was noted in the fourth growing season when deer densities were estimated at 12.0 deer km^{-2} . In the fourth growing season when browsing pressure was high, the average percent of

trees browsed was highest in 20 m gaps ($25.9 \pm 1.1\%$) and on yellow birch ($28.9 \pm 2.1\%$) and lowest in 10 m gaps ($17.4 \pm 3.7\%$) and on hemlock ($10.6 \pm 3.0\%$). However, browsing was highly variable across the study site and differences among gap sizes and species were not significant in any growing season (gap size $F \leq 3.34$, $P \geq 0.09$; species $F \leq 3.07$, $P \geq 0.11$).

3.4. Shrub competition

For hemlock, probability of survival was $\sim 7\%$ higher ($\chi^2 = 7.14$, $P = 0.03$; Pair-wise comparisons, $\chi^2 = 6.84$, $P = 0.02$) and lifespan was ~ 1 year longer ($F = 3.43$, $P = 0.06$) where raspberry cover was low ($10.7 \pm 6.6\%$, 40.2 ± 3.3 months) than when it was high ($3.6 \pm 2.1\%$, 28.2 ± 3.5 months). Survival and lifespan of other species did not differ in a simple way among raspberry levels. Analysis of yellow birch heights within 46 m gaps demonstrated a changing relationship over time with raspberry cover. Taller yellow birch trees were positively associated with increasing raspberry cover in growing season 1 only ($F = 10.65$, $P = 0.01$). In growing season 4, there was no relationship between height and cover, but in growing season 12 the relationship reversed from the first growing season and taller yellow birch were marginally and negatively related to raspberry cover ($F = 9.88$, $P = 0.09$). Mean height increment and diameter were not related to raspberry cover for any species.

4. Discussion

Harvest-created gaps are one tool for influencing future forest composition, an attribute important to biodiversity conservation and attainment of management goals. Thus, based on silvics, a forest manager could prescribe sizes of harvest-created gaps that target desired species traits, such as shade tolerance, and thereby influence future forest composition (Messier et al., 1999). However, our results suggest that gap size effects on growth and survival are complicated for the four study species and only weakly support concepts of the Gap Partitioning Hypothesis as implemented in a complex milieu. In particular, the effect of gap size on tree performance was marginalized by other factors, which resulted in less than half the expected growth and survival after 12 growing seasons. We argue that deer browsing and shrub competition negated the expected positive effects of gap size in this study ecosystem (Fig. 6). Our study suggests that using gap size alone to influence tree growth and survival is challenging in ecosystems with high deer and shrub densities and, in unmanaged forests, could slow succession of the study species. We discuss these ideas in the following subsections.

4.1. Gap size effects

We found that gap size had significant effects on growth and survival of the four planted tree species. Tree survival was commonly higher in intermediate gap sizes for all species (Figs. 2, 3a,b), because the two extreme canopy conditions, open (large gaps) and closed (reference areas), were likely less favorable for seedling persistence. Initially, the very open conditions of large gaps fluctuated greatly in temperature extremes and were probably low in soil moisture, while the closed canopy of reference areas had low light availability as found in previous research at this study site and others (Strong et al., 1997; Wright et al., 1998). Consequently, intermediate gap sizes were likely to be more moderate in microclimate and resources, thus, supporting higher survival. On the other hand, height growth response to gap size was relatively linear: the larger the gap, the taller the tree (Table 1, Figs. 3c, d and 4). The individuals that survived and grew taller than surrounding vegetation (>1 m) in larger gaps benefited from

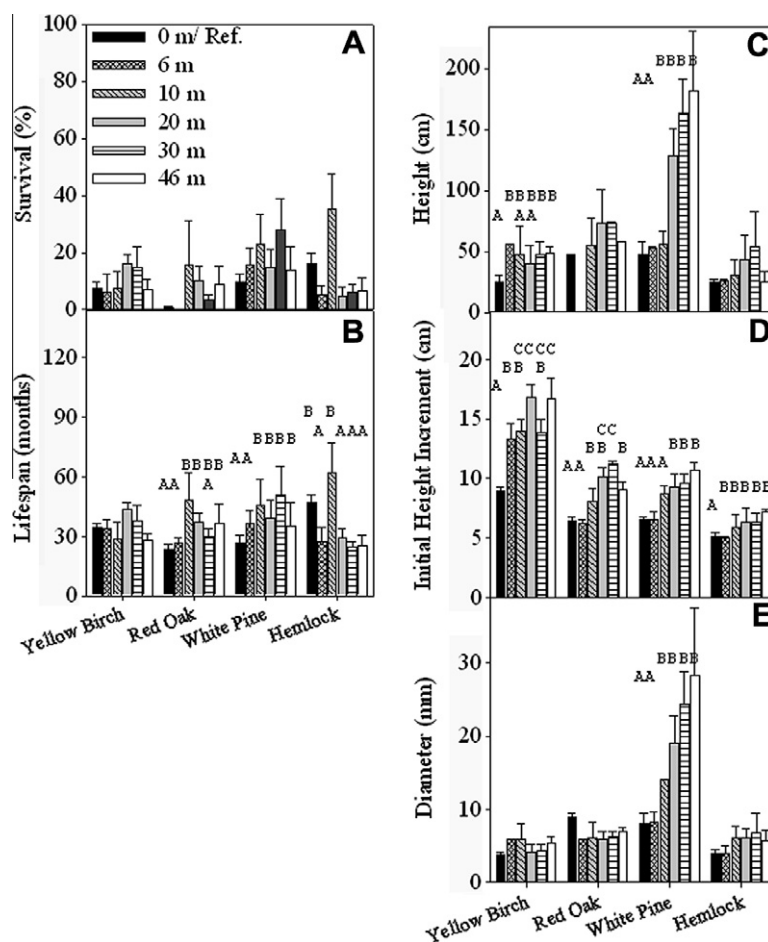


Fig. 3. Planted tree species' growth and survival across gap size treatments in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. (A) Percent survival by gap size in growing season 12. (B) Mean lifespan (months). (C) Mean height (cm) in growing season 12. (D) Mean initial height increment (cm) of growing seasons 1, 2, and 4. (E) Mean stem diameter (mm) at 15 cm in growing season 12. Within species, different letters denote when gap sizes are significantly different from each other ($P < 0.05$). Note that percent survival is illustrated for summary purposes and was not tested for significant pair-wise differences; therefore, letters were not drawn on this graph.

increasing light availability associated with increasing gap size, a likely explanation for the increasing height growth with gap size, as found in other studies (Gray and Spies, 1997; York et al., 2004).

Overall, gap size effects were complex for most of the study species and, generally, a gap size that maximized both growth and survival was not evident, a pattern highlighted elsewhere by Schupp (1995). Instead, the tree growth and survival trends suggest a tradeoff among gap sizes: the majority of survivors were intermediate in height in the intermediate gap sizes, but, in the largest gaps, the few individuals that survived benefited with maximum height growth (Fig. 3d). Similar results have been identified in other experimental gap studies (e.g., Gray and Spies, 1997; Coates, 2002; Raymond et al., 2006; Seiwa, 2007). These results also provide some evidence for the Gap Partitioning Hypothesis, especially for the survival and growth of white pine, which differed across the gap size gradient in nearly every response variable that we tested.

Contrary to our hypotheses, location within 46 m gaps was not a significant factor for most of the responses that we measured on the four study species. Prior research on large gaps of other temperate forests suggest tree seedlings at large gap edges are shorter and longer lived than more central trees, suggesting a growth-survival trade-off among locations in large gaps (e.g., Gray and Spies, 1997; Coates, 2002; Raymond et al., 2006). In our study, white pine was shorter at edges and yellow birch was shorter at southern edges (Fig. 5), but, their survival was similar among locations with-

in 46 m gaps. These results suggest that, within large gaps of this study, a growth-survival trade-off did not exist and that more central locations were advantageous to growth for some species without a higher risk of mortality when compared to edge locations. In addition, our hypothesis, based on gap partitioning concepts, that survival of hemlock, a shade-tolerant species, would be highest at edges and that survival of the other less tolerant species would be highest in more central locations was not supported; survival by location within 46 m gaps was similar among the study species. Thus, in this study, larger canopy gaps do not contribute to species coexistence via survival differences across the gap edge to center gradient as suggested by the Gap Partitioning Hypothesis.

Although gap size effects on growth and survival were statistically significant and likely important for white pine, they were minor for the other species when considered in the context of expected forest stand dynamics. We considered height an important metric of tree performance, where taller trees, those closer to attaining a canopy position, were more successful than shorter trees. Regional silvics manuals suggest that the average heights we observed in the 12th growing season were uniformly low for all species and often less than half the height expected after 12 years of growth (Gilbert, 1960; Godman and Lancaster, 1990; Wendel and Smith, 1990; Morrissey et al., 2010). Only white pine attained heights expected based on regional silvics (>150 cm) and only a small portion of white pine individuals (5% of the

Table 1
Statistical results of four planted tree species' responses to gap size and growing season factors in a randomized complete block experiment in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Polynomial contrasts tested growth responses over gap size (six levels: 0, 6, 10, 20, 30, and 46 m gap diameter classes) as linear (L), quadratic (Q), or Cubic (C) in each growing season (noted as subscript).

Factors	Yellow birch			Red oak			White pine			Hemlock		
	F value	P value	Polynomial contrast	F value	P value	Polynomial contrast	F value	P value	Polynomial contrast	F value	P value	Polynomial contrast
<i>Lifespan</i>												
Gap size	1.9	0.09		4.11	<0.01	L	6.1	<0.01	L, Q	9.86	<0.01	L
<i>Height</i>												
Gap size	5.6	<0.01		4.4	<0.01		10.0	<0.01		2.3	0.05	
Growing season	68.6	<0.01		21.0	<0.01		215.4	<0.01		4.5	<0.01	
Gap size × growing season	2.1	0.02	L _{1,2,4} ; Q _{2,4} ; C ₁₂	4.3	<0.01	L _{2,4} ; Q _{2,4} ; C ₄	3.9	<0.01	L _{2,4,12} ; Q ₁₂ ; C ₄	2.1	0.18	L _{2,4} ; Q ₁₂ ; C ₄
<i>Diameter</i>												
Gap size	1.3	0.31		0.8	0.58		5.6	<0.01	L	0.9	0.51	
<i>Initial Height Increment</i>												
Gap size	10.4	<0.01	L, Q	11.9	<0.01	L	4.9	<0.01	L	2.4	0.05	L

Bold font indicates a test statistic was significant, where $P < 0.05$. *Italic* font indicates a test statistic was marginally significant, where $P \geq 0.05$ and < 0.10 .

original white pine planting and 35% of those surviving to growing season 12) achieved these heights suggesting that these white pine survivors will likely be future canopy dominants.

In sum, tree height and survival after 12 growing seasons was less than half of expected values based on prior empirical and theoretical results. We posit that factors other than gap size and within-gap location impacted their growth and survival. Ungulate browsing and shrub competition are significant influences on forests globally and are two likely mechanisms for the lower-than-expected tree responses to gap size observed in this study ecosystem. General silvics knowledge also suggested that all four study species are sensitive to vegetative competition and browse until trees are taller than the height of competitors and reach of browsers (Crow, 1988; Erdmann, 1990; Godman and Lancaster, 1990; Wendel and Smith, 1990), a height that most study trees did not attain over the 12 year study period.

4.2. Deer and shrub effects

Regionally high deer populations and within-gap dominance of shrubs reduced tree seedling growth and survival in this study ecosystem. We found that yellow birch and hemlock grew taller in the absence of deer during the first few years when deer exclosures were maintained. Browsing likely filtered the effect of gap size and within-gap location on tree growth through the physical removal of biomass that reduces tree stature and on tree survival through frequent compensatory growth that exhausts carbon reserves (Russell et al., 2001; Cote et al., 2004). Furthermore, we found that few trees attained heights >150 cm in the largest gaps after 12 growing seasons, which presumably are nearly above the reach of deer (except during deep snow periods). These few trees may have escaped browse due to the greater distance between individual seedlings or due to greater visual obstruction by ground-layer vegetation, because planting density was more dispersed and shrub density higher in large gaps than in small gaps, both of which were important predictors to browsing patterns in another study (Saunders and Puettmann, 1999). Furthermore, raspberry cover dominated ground-layer vegetation (Fig. 4). In the first growing season, raspberry cover may have facilitated yellow birch growth by moderating microclimate conditions or reducing the abundance of other competitive species, such as grasses and ferns, which were identified to inhibit growth of northern hardwood tree seedlings in Pennsylvania (Horsley and Marquis, 1983). However, by growing season 12, hemlock survival and

yellow birch height were negatively related to raspberry cover. The persistent shrub layer likely filtered the effect of gap size on tree seedling growth and survival through resource competition (both above and belowground), allelopathy, and physical impediment (Lei et al., 2002; Royo and Carson, 2006; Montgomery et al., 2010). Despite the modest evidence, deer browsing and shrub competition were mechanisms that likely dampened tree response to gap size and within-gap location by 12 growing seasons after harvest in this study ecosystem.

4.3. Other factors

Other factors may have influenced the growth and survival of the planted seedlings at this study site. The trees were planted systematically across the gaps to test for gap size and within-gap location effects. Planting locations were not selected for microsites suitable for development. Several recent studies have highlighted the importance of microsite, notably the importance of decaying coarse woody debris to the persistence of hemlock and yellow birch (Rooney and Waller, 1998; Marx and Walters, 2008; Bolton and D'Amato, 2011). Large woody debris was scarce prior to and after harvest when merchantable timber, trees >11.4 cm diameter at breast height, were removed from the site. The microsite limitation idea is further supported by the few observations of naturally regenerated individuals of our study species on site. Even sugar maple regeneration was limited in larger gaps, suggesting that the conditions were not conducive for regeneration of the most prevalent canopy species. The interaction of microsite with gap size and within-gap location warrants further study.

At our study site, the experimental gaps were embedded in a thinned forest matrix that reduced stand density by 25% from uncut, reference condition at the study's initiation. The goal of this thinning was to maintain 80% crown cover thus improving growth and vigor of residual canopy trees (Erdmann, 1986). The reduction of forest canopy cover around the experimental gaps likely dampened the effect of gap size and within-gap location. The thinning likely increased light (e.g., Beaudet and Messier, 2002) and other co-varying microclimate variables at gap edges and moderated the resource and microclimate gradient from forest to gap center among the gap sizes. Despite this, we did find that our experimental gaps influenced the growth and survival of our study species. We anticipate that, if the gap size treatments examined in this study were embedded in an uncut forest, tree seedling growth and survival results among the gap sizes would contrast even

Table 2

Statistical results of four planted tree species' responses to within-gap location and growing season factors in a randomized complete block experiment in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Locations were subset to trees planted along the north-south axis of the 46 m diameter gaps to detect edge to center and north to south difference in growth and survival.

Factors	Yellow birch		Red oak		White pine		Hemlock	
	F value	P value	F value	P value	F value	P value	F value	P value
<i>Initial Height Increment</i>								
N/S Location	1.57	0.22	0.41	0.80	0.18	0.95	1.14	0.36
<i>Height, 46 m</i>								
N/S Location	5.9	<0.01	1.3	0.28	2.7	0.04	1.0	0.44
Growing Season	29.3	<0.01	4.9	<0.01	67.5	<0.01	4.0	0.02
N/S Location x Growing Season	3.3	<0.01	0.5	0.85	1.7	0.10	0.7	0.71
<i>Diameter, 46 m</i>								
N/S Location	1.6	0.38	0.2	0.90	0.7	0.70	0.1	0.99
<i>Initial Height Increment, 46 m</i>								
N/S Location	0.8	0.56	0.6	0.68	1.0	0.44	0.0	1.00

Bold font indicates a test statistic was significant, where $P < 0.05$. *Italic* font indicates a test statistic was marginally significant, where $P \geq 0.05$ and < 0.10 .

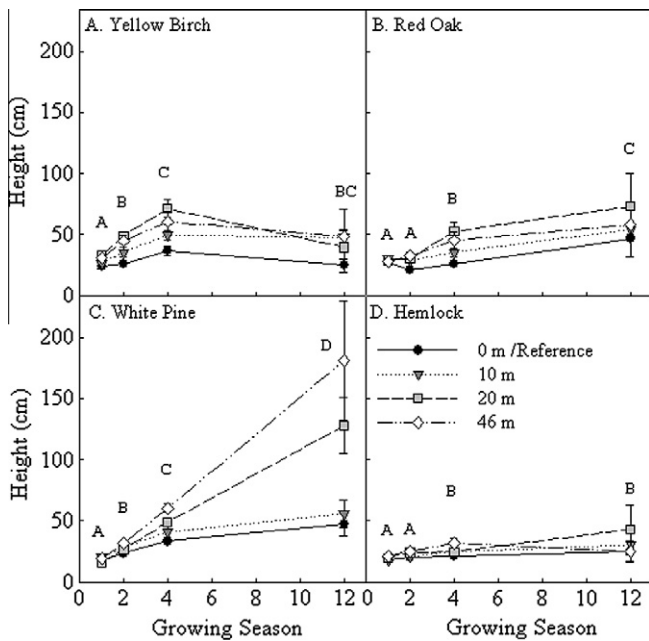


Fig. 4. Planted tree species' mean height (cm) over growing seasons by gap size treatments in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Growing seasons with different letters are significantly different from each other ($P < 0.05$). For ease of interpretation, the 6 and 30 m survival curves are not shown. (Growing season 12 height is also illustrated in Fig. 3c for all gap sizes.)

greater, because resources and microclimate conditions would contrast more from the surrounding forest.

4.4. Implications for forest stand dynamics

The application of our results to other sites and unmanaged forests must be made carefully. Our site represented a single northern hardwood forest in northern Wisconsin. We do not consider the site an anomaly among northern hardwood forests, because the site was selected for its similarity to other forests across the region. Nonetheless, we did not test for variation among other similar locations.

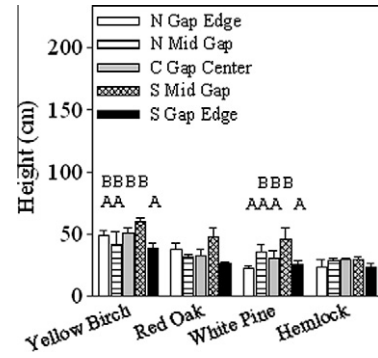


Fig. 5. Planted tree species' mean height (cm) within 46 m diameter gaps two growing seasons after harvest in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Within species, different letters denote when locations are significantly different from each other ($P < 0.05$).

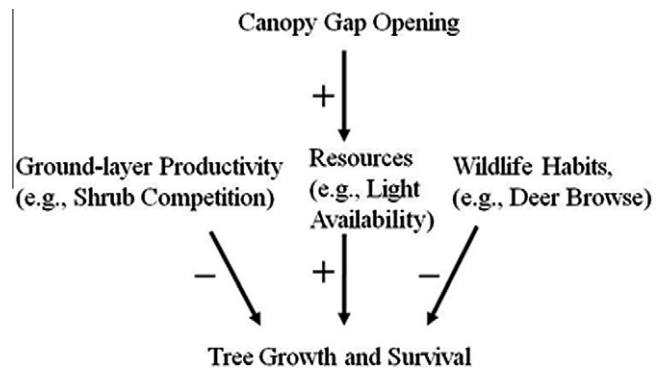


Fig. 6. Conceptual diagram of study. Theoretically, the available resources in gaps are beneficial (+) to tree growth and survival. However, increased vegetative competition and deer browse are detrimental (-) to tree growth and survival. When considered concurrently, the effect of multiple interactions on tree growth and survival are unclear.

Furthermore, our experimental design represented a range of conditions that result from first entry selection harvests. Gap creation through timber harvest differ from natural disturbances in gap size, shape, frequency, within-gap legacies (e.g., woody debris, residual live trees, etc.), and ground disturbances (Franklin et al., 2007). However, we consider our experimental design a model system to test the effect of gap size, which can be difficult to examine in unmanaged forests. In addition, the experiment's context encompasses moderately severe disturbances because timber harvesting removed trees ≥ 2.5 cm diameter at breast height and timber extraction disturbed ground cover. Therefore, while our study represents an opportunity to highlight the effects of gap size, our results must be extrapolated to natural disturbances in unmanaged forests with caution.

In light of these caveats, our results support a conceptual model of interacting factors on this site, where the positive effect of canopy gap size on essential resources for tree growth and survival is dampened by negative effects of competing vegetation and ungulate browsing (Fig. 6). Simulation models often incorporate data from forest structure, such as gap opening and light availability, and species-specific traits, such as shade tolerance, to predict forest stand dynamics (e.g., Pacala et al., 1993). Our results, along with others (e.g., Krueger et al., 2009; Montgomery et al., 2010), suggest that these models should incorporate concurrent interactions of other lifeforms that can mask the relationship between resource availability and tree performance in canopy gaps. Our experiment of trees planted throughout a range of gap sizes showed low survival and minimal growth, which, in an unmanaged forest, would

extend time to gap capture by regenerating trees and thereby slow succession. Elevated deer populations, pervasive shrub layers, and for some species a lack of suitable seedbeds are common to many forest types and their effect on stand dynamics may alter expected outcomes from conventional forest simulation models.

4.5. Implications for forest management

Our results suggest that, under appropriate deer and shrub layer conditions, managers could use medium-sized gaps to enhance the growth and survival of the four species we studied. Although our results span a 12 year period, prior empirical results suggest that raspberry cover should transition to regenerating northern hardwood tree cover within 10–15 years (see review Donoso and Nyland, 2006). Natural regeneration was not an objective of this study but we did observe more natural regeneration in medium than large gaps (data not shown), suggesting that shrub competition to tree regeneration may decrease sooner in medium than large gaps. Furthermore, natural disturbance regimes of northern hardwood forests are primarily characterized by canopy gap disturbances. In particular, moderate-severity disturbances produce gap sizes <500 m² that approximate <30 m treatments in this study although a few very large gaps (up to 5000 m²) do occur (Hanson and Lorimer, 2007). These results in combination with recent studies of other components of northern hardwood management, such as the retention of large woody debris (Smith et al., 2008), gap shelter trees (Shields et al., 2007), and soil preparation treatments (Lorenzetti et al., 2008), could be used to create innovative prescriptions to sustain a wide range of goods and services. Moreover, using more medium than large gaps better emulates natural disturbance and meets goals of natural disturbance-based silviculture.

Regionally, planting trees in northern hardwood stands is uncommon because natural tree regeneration is usually abundant. However, recent declines in northern hardwood tree diversity (Schwartz et al., 2005) and natural tree regeneration (Matonis et al., 2011) in managed forests, which have depended on natural regeneration, suggest that alternative approaches, such as planting, may be necessary. In forests with elevated deer populations and dense shrub populations, our results suggest that planting trees in harvest-created canopy gaps may require additional tools, such as deer protection and vegetation control, to attain desired management outcomes.

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