

The Role of Harvest Gaps in the Plant Diversity of a Northern Hardwood Forest of
Northern Wisconsin, USA

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Abstract

Recent losses of biodiversity in managed forests have invigorated the need for natural disturbance-based management that sustains the many goods and services expected from forests. Regionally, declines in species diversity of managed northern hardwood forests have prompted the need for alternative approaches to forest management. One approach to natural disturbance-based management is using harvest gaps to emulate natural gaps that result from canopy disturbances. In this dissertation, I examine harvest gaps and their influence on ground-layer plants in the context of canopy gap theory. With the help of others, I measured four planted tree species and ground-layer vegetation (woody and herbaceous) abundance within a field experiment located in a second-growth northern hardwood forest of northern Wisconsin. The experimental approach included a gap opening gradient (five gap sizes, 6, 10, 20, 30 and 46 m diameter, and undisturbed reference areas) and a temporal gradient (0, 2, 6, and 13 years after gap creation).

Ground-layer plant community composition and functional traits differed among gap sizes supporting theory. Gaps of all sizes differed in composition from undisturbed areas and all pair-wise combinations of gap size also differed in composition, except the 6 m and 10 m gaps. Compositional differences in gap size were evident two years after gap creation and grew more pronounced over the 13 year period. Species' functional traits and micro-environments were related to variation in ground-layer composition. The correlation between gap size and ground-layer plant composition provides evidence for

gap partitioning by the ground-layer community in this forest. In addition, medium gap sizes were more diverse than smaller or larger gaps, supporting the concept that intermediate disturbances maximize species diversity. Furthermore, survival and growth of planted yellow birch, white pine, red oak, and hemlock seedlings was lower than expected growth and survival based on prior empirical and theoretical results. Growth and survival responses to gap sizes are dampened by deer browsing and shrub competition. This dissertation argues that harvest gaps play a role in plant diversity at multiple scales and provides an ecological framework for management decisions regarding gap size and its relationship to the ground-layer plant community.

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Introduction

Maintaining ecosystem function is vital to forest sustainability as climate, disturbances, pests, and disease change forests in novel ways. Moreover, society's demands and expectations of forests have changed from being solely a timber resource to having multiple uses including timber, recreation, wildlife, and spiritual values (Bengston 1994). The extensive use and changing nature of managed forests require ecosystem management, where practices can meet specific objectives while maintaining the many goods and services that forests provide (Seymour and Hunter 1999). Therefore, as stressors and disturbances continue to change forest ecosystems, grounding management actions in an ecological context is crucial.

One approach to ecosystem management is using natural disturbance as a template for forest management (Seymour and Hunter 1999, Franklin et al. 2007). For instance, gap-based silviculture based on historical range of variation has been proposed in forests where small-scale disturbances dominate (Coates and Burton 1997, Seymour et al. 2002). Canopy gap disturbances create space for tree regeneration and modify microclimate and resource availability. Therefore, testing the applicability of gap theory developed in unmanaged forests to gap-based silviculture in managed forests is a necessary step to developing sustainable forest management practices.

Another approach to ecosystem management is using existing silvicultural practices that use area-based harvest gaps or patch cuts to maintain or increase structure and composition. Single-tree selection modified with harvest gaps, group selection, and

patch cutting use canopy opening size as a tool to influence the proportion of shade intolerant tree composition and facilitate cohort development in forests that are predominately shade tolerant tree species. Group selection and patch cutting has had a long history of success of diversifying tree species in New England northern hardwood forests (Leak and Wilson 1958, Leak and Filip 1977). However, existing practices have been developed to focus growth and productivity on trees and the effects of these practices on the broader ecosystem are not clear (e.g., Crow et al. 2002). Therefore, evaluating existing practices in the context of ecological concepts is important. For example, examining patterns and processes within harvest gaps of existing practices can be compared with gap theory concepts to explain mechanisms of change in the broader forest ecosystem.

In this dissertation, I examine patterns of ground-layer plant diversity in harvest-created gaps in a US Forest Service (USFS) field experiment established by Terry Strong (retired research silviculturist from the USFS Northern Research Station) on the Chequamegon-Nicolet National Forest in northern Wisconsin, USA. The robust experimental design involves more than a decade of repeated measurements beginning prior to gap creation and includes experimental gaps that differ in area by two orders of magnitude. I used this experiment creatively in my dissertation the following ways.

>>Chapter 1: I, along with Rebecca Montgomery, Peter Reich, and Terry Strong, test the GPH among gap sizes and within large gaps on the ground-layer plant community composition and function (in prep, *Journal of Ecology*). >>Chapter 2: We consider the GPH again but as it relates to the growth and survival of several species of planted trees

(accepted after major revisions, *Forest Ecology and Management*). >>Chapter 3: We consider the IDH as it relates to species diversity among gap sizes and among forests with different gap sizes and proportions of forest in gap (in prep, *Ecological Applications*). These chapters synthesize effects of harvest-created gaps on the plant communities and individual species in regard to existing ecological concepts. The results will be useful to managers using harvest-created gaps to maintain a variety of ecosystem goods and services.

**Chapter 1: Canopy gap size influences niche partitioning of the ground-layer plant
community in a northern temperate forest**

Chapter Summary

We used a ground-layer plant community of a temperate deciduous forest in northern Wisconsin, U.S.A, as a model system to test whether the Gap Partitioning Hypothesis (GPH) extends to the relatively species-rich ground layer. Specifically, we used a well replicated experimental approach that included a gap opening gradient (five gap sizes, 6, 10, 20, 30 and 46 m diameter, and undisturbed reference areas), a within-gap location gradient (gap edge to center), and a temporal gradient (0, 2, 6, and 13 years after gap creation). Ground-layer plant composition and traits differed across gap sizes, within gap locations, and over time. Gaps of all sizes differed in composition from undisturbed areas and all pair-wise combinations of gap size also differed in composition, except the 6 m from the 10 m gaps. Large gaps also displayed within-gap compositional gradients from gap edge to center locations. Compositional differences in gap size were evident two years after gap creation and, contrary to our hypotheses, grew more pronounced over the 13 year period. In contrast to neutral theory, species' functional traits and microenvironmental conditions were related to variation in ground-layer composition. Species with smaller seeds, lower shade tolerance, later bloom times, shorter stature, and longer leaves were associated with higher light, more central gap locations, larger gap sizes, and greater time since gap creation. The correlation between gap size and ground-layer plant composition provides evidence for gap partitioning by the diverse ground-layer community in this temperate deciduous forest community.

Introduction

Canopy gaps create heterogeneity in understory conditions important for plant regeneration by modifying local competitive hierarchies, microclimate, and resource availability. The Gap Partitioning Hypothesis (GPH) (Ricklefs 1977, Denslow 1980) provides a theoretical context for understanding whether and how canopy gaps influence species diversity in forest ecosystems. The GPH posits that gaps create heterogeneity in resources crucial for tree regeneration in closed-canopy forests, allowing trees with contrasting strategies to coexist along resource gradients. The interaction between microsite resource availability and species' strategies leads to gap partitioning among species. It contrasts with the neutral model, which suggests that stochastic processes and sink populations regulate diversity, and that niche differences play little role in community assembly or composition (Hubbell et al. 1999).

Examination of tree composition within and among gaps has yielded mixed empirical support for the GPH. Generally, shade intolerant species dominate in large gaps and gap centers, but shade tolerant species are not necessarily restricted to gap edges or small gap sizes in tropical (Brandani et al. 1988, Brokaw and Scheiner 1989, Whitmore 1989, Chandrashekara and Ramakrishnan 1993) and temperate (Minckler and Woerheide 1965, Sipe and Bazzaz 1995, Gray and Spies 1996, Runkle 1998, Holladay et al. 2006) forests. In some forests, no clear evidence for niche partitioning in gaps has been found (Lieberman et al. 1995, Busing and White 1997, Hubbell et al. 1999, Schnitzer and Carson 2001, Coates 2002). Instead, tree species either appeared to be distributed at random and not associated with gap-related gradients (Hubbell et al. 1999);

had higher density in gaps, but did not differ in composition (Denslow 1995, Busing and White 1997, Schnitzer and Carson 2001, Coates 2002); or were related to pre-gap composition (Uhl et al. 1988, Dietze and Clark 2008). The failure of the GPH to routinely explain patterns of tree composition may result from the intersection of the spatial and temporal stochasticity of a canopy gap with recruitment limitation, resilient pre-gap vegetation, or generalist species that occur across a broad range of microsites (Brokaw and Busing 2000).

Few studies have examined gap partitioning of temperate, ground-layer vascular plants. The GPH was supported in ground-layer plant communities of Douglas-fir (*Pseudotsuga menziesii*) forests, where small gaps were dominated by late-successional plants and large gaps contained early-successional plants (Fahey and Puettmann 2007). In contrast, partitioning was not observed in northern hardwood (Moore and Vankat 1986, Collins and Pickett 1988a) or pine-oak forest (Schumann et al. 2003) understories. This could indicate that (i) the theory does not hold in these context of those studies, (ii) the range of openings examined may not have differed enough to identify partitioning (Moore and Vankat 1986, Collins and Pickett 1988a), or (iii) those studies specifically contained gaps with high gap edge to interior ratios that weakened gap size relationships to composition (Schumann et al. 2003).

Here, we test the GPH in the species-rich, ground-layer plant community of a northern hardwood forest. We use a robust field design that involves more than a decade of repeated measurements beginning prior to gap creation and includes experimental gaps that differ in area by two orders of magnitude. We hypothesize that the GPH will explain

ground-layer plant community composition broadly across gap sizes (small, intermediate, and large sizes) and within gaps along the forest-gap gradient (forest, edge, and gap locations) until gap closure. Furthermore, we expect that partitioning in the ground-layer composition will be evident soon after gap creation and weaken over time as the gap closes (and presumably resources revert to more similar to undisturbed conditions). We use species' trait associations with gap size and location along the forest-gap gradient to identify possible partitioning mechanisms, with the expectation that light will be an important mechanism in this closed-canopy forest.

Methods

Study site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located on the Chequamegon-Nicolet National Forest in northern Wisconsin, U.S.A (T40°N R12E). At the start of the study, the forest was 60 years old, having regenerated after harvest, and dominated by sugar maple (*Acer saccharum*). Soils are Stambaugh silt loam loess. The habitat type is classified as *Acer-Tsuga/Dryopteris* (ATD) based on Kotar et al. (2002).

Regionally, the natural disturbance regimes of northern hardwood forests are primarily characterized by canopy gap disturbances. Low intensity disturbance events (10–19% canopy removed) that create small canopy gaps (mean gap areas of 12–121 m²; mean upper limit <250 m²) tend to affect <10% of typical stands per decade (Tyrrell and Crow 1994, Dahir and Lorimer 1996) and are pathways for canopy recruitment for >60%

of trees (Frelich and Lorimer 1991). More moderate disturbances (30–60% canopy removal) are estimated to occur once during the lifetime of a tree cohort (300–390 years) (Frelich and Lorimer 1991) and result in gap area distributions with maxima at $\approx 5000 \text{ m}^2$ and distribution tails with $\approx 50\% < 40 \text{ m}^2$ and $\approx 9\% > 500 \text{ m}^2$ (Hanson and Lorimer 2007).

Study design

The experimental design is a randomized complete block with subsampling. Three replicates of each of six gap sizes (0 [reference area], 6, 10, 20, 30, and 46 m diameter gaps; Fig. 1) were randomly assigned in each of four blocks. Experimental gaps were created by dormant-season timber harvesting in 1994 (2 blocks) and 1995 (2 blocks) that removed trees $> 2.54 \text{ cm}$ diameter at breast height. The resulting design included 12 reference areas (0.4 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). The four blocks were also thinned (except for the reference areas) in 1994–1995, reducing the forest matrix density ($23 \text{ m}^2 \text{ ha}^{-1} [\pm 1.8 \text{ SE}]$).

Deer 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 and were maintained for four years. The responses analyzed in this study showed no relationship with deer exclosures; consequently, the data were combined into the larger dataset.

Data collection

Community composition.—We surveyed permanent sample plots (1 m^2) for vascular plants (including trees $< 0.5 \text{ m}$ tall). Plots were arrayed in four transects radiating in cardinal directions from gap centers to $> 7 \text{ m}$ into the adjacent forest matrix (the

“forest-gap transect”; Fig. 1). We assigned species (taxonomy according to the PLANTS Database (USDA 2009)) into one of eight cover classes (0; 1, 1 or 2 individuals and <1% cover; 2, 2–20 individuals and <1% cover; 3, >20 individuals and/or 1–5%; 4, 5–25%; 5, 26–50%; 6, 51–75%; 7, 76–100%). Surveys were conducted in late June–early August over four survey periods: pre-harvest (1994 [2 blocks]–1995 [2 blocks]; “year 0” hereafter) and post harvest in 1997 (“year 2” hereafter), 2000 (2 blocks) or 2001 (2 blocks) (“year 6” hereafter), and 2008 (“year 13” hereafter)).

Plant traits.—We compiled widely available traits by species (Table A1). Traits included shade tolerance, lifeform, potential maximum height, leaf and seed length, and potential first month of bloom and were reported by community-weighted means (CWM) (Lavorel et al. 2008), except for lifeform, which was evaluated by plot-level dominance of all lifeforms present.

Light.—We modeled light availability at the plot level using MIXLIGHT (v1.15), a light transmission model that calculates a growing-season average value at the microsite level (Stadt and Lieffers 2000). We parameterized the model with site information and canopy tree characteristics to create a relative index of the light environment at the plot-level for each experimental gap (Appendix A).

Data analysis

Ordination. – To test for gap partitioning, two assumptions must first be met: a range of species with diverse traits must be available in the local species pool and canopy gaps must create a gradient of resources and microclimates in the gap understory (Brokaw and Busing 2000). Therefore, before we examined our central question about

gap partitioning, we checked assumptions by developing and assessing metrics regarding the site's species pool and gap environments (Appendix A). Both assumptions were clearly met. We then conducted compositional analysis with Non-metric Multi-dimensional Scaling (NMS), a non-parametric ordination method that uses rank distances. The main data matrix consisted of 5088 sample units (or rows; 1272 plots \times 4 surveys) and 125 species (or columns). The main matrix was reduced to 5042 sample units \times 39 species to remove outliers and rare species. The final main matrix was run 40 times with real data and 70 times with random data running four- to one-dimensional solutions in PC-Ord v5.31 (McCune and Medford 2006). Details of analytical process used to select the end solution of NMS are presented in Appendix A.

Evaluation of compositional partitioning.—We analyzed the ordination first by gap size and second by location along the forest-gap transect, with several approaches: correlations, descriptive statistics, non-parametric tests of group differences, and indicator species' importance values. Details of the methods are available in Appendix A.

Results

Ordination of the ground-layer plant community showed differences that support the GPH and niche partitioning was associated with shifts in species traits among gap sizes and locations along the forest-gap transects. The end, three-dimensional configuration of 5042 sample units and 39 species (Fig. B1) had greater structure than expected by chance ($P = 0.0278$), stress of 21.4, and final instability of 0.00078. The ordination represented two-thirds of the total variance and, after varimax rotation, axis 3 was the major gradient, accounting for the most variation (34%; axis 2 = 17% and axis 1

= 16%). We evaluate axis 3 for compositional partitioning and potential mechanisms in the following subsections. Detailed results from the centroids, MRPP, and indicator species analyses are available in Appendix B. Axis 1 and 2 results are presented in Tables B1–2. For visual 2-D presentation, we used axis 1 as the minor gradient.

Gap partitioning through space

We found strong compositional shifts that were associated with gap size. Gap openings' composition differed significantly from reference areas (MRPP $P < 0.0001$) and the magnitude of that difference increased with gap size (correlation to axis 3, $\tau = 0.48$; Fig. 2). In years 2–13, all pairwise combinations of gap size also significantly differed in composition ($P < 0.0001$), except the 6 m from the 10 m.

Moreover, we found that composition was always different among the general forest-gap transect locations of the reference area, forest matrix, and gap opening. The correlation of location to axis 3 was weaker than gap size ($\tau = 0.19$), because composition along the forest-gap transects varied by gap size. The 46 m gap had the most extensive forest-gap transect, and, consequently, had the greatest changes in composition from forest matrix to gap center and from the reference area as a whole (Fig. 3). In pairwise comparisons within 46 m gaps, gap opening locations were significantly different from each other at 10 m intervals, while adjacent locations (5 m intervals) were not; however composition clearly varied in a continuous manner from forest interior to gap edge to gap center (Fig. 3). Forest matrix locations around the 46 m gaps were similar to each other but significantly different from the reference areas and gap opening locations.

Smaller gap sizes had less extensive forest-gap transects than 46 m gaps. Among

gap sizes, locations within gap openings that were similar distance from and near to dripline differed compositionally between the small (6 and 10 m) and large (20 m, 30 m and 46 m) gaps (Fig 4c). However, mid-gap locations far from dripline did not differ among the three large gap sizes (Fig 4d–e).

Gap size composition through time

Survey year was also positively related to axis 3 ($\tau = 0.33$; $P < 0.0001$). Ordination of the ground-layer community showed compositional trends that grew stronger rather than weaker over time (Fig. 2). Gap composition changed through time in similar vector direction, or successional trajectory, but differed in vector length, or magnitude of change, among gap sizes. From year 0 to year 13, average direction of change for reference areas and gaps was similar with a positive shift along axis 3. However, the magnitude of compositional change from year 0 to year 13 was different across gap sizes ($F_{5,12} = 4.43$; $P = 0.0162$). Compositional change in reference areas was very modest, whereas maximum change occurred in the intermediate to large gaps, which by year 13 were very different from preharvest and reference conditions. The change in small gaps composition was intermediate to larger gaps and the reference areas.

Modeled light

Modeled growing season light transmission increased with gap size (Fig. 5a) and more central gap locations. In the ordination, modeled light was positively related to axis 3 scores ($\tau = 0.51$, $P < 0.0001$), a correlation that was stronger than other design variables of space (gap size and within-gap location) and time (survey year). Taken together, these

results suggest that higher light environments (alone or along with other environmental variation that co-varies with light) in more central gap locations, larger gap sizes, and greater time since gap creation were related to increasing NMS axis 3 scores and thus to overall composition.

Species' associations

Several species were significantly associated with the ordination. The highest correlation resulted between axis 3 and *Rubus idaeus* abundance ($\tau = 0.64$, $P < 0.0001$; Table 1). *Polygonum cilinode*, *Phyrma leptostachya*, *Dryopteris carthusiana*, and *Carex* sp. abundance also showed positive relationships with axis 3 ($\tau = 0.50, 0.50, 0.23, 0.21$; $P < 0.0001$). Indicator species were found for all gap sizes post harvest. Some gap sizes had a common indicator species over all years post harvest: *Maianthemum canadense* in the reference area, *Osmorhiza claytoni* in the 6 m, *Aralia nudicaulis* in the 10 m, and *Rubus idaeus* in the 46 m (Table 1). Locations along the forest-gap transects resulted in different indicator species as well. For instance, 46 m gap centers were associated with *Polygonum cilinode* and the adjacent forest matrix was associated with *Acer saccharum*. The ordination's correlation of axis 3 to the species pool and indicator species results suggest that dominant species changed from more forest-dwelling species to species that can thrive in open, disturbed, or high light environments as axis 3 scores increased.

Trait associations

The species' associations highlighted functional trait relationships to the ordination. Shade intolerance, first month of bloom, and leaf length were positively

related to axis 3 ($\tau = 0.39, 0.35, 0.23$, respectively; $P < 0.0001$), while maximum height and seed length relationships were negative ($\tau = -0.43, -0.47$, respectively; $P < 0.0001$). For all traits, there was a clear gradient from undisturbed reference plots to small to large gaps. However, gap size centroids were more similar among reference areas and small gaps (6 m and 10 m) and among intermediate to large gaps (20 m, 30 m, and 46 m; Fig. 5). Together, these results suggest that shade intolerant, late blooming, longer-leaved, shorter and smaller seeded plants were related to high light environments in more central gap locations, larger gap sizes, and a longer time interval since gap creation. The trait correlations also illustrate high trait diversity and change in community function related to gap size.

Furthermore, the relative proportions of lifeforms in the sample units diverged along the major gradient. Axis 3 scores were correlated positively to shrub and negatively to tree lifeforms ($\tau = 0.42, -0.46$, respectively; $P < 0.0001$). The lifeform correlations suggest that the low light environments of forest matrix locations and small gaps were dominated by tree species that maintain forest cover and a transient gap-phase forest dynamic. In contrast, high light environments in more central gap locations and larger gap sizes were dominated by shrubs over the study period of 13 years.

Discussion

According to the Gap Partitioning Hypothesis (GPH), the coexistence of plant species in closed forests is, in part, the result of niche-partitioning along the environmental gradients created from gap openings to forest interiors. The GPH suggests that no single species can dominate the wide range of environments along such a gradient

and that species have traits that are advantageous or disadvantageous at different locations along the gradient (Ricklefs 1977, Denslow 1980). Our study quantitatively explored compositional shifts within and across gaps, and found evidence that supports niche partitioning in ground-layer plant community composition. Composition increasingly differed from reference (undisturbed) areas with increasing gap size, and composition also differed among gaps as a function of their size (Fig. 2). Moreover, we found evidence that variation within gaps differed by gap size to influence ground-layer composition (Fig. 3–4).

The variation in gap composition was accompanied by differences in species' functional traits (Fig. 5). Species with smaller seeds, lower shade tolerance, later bloom time, shorter stature, and longer leaves were associated with higher light, more central gap locations, larger gap sizes, and a longer time interval since gap creation. The shifts in functional trait distribution suggest that variation in gap size provided contrasting environments in which certain traits were differentially advantageous.

A novel finding from our study was that, over the 13 year study period, compositional differences evident in year 2, and gradually increased over time with no indication of a return to reference conditions in the near future (Fig. 2). Prior longitudinal studies of canopy gaps also showed an initial divergence in composition that was related to gap size, but after canopy gap closure, composition started to converge after intense competition regardless of gap size (Kupfer and Runkle 1996). In contrast, the intermediate to large gap openings in our study were still open (in terms of the overstory) after 13 years and likely facilitated the sustained compositional differences across gap

sizes (Fahey and Puettmann 2007). Our study highlights a decadal effect of gap size on ground-layer community composition and suggests that intermediate to large gaps can harbor community assemblages different from the small gaps, forest matrix, and uncut forest for at least 13 years.

Most previous investigations of the GPH in temperate forests have focused on the tree community, which has low species richness and frequent recruitment limitation as compared to the ground-layer plant community. Alternative hypotheses proposed to explain high tree diversity and composition posit that composition patterns are random (Hubbell et al. 1999), controlled by species density (Denslow 1995), or dominated by pre-gap composition (Brokaw and Busing 2000). In contrast, our study, in a species-rich, ground-layer plant community of a closed-canopy temperate forest, supported the concept that canopy gaps are mechanisms for species coexistence and functional diversity.

Previous studies in northern hardwood forests examined gaps <20 m in diameter and found neither ground-layer compositional partitioning (Moore and Vankat 1986, Collins and Pickett 1988a) nor changes in microclimate (Collins and Pickett 1988a). Such findings are consistent with our results. Gap sizes <20 m in diameter in our study (6 m and 10 m) also showed minimal differences in composition (Fig. 2), and most closed during the 13 year study period. The proportionally small difference in gap area and the short temporal availability of the gap openings may have contributed to the compositional similarity of gaps <20 m in diameter (Collins and Pickett 1988b). Even so, our results show that gaps as small as 6 m or 10 m in diameter (gap diameter to canopy height ratio

(D:H) of 0.2 and 0.3, respectively) shift ground-layer composition away from undisturbed forest conditions.

Because we used a wide range of gap sizes, we were able to detect gap size partitioning, finding distinct communities in gaps <20 m, 20 m, 30 m and 46 m (D:H of 0.7, 1.2, and 1.9 for the 20 m, 30 m and 46 m, respectively). This is consistent with another study that demonstrated gap size partitioning of the ground-layer between two gap sizes (D:H = 1.0 and 2.0) in Douglas fir forest ground-layer vegetation of the Pacific Northwest (Fahey and Puettmann 2007). However, in another study where a wide range of gap sizes were studied (estimated D:H = 0.3–2.4), gap partitioning was not supported (Schumann et al. 2003). Multiple land-use histories and convoluted gap shapes may have weakened the gap size relationships in that study, and, consequently, obscured partitioning patterns. Our study site had a common land use history and fairly circular gap shapes that likely strengthened our ability to detect partitioning patterns.

A compositional dichotomy between forest interior and gap openings has been identified in other forests (e.g, Galhidy et al. 2006), but fine-scale composition across locations within gap openings has been less well studied. We found that composition gradually changed from edge to more central gap locations (Fig. 3). Ruderal species established at gap centers contributed to within-gap partitioning of large gaps in our study and others (Fahey and Puettmann 2007).

Partitioning mechanisms

Our results demonstrated that compositional change was positively related to both environment (modeled light [among gaps], gap size, and gap locations) and plant traits

(leaf length, shade tolerance [among species], and first month of bloom [among species]). Although we were not able to directly test the relationship between composition and microclimate (e.g., soil temperature) or resource factors (e.g., soil moisture) other studies have detected a relationship to gap size and within-gap location (Galhidy et al. 2006) and showed that they co-vary with light.

Experimental gaps at our site were created through timber harvest that likely created more homogeneous microsite conditions than in naturally-occurring canopy gaps. Microsite heterogeneity is important to species composition (Fahey and Puettmann 2007) and may even override larger-scale gap-size environmental gradients (Gray and Spies 1997). Although we did not measure microsite heterogeneity, lack of rotted logs, pit-mounds, etc. could have limited recruitment of more forest interior species in the gaps, and, consequently, strengthened the degree of compositional partitioning across gaps.

Competitive exclusion may have also strengthened partitioning patterns. Composition of large gaps and gap centers were characterized by establishment of ruderal species that can create recalcitrant layers that competitively exclude other species (see review Royo and Carson 2006). The shrub genus, *Rubus*, is known for its affinity for highly disturbed sites, establishing early and dominating sites after disturbance. Such post-disturbance competition has set back tree establishment for 10 to >15 years (see review Donoso and Nyland 2006). At our sites, *Rubus* patches still dominated large gaps 13 years after gap creation and may have limited recruitment of other species, fortifying compositional partitioning across gaps.

The major compositional gradient from small to large gaps was also marked by a

shift towards species with smaller seeds. Since most woodland herbs are clonal and large gaps were likely too large for colonization by vegetative reproduction, seed-based regeneration was likely important in the larger gaps. Because small seeds disperse farther on average, they may have been more likely to reach the center of large gaps.

Alternatively, the harvesting disturbance may have triggered germination of small seeds in the seed bank, such as seed from *Rubus* and *Stellaria* (Donoso and Nyland 2006).

This experiment highlights the potential significance of niche partitioning in the ground-layer plant community of natural forests. Our results support the GPH and, therefore, support the idea that a few large gaps could maintain diversity over space and time in a forested landscape. Because our study was experimental, we were able to isolate the effect of gap size. In unmanaged forests, the variability of natural canopy gap conditions (e.g., pre-existing vegetation, large woody debris, etc.) could weaken the relationship to ground-layer composition found here. Nonetheless, the correlation between gap size and ground-layer plant composition provides evidence for gap partitioning by this functionally-diverse ground-layer community.

Implications to forest management

Finally, our experimental gaps were created through timber harvest. Therefore, our experiment isolated how harvest-created gaps and their size affect community composition and functional trait distribution. The gradient of composition and traits among the gap sizes suggests that forest management actions based on the GPH create heterogeneity in ground-layer community function, a finding important to building science-based management strategies (Coates and Burton 1997, Lindenmayer et al.

2006). The use of harvest-created gaps to increase forest heterogeneity and complexity could also be enhanced by other strategies, including gap-level (e.g., shape, within-gap legacies) and stand-level (e.g., size distribution, frequency, spatial array, timing) approaches that influence stand characteristics and meet larger-scale objectives.

Table 1. Species correlations (Kendall's tau) to axis 3 and significant indicator species' importance values (IV) for gap size (diameter) in survey years after gap creation in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A.

Genus	Species	tau	Year 2	Year 6	Year 13
			Size (IV)	Size (IV)	Size (IV)
<i>Rubus</i>	<i>idaeus</i>	0.638	46 m (29.5)	46 m (26.7)	46 m (26.5)
<i>Phryma</i>	<i>leptostachya</i>	0.503	30 m (13.9)	30 m (16.8)	46 m (22.4)
<i>Polygonum</i>	<i>cilinode</i>	0.496	46 m (20)	20 m (17.7)	46 m (22.4)
<i>Dryopteris</i>	<i>carthusiana</i>	0.233		20 m (13.1)	
<i>Carex</i>	<i>spp</i>	0.209			
<i>Stellaria</i>	<i>media</i>	0.166			30 m (11.6)
<i>Galium</i>	<i>spp</i>	0.164	6 m (12.2)	6 m (33.8)	
<i>Betula</i>	<i>alleghaniensis</i>	0.130			
<i>Circaea</i>	<i>alpina</i>	0.090			30 m (4.7)
<i>Sambucus</i>	<i>racemosa</i>	0.087			
<i>Circaea</i>	<i>lutetiana</i>	0.087			
<i>Viola</i>	<i>spp</i>	0.083	6 m (17.5)	6 m (24.7)	
<i>Arisaema</i>	<i>triphillum</i>	0.083			
<i>Tilia</i>	<i>americana</i>	0.077			
<i>Aralia</i>	<i>nudicaulis</i>	0.070	10 m (6.6)	10 m (6.3)	10 m (11.1)
<i>Cinna</i>	<i>latifolia</i>	0.057			
<i>Brachyelytrum</i>	<i>erectum</i>	0.055			10 m (3.8)
<i>Ribes</i>	<i>cynosbati</i>	0.053			
<i>Elymus</i>	<i>hystrix</i>	0.039			

<i>Athyrium</i>	<i>felix-femina</i>	0.035		6 m (22.4)	6 m (5,5)
<i>Aster</i>	<i>macrophyllus</i>	0.017		10 m (4.1)	10 m (8.2)
<i>Anemone</i>	<i>quinquefolia</i>	0.016			
<i>Acer</i>	<i>rubrum</i>	-0.013		<i>10 m (4.6)</i>	10 m (7)
<i>Polygonatum</i>	<i>pubescens</i>	-0.013			10 m (10.5)
<i>Osmorhiza</i>	<i>claytoni</i>	-0.014	6 m (19.1)	6 m (22.4)	6 m (20.8)
<i>Prunus</i>	<i>serotina</i>	-0.014	6 m (7.2)	6 m (8.7)	
<i>Ostrya</i>	<i>virginiana</i>	-0.024			
<i>Abies</i>	<i>balsamea</i>	-0.024			10 m (4.8)
<i>Populus</i>	<i>tremuloides</i>	-0.026			
<i>Torientalis</i>	<i>borealis</i>	-0.028		<i>0 m (6.7)</i>	<i>20 m (6.5)</i>
<i>Streptopus</i>	<i>lanceolatus</i>	-0.032	10 m (8.2)		
<i>Trillium</i>	<i>grandiflorum</i>	-0.034		6 m (3.8)	
<i>Osmunda</i>	<i>claytoniana</i>	-0.044			6 m (5.2)
<i>Oryzopsis</i>	<i>asperifolia</i>	-0.044		10 m (8.7)	0 m (10.7)
<i>Quercus</i>	<i>rubra</i>	-0.057		6 m (8.5)	
<i>Lycopodium</i>	<i>obscurum</i>	-0.101	<i>10 m (6.8)</i>		<i>0 m (6)</i>
<i>Maianthemum</i>	<i>canadense</i>	-0.135	<i>0 m (11.6)</i>	0 m (14.4)	0 m (14.4)
<i>Fraxinus</i>	<i>americana</i>	-0.140	6 m (15.3)	6 m (18.6)	
<i>Acer</i>	<i>saccharum</i>	-0.146	0 m (20.7)	6 m (21.4)	<i>6 m (17.5)</i>

Note: Kendall's tau values in bold are significant ($P < 0.05$) and values with an asterisk have Bonferroni protection. Gap sizes with indicator species are listed if $P < 0.05$ and listed in italics if $P = 0.5-0.1$.

Figure 1. Gap sizes and plot 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). Black, filled squares represent sample plot (1 x 1 m) locations along the forest-gap transects. Circles with dotted line perimeters represent ideal experimental gap driplines, but, in reality, opening shape, diameter, and proximity to sample plot layout varied. In reference areas and 30 m and 46 m gaps, sample plots were spaced 5.5 m apart along transects, and, in 6 m, 10 m, and 20 m gaps, sample plots were spaced 3.7 m apart.

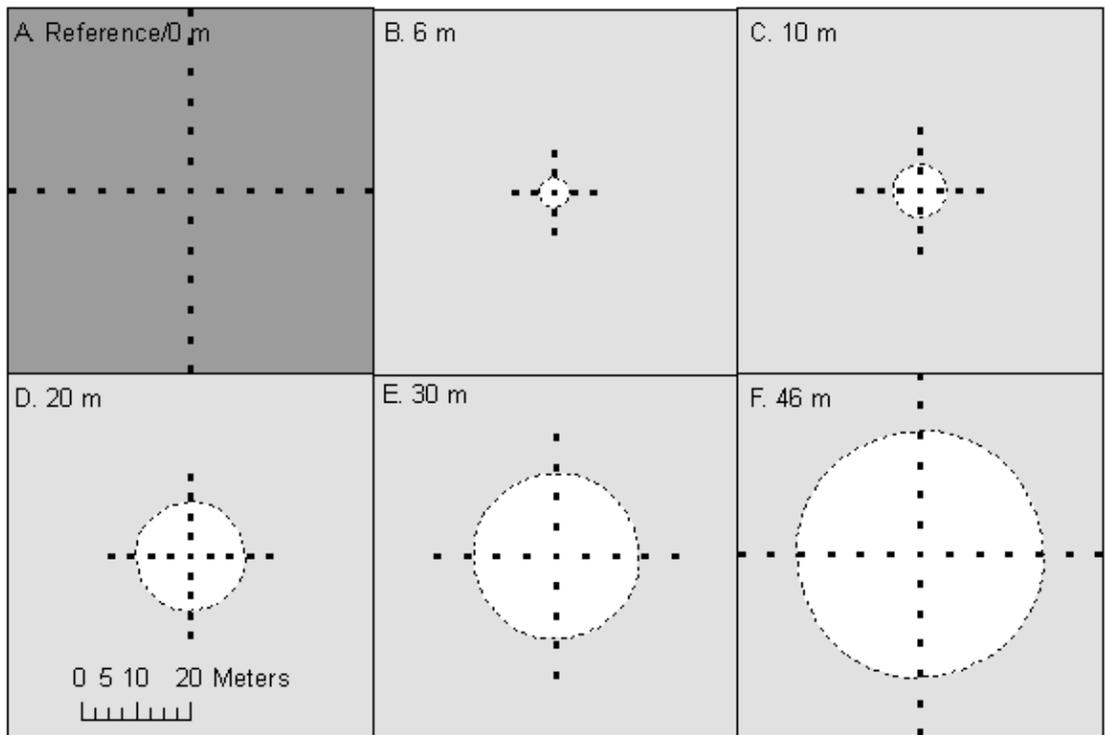


Figure 2. Centroids (\pm 95% confidence intervals) of gap size ground-layer vegetation composition by survey year in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. Gap size centroids were based on plots located within gap openings and excluded adjacent forest matrix plots.

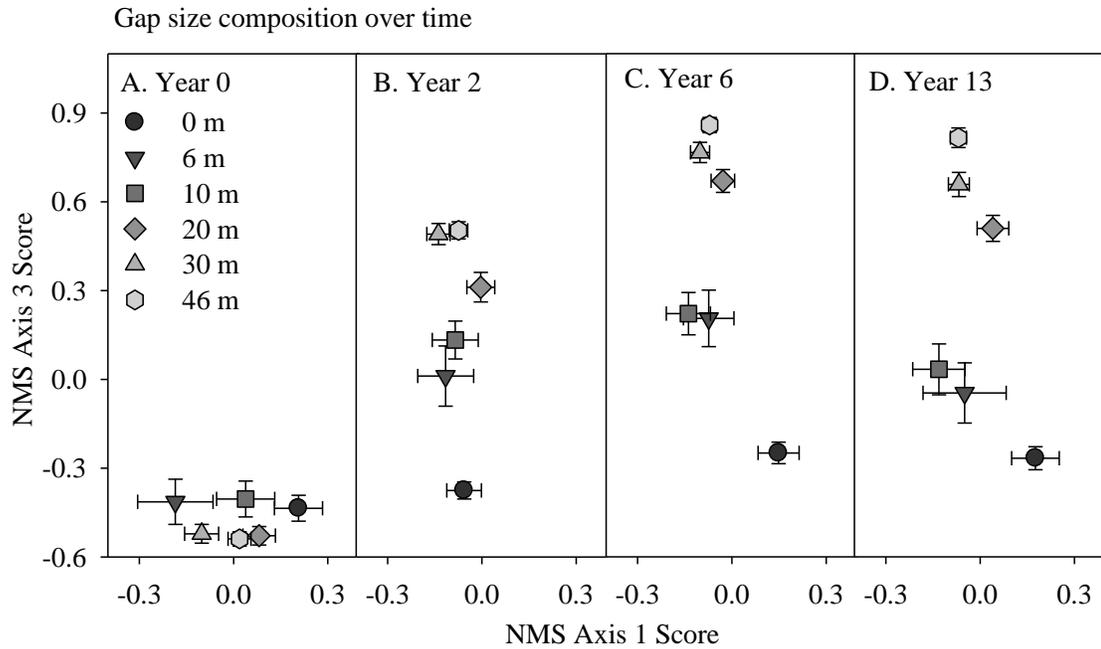


Figure 3. Year 13 centroids (\pm 95% confidence interval) of ground-layer vegetation composition in reference areas and locations along the 46 m forest-gap transects in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. Symbols represent distance from dripline into the adjacent forest matrix (negative numbers) or into the gap opening (positive numbers).

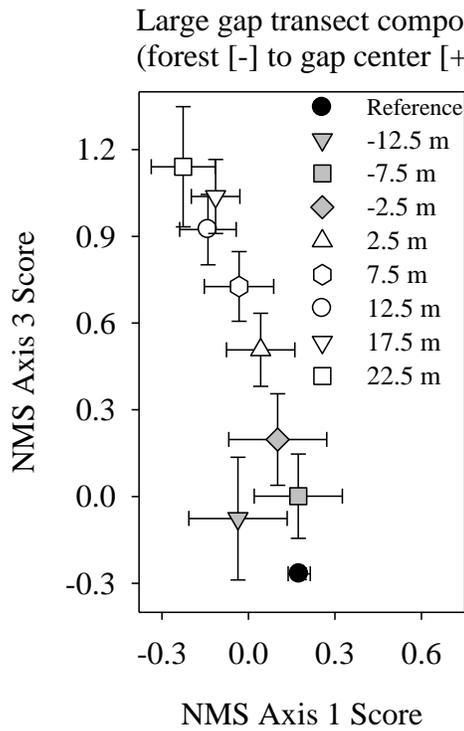


Figure 4. Year 13 gap size centroids (\pm 95% confidence interval) of ground-layer vegetation composition along forest-gap transects in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. Panels represent distance from dripline into the adjacent forest matrix (-7.5 m [A] and -2.5 m [B]) and into the gap opening (2.5 m [C], 7.5 m [D], and 12.5 m [E]).

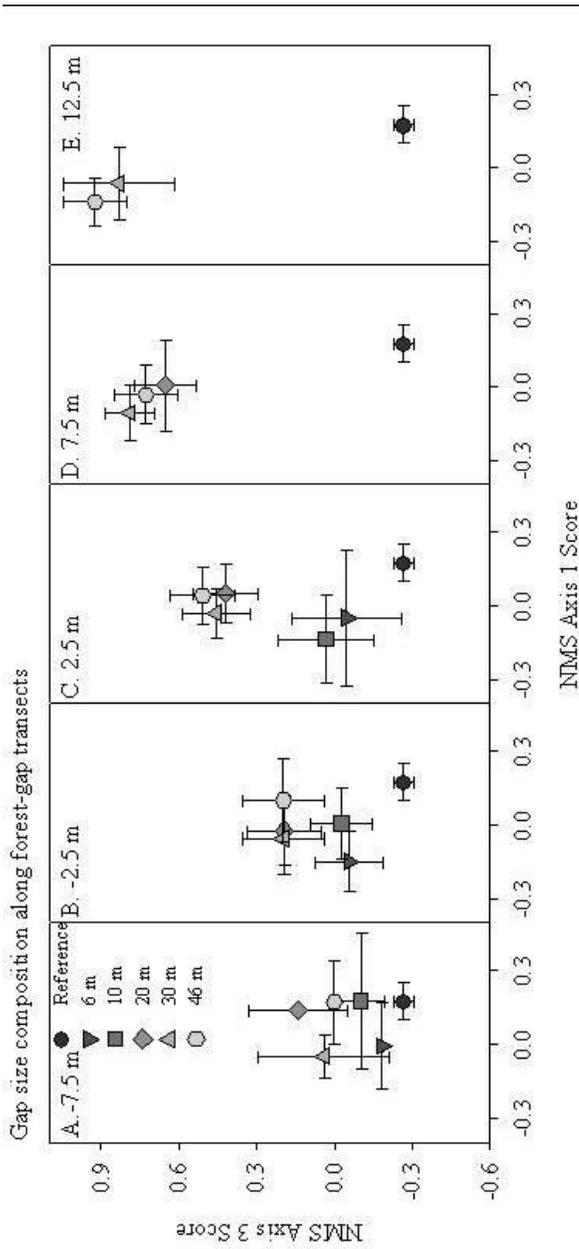
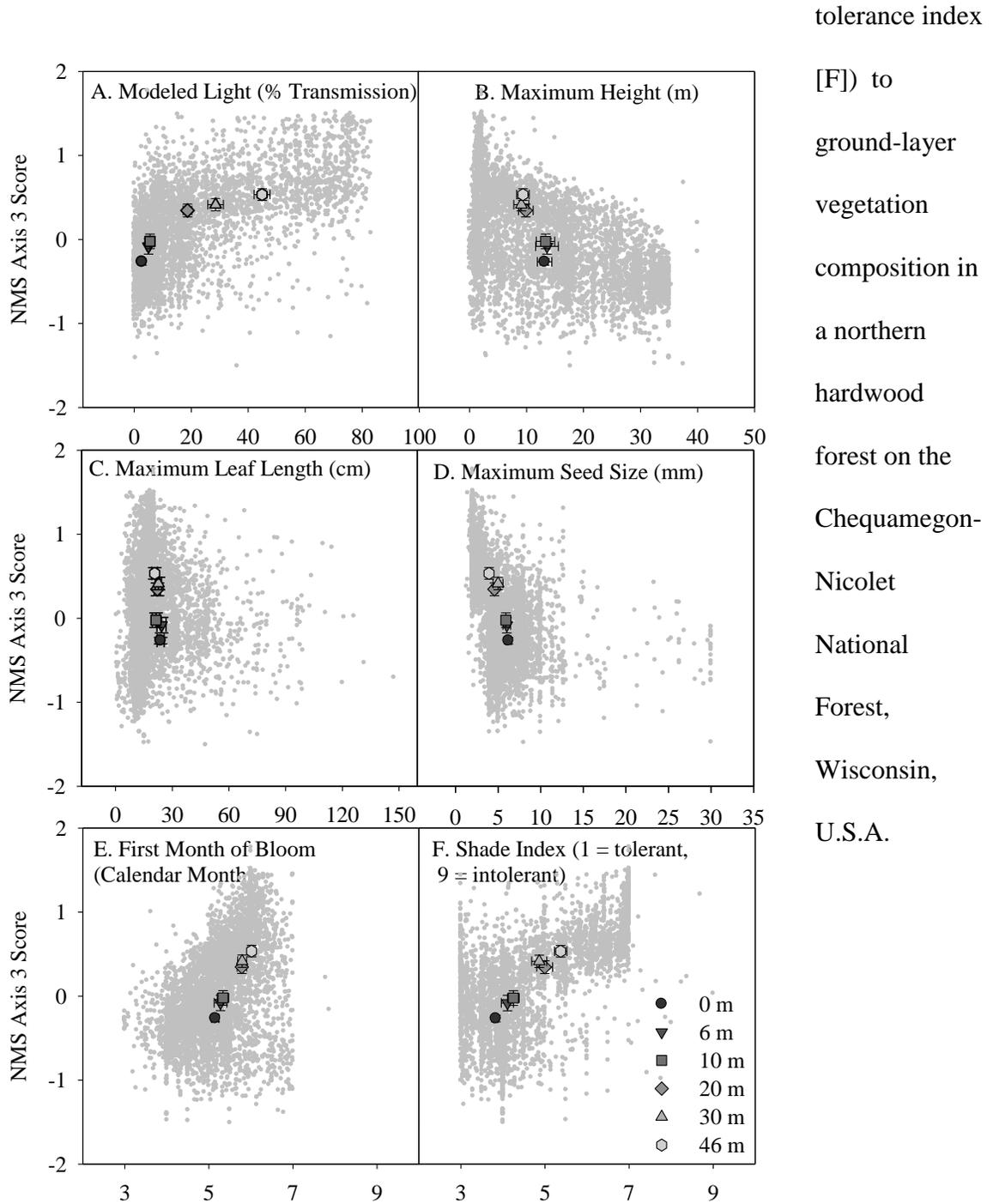


Figure 5. Scatter plot and centroids (\pm 95% confidence intervals) of plot- and gap-level modeled light (A) and species' traits (potential maximum height [B], potential maximum leaf length [C], potential maximum seed length [D], first month of bloom [E] and shade



tolerance index
[F]) to
ground-layer
vegetation
composition in
a northern
hardwood
forest on the
Chequamegon-
Nicolet
National
Forest,
Wisconsin,
U.S.A.

**Chapter 2: Tree seedling growth and survival in northern temperate forest: Do deer
and shrubs override canopy gap size effects?**

Chapter Summary

Detailed assessments of silvicultural approaches are needed to provide flexibility in future management options and sustain ecosystem goods and services. We evaluated the influence of harvest-created gap size 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. We expected, based on silvics, that our three midtolerant 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 differences were minor. With the exception of a small portion of white pine individuals, 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 overwhelmed 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 compositions in forests that have overly abundant deer and pervasive shrub layers and underscore the importance of silvicultural prescriptions that include measures for reducing these impacts.

Introduction

The ecological sustainability of managed forests is uncertain in the face of an increasing range of forest threats, such as global climate change, nonnative disease and pest outbreaks, and landscape fragmentation (Millar et al. 2007). Historically, management strategies simplified forests to meet narrowly-focused, short-term economic gains (Christensen et al. 1996, Puettmann et al. 2009). 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) and sustain ecosystem goods and services as forest threats change.

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 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 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 ecological theory, gap sizes targeted towards the shade tolerance of desired species and thereby influence future forest composition.

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 & Busing (2000) found 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 forest understory 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.

The degree to which gap size influences tree performance in forests in the face of changing forest conditions is unclear, yet is important to understanding tree persistence and ascension to the canopy. 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 et al., in review). This design allowed us to test several hypotheses. We hypothesized, based on silvics, that our three midtolerant 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.

Methods

Study site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located in the Chequamegon-Nicolet National Forest in northern Wisconsin, U.S.A (T40°N R12E). 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.

Regionally, the natural disturbance regime of northern hardwood forests is primarily characterized by canopy gap disturbances. Low intensity disturbance events (10–19% canopy removed) that create small canopy gaps (mean gap areas of 12–121 m²; mean upper limit <250 m²) tend to affect <10% of stands per decade (Tyrrell and Crow 1994, Dahir and Lorimer 1996) and are pathways for canopy recruitment for >60% of trees (Frelich and Lorimer 1991). More moderate disturbances (30–60% canopy removal) are estimated to occur once during the lifetime of a tree cohort (300–390 years) (Frelich and Lorimer 1991) and result in gap area distributions with maxima at ≈ 5000 m² and distribution tails with $\approx 50\%$ <40 m² and $\approx 9\%$ >500 m² (Hanson and Lorimer 2007).

A field reconnaissance of the study site in 1993 resulted in delineation of seven uniform blocks of which four were selected for study. The topography 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*) dominated the site but 12 other species of trees were identified, in addition to 6 shrubs, 23 herbs and forbs, 6 fern and clubmosses, and 1 sedge species. Tree basal area ranged from 20 to 39 m² ha⁻¹ and tree density ranged from 89 to 285 trees ha⁻¹. The forest canopy was closed with an occasional small canopy gap created by recent single-tree blowdown.

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 (*Acer saccharum*) at the expense of these study species (Schwartz et al. 2005), when compared to tree composition of old-growth forests (Goodburn & 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 microsites for regeneration (Rooney et al. 2000, Witt and Webster 2010). Moreover, microsite availability is often limited in managed stands for yellow birch and hemlock further complicating their regeneration

(Tubbs 1969, 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.

Study design

Treatments.—The experimental design is a randomized complete block with subsampling. Three replicates of each of six gap sizes (0 [reference area], 6, 10, 20, 30, and 46 m diameter gaps) were randomly assigned in each of four blocks. Experimental gaps were created by dormant-season timber harvesting in 1994 (2 blocks) and 1995 (2 blocks). The resulting design consisted of 12 reference areas (0.4 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). Openings were measured in 1997 and 2008 from gap center to dripline in cardinal and sub-cardinal directions (8 total radii). In 1997, gap area ranged from 9.9 m² to 1986 m² (gap diameter to tree height ratio 0.1 to 2.2). By 2008, 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).

Planting layout of the sample population.—In May 1997, we planted containerized seedlings of yellow birch and hemlock and bare-root (3-0) red oak and white pine in groups of four individuals (one individual per species). Spacing between individuals within a group ranged from 0.5–2 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. To isolate the effect of gap size, individuals that were located in the forest matrix adjacent to canopy gap openings were excluded from analysis.

Deer exclosure 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 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. We chose this design to reduce costs and to deter deer from dwelling in the confined area of the 1.8-m wide exclosure segments.

Plot layout for competing vegetation.—We evaluated the relationship between

shrub layer competition and tree growth and survival within the context of canopy gaps by compiling data from a companion study of ground-layer composition in these same gaps (Kern et al., in review). Permanent sample plots (1 m²) were arrayed along the forest-gap transects. These plots were adjacent to, but did not include, the planted seedlings.

Data collection

Growth and survival.—We measured the growth and survival of planted trees 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. Gap-level (and reference area-level) means were used in growth analyses.

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 conservative assessment 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).

Shrub competition.—Ground-layer vegetation within the gaps was assessed within the study site in a companion study (Kern et al., in review). In that companion study,

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 [2 blocks]–1995 [2 blocks]) and post harvest in 1997, 2000 (2 blocks)–2001 (2 blocks), and 2008. For the current study, only plots located within gap openings (and all plots 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).

Data analysis

Gap size and location categories.—We categorized gap size by 1997 gap diameter measurements and labeled them as “0 m” (or reference), “6 m”, “10 m”, “20 m”, “30 m”, or “46 m”. The 46 m gap was the only gap large enough to examine within-gap location responses. Locations within 46 m gaps were categorized by distance from dripline, in 5-m increments. This resulted in five location categories that were labeled by their midpoints: “2.5 m”, 0–5 m; “7.5 m”, 5.1–10 m; “12.5 m”, 10.1–15 m; “17.5 m”, 15.1–20 m; and “22.5 m”, 20.1–25 m.

Statistical approach.—The first step in analysis tested the growth and survival responses of each species in a randomized complete block with subsampling. The design was split into two separate mixed effects models: 1) among gap sizes (fixed effect) and 2) among locations within 46 m gaps (fixed effect). Blocks were considered random effects

and gap size replicates were random subsamples within each block. The effects of gap size and within-gap location on height were analyzed with repeated measures. Serial correlation was modeled with heterogeneous autoregressive-1 error structure. When gap size or location was significant, polynomial contrasts were used to test for linear, quadratic, and cubic trends across increasing gap size (0–46 m) within each growing season. To meet ANOVA assumptions, responses were log-transformed. Analyses were conducted with the MIXED Procedure in SAS (SAS Institute Inc. 2008).

Seedling survival was also tested in two separate models, among gap sizes and among locations within 46 m gaps. Survival was analyzed with nonparametric estimates of survivor function with the product-limit (Kaplan-Meier) method. Lifespan was calculated in months and right-censored if the individual was still alive in growing season 12. 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, the 0 m, 20 m, and 46 m gap sizes. Exclosure effects were evaluated on planted tree seedlings' growth and survival. Responses were analyzed as described in the first step of analysis but with the addition of a binary variable, the presence or absence of a deer exclosure. To further explore the effect of browsing on the study site, we used the gap-level browse (% of trees noted as browsed) as a response in the ANOVA models described in first step of analysis to determine if browse varied by gap size and time.

Lastly, 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 (Metzger and Tubbs 1971). Previous research on site (Kern et al., in review) showed that gap size and raspberry cover were similarly correlated to the major gradient of ordination analysis ($\tau = 0.48$ and $\tau = 0.64$, respectively) such that increasing gap size was associated with increasing raspberry cover. Based on this, we subset the data to isolate the effects of raspberry competition from gap size. For growth responses, we subset the data to the 46 m gaps and tested raspberry abundance effects by species and growing season with the MIXED Procedure in SAS. For survival analysis, we subset the data to 20–46 m gaps to capture a range of lifespans. Because raspberry cover varied among growing seasons, we relativized 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). The data were then classed 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 in each growing season, each with similar numbers of observations. Survival curves were then derived after stratification by raspberry cover level with the LIFETEST Procedure in SAS.

Results

Survival

After 12 years, overall planted species' survival was <30% across all gaps and was highest in intermediate gap sizes (Figs. 1 and 2a). With the exception of yellow

birch, survival was greater in gaps than in reference conditions (Table 1, Pair-wise comparisons, $P < 0.0508$). Survival was not significantly different by location within 46 m gaps ($\chi^2 \leq 8.2237$, $P \geq 0.0837$).

Growth

Most species grew taller with time, as expected, and with increasing gap size (Table 2 and 3, Fig. 2b and 3). For yellow birch and red oak, the height responses followed quadratic trends, with height increases greatest at intermediate gap sizes (Table 3). 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 46 m, the largest gap size. In addition, initial height increment (growing seasons 1–4) increased with gap size (Table 2 and 3, Fig. 2c) with yellow birch having the greatest initial growth rate, 13.9 ± 1.0 cm y^{-1} , of the planted species. Furthermore, diameter in the 12th growing season was similar among the gap sizes for yellow birch, red oak, and hemlock each. White pine diameter increased with increasing gap size (Table 2 and 3, Fig. 2d) and had the largest overall mean diameter (28.2 ± 9.2 mm) of the planted species in the 46 m gap. Growth measures examined by location within 46 m gaps were not significantly different for any species.

Deer herbivory

In growing seasons 1–4, mean height was greater when deer were excluded for yellow birch ($F = 7.71$, $P = 0.0073$) and hemlock ($F = 5.47$, $P = 0.0224$) regardless of the gap size (0 m, 20 m, or 46 m). In addition, yellow birch within deer exclosures had a marginally greater initial height increment than those without a deer exclosure regardless

of the gap size ($F = 3.82$, $P = 0.0624$). Presence or absence of a deer exclosure did not affect diameter or survival for any species.

Percent of trees noted for browse ($F = 37.07$, $P < 0.0001$) 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} . Within each growing season, the percent of trees browsed was similar among gap sizes ($F \geq 3.34$, $P \leq 0.0869$) and species ($F \geq 3.07$, $P \leq 0.1124$).

Shrub competition

Raspberry cover varied over time and increased with gap size (Fig. 4). After accounting for gap size, hemlock survival through growing season 12 was greater where raspberry cover was low ($\chi^2 = 7.14$, $P = 0.0281$; Pair-wise comparisons, $\chi^2 = 6.84$, $P = 0.0242$). Survival curves did not differ among raspberry levels for other species.

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 ($F = 10.65$, $P = 0.0085$). 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 ($F = 9.88$, $P = 0.0880$). Mean height increment and diameter were not related to raspberry cover for any

species.

Discussion

Harvest-created gaps are one tool for influencing future forest composition, an attribute important to biodiversity conservation and attainment of management goals. However, our results suggest that a gap size that simultaneously maximizes both growth and survival did not exist for the four study species. In fact, the effect of gap size on tree performance was marginalized by other factors, which resulted in lower than 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. 5). Our study suggests that using gap size alone to influence tree growth and survival is challenging in ecosystems with high deer and shrub densities. Instead, a combination of management tools may be necessary to attain management goals. We discuss these ideas in the following subsections.

Gap size effects

Gaps increase availability of key resources (e.g., light, water, nutrients) compared to closed forest understories, and resource availability increases as size of gap increases creating a resource gradient from closed forest to gap centers. Theoretically, this should allow species to coexist in a forest, because species have traits that are advantageous or disadvantageous at different locations along the gradient (Ricklefs 1977, Denslow 1980). 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). We tested this relationship between harvest-created gap size and performance of four planted tree species.

We found that gap size had significant effects on growth and survival of the four planted tree species. Tree survival was highest in intermediate gap sizes for all species (Fig. 1 and 2a), 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 tended to be linear: the larger the gap, the taller the tree (Table 3, Figure 2b and 3). The individuals that survived and grew taller than surrounding vegetation (>1 m) of larger gaps benefited from 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).

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. Similar spatial differences in growth and survival have been identified in other experimental gap studies (e.g., Gray and Spies 1997, Coates 2002, Raymond et al. 2006, Seiwa 2007). Therefore, an important finding from our study was that a gap size that

maximizes both growth and survival did not exist for the study species similar to another study (Schupp 1995).

Although gap size effects were statistically significant on growth and survival, they were minor 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 (Gilbert 1960, Godman and Lancaster 1990, Wendel and Smith 1990, Morrissey et al. 2010), but not for all individuals. A small portion of white pine individuals (5% of the original white pine planting) grew to heights >150 cm, an expected height after 12 growing seasons. 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. Moreover, location within 46 m gaps was not a significant factor for the responses that we measured for 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 (e.g., Gray and Spies 1997, Coates 2002, Raymond et al. 2006). We did not detect this pattern possibly due to other factors dampening the effect of edge-to-center gradients within the large gaps. In sum, tree performance was lower than expected from prior empirical and theoretical results, and we posit that factors other than gap size 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.

Deer browse effects

As in many forests worldwide (see reviews Russell et al. 2001, Cote et al. 2004), northern Wisconsin white-tailed deer populations have reached historically high densities and impacted regional forests (Stoekeler et al. 1957, Rooney and Waller 2003). At our study site, yellow birch and hemlock grew taller in the absence of deer during the first few years when deer exclosures were maintained. Furthermore, 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 1999b). Browsing filters the effect of gap size 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). For example, one study demonstrated that browsing occurred on white pine seedlings that were <130 cm tall and had been previously browsed (Saunders and Puettmann 1999b) and browsed trees had greater mortality rates than unbrowsed trees (Saunders and Puettmann 1999a). Such findings suggest that our study design likely

failed to fully capture effects of deer browse if some trees were browsed and subsequently died between surveys. The combination of evidence from the deer exclosures, the regionally high deer density and prior empirical results from other studies suggest that deer browsing had potentially large negative effects on tree growth and survival.

Shrub competition effects

Shrub competition also likely diminished the effect of gap size. Royo and Carson (2006) noted that formation of recalcitrant understory layers have altered forest dynamics worldwide. Shrub cover dominated ground-layer vegetation and was correlated to gap size in this study (Fig. 4; Kern et al., in review). By growing season 12, hemlock survival and yellow birch height were negatively related to raspberry cover. Shrub cover has been shown to increase with light availability and neutralize the effect of canopy openness in other temperate forest studies (George and Bazzaz 1999, Beckage et al. 2000). Shrubs reduce 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). Thus, intense above- and belowground shrub competition likely contributed to the overall low tree survival and growth in our study. Despite the modest evidence, deer browsing and shrub competition were likely mechanisms that dampened tree response to gap size in this study ecosystem.

Implications for forest stand dynamics

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. 5). 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), 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 a unmanaged forest, would extend time to gap capture by regenerating trees and thereby slow succession. Elevated deer populations and pervasive shrub layers are common to many forest types and their effect on stand dynamics may alter expected outcomes from conventional forest simulation models.

Implications for forest management

Experimenting with components of silvicultural systems to create forest conditions similar to patterns of natural disturbance is important to sustaining the goods and services that managed forests provide. Here, we investigated harvest-created gaps, a tool where stand spatial heterogeneity can be manipulated to influence the distribution of understory resources and subsequent regenerating tree composition. Increasing gap size increased tree growth, while survival maximized in intermediate sized gaps for yellow birch, white pine, red oak, and hemlock. However, overall we found lower than expected growth and survival based on prior empirical and theoretical results, despite statistical

significance of our experiment. Our results suggest that growth and survival responses to gap sizes are filtered and potentially neutralized by deer browsing and shrub competition, factors common in forests worldwide.

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.

Finally, the use of harvest-created gaps to emulate natural disturbance regimes could be enhanced by other management approaches, including gap-level (e.g., shape, within-gap legacies) and stand-level (e.g., size distribution, frequency, spatial array, timing) manipulations that influence stand characteristics and meet larger-scale objectives. Our study isolated the effect of a harvest-created gap and its size on planted seedling growth and survival. 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.

Table 1. Planted tree species' survival curve test statistics by stratification (Chi-square) and linear trend (z-Score) among gap size classes in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A.

Species	Chi-Square ¹	z-Score ²
Yellow Birch	<i>10.57</i>	<i>1.8719</i>
Red Oak	21.1294	-3.3368
White Pine	17.608	-2.9311
Hemlock	46.6548	6.0115

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 .

¹Log-rank test statistic of equality over gap size strata

²Log-rank linear trend test statistic

Table 2. ANOVA test statistics (F -values) of planted tree species' growth response to gap size and growing season factors in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A.

Response	Factors	Yellow	Red	White	
		Birch	Oak	Pine	Hemlock
Height					
	Gap Size	6.83	4.14	10.07	4.12
	Growing Season	83.85	16.16	203.93	4.2
	Gap Size x Growing Season	2.62	3.24	4.02	2.46
Diameter					
	Gap Size	1.28	0.74	5.59	1.01
Initial Height Increment					
	Gap Size	18.46	9.75	8.39	3.13

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 .

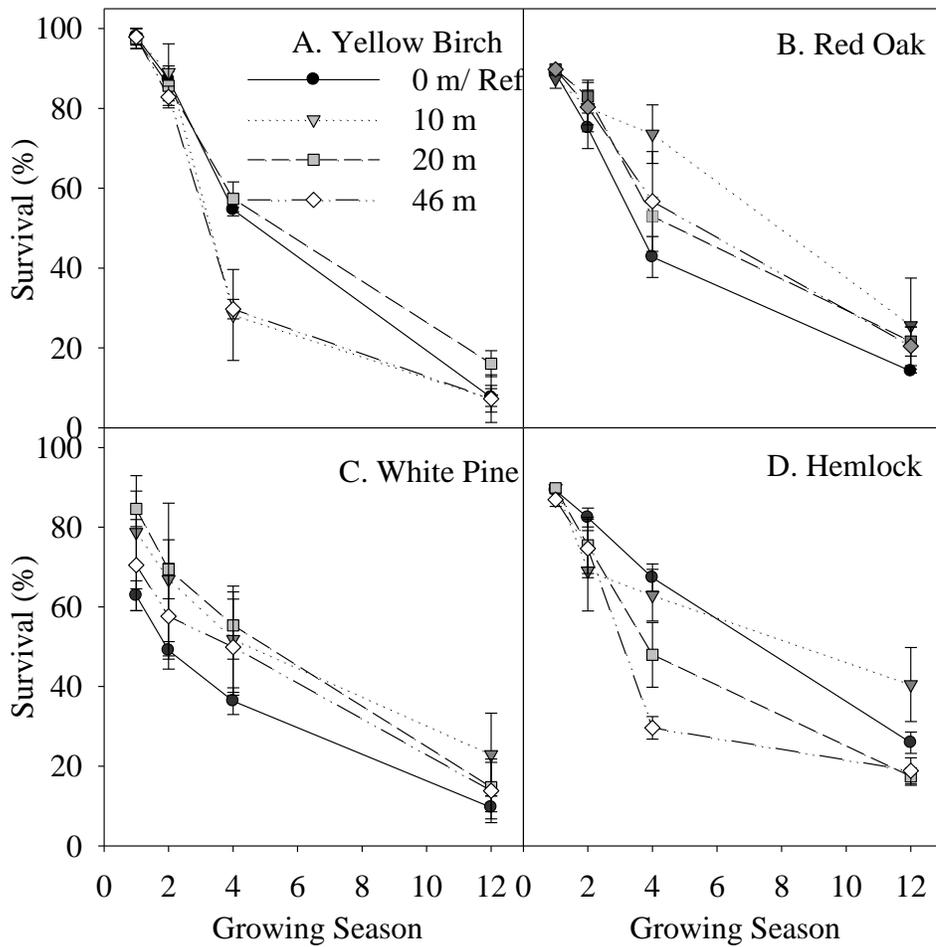
Table 3. Polynomial contrast test statistics (*t*-values) of planted tree species' growth response over gap size (6 levels: 0, 6, 10, 20, 30, and 46 m gap diameter classes) in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A.

	Polynomial	Growing	Yellow	Red	White	
Response	Contrast	Season	Birch	Oak	Pine	Hemlock
Height						
	Linear	1	2.91	1.92	0.88	2.3
		2	5.43	5.22	4.55	3.7
		4	4.59	5.3	7.35	4.09
		12	.	.	4.34	.
	Quadratic	1	1.54	1.13	-0.7	-0.68
		2	2.57	2.92	1.01	0.05
		4	2.5	2.69	1.09	-1.79
		12	.	.	1.71	.
	Cubic	1	0.98	0.24	1.53	0.88
		2	-1.27	0.53	0.77	-1.87
		4	-1.16	-1.49	-2.13	-2.3
		12	.	.	-0.42	.
Diameter						
	Linear	12	1.94	-0.65	4.38	1.42
	Quadratic	12	-0.19	-1.55	1.81	1.05

	Cubic	12	-0.19	-0.96	0.7	0.37
Mean Height Increment						
	Linear	1-4	4.74	6.72	4.3	<i>1.68</i>
	Quadratic	1-4	4.81	0.72	1.48	-1.4
	Cubic	1-4	3.1	-0.96	1.63	-1.2

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 .

Figure 1. Planted tree species' survival by gap size treatment in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. For ease of interpretation, the 6 m and 30 m survival curves are not shown. (Growing season 12 survival is also illustrated in Fig. 2a for all gap sizes.)



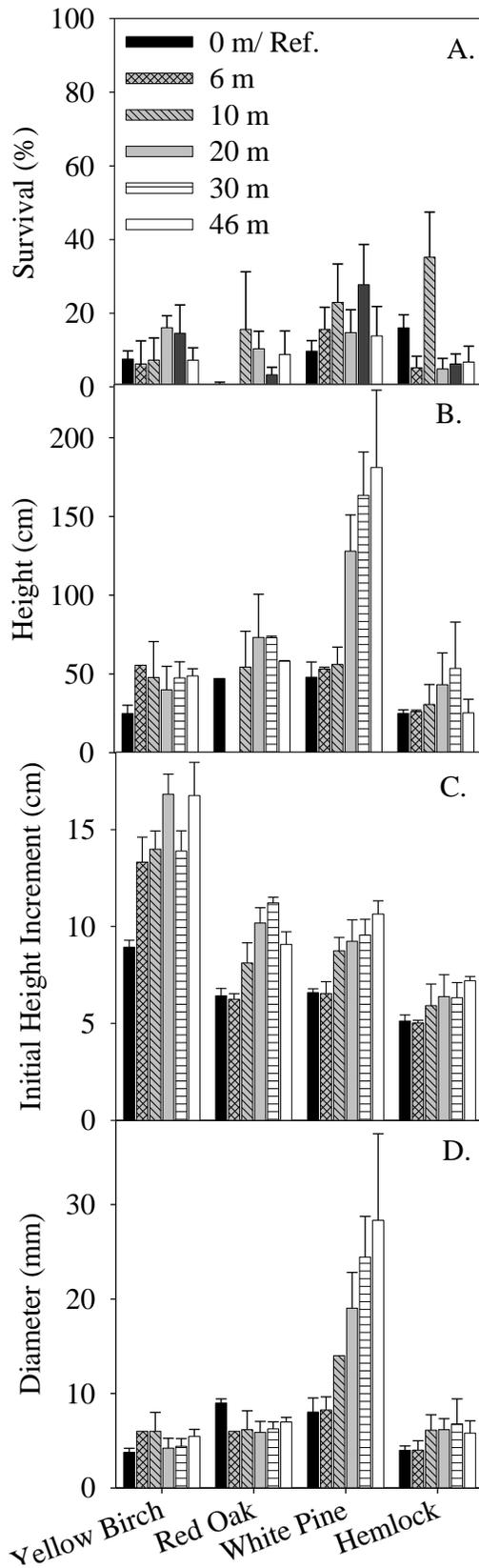


Figure 2. Planted tree species' growth and survival across gap size treatments in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. A. Percent survival by gap size in growing season 12. B. Mean height (cm) in growing season 12. C. Mean initial height increment (cm), or mean of current leader extension in growing seasons 1, 2, and 4. D. Mean stem diameter (mm) at 15 cm in growing season 12.

Figure 3. 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, U.S.A. For ease of interpretation, the 6 m and 30 m survival curves are not shown. (Growing season 12 height is also illustrated in Fig. 2b for all gap sizes.)

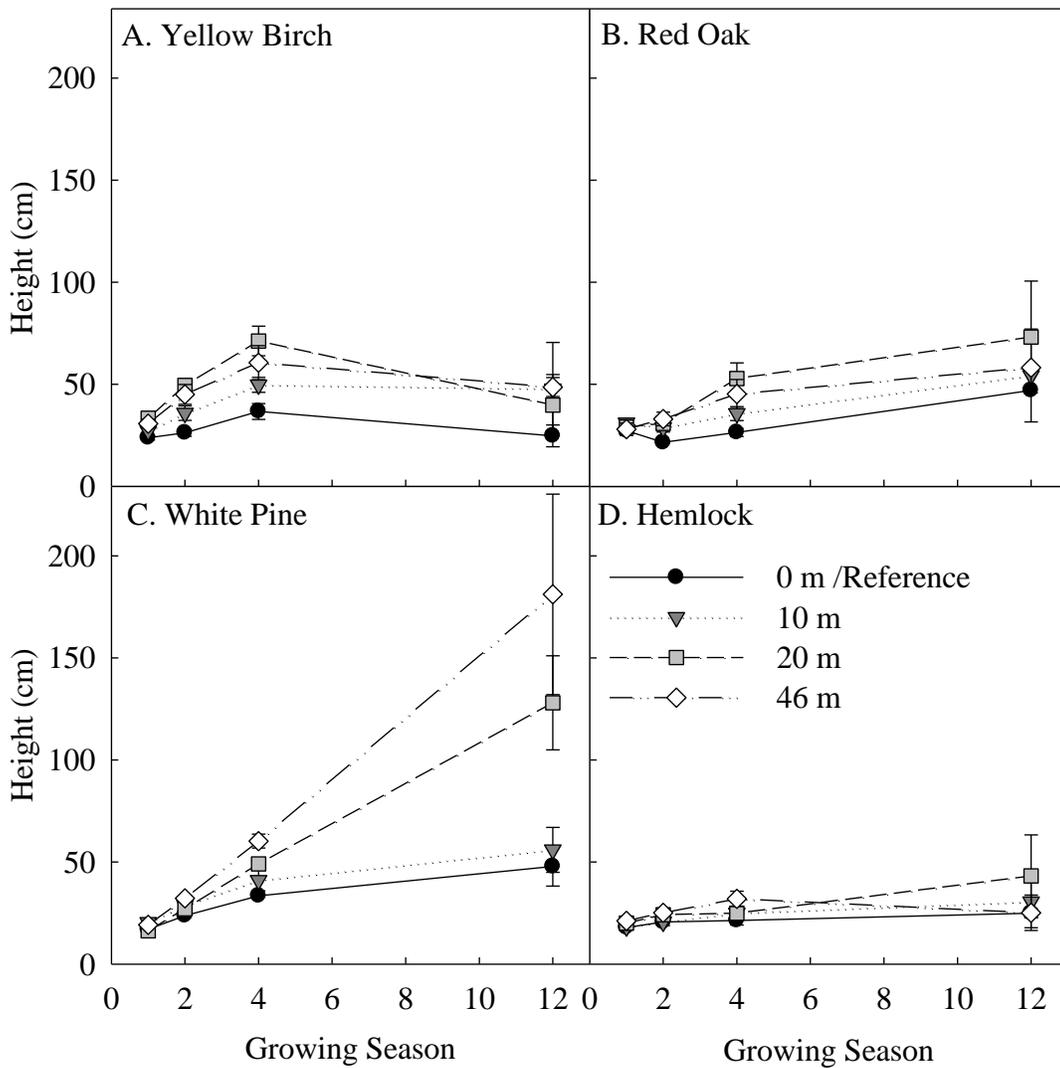


Figure 4. Raspberry abundance by gap size and growing season in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. Bars represent gap-level means (+ SE) and bar shading represents growing season.

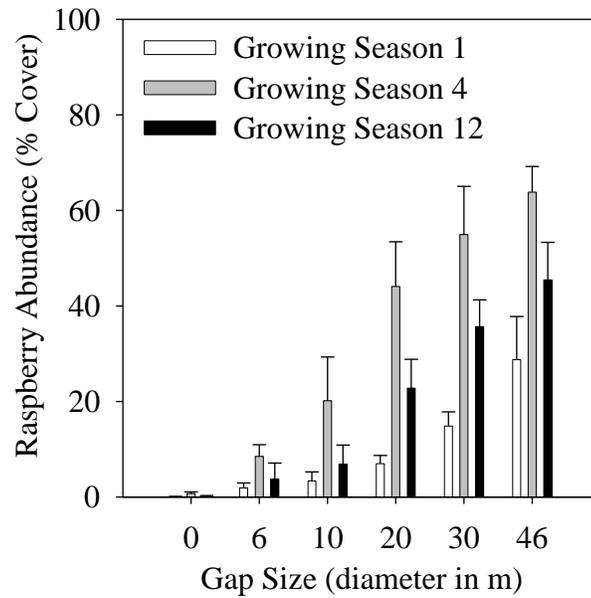
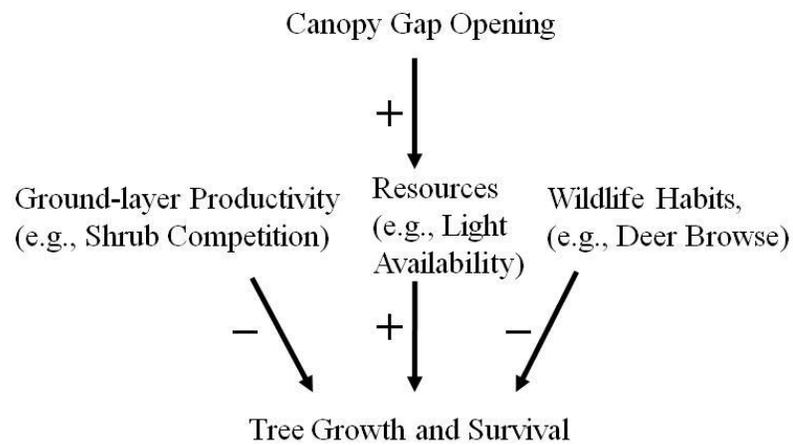


Figure 5. Conceptual diagram of study. Theoretically, the available resources in gaps are beneficial ('+') to tree growth and survival. However, other lifeforms may benefit from gaps, including increased ground-layer productivity and forage for wildlife. When considered alone, increased vegetative competition and deer browse are detrimental ('-') to tree growth and survival. However, when considered concurrently, the effect of multiple interactions on tree growth and survival are unclear.



**Chapter 3: Harvest gap size and proportion of forest area in gaps influence species
diversity of ground-layer vascular plants**

Chapter Summary

Biodiversity conservation in managed forests depends, in part, on management practices that promote components of diversity, such as species richness. In temperate forests the ground-layer vegetation represents a major component of plant diversity. Canopy gaps increase available resources and the range of microsite conditions in the ground layer, facilitating species coexistence. Patterns of harvesting can be manipulated to vary individual gap size and proportion of forest area in gaps, influencing the range and distribution of understory conditions, and thus potentially ground-layer plant diversity. We tested this hypothesis with a well-replicated gap-size experiment in a second-growth northern hardwood forest. We evaluated ground-layer vascular plant species richness within and among gaps of differing size, 13 years after an initial harvest. We also used a novel resampling approach to estimate how richness might vary in forests with differing gap sizes and proportions of forest area in gaps. Results from our field experiment showed that medium-sized gaps (20–30 m dia.) were most diverse, although all gap sizes (6–46 m dia.) had more species than uncut, closed forest understories. For all gap sizes, total species richness (aggregate) was largely composed of uncommon species that differed among individual gaps (β -diversity) rather than the common species that dominated individual gaps (α -diversity). In harvest scenarios created by resampling our empirical data, we found that gaps increased estimated species richness from closed forest and the magnitude of increase was associated with gap size and the proportion of forest in gaps. Overall, harvest scenarios with larger gaps resulted in higher and less

variable species richness estimates than forests with smaller gaps. Intermediate proportions of forest in gaps had more diversity than those with high or low proportions in gaps. Our results support the concepts that harvest-created gaps increase forest diversity in previously-unmanaged, second-growth forests and that gap size and their proportion in a forest can be manipulated to attain biodiversity goals.

Introduction

Global declines in biodiversity have prompted the need for site-specific conservation practices to sustain species assemblages (Dawson et al. 2011). Managing for biodiversity is challenging in forest ecosystems, because forests are expected to provide a wide-range of goods and services, such as commodities and recreation, in addition to biodiversity (Burger 2009). Success in sustaining productive forests that provide diverse ecosystem goods and services is measured by a multitude of metrics, including species richness in managed forests (e.g., Montreal Process Working Group 2009). Species richness, or the number of species per unit area, is a fundamental measure of biodiversity, representing the variety of species and their functional roles within an ecosystem (Diaz and Cabido 2001). Harvest-created canopy gaps represent one silvicultural practice that influences the species richness of managed forests. Canopy gaps influence species assemblages by increasing the available resources and the range of microclimate conditions compared to closed forest understories, allowing species with contrasting life-history traits, such as shade tolerance, to coexist (Leak and Wilson 1958, Leak and Filip 1977, Ricklefs 1977, Denslow 1980). Therefore, harvest-created gaps represent a management strategy for attaining multiple goals that include species diversity.

The association between canopy gaps and ground-layer species diversity is dependent upon individual gap size and proportion of forest area in gaps. Specifically, the Intermediate Disturbance Hypothesis (IDH) argues that disturbances intermediate in scale maintain the highest species richness (Connell 1978). At the scale of individual gaps, the IDH posits that small and large gaps have similar effects on ground-layer plant diversity. The extreme microclimate and high resource conditions of large gaps may be composed of a few dominant species, while the moderate microclimate and low resource conditions of small gaps may also be dominated by a few species, functionally different than those found in large gaps. However, medium gaps create resource conditions intermediate to small and large gaps, capable of supporting many species, including those also found in small and large gaps (Connell 1978). The same idea could be expressed at the forest scale as proportion of forest area in gaps, where highest diversity would be found at intermediate proportions. Some authors have argued that the IDH is the most applicable ecological framework for forest management and ground-layer plant diversity (Roberts and Gilliam 1995). Hence, gap size and proportion of forest in gaps are measures with potentially predictable effects on plant diversity that can be emulated in managed forests (Coates and Burton 1997).

Despite the potential for canopy gaps to aid in designing sustainable forestry practices, the relationship between harvest-created gaps and plant diversity has had little examination at gap and stand scales simultaneously. Gap-level studies have focused on ground-layer plant diversity and found that harvest-created gaps increase species diversity relative to uncut forest patches (Collins and Pickett 1987, Schumann et al. 2003,

Shields and Webster 2007). However, species diversity did not differ among gaps of differing size. The similar effects of gap size across these studies was attributed to different factors: land-use history (Schumann et al. 2003), irregular gap shape (Schumann et al. 2003), small gap sizes (Collins and Pickett 1988b) or microclimate moderation by residual trees (Collins and Pickett 1987, Shields and Webster 2007). Therefore, it remains unclear whether the IDH framework is applicable to harvest gap size, such that gaps intermediate in size can increase gap-level species diversity more than small or large gaps.

Stand level studies have typically focused on gap size effects on plant diversity through conventional management approaches that use harvest-created gaps. For example, selection cuttings create small or large canopy gap openings through dispersed single-tree or group harvesting, respectively. Forests managed with these practices were similar in stand-level diversity of ground-layer plants (Metzger and Schultz 1984, Falk et al. 2008, Smith et al. 2008), suggesting that changing gap size at the stand level had no effect on species diversity. It is not clear from comparisons of only two stand-level gap size treatments whether the IDH is applicable to harvest-created gaps, because a greater range of gap sizes is needed in the humped-shaped curve proposed in the IDH.

In addition, studies of ground-layer plant diversity in managed forests have not directly tested the effects of proportion of forest that is in gaps. Canopy disturbance in managed forests is typically quantified by other measures such as percent canopy openness and basal area. In some managed forests, harvesting that increased canopy openness increased herbaceous species richness (Zenner et al. 2006, von Oheimb and

Hardtle 2009). Intermediate canopy openness did not maximize species diversity but the size of openings was not constant among levels of canopy openness. Furthermore, in studies where gap size was controlled (e.g., in selection cuts), basal area was sometimes equal (Smith et al. 2008) and sometimes unequal (Metzger and Schultz 1984, Falk et al. 2008), leaving the interaction between individual gap size and the proportion of forest in gap, if any, unclear. We are not aware of any study that simultaneously linked individual gap and stand scales to examine stand-level diversity in the context of the IDH. This information is paramount to understanding how components of harvest design, such as gap size and proportion of forest in gaps, can serve as mechanisms to increase stand-level diversity.

Here, we test the applicability of IDH concepts for designing harvest patterns to increase diversity of ground-layer vascular plants in a northern hardwood forest. To examine the effect of individual gap size, we use a robust field design that included circular, harvest-created gaps that were cleared of trees and tall saplings, differed in area by two orders of magnitude, and were replicated randomly across a uniform site. To estimate forest-level diversity, we use a resampling approach to extrapolate our empirical gap data to harvest scenarios that emulate forests with varying gap sizes and proportions of forest in gaps (% gap). Based on early, gap-level results (Strong et al. 1998), we expected that gaps will increase diversity from uncut forest conditions and, among gap sizes, intermediate gap sizes will maximize diversity, supporting the IDH. Based on the IDH, the gap size and % gap could have a synergistic effect on species richness for harvest scenarios, where medium gap sizes at intermediate % gap result in higher species

richness than smaller or larger gap sizes and % gaps.

Methods

Study site

The study ecosystem is a 136 ha second-growth, northern hardwood forest located in the Chequamegon-Nicolet National Forest in northern Wisconsin, U.S.A (T40°N R12E). 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.

Regionally, the natural disturbance regimes of northern hardwood forests are primarily characterized by canopy gap disturbances. Low intensity disturbance events (10–19% canopy removed) that create small canopy gaps (mean gap areas of 12–121 m²; mean upper limit <250 m²) tend to affect <10% of typical stands per decade (Tyrrell and Crow 1994, Dahir and Lorimer 1996) and are pathways for canopy recruitment for >60% of trees (Frelich and Lorimer 1991). More moderate disturbances (30–60% canopy removal) are estimated to occur once during the lifetime of a tree cohort (300–390 years) (Frelich and Lorimer 1991) and result in gap area distributions with maxima at ≈ 5000 m² and distribution tails with $\approx 50\%$ <40 m² and $\approx 9\%$ >500 m² (Hanson and Lorimer 2007).

The study ecosystem was inventoried in 1993 to describe site conditions. Sugar maple (*Acer saccharum*) dominated the site. There were 12 other tree species and also 6 shrub, 23 herb and forb, 6 fern and clubmoss, and 1 sedge species identified. Tree basal area ranged from 20 to 39 m² ha⁻¹ and tree density ranged from 89 to 285 trees ha⁻¹. The

forest canopy was closed with an occasional small canopy gap created by recent single-tree blowdown. The topography 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) by Kotar et al. (2002).

Treatments

Four relatively uniform areas were delineated within the study site as blocks for a randomized complete block experiment with subsampling. Blocks were subdivided into 0.4-ha sections of which 18 were randomly assigned to one of six gap diameters (0 [reference area], 6, 10, 20, 30, and 46 m gaps) thrice (3 replicates gap size⁻¹ block⁻¹). Experimental gaps were created by dormant-season timber harvesting in 1994 (2 blocks) and 1995 (2 blocks). The resulting design consisted of 12 reference areas (0.4 ha square, uncut patches) and 56 experimental gaps (four marked gaps were not cut). Gap openings were measured in 1997 and 2008 from gap center to dripline in cardinal and sub-cardinal directions (8 total radii). In 1997, gap area ranged from 9.9 m² to 1986 m² (gap diameter to canopy height ratio [D:H] range from 0.1 to 2.2). By 2008, 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 those that have minimal potential to gain economic value before the next harvest entry in 20 years. The thinning reduced the forest matrix density to a mean basal area of $23 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 1.8 \text{ SE}$), while reference areas remained uncut at $31.1 \text{ m}^2 \text{ ha}^{-1}$ (± 0.3).

Sample plots

Sample plots (1 m^2) were arrayed in four transects radiating in cardinal directions from gap centers to $>7 \text{ m}$ into the adjacent forest matrix (the “forest-gap transect”). In reference areas and 30 and 46 m gaps, sample plots were spaced 5.5 m apart along transects. Sample plots were spaced 3.7 m apart in 6, 10, and 20 m gaps. In these plots, we assessed vascular plant species (including trees less than 0.5 m tall) for abundance by cover class: 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%. Individuals were identified to species except the following six genera: *Botrychium*, *Carex*, *Galium*, *Viola*, *Equisetum*, and *Fragaria*. Nomenclature follows PLANTS Database (2009). Field data were collected during mid-summer (late June–early August) over four survey periods: pre-harvest (1994 [2 blocks]–1995 [2 blocks]) and post harvest in 1997, 2000 (2 blocks)–2001 (2 blocks), and 2008. Only 2008 data, the $\sim 13^{\text{th}}$ year after harvest, were analyzed in this study.

Data analysis

Size categories.—Many diversity measures are sensitive to sampling effort

(number of sample plots), so we reclassified the gap-level diameter classes into four broader categories of closed, small, medium, and large gaps to minimize sampling effort differences and increase overall sample sizes. “Closed” gaps were the uncut reference areas (only 0 m sample plots). Because ground-layer composition was similar among 6 and 10 m gap diameter classes (Kern et al., submitted), we combined their sample plots into a “small” gap category. “Medium” gaps included plots from the 20 and 30 m gap diameters, while only the 46 m gap diameters were categorized as “large” gaps. The medium and large gap categories encompassed similar ranges in gap area and D:H (unpublished data, Kern). Medium and large gaps categories used only plots located in gap openings, because, in a prior study, composition in openings differed from the adjacent forest matrix in 20, 30, and 46 m gaps (Kern et al., submitted). The closed, small, medium, and large gap size categories yielded 300, 246, 199, and 189 sample plots, respectively, from the field experiment. We considered a finding of maximum species diversity in medium gaps as support for the IDH.

Additive diversity partitioning.—We evaluated the effect of gap size on species diversity using additive diversity partitioning. Additive diversity partitioning breaks total species richness into additive components comparable at multiples scales in the same units (e.g., number of species) as outlined by Lande (1996) and Veech et al. (2002). We partitioned diversity at three scales following the experimental design (Fig. 1): sample plot (α_1), gap or closed patch replicate (“replicate” hereafter) (α_2), and gap size (α_3) in aggregate across the site.

We partitioned three species diversity indices (equations in Lande 1996): richness

(S_{obs}), Shannon diversity (H_{obs}), and Simpson diversity (λ_{obs}). These measures weigh rare species high to low, respectively. Thus, we interpreted these indices to represent the diversity of all, dominant, and very dominant species, respectively. We used PARTITION 3.0 software (Veech and Crist 2009) to partition the diversity measures, specifying our unequal sampling efforts and equal sample plot weight. Significance tests were computed with 1,000 replications of individual-based randomization on richness. For Shannon and Simpson diversities, we used sample-based randomization because our abundance data were based on cover, not individuals. To facilitate interpretation of Shannon and Simpson indices, we present results as “effective number of species” by $\exp(H_{\text{obs}})$ and $1/\lambda_{\text{obs}}$ transformations, respectively, which convert indices into units comparable to richness (Jost et al. 2010).

Rarefaction.—As another measure of diversity, we used sample based-rarefaction to compare gap size by the number of species encounters. The process of rarefaction averages random resampling of pooled individuals or samples within a defined area, providing a measure of diversity without the influence of unequal sampling or species’ densities (Denslow 1995, Gotelli and Colwell 2001). Because the rarefaction curves did not reach asymptotes, we estimated rarefaction curve asymptotes with a non-parametric species richness estimator, the first-order jackknife procedure. We used 1,000 randomizations and default settings in EstimateS 8.2 software (Colwell 2006) to calculate rarefaction curve and jackknife estimates. We compared curves and estimates with 95% confidence intervals.

Validation of gap size effects.—To determine if sample size influenced our field

experimental results, we compared results of analyses based on the complete, unequal sampling efforts (additive diversity partitioning and rarefaction) to analyses based on equal sampling efforts. To do this, we used a non-parametric approach, where we resampled the field experiment observations to generate multiple, random “subsets” of data for each gap size ($N = 1,000$). Subsets were created through random selection without replacement. The random selection of plots was also stratified by replicate to capture the heterogeneity among replicates and maintain inference at the study site scale. One-hundred and seventy five plots were selected for each subset with the SURVEYSELECT procedure in SAS 9.2 (SAS Institute Inc. 2008). Then, for each subset, we calculated species richness (α_3^* [* indicates estimation from re-sampling field observations]) with jackknife procedures using 1,000 permutations in BiodiversityR (Kindt and Coe 2005), an R software (R Development Core Team 2005) package built primarily on vegan (Oksanen et al. 2011) and Rcmdr (Fox et al. 2011) packages. The resulting richness estimates and distributions were compared by gap size using 95% confidence intervals and seven-number summary box plots, respectively.

Estimation of species diversity in forests.—We generated five harvest scenarios that varied in gap sizes and %gaps to estimate the species diversity of ground-layer plants in managed forests. In the first scenario, we varied proportion of forest in large gaps from 0 to 0.9 (1GF, see table in Fig. 4a) and, in the second scenario, we varied gap size at constant %gap (2GS, see table in Fig. 4b). In the third scenario, we varied the ratio of small to large gaps (3GR, see table in Fig. 4c), while in the fourth scenario we varied the number of gap sizes (4GN, see table in Fig. 4d). Our fifth scenario depicted four

silvicultural practices common in northern hardwood forests (5GM, see table in Fig. 5): no cutting, thinning, or age-class conversion through modified single-tree or group selection cutting. The focal scale of all scenarios was equivalent to our study site (136 ha). We considered a scenario finding with maximum species richness in intermediate gap measures (50% gap [1GF], medium gaps [2GS], 1:1 ratio [3GR], and 2 sizes [4GN]) to provide support for the IDH.

Similar to the resampling techniques used in the gap size validation analysis (see Methods/Data analysis/Validation of gap size effects), we resampled our field experiment observations to create data subsets ($N = 1,000$) for each scenario, where subsets had common sampling efforts of 175 plots that were selected with stratified, random sampling without replacement. However, in the scenario analysis, additional controls on plot selection within each subset were necessary; the 175 plots were allocated uniquely among gap sizes and gap fractions (following tables in Fig. 4 and 5). Then, for each subset, we estimated forest-level species richness (γ^*) of the ground-layer plants using jackknife procedures in BiodiversityR (same procedure as Methods/Data analysis/Validation of gap size diversity). This process was repeated for all scenarios. We used 7-number summaries (displayed as box plots) to compare species richness distributions of each scenario.

Results

Gap size effects on species diversity

Diversity among gap sizes.—Medium-sized gaps had the highest aggregate species richness (S_{obs}) at 74 species (α_3). Compared to medium gaps, small ($\alpha_3 = 70$) and

large gaps ($\alpha_3 = 66$) were slightly lower in species richness, but both were more diverse than the aggregate richness across closed forest patches ($\alpha_3 = 55$) (Fig 2a). These patterns among gap sizes were consistent regardless of whether species richness estimates were based on unequal (full dataset) or equal (resampled) sampling efforts (Fig 2a) or rarefaction (Fig. 3). However, when comparing species richness using Shannon (H_{obs}) and Simpson (λ_{obs}) indices, the effects of gap size on species richness were less distinct and ranged from 8 to 11 dominant and 5 to 8 very dominant species, respectively (Fig. 2b–c). In summary, medium gaps were most rich in species, but gap size differences were minimal when measured by dominant species only. The effects of gap size on species diversity suggest that the IDH is applicable to the full plant community, which includes all species regardless of their dominance in the ground layer.

Diversity within gaps.—Partitions of species richness (α_3) were similar within gap sizes ($P < 0.001$). Species richness within plots (α_1) composed a small portion (~10%) of the aggregate richness found in each gap size (α_3), while the heterogeneity of species richness among replicates (β_2) composed a large portion (57–70%) (Fig. 2a). Furthermore, partitions of Shannon and Simpson indices were largely composed of dominant species found within replicates (α_2), but the heterogeneity of dominant species among replicates (β_2) was significant ($P < 0.001$) in the medium and large gap sizes. Furthermore, the overall drop in species richness (α_3) from all species to richness of dominant and very dominant species (S_{obs} to H_{obs} and λ_{obs} , Fig. 2a–c, respectively) suggests that uncommon species comprise a large portion of the observed diversity found across all gap sizes.

Estimation of species diversity in forests

Harvest scenarios with a single gap size increased the estimated species richness relative to closed forest conditions. In scenario 1GF, including small fractions (>10%) of canopy in large gaps increased species richness by >10 species (~20%) relative to closed forest diversity in most (>90%) of the resampling subsets. Moreover, average estimated species richness peaked when forests were 50% (large) gap and was 37% higher than relative closed forest conditions (Fig. 4a). In scenario 2GS, estimated species richness means were similar in forests with medium or large gaps at common %gaps. Forests with small gaps resulted in highly variable and slightly lower species richness estimates that overlapped with closed forest and forests with larger gap sizes (Fig 4b). In summary, the estimated species richness in harvest scenarios with a single gap size was high (approximately 80–90 species) at intermediate %gaps with larger (medium or large) gap sizes. These results suggest that the IDH is applicable to gap size effects on species diversity at the forest-scale when measured by proportion of forest in gap and, in part, by gap size.

Harvest scenarios with multiple gap sizes had variable effects on estimated species richness. In scenario 3GR, mean estimated species richness changed by only a few species (~80–84 species) when two gap sizes were used in various ratios, but the overall range of richness values decreased by a third as proportions of large gaps increased (Fig. 4c). In scenario 4GN, species richness ranges and maxima increased by 47 and 125% or by 3 and 17 species in forests with two and three different gap sizes, respectively, relative to scenarios with a single, large gap size. However, the mean

estimated species richness in these forests was similar (Fig. 4d). In contrast, when compared to forests with small gaps only, forests with multiple gap sizes had higher mean estimated species richness but similar richness estimates (Fig. 4d). The resulting species richness in harvest scenarios with multiple gap sizes suggests that adjusting both ratios and numbers of gap sizes results in minor changes to richness, which does not provide support for the IDH.

Harvest scenarios with canopy patterns similar to common management practices increased estimated species richness relative to no cutting alternatives (5GM, Fig. 5). The two conversion practices of modified single-tree and group selection were similar to each other in mean, 10th and 90th percentile of estimated species richness, although maxima reached 95 species in modified single-tree compared to 87 species in group selection. The two conversion cutting patterns also increased species richness more (~20%) than thinning patterns. Canopy patterns that emulated thinning increased species richness by 8%, with species richness estimates ranging from 54–86 species and a minima lower than no cutting (<60 species). These harvest scenarios suggest that canopy openness patterns of common harvesting practices increase diversity relative to no cutting and that conversion practices result in greater ground-layer diversity 13 years after the first entry than thinning practices.

Discussion

An understanding of the impacts of stand-level forestry practices on ground-layer plant species diversity is important to efforts aimed at restoring biodiversity to managed forests. Here, we tested the influence of manipulating both gap size and the proportion of

forest in gaps on ground-layer vascular plant species richness of a northern hardwood forest. Our novel approach used both observed gap-level and extrapolated forest-level data. One key finding was that harvest-created gaps increased ground-layer plant diversity compared to closed forest patches and that diversity increased most in medium gaps. Diversity differences among gap sizes was largely attributed to compositional heterogeneity among gap replicates, which captured uncommon species, and suggested that stochastic processes may be important to structuring gap diversity. Another key finding was that, at the forest-level, impacts of individual gap size on richness changed. Forests with only medium gaps did not have higher diversity than forests with only large gaps; rather, these forests had similar increases in species richness. Furthermore, forest-level diversity results highlighted the importance of %gap to species richness with intermediate %gap highest in diversity. Our findings also suggest that the effect of harvest-created gaps on ground-layer plant diversity were not transient, as the gap size effects presented here are the effects in the 13th year post initial harvest. We further discuss these findings in the following subsections.

Gap size effects on species diversity

Overall, the presence of gaps increased species richness from closed forest conditions, but the degree of increase depended on gap size. Other studies have found gaps increase the number of species by providing space and resources unavailable under closed forest canopy (Schumann et al. 2003, Galhidy et al. 2006, Naaf and Wulf 2007). In some contexts, gap size was important to species diversity; for example, diversity increased with gap size in European beech forests (Naaf and Wulf 2007) and Florida

scrubland communities (Menges et al. 2008). However, the effect of gap size on species richness has been negligible in other contexts due to resilience of preexisting vegetation (Collins and Pickett 1988b), gap treatments convoluted in shape (Schumann et al. 2003), or examination of a narrow range of gap sizes (Moore and Vankat 1986). Our study did not have these confounding factors: our study gaps were clear-felled, circular, and ranged widely in gap size. In contrast to past studies, we found that medium gap sizes were most species rich; as gap size increased, species diversity increased then decreased. The difference in diversity between medium and large gaps was likely due to the fewer number of dominant species in large gaps; a few species increased abundance at the cost of other species presence, thereby decreasing diversity. This result supports the Intermediate Disturbance Hypothesis (Connell 1978), where advantageous colonization traits are limited to a few species that can establish and persist in the extreme conditions of small and large gaps, but a mix of traits and species coexist in intermediate gap sizes. In our study site, larger gaps were correlated to high *Rubus idaeus* abundance (Kern et al., submitted). This shrub regenerates from persistent seed banks and grows at high densities that limit persistence of competing species (Donoso and Nyland 2006), thus, has the potential characteristics to decrease diversity (Decocq et al. 2004). Furthermore, large gaps have high resource availability and microclimate extremes that were likely detrimental to any pre-existing vegetation and limited species colonization to those species with seed dispersal by wind or animal or persistent seed banks (Naaf and Wulf 2007) (e.g., *Rubus*). Or, large gap conditions discriminated against species establishment in extreme conditions (e.g., Tubbs 1969).

Our additive partitioning results highlight that gap diversity was partly structured by stochastic processes. Gap diversity was composed, in part, of uncommon species, regardless of gap size (Fig 1 and 2), which were likely the result of dispersal or recruitment limitations. This finding supports the idea of species neutrality and randomness structuring species assemblages (Hubbell et al. 1999, Hubbell 2001). Gap studies in unmanaged forests have also detected the importance of uncommon species, but with little support for niche-related processes (Grau 2002, Obiri and Lawes 2004). Therefore, our research highlights that gap diversity is not completely a result of deterministic or stochastic processes; rather, our study supports concurrent mechanisms structuring ground-layer plant diversity in canopy gaps as found in another study (Fahey and Puettmann 2007).

Estimation of species diversity in forests

Surprisingly, harvest scenarios with only medium or only large gaps had similar species richness means and ranges at constant %gap (Fig. 4) even though our gap level results suggested that medium gaps were more diverse than large gaps (Figs. 1 and 2). Although these forest scale findings do not provide support for the IDH, our results are similar to results from other stand-level applications of gap size, where ground-layer species diversity did not differ between two gap sizes (Metzger and Schultz 1984, Jenkins and Parker 1999, Falk et al. 2008, Smith et al. 2008). Our results from the comparison of three gap sizes suggest that species diversity may reach a maximum threshold in forests with medium gap sizes, rather than the decreasing effect proposed in the IDH. Medium and large gaps may not differ at the forest scale because stochastic processes that likely

structure diversity within gaps may have marginalized gap size differences at the forest scale. Our findings suggest that forest scale application of medium and large gaps can be used similarly to maximize species diversity, creating flexibility to base harvest gap size on other management goals.

Furthermore, our harvest scenario results provide evidence for the IDH framework in terms of % gap. Intermediate proportions of forest in gap were most diverse (Fig. 4), whereas species diversity was lower when forests were mostly closed or mostly open with few species dominated each extreme condition. Other forest management studies have not simultaneously controlled for harvest gap size and proportion of forest in gap, so direct comparison of past research to our results is difficult. However, studies of stand-level silvicultural systems have suggested that treatments intermediate in intensity result in high diversity as well (Battles et al. 2001, Haeussler et al. 2002, Wang and Chen 2010), while others have detected a threshold effect (Pawson et al. 2006, Zenner et al. 2006). Our results tested a full range of % gap, facilitating the detection of the hump-shaped curve proposed in the IDH. Our harvest scenario results suggest the IDH framework is applicable to the proportion of forest in gaps and its relationship to ground-layer plant diversity.

Implications to forest management

Understanding how harvest patterns affect diversity is important to sustainable management. For instance, common forestry certifications use native species diversity as criterion to meet sustainable management guidelines. In unmanaged, second growth-forests like our study site, species diversity is typically low when compared to old-growth

and managed forests (Crow et al. 2002) and increasing species diversity is often a management goal. The common management practices that we depicted increased species diversity compared to the relatively uniform closed canopy conditions of unmanaged second-growth forests. In addition, our experimental framework provides managers with the potential direction and magnitude of change in species diversity when using gap sizes and %gaps attributes outside common practices.

Our study also depicted harvest-created gaps 13 years after the first entry into a closed forest composed primarily of native species. Stands managed with multiple entries, which result in gaps of different age, have homogenized the plant community to species that thrive on regular disturbance at some sites (Scheller and Mladenoff 2002, Decocq et al. 2004), but not others (Metzger and Schultz 1984, Kern et al. 2006). In addition, some forests managed with large gaps have resulted in invasion by exotic species (Burnham and Lee 2010). We were not able to test the effects of multiple harvests or the risks of harvesting near large source populations of exotics. However, our results suggest that maintaining undisturbed patches through cutting cycles could help maintain native species diversity over time, because our forest scenarios with uncut forest patches increased diversity of ground-layer plants more than forests composed mainly of gaps. Undisturbed forest patches preserve late successional species and those slow to colonize in addition to many elements of biodiversity including structural complexity, as discussed by others (Battles et al. 2001, Smith et al. 2008). Nonetheless, our results illustrate that the effects of canopy gaps are not transient and influence ground-layer species diversity for at least 13 years after harvest.

Lastly, we examined two attributes of a harvest, gap size and %gap, and one value of plant communities within gaps, diversity. In practice, managers would likely be considering numerous factors in addition to gap size and %gap such as spatial location and arrangement of gaps in relation to site features (e.g., topography) and residual tree vigor, stem quality, and crown development. In addition, other values besides diversity may require additional tools and attributes to design management practices. For instance, recent work on selection system modifications for a range of goods and services include retention of gap seed trees (Shields and Webster 2007) and various sources of large woody debris (Smith et al. 2008). Recent reviews of gap-based silviculture (Coates and Burton 1997) and herbaceous layer response to management (Roberts 2004) both suggested that future research explore harvest disturbance extremes to provide a framework to guide management. Our results provide this within an ecological context and can be combined with other management tools to meet a wide range of goods and services.

Study limitations

The harvest scenario results provide unique insights into forest scale plant diversity under various management practices. However, the approach does have some limitations. First, the models were created from plots located in gap openings and/or closed, uncut forest. In reality, such conditions would also have “edge” conditions where side light and temperatures of the gap opening would be influencing conditions under closed forest adjacent to the gap. The edge condition would likely increase absolute estimates of species diversity in the harvest scenarios but the relative differences between

scenarios would likely be similar to our results. Second, scenarios with high %gap represented numerous large gaps surrounded by narrow strips of trees that were simulated with plots from large gaps and uncut, closed forest conditions. This approach would not represent the prevailing edge condition within strips of trees in a real landscape. In this situation, the influence of edge would likely decrease or be similar to the absolute estimates of species diversity to our results. However, the general patterns of %gap to species richness would likely remain.

Figure 1. Diagram of ground-layer vascular plant α -, β -, and γ -diversity within a canopy gap size field experiment in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A. Estimates of species diversity were partitioned additively among levels of the study design, such that diversity at cumulative gap size (α_3) equaled the sum of diversity within sample plot (α_1), among sample plots (β_1), and among gap replicates (β_2). Spatial extent of each level is noted in parentheses. The spatial extent of diversity within gap size (α_3) was ~136 ha, which represented diversity of gap sizes in aggregate across the study site. Because the study's inference was gap level, we did not directly analyze diversity among gap sizes (β_3). However, the variation in species among gap sizes (β_3) plus the diversity within gap sizes (α_3) equaled the total observed species richness (γ) in our field experiment. (Adapted from Chandy et al. 2006)

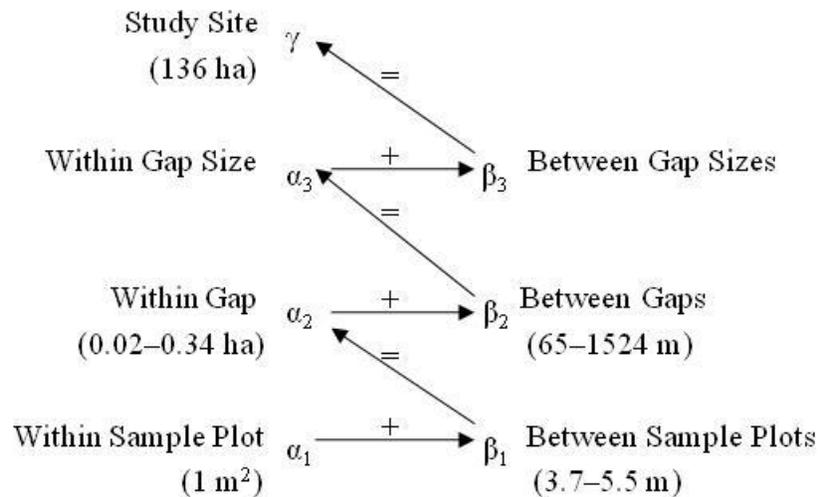


Figure 2. Ground-layer vascular plant diversity by canopy gap size in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A., 13 years after harvest. Stacked bars represent additive partitioning of (A.) species richness, S_{obs} , (B.) Shannon diversity, transformed to $\exp(H_{\text{obs}})$, and (C.) Simpson diversity, transformed to $(1/\lambda_{\text{obs}})$, where bars are shaded solid black, hatched grey, and solid white to represent diversity within sample plot (α_1), among plots (β_1), and among gap replicates (β_2) of aggregate gap sizes (α_3). Additive partitioning included complete sampling efforts of 300, 246, 199, and 189 sample plots in closed, small, medium, and large gap sizes, respectively. Box plots (A.) represent jackknife estimates of gap size species richness (α_3^*) at equal sampling effort (175 sample plots stratified by replicate and randomly-selected without replacement; $N = 1000$). The richness distributions (A.) are denoted with box and whiskers indicating the 10th percentile, lower quartile, median, upper quartile, and 90th percentile and with individual points indicating the outliers.

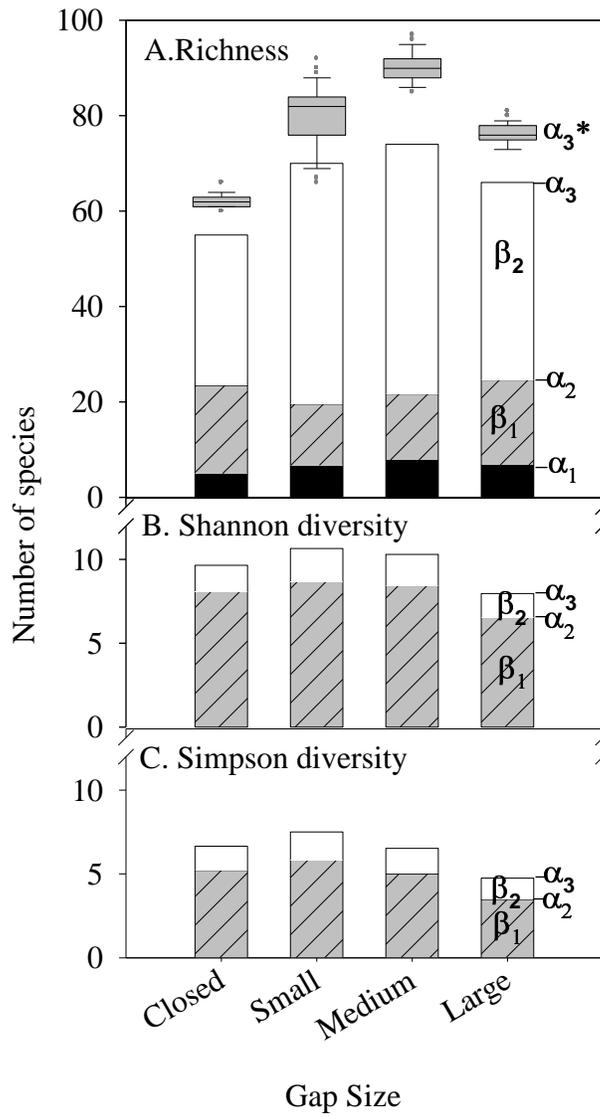


Figure 3. Estimates of ground-layer vascular plant diversity by canopy gap size in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, U.S.A., 13 years after harvest. Symbols are jackknife estimates of species richness ($\alpha_3 \pm 95\%$ CI; $N = 1000$) at cumulative species occurrences, where sampling effort was 300, 246, 199, and 189 sample plots in closed (circle), small (triangle), medium (square), and large (diamond) gap sizes, respectively. To aid interpretation, error bars are only illustrated for the final estimate of each gap size.

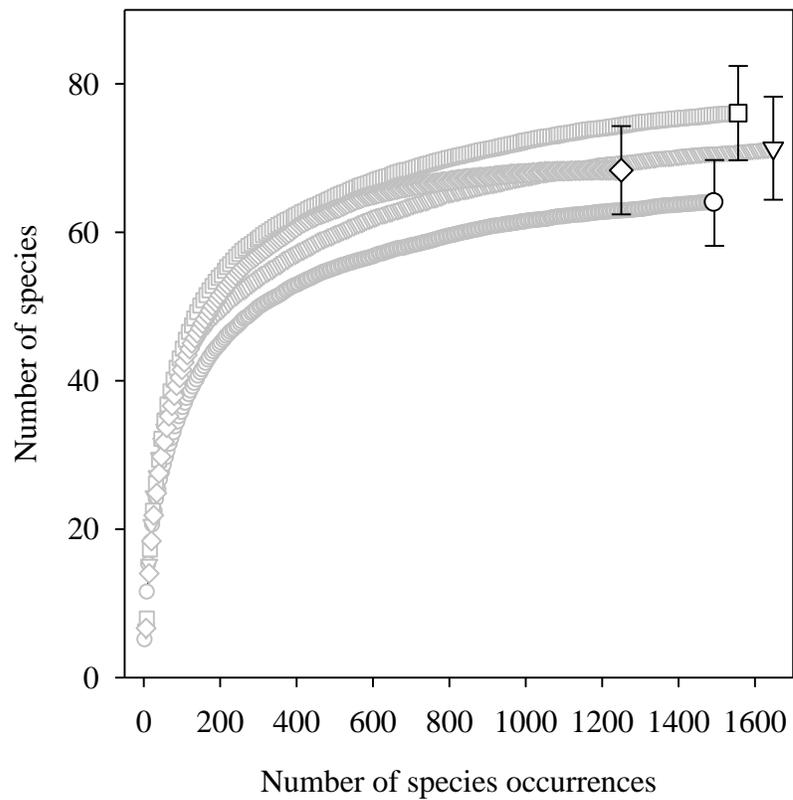


Figure 4. Box plots of ground-layer vascular plant species richness for harvest scenarios of varying gap sizes and total gap fractions in a northern hardwood forest 13 years after harvest. Jackknife procedures estimated forest species richness (γ^* , ~136 ha) at equal sampling effort (175 sample plots stratified by replicate and randomly-selected without replacement; $N = 1000$). The richness distributions are denoted with box and whiskers indicating the 10th percentile, lower quartile, median, upper quartile, and 90th percentile and with individual points indicating the outliers. A. Large gaps (L) by forest canopy gap fractions. C = Closed forest canopy. B. Small (S), medium (M), and large gaps by total gap fractions. C. Small to large gap ratios at 50% closed forest. D. Increasing number of gap sizes at 50% closed forest.

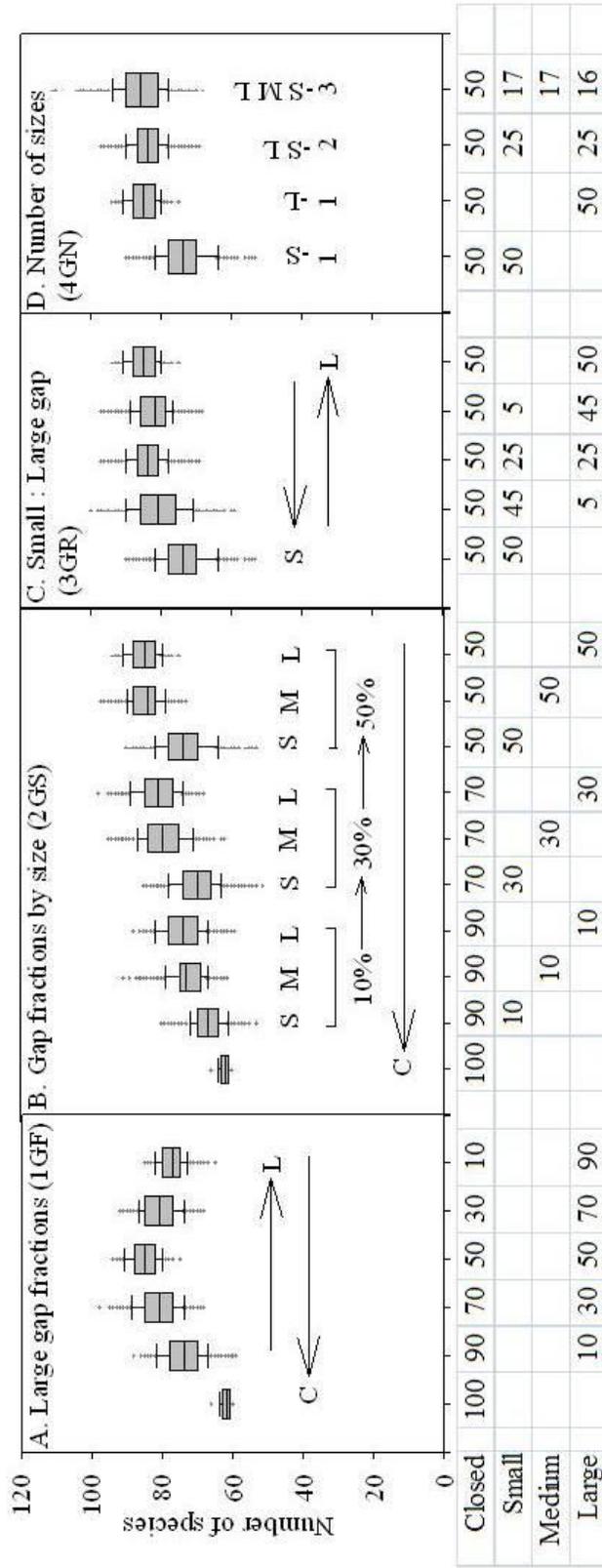
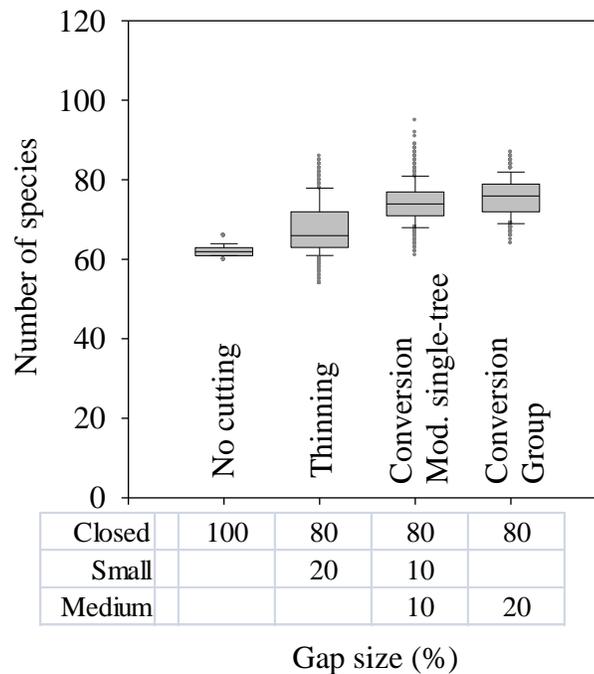


Figure 5. Box plots of ground-layer vascular plant species richness for harvest scenarios of management alternatives in a northern hardwood forest 13 years after harvest. Four common practices were depicted by canopy openness on the x-axis (left to right): no cutting, thinning, conversion by modified single-tree selection, and conversion by group selection. Jackknife procedures estimated forest species richness (γ^* , ~136 ha) at equal sampling effort (175 sample plots stratified by replicate and randomly-selected without replacement; $N = 1000$). The richness distributions are denoted with box and whiskers indicating the 10th percentile, lower quartile, median, upper quartile, and 90th percentile and with individual points indicating the outliers.



Conclusions

Experimenting with components of silvicultural systems to create forest conditions similar to patterns of natural disturbance is important to sustaining the goods and services that managed forests provide. Here, I, along with others, investigated harvest-created gaps, a management tool that creates stand spatial heterogeneity and influences the distribution of understory resources available to ground-layer plants. We tested the applicability of some theories devised from gap research in unmanaged forests to harvest-created gaps in a field experiment in northern Wisconsin. The robust experimental design provided a model system with more than a decade of repeated measurements beginning prior to gap creation and included experimental gaps that differ in area by two orders of magnitude. I learned the following:

>>Chapter 1: Ground-layer plant community composition and traits differed among gap sizes, within-gap locations, and over time. Species with smaller seeds, lower shade tolerance, later bloom times, shorter stature, and longer leaves were associated with higher light, more central gap locations, larger gap sizes, and greater time since gap creation. The correlation between gap size and ground-layer plant composition provided evidence for gap partitioning by the diverse ground-layer community in this temperate deciduous forest community.

>>Chapter 2: The strong relationship between gap size and plant community responses in Chapter 1 was not consistent for several individual species. The effect of gap

size on yellow birch, red oak, white pine, and hemlock growth and survival was marginalized by other factors that resulted in lower than expected growth and survival after 12 growing seasons. Evidence from deer exclosures and gaps with high shrub (*Rubus idaeus*) density suggested that browsing and shrub competition were mechanisms for the poor tree seedling performance. Therefore, for these species, gap partitioning evidence was weak and the study highlighted the management challenges of using gap size as a tool to influence future forest composition in forests that have overly abundant deer and pervasive shrub layers.

>>Chapter 3: Gap-level results from the field experiment showed that gaps intermediate in size (20–30 m dia.) had the most species, although all gaps (6–46 m dia.) had more species than uncut, closed forest understories. Furthermore, at the forest-level, the relationship between species diversity and gap size was different. Forests with medium or large gaps increased species richness similarly and were more diverse than forests with only small gaps. Forest-level diversity results highlighted the importance of the proportion of forest in gaps to species richness with intermediate proportions highest in diversity. We found that the Intermediate Disturbance Hypothesis was applicable to gap size at the gap level and, in part, to proportions of forest in gap at the forest level. Our results also illustrate that the effects of harvest-created gaps are not transient and influence ground-layer species diversity for at least 13 years after harvest.

This dissertation found that the Gap Partitioning Hypothesis and Intermediate Disturbance Hypothesis are useful frameworks to use in management with some caveats. The studies took place in a field experiment to isolate the effect of gap size; therefore, the

study gaps were clear-felled, circular, and wide ranging in gap size. In application, harvest-created gaps could contain residual trees, be more convoluted in shape, and be more uniform in size. Therefore, future research should consist of testing the effect of harvest-created gap sizes at an operational scale in managed forests. In addition, this study evaluated a decadal period after an initial harvest, but future work should focus on gap size and gap age as the patterns detected here could change with time and multiple harvests. Finally, deer browsing and shrub competition were identified as important factors that dampened gap size effects on tree regeneration. These effects do not necessarily confound canopy gaps at all sites; however, managers should be aware of local confounding factors including herbivores, non-native earthworms, invasive species, resilient preexisting vegetation, and potential recruitment limitations. This dissertation shows the range of effects from harvest-created gaps and can be used in combination with other management tools to maintain a range of goods and services in managed forests.

Management Applications

Silvicultural roots to the Divide Canopy Gap Study

The Divide Canopy Gap Study was established following a legacy of northern hardwood silviculture in the Lake States. The research started in 1926 when cutting-edge research on uneven-aged silviculture, an alternative to the commonly practiced, exploitive cuttings in the region, was established by the Lake States Forest Experiment Station (now part of the Northern Research Station) on the Dukes (a.k.a. Upper Peninsula) Experimental Forest (EF). By the 1950s, selection silviculture was established as a productive management approach in northern hardwood forests that sustained timber yield, where “growth balances cut” (Eyre and Zillgitt 1953). Uneven-aged management guides and trainings were developed (Arbogast 1957) and influenced the management practices of many major landowners at that time (e.g., National Forests, Menominee Indian Reservation, Goodman Lumber Company, American Can Co., U.S. Steel).

During the 1960s, forestry began moving into the Production Forestry Era (1960 - 1990); research and management emphasized high forest productivity with even-aged silviculture (Seymour and Hunter 1999). In the northern hardwoods of the Lake States, even-aged methods were tested and shown to be feasible and productive for the northern hardwood forest (e.g., Godman and Tubbs 1973), unlike the turn-of-the-century exploitive cuttings. However, selection silviculture research continued.

During the Production Forestry Era, adaptations of uneven-aged approaches to convert even-aged stands to uneven-aged stand structures were developed. Gus Erdmann, research silviculturist at the Argonne EF, recognized a hybrid approach to uneven-aged management, where a single-tree selection approach is supplemented by area-based group cuts, or harvest gaps, to regenerate trees (Erdmann 1986). Publishing this idea was important because trees were not regenerating adequately through single-tree removals. This observation came from long-term monitoring of single-tree selection treatments at varying residual basal areas in second-growth forests, where the heavier cuts (lower residual basal areas) resulted in larger openings and better stocking of saplings. As a result, Erdmann recommended the creation of 30-40 ft. (10-12 m) harvest gaps throughout the stand (~10% of stand area with a max tree age of 100 years and a 20-year cutting cycle) that were cleaned of poor quality saplings (>1" DBH) and applied in conjunction with established guidelines for single tree selection (Erdmann 1986). In light of the profession's push to focus largely on even-aged management in many other forest types during this time period, uneven-aged management remained the predominant management approach in northern hardwood forests of the Lake States (Jacobs 1987).

By the early 1990s the ecological forestry paradigm became widely popularized (e.g., Franklin 1989) and the issue of maintaining and restoring biodiversity was elevated in importance in the profession of forestry. All silvicultural systems were being evaluated in a new light. Single-tree selection systems were known to increase shade tolerant species (Smith et al. 1997, Nyland 2002). Although maintaining tree diversity in Lake States northern hardwood forests has always been ideal (Eyre and Zillgitt 1953),

management practices other than selection were rarely applied. To address this limitation, Lake States silvicultural research had focused on increasing or maintaining yellow birch in uneven-aged stands. Yellow birch is an economically valuable species and, when multiple-use legislation of the 1960's changed the forestry profession to focus on wildlife, soil, and water, in addition to timber, regenerating yellow birch became even more important for wildlife habitat. One suggested approach in uneven-aged management to incorporate less tolerant species, such as yellow birch, into a stand of predominately shade tolerant species is group selection. A group selection treatment was tested in the 1926 experiment in the old growth forests at Dukes EF and resulting gaps <0.1 ac. (0.04 ha) regenerating greater yellow birch abundance than larger gaps, where shrubs were the dominant vegetation. Similar patch cutting tests were implemented in second-growth forests at the Argonne EF in Wisconsin. Most openings were dominated by shrubs and grasses for at least 15 years post harvest and were not successful in recruiting trees of any species that were uniform distribution and size (Metzger and Tubbs 1971). More recent work on group selection cuts suggest that yellow birch establishment is associated with coarse woody debris, which is often missing in larger harvest gaps (Shields et al. 2007). This is contrary to a long history of success with larger gap sizes (0.1-0.4 ha) via patch cutting in northern hardwood forests of northeastern U.S., where patch cutting has successfully recruited shade-intolerant species, such as birches and cherries, into sugar maple and beech stands (Leak and Wilson 1958, Leak and Filip 1977). Patch cutting continues to be a dominant management approach with some major landowners in the northeast (e.g., White Mountain National Forest).

In light of the early recognition to diversify tree species in northern hardwoods of the Lake States, single-tree selection remained a popular choice for managers for decades. Early research clearly showed that single-tree selection would favor regeneration of sugar maple (Eyre and Zillgitt 1953). Sugar maple has been an economically valuable species and developing this species into high quality sawlogs has often been a management goal (Godman and Books 1971, Erdmann 1986, Strong et al. 1995). So, perpetuating this species had no negative effects in the near term on sustained-yield forestry in this forest type.

However, during the beginnings of the ecological forestry era of the 1990's, a more encompassing view of managing entire forest ecosystems was prevalent and current management regimes were being evaluated in terms of their influence on native biodiversity. For northern hardwood forests, selection practices were falling short of new expectations in structure (Kenefic and Nyland 2007, Gronewold et al. 2010) and composition (Crow et al. 2002). In the early 1990's, harvest gap size studies were limited to the couple group selection tests in the Lakes States that were only evaluated for tree regeneration. Uneven-aged management was at a critical time for further development and a time to revisit harvest gap size and its relationship to tree regeneration, tree diversity, shrub abundance, and overall plant community diversity. There may be a role for one or many harvest gap sizes in uneven-aged management when broader objectives include restoring biodiversity. Hence, Terry Strong, silviculturist, designed and established the Divide Canopy Gap Study in 1994.

Relevance of the study design to uneven-aged management of northern hardwood forests

In northern hardwood forests of the Lake States, harvest gaps (cleaned of trees >1 in. dbh) are used in uneven-aged management as an area-based tool to establish new age classes or cohorts and to increase or maintain stand tree diversity. In some cases, the purpose of harvest gaps is also created for maintenance or restoration of biodiversity (e.g., Silviculture Handbook #2431.5, State of Wisconsin, Department of Natural Resources, 2006). However, at the establishment of the Divide Canopy Gap Study in 1994, there was little empirical data to support harvest gap size relationships to cohort development or biological diversity. Evidence was limited to an initial group selection cuts, which suggested that gaps larger than 100 ft. (30 m) diameter were dominated by shrubs and grasses in old growth forests (Eyre and Zillgitt 1953) and, in second growth, potential regeneration failure with any gap size (Metzger and Tubbs 1971). In addition, field observations by Gus Erdmann (1986) suggested that gaps 30-40 ft. (10-12 m) could establish shade-tolerant cohorts. Therefore, the Divide Canopy Gap Study was created to evaluate harvest gap size effects on tree regeneration and plant diversity. The design includes uncut forest patches (1 ac. [0.04 ha]) and 5 harvest gap sizes. The 18 ft. (6 m) dia. gap treatment represent the average crown size of a mature sugar maple at the study site, while the 18-33 ft. (6-10 m) dia. gap treatments represented the range of canopy opening sizes in single-tree selection (where trees are removed singly or in groups of 2 or 3 trees). Based on past evidence and field observations, the 66 ft. (20 m) dia. gap treatment was anticipated to regenerate the most yellow birch and other midtolerant tree

species to increase stand tree diversity. The 66 ft. gap was also anticipated to increase diversity in the broader ground-layer plant community as well because larger gaps were anticipated to be dominated by shrubs (raspberry) at the expense of tree and herbaceous species persistence - - thereby, lowering diversity in larger gaps. In order to detect trends among harvest gap sizes, the harvest gap size treatments were extended to 150 ft. (46 m) dia.

The uncut patches and harvest gap size treatments were established in an unmanaged second-growth stand. This stand represented an opportunity for a first harvest entry aimed to both improve stand vigor and quality and begin converting the stand to an uneven-aged structure. In practice, this would be an “improvement cut” with harvest gaps. Improvement cuts remove trees anticipated to die from self-thinning, disease, or damage or have minimal potential to gain economic value before the next harvest entry (approximately 20 years) to develop quality in the established age class(es). The canopy openings created through improvement cuts alone are too small and ephemeral to develop new age classes or cohorts and is usually combined with additional harvest gaps, which facilitate regeneration or cohort establishment. Therefore, in order to make the study applicable to practice, the study treatments (uncut patches and harvest gaps) were embedded in a forest that was thinned following improvement cut methods. The thinning reduced stand basal area by 17 % in the forest matrix averaging 100 ft²/ac (\pm 8 ft²/ac (standard error)) (23 ± 2 m²/ha).

The responses highlighted in this dissertation were focused on the broad ground-layer plant community and several tree species of ecologic and economic concern. The

analyses of the ground-layer plant community were focused to explore the relationship between composition, function, and diversity and harvest gaps as measures of biodiversity among the gap sizes. The analyses of the planted trees species (yellow birch, red oak, white pine, and hemlock) were focused to identify optimal performance among the gap sizes and potential gap sizes to increase these species abundances when recruitment is not limiting. This is particularly important given the recruitment limitations affecting these four species across the region.

Inference limitations of the results

The recommendations from this study should be limited to sites similar to the study ecosystem. Interpretation of the results to forests dissimilar to the study site should be used with caution.

Study site description: The site consists of a 340 ac. second-growth, northern hardwood forest embedded in the Chequamegon-Nicolet National Forest of northern Wisconsin, U.S.A. The management history of the area was relatively unknown but notes at the Eagle River district office suggested that the forest regenerated after heavy cutting in the early twentieth century (similar to many forests in the region). In 1994, the forest was unmanaged (29 m²/ha basal area) and estimated to be 60 years old. Sugar maple (*Acer saccharum*) dominates the site (relative basal area > 0.76) but 17 other trees species, in addition, to 12 shrubs, 70 herbs and forbs, 15 fern and clubmoss species, and 18 grass, sedge, and rush species were identified during a releve prior to study installation. Soils are silt loam loess, overlying stratified sand and gravel (Strong *et al.*, 1994). The

habitat type is ATD (*Acer-Tsuga/Dryopteris*), a rich, mesic site well suited for sugar maple growth (Kotar *et al.*, 2002).

Therefore, this study represented a second-growth, unmanaged forest before harvest to 13 years post an initial harvest to improve the existing age class quality and development and to begin converting the stand to an uneven-aged stand structure with harvest gaps.

Pertinent results and recommendations for management

There are three key findings, one for each chapter, pertinent to the development of uneven-aged silviculture.

- 1) Ch1/Herb Composition: the ground-layer plant community composition moved away from uncut ground-layer plant composition as gap size and time since harvest increased. Spatially, the change in composition among harvest gap sizes was similar in direction towards raspberry dominance, or successional trajectory towards an early successional stage. In addition, the degree or magnitude of compositional change was related to harvest gap size, where larger gap sizes resulted in a greater compositional shift away from uncut conditions. Temporally, the ground-layer plant community composition shifted away from pre harvest conditions immediately at year 2 and remained different for the 13 year study period.

Operationally, harvest gaps are a tool to facilitate stand development when management objectives include conversion of an even-aged to uneven-aged stand structure. In practice, gaps larger than 80 ft. dia. are rarely implemented

by major landowners in the Lake States (e.g., national forests, state agencies, and Indian reservations) that use selection methods. This study provided empirical evidence that larger gaps facilitated regression of stand development to early succession and the dominance of shrubs. The evidence also supports the idea that the larger gaps are not operationally acceptable when the goal is to perpetuate tree dominance. In order to avoid regression to early successional stages in larger gaps, scarification would be necessary if seed trees are nearby for natural regeneration of less tolerant species. However, if the goal includes creating variability in ground-layer plant community composition between the developmental stages of stand initiation and stem exclusion, then a range of gap sizes would be recommended.

Recommendation: maintain existing practices that use intermediate gap size to maintain or restore species diversity while maintaining tree cover.

The results here specifically provide empirical data to support gaps 60 ft. (20 m) dia. (e.g., Wisconsin DNR silvicultural handbook) that are related to high species diversity and a compositional mix of trees, herbs, and shrubs in ground-layer plants.

Recommendation: when objectives include openings for wildlife, use harvest gaps >100 ft. (30 m) dia. Large harvest gaps facilitate shrub dominance and revert the parts of the stand to early successional patches conducive for some wildlife species. These gaps will maintain for small

mammal cover and wildlife food through the dominance of raspberry for at least 13 years.

- 2) Ch2/Planted tree seedlings: a limited amount of statistically significant results demonstrated that gap size affected the growth and survival of yellow birch, white pine, red oak, and hemlock, suggesting the potential for harvest gap size prescriptions to perpetuate established seedlings of these species. However, overall low survival and growth highlight that harvest gap size effects are of less importance to the performance of these species where shrubs are abundant and deer populations are elevated. In addition, of these trees surviving to year 13, most trees were of poor form and vigor (personal observation) such that most survivors had little chance to survive and grow to forest canopy height. A limitation to this study was the small number trees planted in each gap and the limited data collected on each tree over time. In addition, there was limited data available on the effects of raspberry abundance and deer browsing, making specific recommendations difficult without further investigation.

Operationally, the low survival and growth would not be acceptable.

Moreover, planting trees is not a conventional practice in northern hardwood management, which has traditionally relied on natural tree regeneration.

However, this work highlights some potential for planting in harvest gaps if additional tools (scarification, release, browse deterrents) are used to facilitate

survival and growth. This approach might be necessary in the future as all for study species have major recruitment limitations in the region. *Additional research will be necessary to make recommendations on planting and harvest gap size.*

- 3) Ch3/Ground-layer plant diversity: at the gap level, these results identified a non-linear trend between harvest gap size and species diversity, where maximum diversity was detected in gaps 66-100 ft. (20-30 m) dia. Furthermore, estimations of species diversity among common management practices suggested that using 66-100 ft. (20-30 m) dia. gaps in a first entry to convert from an even-aged to uneven-aged structure resulted in greater species diversity than thinning (crop tree release) practices. Furthermore, estimations of a multi-cohort approach, which uses a range of harvest gap sizes from small to large that emulate natural wind disturbance, resulted in the highest species diversity of all harvest scenarios.

Operationally, management goals are usually more complex than to just simply increase species diversity as demonstrated here. In practice, managers would also be weighing other objectives and management practices to meet forest goals. The work here highlights one measure of biodiversity, species diversity, and one parameter of designing sustainable forest management approaches, harvest gap size. Even so, if the goal is to maintain or restore

native biodiversity, managers should consider additional metrics of biodiversity and additional practices that follow principles of ecological forestry and emulate other aspects of natural wind disturbances (e.g., tip-up mounds, down and standing woody debris, and live trees).

Moreover, because species diversity is a measure of biodiversity, the effects of harvest gaps at a larger scale are important. The forest scale results from this study were estimates based on empirical data collected at the gap level. In addition, we could not account for the influence of other aspects of managed forest landscapes, such as skid trails and forest roads, which would also influence the patterns of species occurrence across this landscape.

Therefore, the relationship between harvest gap size and species diversity in operational scale treatments warrant further study to test the results from this study before recommendations can be made.

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APPENDIX A, Supplementary information for chapter 1 methods.

Modeled light methods.

We modeled light availability at the plot level using MIXLIGHT (v1.15), a light transmission model that calculates a growing-season average value at the microsite level (Stadt and Lieffers 2000). Input parameters included site information and species characteristics. For site parameterization, default site and sky conditions were used, except for longitude (45° 54' N), latitude (88° 50' W), date (May 15–September 15 in 1997 and 2008), and time (04:00–22:00), which were specified for the study site. Since our intention was to create a relative index of the light environment (not predict actual light environment at specified locations), parameters for species characteristics were based on published sugar maple data. When published results could not be found, parameters were estimated in the field. Species characteristics included crown shape (ellipsoid), crown class (<12.7 cm diameter at breast height [DBH] = Intermediate, ≥ 12.7 cm DBH = Codominant), height (< 18 cm DBH: $(DBH / 0.266)^{1/1.44}$; ≥ 18 cm DBH: $(DBH / 0.00546)^{1/2.87}$ (King 1986)), height to live crown (Height * 0.7), crown ratio $(1.65 + 6.37 * DBH / 100)$ (Canham et al. 1994), leaf area $(10^{(-0.01 + 1.434 * (\log(DBH))))}$ (Tucker et al. 1993)), and leaf inclination (1.4).

The model was run in two virtual forests, an uncut (representing reference area conditions) and a thinned forest matrix (representing conditions around experimental gaps). The virtual forests were based on DBH measurements collected from reference area and forest matrix conditions on the study site. The resulting virtual forests had stand

average growing season light transmission values at 1-m height of 2.8% (range: 0.2–7.7%) in the uncut and 5.2% (range: 0.7–10.4%) in the thinned forest matrix. The model was run once in the virtual, uncut forest for plot-level indices of the reference areas. To simulate experimental gaps, we used the harvest tool option in MIXLIGHT to create circular openings in the virtual, thinned forest. Harvest parameters were setup to (i) orient gap center and sample plot transects in a similar layout as in the field (e.g., Appendix A4) (ii) represent each experimental gap's average radius, and (iii) cut all trees within gaps regardless of species and size. The harvest tool and model were run twice, representing years 2 and 13 (years in which gap opening measurements were taken), to create plot-level indices for each experimental gap. The light values in the gaps were estimated at 1 m aboveground in circular openings and did not include shading of a potential sapling layer.

Model check for the assumptions of the Gap Partitioning Hypothesis.

To test for gap partitioning, two assumptions must first be met: a range of species with diverse traits must be available in the local species pool and canopy gaps must create a gradient of resources and microclimates in the gap understory (Brokaw and Busing 2000). Before we examined our central question about gap partitioning, we considered a model check of these assumptions as a methodological step necessary before data analysis. We checked assumptions by calculating descriptive summaries of the site's species pool and gap environments as follows.

Species pool

From our vascular plant field surveys, we identified a species pool of 119 species, plus six taxa not identified to species, for a total of 125 “species” (hereafter). Of these, one-third were found in 2% (i.e. 102) or more of the sample units (or matrix “cells”) and were used in analyses to test the GPH. The 39 species consisted of six lifeforms (*n* species in parentheses): ferns (4), graminoids (5), forbs (16), herbaceous vine (1), shrubs (3), and trees (10). In total, the 39 species represented 37 genera, 28 families and only one introduced species, *Stellaria media* (a forb). Potential leaf and seed length had maximum values of 160 cm and 30 mm, respectively. Shade tolerance ranged from 3 to 9 (tolerant to intolerant, on a scale of 1–9) and first month of bloom ranged from February to September. These data suggest that a range of species traits were available in the local pool met one of the assumptions of the GPH.

Gap microenvironments.—To determine if a range of conditions were created within and among the gaps, light was modeled based on gap dimensions. In addition, light availability was measured with quantum sensors (LI-190SB; Campbell Scientific, Inc., Logan, UT) in a subset of the gap centers between year 2 and year 6 to validate modeled light. Gap size influenced light transmission at gap centers, suggesting that our treatment design was extensive enough to create some resource and microenvironment heterogeneity among gap sizes. Modeled light also demonstrated within-gap variation with maximum light just north of gap center, suggesting that, at least in the large gaps, the experimental gaps potentially created within-gap light heterogeneity. These data suggest that a gradient of resources and microclimates were available in the gap understories and that our design met the assumptions of the GPH.

Details of analytical process used to select end solution of Non-metric Multi-dimensional Scaling

We chose the Non-metric Multi-dimensional Scaling (NMS) end solution using several principles: appropriate dimensionality, randomization tests, stability, and low stress (McCune and Grace 2002). First, we selected dimensionality based on examination of scree plots to identify when additional axes resulted in small reductions in stress. We further examined dimensionality with probability tests (Monte Carlo tests: $P < 0.05$) to determine if the real data resulted in lower stress for a given dimensionality than expected from chance (McCune and Grace 2002). This resulted in an end, three-dimensional solution significantly different from randomized runs of the data. Second, we examined stability using plots of stress versus iteration number to examine if stress stabilized with increasing number of iterations (McCune and Grace 2002). Our plots did show stability with a sharp, initial decline in stress that stabilized after the 27th iteration (out of 200). Third, we evaluated stress with several interpretive scales by Kruskal (1964), Clarke (1993), and McCune and Grace (2002). Our end solution had a total stress of 21.4, a sign of potential poor model fit by all three interpretive scales. Eliminating outliers and transforming (including relativizations) are ways to reduce stress (McCune and Grace 2002), but were not effective in reducing the stress in our analysis. Therefore, the high stress was a result of poor model fit that could lead to (i) misinterpretation of a solution that is no better than random chance or (ii) a result of high sample-unit heterogeneity from our sampling design. We were interested in using all 5042, 1×1 -m

plot-level sample units to determine if average trends in composition were possible given the heterogeneous understory conditions across the study site. To test if our high stress represented random chance or plot heterogeneity from our sampling design, we simplified the dataset to experimental unit centroids and reanalyzed the data with NMS. This reduced stress to 8.4, a more satisfactory result by all three interpretive scales. This post-ordination analysis suggested that the high stress of our end solution of 5042 sample units was a consequence of a small plot size (1×1 m) that detected high site heterogeneity and was not a result of a random configuration (Bruce McCune, personal communication). Therefore, we concluded that our end stress of 21.4 was acceptable to continue with analysis.

To determine if the ordination was skewed by a few highly abundant species, we ran another NMS analysis on a binary dataset that represented the 39 species' presence or absence in the 5042 sample units. Results from these data were similar in stress, overlays, and correlations to the abundance (cover) dataset suggesting that a few dominant species were not driving the compositional patterns. Because we were interested in using the results that incorporated both the presence and abundance of species in composition, we continued analysis with the species abundance data.

Evaluation of compositional partitioning.

We analyzed the ordination by gap size and location along the forest-gap transect with several approaches: correlations, descriptive statistics, non-parametric tests of group differences, and indicator species' importance values.

Correlations.—Correlations were used to evaluate broad trends in the ordination of species abundance data. The Kendall tau rank correlation coefficient (τ) was calculated to evaluate broad trends between ordination axes and explanatory variables: modeled light, gap size, location along the forest-gap transect, and survey year. Species, lifeform and plant traits were also examined to evaluate functional shifts in composition.

Gap size and location categories.—To evaluate compositional partitioning of the ordination, we classified each plot by gap size and location along the forest-gap transect. Gap size was categorized by year 2 gap diameters and labeled as “0 m”, “6 m”, “10 m”, “20 m”, “30 m”, or “46 m”. Location was assigned by creating 5m distance bins in each experimental gap from gap edge dripline into both gap center (positive distance classes) and the adjacent forest matrix (negative distance classes) using year 2 dripline measurements. This resulted in eight distance classes labeled by midpoints (relevant gap sizes in parentheses): “-12.5 m” (46 m only); “-7.5 m” (all gap sizes); “-2.5 m” (all gap sizes); “2.5 m” (all gap sizes); “7.5 m” (gap size ≥ 20 m); “12.5 m” (gap size ≥ 30 m); “17.5 m” (46 m only); and “22.5 m” (46 m only).

Gap partitioning through space.—We calculated descriptive statistics using centroids and 95% confidence intervals to determine if different gap sizes and locations along the forest-gap transect occupied different areas of the ordination space. We used multi-response permutation procedure (MRPP) to test for gap size and location group differences in PC-Ord v5.31 (McCune and Medford 2006), which accommodated our unbalanced design. Post-hoc pair-wise comparisons were made when group differences were detected ($P < 0.05$). Lastly, we used indicator species analysis (in PC-Ord v5.31) to

understand species associations with group differences detected with MRPP. Indicator values (0 to 100; no indication to perfect group indication) were calculated on both frequency and abundance with gap size and location along the forest-gap transect. Species were considered significant indicators of a group when $P < 0.1$ in a Monte Carlo procedure (McCune and Grace 2002).

Gap composition over time.—We examined whether change in gap composition through time was similar across gap sizes. To do this, we calculated vector lengths and azimuths of plots within gap openings and reference areas between year 0 and 13. Vector lengths and azimuths were tested for gap size effects in a mixed model ANOVA with gap size as a fixed factor and gap size \times block as a random factor in SAS version 9.2 (SAS Institute Inc. 2008).

Table A1. Species' trait data used in compositional analysis. Shade tolerance (Humbert et al. 2007), lifeform (USDA 2009), potential maximum height, leaf and seed length, and potential first month of bloom (Gleason and Cronquist 1991, Unknown 2009) were compiled for each species. Species traits were estimated in the field when published data were not found.

Lifeform	Family	Genus	Species	Maximum Height (cm)	Maximum Leaf Length (cm)	Maximum Seed Length (mm)	Shade Index (1= tolerant; 9= intolerant)	First Month of Bloom (Calendar month)
Fern	Dryopteridaceae	<i>Athyrium</i>	<i>filix-femina</i>	91	100	.	3	.
Fern	Dryopteridaceae	<i>Dryopteris</i>	<i>carthusiana</i>	91	50	.	3	.
Fern	Lycopodiaceae	<i>Lycopodium</i>	<i>obscurum</i>	30	0.5	.	3	.
Fern	Osmundaceae	<i>Osmunda</i>	<i>claytoniana</i>	183	160	.	5	.
Forb	Ranunculaceae	<i>Anemone</i>	<i>quinquefolia</i>	20	5	4.5	3	4
Forb	Araliaceae	<i>Aralia</i>	<i>nudicaulis</i>	50	15	3	5	5
Forb	Araceae	<i>Arisaema</i>	<i>triphillum</i>	150	20	10	3	3
Forb	Asteraceae	<i>Aster</i>	<i>macrophyllus</i>	120	30	1	5	7
Forb	Verbenaceae	<i>Phryma</i>	<i>leptostachya</i>	100	15	5	5	6
Forb	Onagraceae	<i>Circaea</i>	<i>alpina</i>	30	6	3	4	6
Forb	Onagraceae	<i>Circaea</i>	<i>lutetiana</i>	100	12	5	3	6
Forb	Rubiaceae	<i>Galium</i>	spp.	5
Forb	Liliaceae	<i>Maianthemum</i>	<i>canadense</i>	20	10	4	4	5
Forb	Apiaceae	<i>Osmorhiza</i>	<i>claytoni</i>	80	10	.	3	5
Forb	Polygonaceae	<i>Polygonatum</i>	<i>pubescens</i>	91	12	12.7	.	5
Forb	Caryophyllaceae	<i>Stellaria</i>	<i>media</i>	40	3	1.2	8	2
Forb	Liliaceae	<i>Streptopus</i>	<i>lanceolatus</i>	80	9	3	4	4
Forb	Primulaceae	<i>Trientalis</i>	<i>borealis</i>	20	10	0.5	3	5
Forb	Liliaceae	<i>Trillium</i>	<i>grandiflorum</i>	40	12	1.6	0	4
Forb	Violaceae	<i>Viola</i>	spp.	4
Vine	Liliaceae	<i>Polygonum</i>	<i>cininode</i>	200	10	3	6	6
Graminoid	Poaceae	<i>Brachyelytrum</i>	<i>erectum</i>	100	18	7.5	4	6
Graminoid	Cyperaceae	<i>Carex</i>	spp.	3
Graminoid	Poaceae	<i>Cinna</i>	<i>latifolia</i>	150	1.5	2.8	.	7
Graminoid	Poaceae	<i>Elymus</i>	<i>hystrix</i>	150	1.5	2	0	6
Graminoid	Poaceae	<i>Oryzopsis</i>	<i>asperifolia</i>	40	80	5	4	.
Shrub	Grossulariaceae	<i>Ribes</i>	<i>cynosbati</i>	152	5	4.5	4	5
Shrub	Rosaceae	<i>Rubus</i>	<i>idaeus</i>	213	20	2	7	5
Shrub	Caprifoliaceae	<i>Sambucus</i>	<i>racemosa</i>	300	15	5	5	5
Tree	Pinaceae	<i>Abies</i>	<i>balsamea</i>	2500	2.5	6	3	9
Tree	Aceraceae	<i>Acer</i>	<i>rubrum</i>	2500	10	9	5	3
Tree	Aceraceae	<i>Acer</i>	<i>saccharum</i>	3500	15	10	4	4
Tree	Betulaceae	<i>Betula</i>	<i>alleghaniensis</i>	3000	10	4.5	5	4
Tree	Oleaceae	<i>Fraxinus</i>	<i>americana</i>	3000	10	5	5	4
Tree	Betulaceae	<i>Ostrya</i>	<i>virginiana</i>	2000	10	5	.	4
Tree	Salicaceae	<i>Populus</i>	<i>tremuloides</i>	2250	10	6	9	4
Tree	Rosaceae	<i>Prunus</i>	<i>serotina</i>	2500	12	10	8	5
Tree	Fagaceae	<i>Quercus</i>	<i>rubra</i>	3000	20	30	7	4
Tree	Tiliaceae	<i>Tilia</i>	<i>americana</i>	4000	15	8	5	7

APPENDIX B, Supplementary information for chapter 1 results.

Partitioning along the forest-gap transect

Broadly, the ordination showed weak correlation to plot location along the forest-gap transects ($\tau = 0.19$). Although there was high variability ($A = 0.1-0.2$), Multiple Response Permutation Procedure (MRPP) detected locational differences along the forest-gap transect (distance classes ranged from -12.5 m into the forest matrix to 22.5 m into the gap center ($P < 0.0001$)). In pair-wise comparisons, reference areas were always different than forest matrix and gap opening locations in post harvest years ($P < 0.0001$). Whereas, forest matrix locations (-12.5 m, -17.5 m and -2.5 m distance classes) were always similar to each other but different from the reference area and gap opening locations (2.5 m–22.5 m distance classes, $P < 0.0001$)¹. Generally, gap edge locations, the 2.5 m distance class, were different in composition from more central gap locations ($P < 0.04$) in all years post harvest². The 2.5 m, 7.5 m, and 12.5 m distance classes were different from each other and from the two most central locations, the 17.5 and 22.5 m distance classes ($P < 0.003$), but the 17.5 and 22.5 m classes were not significantly different from each other in any year ($P > 0.1$)³. Regardless of gap size, location centroids differentiated between forest matrix and gap centers and from the reference areas.

¹ Although in year 13, without Bonferroni protection ($P = 0.001$), forest matrix positions closer to the gap edge, -2.5 m, were different than positions further into the forest matrix, -7.5 m ($P = 0.007$).

² After Bonferroni protection ($P = 0.001$), 2.5 m was not different from 7.5 m and 22.5 m in year 2 only

³ After Bonferroni protection, 7.5 m was not significantly different from 12.5 and 22.5 and 12.5 m was not significantly different from 17.5 m

Indicator species were identified for forest-gap transects locations. Central gap locations (12.5 m, 17.5 m, and 22.5 m distance classes) always included *Rubus idaeus*, *Phryma leptostachya*, and *Polygonum cilinode*. Forest matrix locations (-12.5 m, -7.5 m distance classes) and reference areas always included *Maianthemum canadense*, *Acer saccharum*, and *Fraxinus americana*. Indicator species were not identified for locations near the gap edge (-2.5 m, 2.5 m, and 7.5 m).

Interaction of gap size along the forest-gap transect

Although there was broad evidence for compositional partitioning as a function of plot location along the forest-gap transect, gap size had high correlation within the ordination ($\tau = 0.48$) of the explanatory variables. Therefore, we next examined how gap size affect the NMS score within each location along the forest-gap transect. To assess this, gap size composition was examined following stratification by location.

In forest matrix locations (-7.5 m and -2.5 m distance classes), the gap size centroids were similar with high variability in more interior locations (-7.5 m distance class), but, in forest matrix locations closer to the gap edge (-2.5 m distance class), the intermediate to large gap sizes (20 m–46 m) centroids were different than the smaller gap sizes centroids (6 m and 10 m; $A < 0.03$ – 0.05 , $P < 0.0001$; Fig. 4). Even with high variability, MRPP results detected gap size differences (except between 30 m and 46 m gap sizes) in the -7.5 m distance class in year 6⁴ ($A = 0.03$ – 0.06 , $P < 0.0004$). Year 6 indicator species for the -7.5 m distance class included *Stellaria media* (Indicator value (IV) = 7.9) and *Rubus idaeus* (IV = 23.6) around large gaps (30 m and 46 m gap sizes,

⁴ After Bonferroni protection, the 6 m was not different from the 10 and 20 m and the 20 m was not different from the 30 m.

respectively); however, by year 13, the indicator species *Carex* sp. (IV = 20.8) was important in the forest matrix of the 46 m gap size and no indicator species was detected for the 30 m gap size. The -2.5 m distance class also was marked by the presence of *Carex* sp. (IV = 18.5 - 19.9) in forest matrix of the 46 m in all years post harvest.

Within the gap opening, the gap edge location (2.5 m distance class) was the only location within the gap opening where all gap sizes could be compared. This location's centroids differentiated between the intermediate to large gap sizes (20 m, 30 m and 46 m) and small gap sizes (6 m and 10 m; $A < 0.08$, $P < 0.0001$) by years 6 and 13 (Fig. 4). *Osmorhiza claytoni* and *Rubus idaeus* were indicator species for the smallest (6 m, IV = 20.9–24.9) and largest gap sizes (46 m, IV = 21.5–25.1), respectively, in years 6 and 13.

Within the gap opening, the 7.5 m distance class of the intermediate to large gap sizes (20–46 m) was significantly different between gap sizes in years post harvest ($A = 0.01 - 0.04$, $P < 0.04$). In year 2, the 20 m was different than the 30 m and 46 m gap sizes, and, by year 13, the 30 and 46 m gap sizes were significantly different from each other as well. Indicator species with the highest importance values for the 20 m in year 2 and 13 were *Osmorhiza claytoni* (IV = 21.9) and *Viola* spp. (IV = 24.4), respectively. Whereas, *Rubus idaeus* (IV = 38) and *Carex* spp. (IV = 31) were important in the 46 m gap size in years 2 and 13, respectively.

The 12.5 m distance class was limited to only the 30 m and 46 m gap sizes. This location had overlapping gap size centroids, but MRPP still detected compositional differences between the 30 m and 46 m gap sizes ($A = 0.02$, $P < 0.02$). In year 13,

Dryopteris carthusiana had the strongest affinity for the 30 m gap size, while no indicator species was detected for the 46 m gap.

The 17.5 m and 22.5 m distance classes (within the gap opening) were only found in the largest gap size, 46 m, and could not be tested for gap size variability within these locations.

Forest-gap transects within each gap size

Since there was evidence for an interaction between location along the forest-gap transect and gap size, we next tested for partitioning along the forest-gap transect within a single gap. To assess this, composition along the forest-gap transect was examined following stratification by gap size. The smallest gap size, 6 m, had only one gap opening location (2.5 m distance class) in addition to two forest matrix locations (-2.5 m and -7.5 m distance classes), and, although the centroids tended to increase from forest matrix to gap opening locations, MRPP results were insignificant in all years.

The forest-gap transect of the 10 m gap size was similar to the 6 m (3 distance classes: -7.5 m, -2.5 m and 2.5 m), but, in the 10 m, composition along the transect was significantly different in year 6⁵ ($A = 0.02-0.03$; $P < 0.04$). Pair-wise comparisons in MRPP showed that the gap location (2.5 m) was different than the forest matrix locations (-7.5 and -2.5 m, $P < 0.003$). *Polygonum cilinode* was important to gap opening locations (IV = 36.3, 2.5 m distance class) and *Carex* spp. was important to interior forest matrix locations (IV = 28.8, -7.5 m distance class).

The forest-gap transect of the 20 m gap size was more extensive than the 6 m and 10 m gap sizes with four distance classes (-7.5 m, -2.5 m, 2.5 m, and 7.5 m). Location

⁵ Without Bonferroni protection, location along the forest-gap transect was significant in year 2 as well.

composition differed along the forest-gap transect of the 20 m gap size in all years post harvest ($A = 0.03\text{--}0.06$; $P < 0.0008$). Pair-wise comparisons found gap opening locations (2.5 m and 7.5 m classes) different than forest matrix locations (-7.5 and -2.5 m classes) in all years post harvest⁶. Indicator species were identified at the opposing ends of the forest-gap transect in year 13. *Phryma leptostachya* (IV = 39), *Rubus idaeus* (IV = 26.9), *Polygonum cilinode* (IV = 25.8), and *Dryopteris carthusiana* (IV = 25.8) had strong affinity for 20 m gap centers (7.5 m distance class); whereas, *Lycopodium obscurum* (IV = 8.2) was the only indicator species with significant association with interior forest locations (-7.5 m distance class) around 20 m gaps.

Composition also differed across the forest-gap transect of the 30 m gap size, which extended from the -7.5 m to 12.5 m distance class. In all years, gap opening locations were different from forest matrix locations ($A = 0.03\text{--}0.1$; $P < 0.04$). In year 6, gap opening composition differentiated between gap edge (2.5 m class) and gap center locations (7.5 m and 12.5 m; $P < 0.001$).⁷ End locations of the forest-gap transect had significant indicator species identified in year 13: *Rubus idaeus* (IV = 29.3), *Dryopteris carthusiana* (IV = 27.8) *Phryma leptostachya* (IV = 26.3), *Polygonum cilinode* (IV = 25), and *Stellaria media* (IV = 24.2) in gap centers (12.5 m distance class) and *Acer saccharum* (IV = 23.9) in the interior forest (-7.5 m distance class) around 30 m gaps.

In the 46 m gap size, composition differed between forest matrix and gap opening locations in all years post harvest ($A = 0.06\text{--}0.2$; $P < 0.0001$). In year 6 and 13,

⁶ With Bonferroni protection, the 2.5 m distance class was not different from forest matrix locations (-2.5 m and -7.5 m) in year 13.

⁷ Without Bonferroni protection, 2.5 m distance class was different from 7.5 m and 12.5 m classes in year 13.

composition within the gap opening was different between edge (2.5 m distance class) and center (12.5 m to 22.5 m distance classes) locations ($P < 0.04$)⁸. However, in year 13, composition within the gap opening differentiated even more, so that, composition was significantly different in every other distance classes ($P < 0.0004$). For example, the 12.5 m distance class was different from 2.5 m and 22.5 m distance classes but was similar to the adjacent 7.5 m and 17.5 m distance classes. Centroids of the 46 m positions displayed a gradient of compositional change along axis 3 from forest interior to gap edge to gap center locations (Fig. 3). Again, indicator species were identified for the opposing ends of the forest-gap transect. The 46 m gap center (22.5 m distance class) was marked by *Polygonum cilinode* (IV = 22) and the interior forest matrix (-12.5 m distance class) was marked by *Acer saccharum* (IV = 17).

Gap size partitioning

Since location along the forest-gap transect was not uniform across gap sizes, we specifically tested composition for only gap size partitioning. To do this, gap size composition was tested after stratification to gap opening locations (2.5 m to 22.5 m distance classes). Gap size centroids were different in all survey years post harvest, except the 6 m and 10 m which had overlapping confidence intervals throughout the study period (Fig. 2). The centroids also differentiated the most along axis 3, the major gradient, with the largest gap size, 46 m, most different from the reference areas.

MRPP results detected group differences in gap size categories for all years post harvest ($P < 0.0001$) as well, even though there was high variability, $A = 0.2-0.3$. In MRPP pair-wise comparisons, the 20 m, 30 m, 46 m, and reference area were different

⁸ Without Bonferroni protection, 2.5 m distance class was also different from the 7.5 m distance class.

from each other and other gap sizes ($P < 0.02$)⁹. The two smallest gap sizes, the 6 m and 10 m gaps, were not distinguished as separate groups throughout the study, except in year 6 there was significant pair-wise difference detected ($P = 0.04$ without Bonferroni protection ($P = 0.003$)).

Indicator species were found for all gap sizes post harvest. Some gap sizes had a common indicator species over all years post harvest: *Maianthemum canadense* in the reference area, *Osmorhiza claytoni* in the 6 m, *Aralia nudicaulis* in the 10 m, and *Rubus idaeus* in the 46 m. At the end of the study period (year 13), the highest importance values (22.4 – 26.5) were found for 46 m gap size indicator species, *Rubus idaeus*, *Phryma leptostachya*, and *Polygonum cilinode*, followed by 6 m gap indicator species, *Acer saccharum* (17.5) and *Osmorhiza claytoni* (20.8). While *Stellaria media* (11.6), *Trientalis borealis* (6.5), and *Polygonatum pubescens* (10.5) had lower importance values, they were still detected as significant indicators for the 30 m, 20 m and 10 m gap sizes, respectively, in year 13 (Table 1).

Cardinal direction of forest-gap transects

Cardinal direction (north, south, east, and west) of forest-gap transect locations was not an important group variable, except when composition was stratified by location in year 13. Direction was only important to the composition of edge locations (-2.5 m and 2.5 m distance classes) in year 13. The forest matrix location near gap edge, -2.5 m distance class, on the north side of gaps were marked by *Carex* sp. (IV = 22.5) and *Phryma leptostachya* (IV = 20.9) and was different ($A = 0.01$; $P = 0.008$) from south side

⁹ After Bonferroni protection ($P = 0.003$), only the largest gap sizes, 46 m and 30 m, and reference area were significantly different ($P < 0.0001$) from each other and from the other gap sizes in year 2.

locations (*Dryopteris carthusiana*, IV = 20.9). In the gap opening edge location (2.5 m distance class), the south gap edge was different from north and east gap edges ($A = 0.01$; $P = 0.035$). Indicator species for the south gap edge included *Dryopteris carthusiana* (IV = 29.1), whereas north and east were noted by *Polygonum cilinode* (IV = 17.3) and *Elymus hystrix* (IV = 14.9), respectively.

Table B1. Explanatory variables' correlations (Kendall's tau) to axis 1 and 2. Bolded numbers are significant (Bonferroni protection applied).

	Axis 1	Axis 2
Modeled Light	-0.044	0.072
Distance from Dripline	-0.032	-0.028
Gap Diameter	-0.031	0.049
Time Period	0.020	0.150
Maximum Height	-0.194	0.170
Maximum Seed Length	-0.173	0.117
First Month of Bloom	-0.153	-0.091
Tolerance Index	-0.014	0.029
Maximum Leaf Length	0.069	-0.032

Table B2. Species' correlations (Kendall's tau) to axis 1 and 2. Bold numbers are significant (Bonferroni protection applied).

Genus	Species	Axis 1	Axis 2
<i>Acer</i>	<i>saccharum</i>	-0.225	0.338
<i>Osmorhiza</i>	<i>claytoni</i>	-0.216	-0.308
<i>Viola</i>	spp.	-0.144	-0.415
<i>Phryma</i>	<i>leptostachya</i>	-0.126	-0.124
<i>Arisaema</i>	<i>triphillum</i>	-0.083	-0.112
<i>Fraxinus</i>	<i>americana</i>	-0.069	-0.297
<i>Sambucus</i>	<i>racemosa</i>	-0.066	-0.096
<i>Polygonum</i>	<i>cilinode</i>	-0.039	0.033
<i>Circaea</i>	<i>alpina</i>	-0.029	-0.084
<i>Osmunda</i>	<i>claytoniana</i>	-0.027	-0.038
<i>Elymus</i>	<i>hystrix</i>	-0.020	-0.037
<i>Rubus</i>	<i>idaeus</i>	-0.016	0.079
<i>Circaea</i>	<i>lutetiana</i>	-0.014	-0.055
<i>Prunus</i>	<i>serotina</i>	-0.009	0.022
<i>Athyrium</i>	<i>felix-femina</i>	-0.001	-0.078
<i>Ribes</i>	<i>cynosbati</i>	0.001	-0.012
<i>Cinna</i>	<i>latifolia</i>	0.002	-0.018
<i>Tilia</i>	<i>americana</i>	0.009	-0.013
<i>Polygonatum</i>	<i>pubescens</i>	0.010	-0.033

<i>Stellaria</i>	<i>media</i>	0.016	-0.048
<i>Galium</i>	spp.	0.017	-0.120
<i>Brachyelytrum</i>	<i>erectum</i>	0.023	0.038
<i>Trillium</i>	<i>grandiflorum</i>	0.030	-0.017
<i>Anemone</i>	<i>quinquefolia</i>	0.031	0.009
<i>Populus</i>	<i>tremuloides</i>	0.042	0.014
<i>Dryopteris</i>	<i>carthusiana</i>	0.053	-0.165
<i>Betula</i>	<i>alleghaniensis</i>	0.056	0.062
<i>Ostrya</i>	<i>virginiana</i>	0.069	0.023
<i>Streptopus</i>	<i>lanceolatus</i>	0.077	0.022
<i>Aralia</i>	<i>nudicaulis</i>	0.079	0.011
<i>Acer</i>	<i>rubrum</i>	0.096	0.147
<i>Quercus</i>	<i>rubra</i>	0.097	0.105
<i>Abies</i>	<i>balsamea</i>	0.124	0.083
<i>Lycopodium</i>	<i>obscurum</i>	0.130	0.228
<i>Aster</i>	<i>macrophyllus</i>	0.158	0.048
<i>Trientalis</i>	<i>borealis</i>	0.192	0.158
<i>Oryzopsis</i>	<i>asperifolia</i>	0.244	0.133
<i>Maianthemum</i>	<i>canadense</i>	0.430	0.223
<i>Carex</i>	spp.	0.559	0.110

Figure B1. Scatter plot of all 5042 sample units on axes 1 and 3. Preharvest (year 0) symbols follow the legend's shapes and are filled with grey. Postharvest (years 2, 6, and 13) symbols' shape and color follow the legend.

