

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

Christel C. Kern^{1,2,*}, Rebecca A. Montgomery², Peter B. Reich^{2,3} and Terry F. Strong⁴

¹ USDA Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA

² Department of Forest Resources, University of Minnesota-Twin Cities, 1530 North Cleveland Avenue, Saint Paul, MN 55108, USA

³ Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith NSW 2751, Australia

⁴ USDA Forest Service, USA, Retired

*Correspondence address. USDA Forest Service, Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 55744, USA. Tel: +1 218-326-7134; Fax: +1 218-326-7123; E-mail: cckern@fs.fed.us

Abstract

Aims

The Gap Partitioning Hypothesis (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. Few studies have examined gap partitioning of temperate, ground-layer vascular plants. We used a ground-layer plant community of a temperate deciduous forest in northern Wisconsin, USA, as a model system to test whether the GPH extends to the relatively species-rich ground layer.

Methods

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). The data were observations of ground-layer plant abundance, published plant traits, and a modeled index of understory light environments. We ordinated the plant abundance data and evaluated the relationships of composition, traits and light environment by gap size, location along the forest-gap transect and time, with several approaches such as correlations, descriptive statistics, non-parametric tests of group differences and indicator species importance values.

Important Findings

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 (46 m) also displayed within-gap compositional gradients from gap edge to center locations. Compositional differences in gap size were evident 2 years after gap creation and, contrary to our hypotheses, remained different over the 13-year period, even in gaps with crown closure. In contrast to the 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 and traits provides evidence for gap partitioning by the diverse ground-layer community in this temperate deciduous forest community.

Keywords: herbaceous layer • experimental gaps • proximity to edge • functional diversity • plant traits

Received: 06 Dec 2011 Revised: 18 April 2012 Accepted: 22 April 2012

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) (Denslow 1980; Ricklefs 1977) 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; Chandrashekara and Ramakrishnan 1993; Whitmore 1989) and temperate (Gray and Spies 1996; Holladay *et al.* 2006; Minckler and Woerheide 1965; Runkle 1998; Sipe and Bazzaz 1995) forests. In some forests, no clear evidence for niche partitioning in gaps has been found (Busing and White 1997; Coates 2002; Hubbell *et al.* 1999; Lieberman *et al.* 1995; Schnitzer and Carson 2001). Instead, tree species 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 (Busing and White 1997; Coates 2002; Denslow 1995; Schnitzer and Carson 2001), or were related to pregap composition (Dietze and Clark 2008; Uhl *et al.* 1988). 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 pregap 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 (Collins and Pickett 1988a; Moore and Vankat 1986) or pine-oak forest (Schumann *et al.* 2003) understories. This could indicate that (i) the theory does not hold in these contexts of those studies, (ii) the range of openings examined may not have differed enough to identify partitioning (Collins and Pickett 1988a; Moore and Vankat 1986) 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 a state more similar to undisturbed conditions). We use associations between species traits and gap characteristics to identify possible partitioning mechanisms, with the expectation that light will be an important mechanism in this closed-canopy forest.

MATERIALS AND 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, USA (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* in 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 (Dahir and Lorimer 1996; Tyrrell and Crow 1994) 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 ≈50% <40 m² and ≈9% >500 m² (Hanson and Lorimer 2007).

Study design

The experiment was established in a randomized complete block. 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 (two blocks) and 1995 (two blocks). 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 m² ha⁻¹ [±1.8 SE]). Reference areas remained uncut at 31.1 m² ha⁻¹ (±0.3).

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 4 years. The responses analyzed in this study showed no relationship with deer exclosures; consequently, the data were combined into the larger data set.

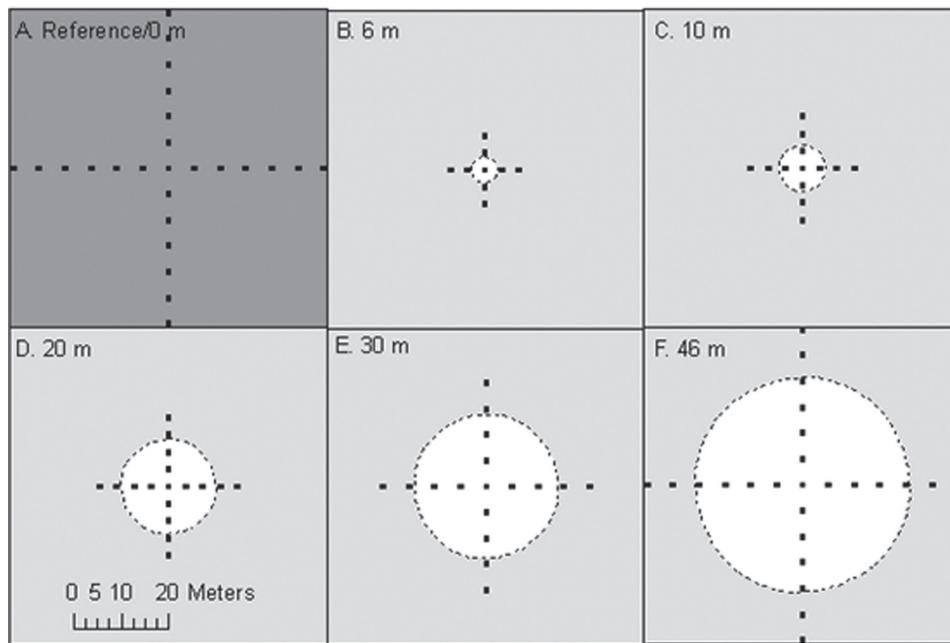


Figure 1: gap sizes and plot layout. Each panel represents a 0.4 ha square, the size of the reference area. (A) Uncut reference area (0.4 ha). (B–F) Experimental gaps embedded in a thinned forest matrix (gap diameters are labeled in each panel). Black, filled squares represent sample plot (1 × 1 m) locations 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 and 46 m gaps, sample plots were spaced 5.5 m apart along transects, and, in 6, 10 and 20 m gaps, sample plots were spaced 3.7 m apart.

Data collection

Community composition

We used the study design to measure fine-scale plant community composition by surveying permanent sample plots (1 × 1 m, the sample unit) for vascular plants (including trees <0.5 m tall). Plots were arrayed in four transects radiating in cardinal directions from experimental gap centers to >7 m into the adjacent forest matrix (the ‘forest-gap transect’; Fig. 1). We assigned species (taxonomy according to the PLANTS Database (USDA NRCS, 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: preharvest (1994 [two blocks]–1995 [two blocks]; ‘year 0’ hereafter) and postharvest in 1997 (‘year 2’ hereafter), 2000 (two blocks) or 2001 (two blocks) (‘year 6’ hereafter) and 2008 (‘year 13’ hereafter)).

Plant traits

We compiled widely available traits by species (Table S1). Traits included shade tolerance, life-form, potential maximum height, leaf and seed length and potential first month of bloom and were reported by community-weighted means (Lavorel et al. 2008), except for life-form, which was evaluated by plot-level dominance of all life-forms 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. 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 to 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: $(\text{DBH}/0.266)^{(1/1.44)}$; ≥18-cm DBH: $(\text{DBH}/0.00546)^{(1/2.87)}$ (King 1986)), height to live crown (Height * 0.7), crown ratio $(1.65 + 6.37 * \text{DBH}/100)$ (Canham et al. 1994), leaf area $(10^{(-0.01 + 1.434 * (\log(\text{DBH})))})$ (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, (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.

Data analysis

Model check for the assumptions of the GPH

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 S1). Both assumptions were clearly met.

Ordination

We then conducted compositional analysis with Non-metric Multidimensional 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 (>3.5 SD from the average distance [Sørensen measure of similarity] among sample units) and rare species (presence in $<2\%$ of the sample units). 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).

We chose the 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 whether 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 whether 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- \times 1-m plot-level sample units to determine whether trends in composition (in response to gap size and position) were possible given the heterogeneous understory conditions across the study site. To test whether our high stress represented random chance or plot heterogeneity from our sampling design, we simplified the data set to block means and reanalyzed the data with NMS. This reduced stress to 8.4, a more satisfactory result by all three interpretive scales. This postordination analysis suggested that the high stress of our end solution of 5042 sample units was a consequence of a small plot size (1 \times 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 whether the ordination was skewed by a few highly abundant species, we ran another NMS analysis on a binary data set that represented the presence or absence of the 39 species among the 5042 sample units. Results from these data were similar in stress, overlays and correlations to the abundance (cover) data set, 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.

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', '6', '10', '20', '30' or '46 m'. Location was assigned by creating 5-m-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). We analyzed the ordination by these gap sizes and locations along the forest-gap transect categories, with several approaches such as 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 τ 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, life-form and plant traits were also examined to evaluate functional shifts in composition.

Gap partitioning through space

We calculated descriptive statistics using centroids and 95% confidence intervals of sample units to determine whether different gap sizes and locations along the forest-gap transect occupied different areas of the ordination space. We used multiresponse 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 (with Bonferroni correction, $P < 0.003$) 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; ranging from 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).

RESULTS

Ordination of the ground-layer plant community showed differences that support the GPH; moreover, this 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. S1) 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 S2. Axis 1 and 2 results are presented in Tables S2–3. For visual 2D presentation, we used axis 1 as the minor gradient.

Gap partitioning through space

We found strong compositional shifts that were associated with gap size. The composition of gap openings differed significantly from reference areas ($P < 0.0001$), and the magnitude of that difference increased with gap size (correlation to axis 3, $\tau = 0.48$; Fig. 2). In years 2 and 6, all pair-wise combinations of gap size also significantly differed in composition ($P < 0.0001$), except the 6, 10 and 20 m were similar in composition to each other ($P > 0.01$). By year 13, gap composition remained different among the gap sizes ($P < 0.0001$), except the 6 m from the 10 m ($P = 0.57$).

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 ($\tau = 0.19$) was weaker than gap size 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 pair-wise comparisons within 46-m gaps, gap opening locations were significantly different from each other at 10-m intervals ($P < 0.0001$), whereas adjacent locations (5-m intervals) were not ($P > 0.01$); 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 ($P > 0.03$) but significantly different from the reference areas and gap opening locations ($P < 0.0001$).

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, 30 and 46 m) gaps (Fig. 4C). However, mid-gap locations far from dripline did not differ among the three large gap sizes (Fig. 4D and 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 for larger gap sizes and slightly weaker for smaller gap sizes 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

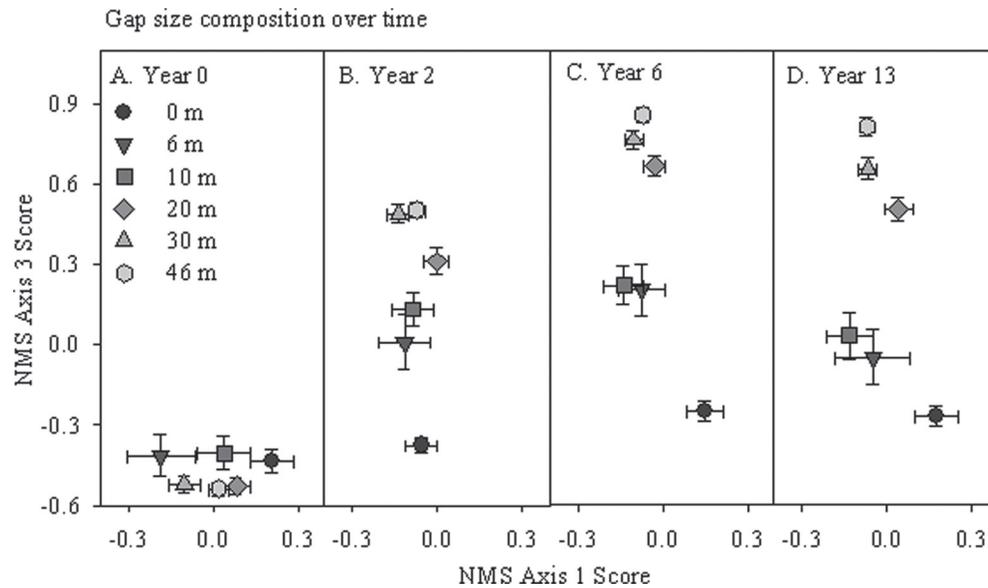


Figure 2: centroids ($\pm 95\%$ confidence intervals) of gap size ground-layer vegetation composition by survey year in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Gap size centroids were based on plots located within gap openings and excluded adjacent forest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

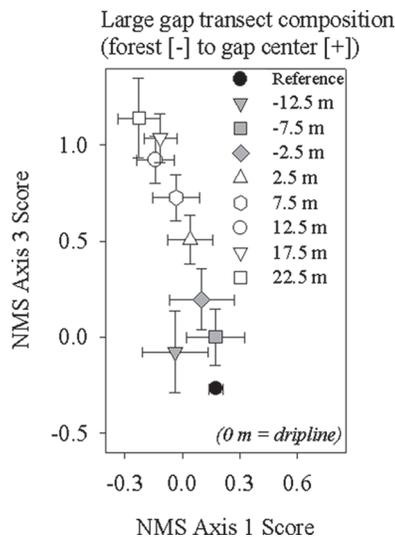


Figure 3: year 13 centroids ($\pm 95\%$ confidence interval) of ground-layer vegetation composition in reference areas and locations along the 46-m forest-gap transects in a northern hardwood forest in the Chequamegon-Nicolet National Forest, Wisconsin, USA. Symbols represent distance from dripline (0 m) into the adjacent forest matrix (negative numbers) or into the gap opening (positive numbers).

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 pre-harvest and reference conditions. The change in small gaps composition was intermediate to that in 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 and larger gap sizes 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*, *Phryma leptostachya*, *Dryopteris carthusiana* and *Carex* sp. abundance also showed positive relationships with axis 3 ($\tau = 0.50$, 0.50 , 0.23 and 0.21 ; $P < 0.0001$). Indicator species were found for all gap sizes postharvest. Some gap sizes had a common indicator species over all years postharvest: *Maianthemum canadense* in the reference area, *Osmorhiza claytonii* in the 6 m, *Aralia nudicaulis* in the 10 m and *R. 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 *P. cilinode*, and the adjacent forest matrix was associated with *A. 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.

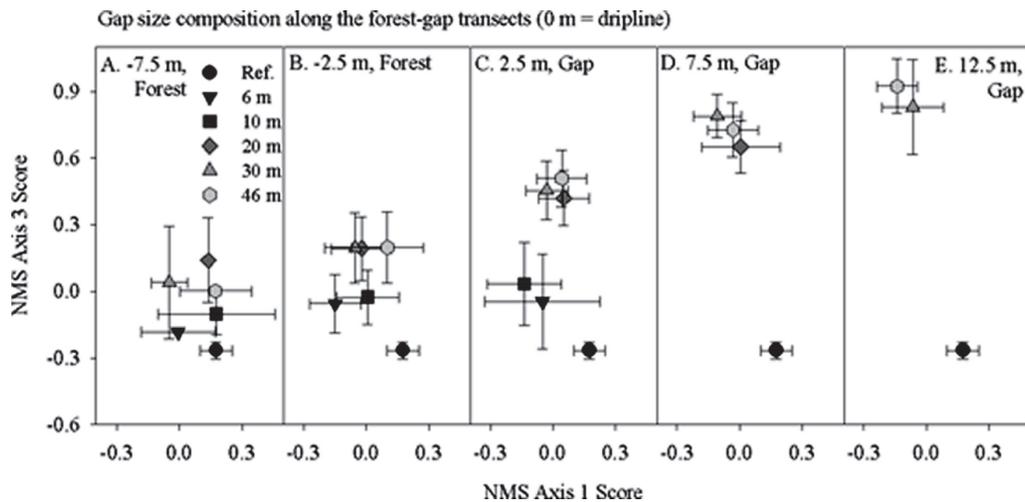


Figure 4: year 13 gap size centroids ($\pm 95\%$ confidence interval) of ground-layer vegetation composition along forest-gap transects in a northern hardwood forest in the Chequamegon-Nicolet National Forest, Wisconsin, USA. Panels represent distance from dripline (0 m) into the adjacent forest matrix (-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]).

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 and 0.23, respectively; $P < 0.0001$), whereas maximum height and seed length relationships were negative ($\tau = -0.43$ and -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 and 10 m) and among intermediate to large gaps (20, 30 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, more central gap locations, larger gap sizes and later years of the 13-year study period. The trait correlations also illustrate high trait diversity in relation to gap size.

Furthermore, the relative proportions of life-forms in the sample units diverged along the major gradient. Axis 3 scores were correlated positively to shrubs and negatively to trees ($\tau = 0.42$ and -0.46 , respectively; $P < 0.0001$). The life-form 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 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 (Denslow 1980; Ricklefs 1977). 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 gap partitioning within gaps varied among gap sizes to influence ground-layer composition (Figs 3 and 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 among the gap sizes were evident in year 2 and continued to differentiate into year 6. By year 13, composition remained different among the gap sizes although the composition of intermediate to small gaps moved closer to reference conditions (Fig. 2). The composition of 46-m gaps showed little or no indication of a return to reference conditions at year 13. Moreover, contrary to our hypotheses, ground-layer plant community composition in gaps with crown closure (small gaps) was still different in composition from reference conditions. Prior longitudinal studies of canopy gaps also showed an initial divergence in composition that was related to gap size, but after canopy gap

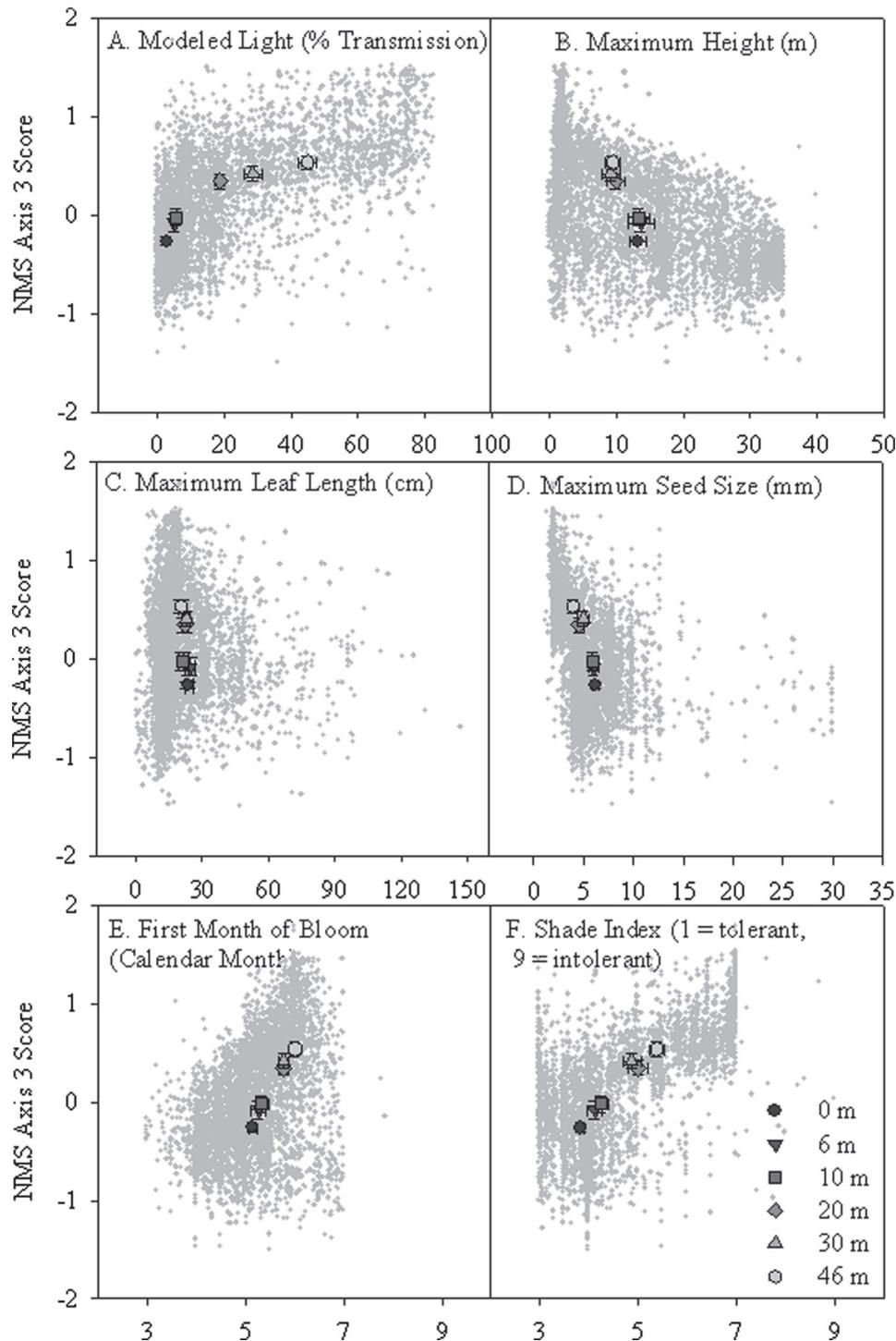


Figure 5: scatter plot and centroids ($\pm 95\%$ confidence intervals) of plot- and gap-level modeled light (A) and species traits (potential maximum height [B], potential maximum leaf length [C], potential maximum seed length [D], first month of bloom [E] and shade tolerance index [F]) to ground-layer vegetation composition in a northern hardwood forest on the Chequamegon-Nicolet National Forest, Wisconsin, USA. Horizontal axis units are noted in parentheses of each panel.

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

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 in the Chequamegon-Nicolet National Forest, Wisconsin, USA

Genus species	<i>Tau</i>	Year 2	Year 6	Year 13
		Size (IV)	Size (IV)	Size (IV)
<i>R. idaeus</i>	0.638	46 m (29.5)	46 m (26.7)	46 m (26.5)
<i>P. leptostachya</i>	0.503	30 m (13.9)	30 m (16.8)	46 m (22.4)
<i>P. cilinode</i>	0.496	46 m (20)	20 m (17.7)	46 m (22.4)
<i>D. carthusiana</i>	0.233		20 m (13.1)	
<i>Carex</i> spp	0.209			
<i>Stellaria media</i>	0.166			30 m (11.6)
<i>Galium</i> spp	0.164	6 m (12.2)	6 m (33.8)	
<i>Betula alleghaniensis</i>	0.130			
<i>Circaea alpina</i>	0.090			30 m (4.7)
<i>Sambucus racemosa</i>	0.087			
<i>C. alpina</i>	0.087			
<i>Viola</i> spp	0.083	6 m (17.5)	6 m (24.7)	
<i>Arisaema triphyllum</i>	0.083			
<i>Tilia americana</i>	0.077			
<i>A. nudicaulis</i>	0.070	10 m (6.6)	10 m (6.3)	10 m (11.1)
<i>Cinna latifolia</i>	0.057			
<i>Brachyelytrum erectum</i>	0.055			10 m (3.8)
<i>Ribes cynosbati</i>	0.053			
<i>Elymus hystrix</i>	0.039			
<i>Athyrium filix-femina</i>	0.035		6 m (22.4)	6 m (5.5)
<i>Aster macrophyllus</i>	0.017		10 m (4.1)	10 m (8.2)
<i>Anemone quinquefolia</i>	0.016			
<i>Acer rubrum</i>	-0.013		10 m (4.6)	10 m (7)
<i>Polygonatum pubescens</i>	-0.013			10 m (10.5)
<i>O. claytonii</i>	-0.014	6 m (19.1)	6 m (22.4)	6 m (20.8)
<i>Prunus serotina</i>	-0.014	6 m (7.2)	6 m (8.7)	
<i>Ostrya virginiana</i>	-0.024			
<i>Abies balsamea</i>	-0.024			10 m (4.8)
<i>Populus tremuloides</i>	-0.026			
<i>Trientalis borealis</i>	-0.028		0 m (6.7)	20 m (6.5)
<i>Streptopus lanceolatus</i>	-0.032	10 m (8.2)		
<i>Trillium grandiflorum</i>	-0.034		6 m (3.8)	
<i>Osmunda claytoniana</i>	-0.044			6 m (5.2)
<i>Oryzopsis asperifolia</i>	-0.044		10 m (8.7)	0 m (10.7)
<i>Quercus rubra</i>	-0.057		6 m (8.5)	
<i>Lycopodium obscurum</i>	-0.101	10 m (6.8)		0 m (6)
<i>M. canadense</i>	-0.135	0 m (11.6)	0 m (14.4)	0 m (14.4)
<i>Fraxinus americana</i>	-0.140	6 m (15.3)	6 m (18.6)	
<i>A. saccharum</i>	-0.146	0 m (20.7)	6 m (21.4)	6 m (17.5)

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

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 compared with that of 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 pregap composition (Brokaw and Busing 2000). Compositional patterns in our study of a species-rich, ground-layer plant community of a closed-canopy temperate forest were not random, a result of species density (See Methods/Data analysis/Ordination) or dominated by pregap vegetation (Fig. 2). In contrast, our results supported the concept that canopy gaps are mechanisms for maintaining species coexistence and functional diversity.

Previous studies in northern hardwood forests examined gaps <20 m in diameter and found neither ground-layer compositional partitioning (Collins and Pickett 1988a; Moore and Vankat 1986) 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 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 or 10 m in diameter (gap diameter to canopy height ratio (D:H) of 0.2 and 0.3, respectively) initially shift ground-layer composition away from uncut 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, 20, 30 and 46 m (D:H of 0.7, 1.2 and 1.9 for the 20, 30 and 46 m, respectively). This is consistent with another published 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 in which 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 (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 and applicability to managed forests

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.

From the alternative perspective of managed forests, though, our findings are more relevant, as our experimental gaps were created through timber harvest. The gradient of composition and traits among the gap sizes suggests that forest management actions based on the GPH create heterogeneity in the ground-layer community, a finding important to building ecology-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. Specifically, recent studies of harvest gaps suggest that creating woody debris and tip-ups (Smith *et al.* 2008) and ground disturbance (Fahey and Puettmann 2007) and leaving shelter trees (Shields and Webster 2007) could be used in combination to emulate characteristics of natural gaps and influence the composition and diversity of the ground-layer plant community of managed forests.

Dominant species may have also strengthened partitioning patterns. Composition of large gaps and gap centers was characterized by establishment of ruderal species that can create recalcitrant layers, which 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 postdisturbance 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. It could be that *Rubus* patches competitively excluded species with similar traits (*sensu* Gause 1934) or inhibited the limited recruitment of other species (*sensu* Connell and Slatyer 1977). Nonetheless, the *Rubus* patches may have fortified compositional partitioning across gaps.

The major compositional gradient from small to large gaps was also marked by a shift toward species with smaller seeds. Since most woodland herbs were 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).

Caveats and implications

It is important to note that our results are limited by the study design and should not be directly extrapolated to other sites. For example, our experimental gaps were embedded in a thinned forest matrix. If these gaps were located within an uncut forest, we expect that compositional partitioning among the gap sizes would be stronger than partitioning in our study because microclimatic and resource conditions along forest-gap transects would contrast to a greater degree than microclimate gradients along our forest-gap transects. Also, we did not directly measure light or plant traits. However, we expect that exact light and trait measurements would clarify the relationships that we identified with the estimated data that we used.

CONCLUSION

Ground-layer plant composition and traits differed across experimental gap sizes and within-gap locations as predicted by GPH theory. These compositional differences were evident 2 years after gap creation and, contrary to our hypotheses, persisted over the 13-year period. In contrast to the 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. This experiment highlights the potential significance of niche partitioning in the ground-layer plant community of both natural and managed forests and, therefore, supports the idea that a few large gaps could maintain diversity over space and time in a forested landscape.

SUPPLEMENTARY MATERIAL

Supplementary information for Appendices S1 and S2, Tables S1–S3 and Figure S1 is available at *Journal of Plant Ecology* online.

FUNDING

US Department of Agriculture Forest Service: specifically, the Northern Research Station (and former North Central Research Station); the Chequamegon-Nicolet National Forest (and former Nicolet National Forest); and the Washington Office Research & Development (Scientist Recruitment Initiative). *Conflict of interest statement.* None declared.

ACKNOWLEDGEMENTS

The research could not have been completed without the additional mentoring and leadership of Brian Palik, Anthony D'Amato and John Zasada. We greatly appreciate the technical assistance from the Reich and Montgomery Labs, Adam Weise, Kris Gray, Emma Schultz and Ben Gosack, among many other field technicians. We also thank three anonymous reviewers and the Associate Editor for providing helpful comments on the manuscript. T.F.S. designed the study and led data collection in years 0–6. C.C.K. led data collection in year 13, analyzed the data and wrote the initial and most of the subsequent drafts of the article. R.A.M. and P.B.R. contributed equally to the manuscript providing guidance and ideas in data analyses and interpretation and contributed to the writing.

REFERENCES

- Brandani A, Hartshorn GS, Gordon HO (1988) Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. *J Trop Ecol* **4**:99–119.
- Brokaw NVL, Busing RT (2000) Niche versus chance and tree diversity in forest gaps. *Trends Ecol Evol* **15**:183–8.
- Brokaw NVL, Scheiner SM (1989) Species composition in gaps and structure of a tropical forest. *Ecology* **70**:538–41.
- Busing RT, White PS (1997) Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos* **78**:562–8.
- Canham CD, Finzi AC, Pacala SW. *et al.* (1994) Causes and consequences of resource heterogeneity in forests - interspecific variation in light transmission by canopy trees. *Can J For Res* **24**:337–49.
- Chandrashekhara U, Ramakrishnan P (1993) Gap phase regeneration of tree species of differing successional status in a humid tropical forest of Kerala, India. *J Biosci* **18**:279–90.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Aust J Ecol* **18**:117–43.
- Coates KD (2002) Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *For Ecol Manage* **155**:387–98.
- Coates KD, Burton PJ (1997) A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *For Ecol Manage* **99**:337–54.
- Collins BS, Pickett STA (1988a) Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J Ecol* **76**:437–50.
- Collins BS, Pickett STA (1988b) Response of herb layer cover to experimental canopy gaps. *Am Midl Nat* **119**:282–90.
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**:1144.
- Dahir S, Lorimer C (1996) Variation in canopy gap formation among developmental stages of northern hardwood stands. *Can J For Res* **26**:1875–92.
- Denslow JS (1980) Gap partitioning among tropical rainforest trees. *Biotropica* **12**:47–55.
- Denslow JS (1995) Disturbance and diversity in tropical rain forests: the density effect. *Ecol Appl* **5**:962–8.

- Dietze MC, Clark JS (2008) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecol Monogr* **78**:331–47.
- Donoso PJ, Nyland RD (2006) Interference to hardwood regeneration in northeastern North America: the effects of raspberries (*Rubus* sp.) following clearcutting and shelterwood methods. *N J Appl For* **23**:288–96.
- Fahey RT, Puettmann KJ (2007) Ground-layer disturbance and initial conditions influence gap partitioning of understorey vegetation. *J Ecol* **95**:1098–109.
- Frelch LE, Lorimer CG (1991) Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecol Monogr* **61**:145–64.
- Galhidy L, Mihok B, Hagyo A. *et al.* (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecol* **183**:133–45.
- Gause GF (1934) *The Struggle for Existence*. Maryland, USA: Williams and Wilkins.
- Gray AN, Spies TA (1996) Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *J Ecol* **84**:635.
- Gray AN, Spies TA (1997) Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* **78**:2458–73.
- Hanson J, Lorimer C (2007) Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. *Ecol Appl* **17**:1325–40.
- Holladay C-A, Kwit C, Collins B (2006) Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size. *For Ecol Manage* **223**:218–25.
- Hubbell SP, Foster RB, O'Brien ST, *et al.* (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**:554–7.
- King DA (1986) Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. *Ecology* **67**:980–90.
- Kotar J, Kovach JA, Burger TL (2002) *A Guide to Forest Communities and Habitat Types of Northern Wisconsin*. Madison, WI: University of Wisconsin, 488.
- Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**:1–27.
- Kupfer JA, Runkle JR (1996) Early gap successional pathways in a *Fagus-Acer* forest preserve: pattern and determinants. *J Veg Sci* **7**:247–56.
- Lavorel S, Grigulis K, McIntyre S, *et al.* (2008) Assessing functional diversity in the field—methodology matters! *Funct Ecol* **22**:134–47.
- Lieberman M, Lieberman D, Peralta R, *et al.* (1995) Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *J Trop Ecol* **11**:161–77.
- Lindenmayer DB, Franklin JF, Fischer J (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol Cons* **131**:433–45.
- McCune B, Grace JB (2002) *Analysis of Ecological Communities*. Glendened Beach, OR: MjM Software Designs, 300.
- McCune B, Medford MJ (2006) *PC-ORD, Multivariate Analysis of Ecological Data*, Version 5. Glendened Beach, OR: MjM Software.
- Minckler LS, Woerheide JD (1965) Reproduction of hardwoods 10 years after cutting as affected by site and opening size. *J For* **63**:103–7.
- Moore MR, Vankat JL (1986) Responses of the herb layer to the gap dynamics of mature beech-maple forest. *Am Midl Nat* **115**:336–47.
- Ricklefs RE (1977) Environmental heterogeneity and plant species diversity: a hypothesis. *Am Nat* **111**:376–81.
- Royo AA, Carson WP (2006) On the formation of dense understorey layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can J For Res* **36**:1345–62.
- Runkle JR (1998) Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* **79**:1768–80.
- SAS Institute Inc. (2008) *SAS Version 9.2*. Cary, NC: SAS Institute Inc.
- Schnitzer SA, Carson WP (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**:913–9.
- Schumann ME, White AS, Witham JW (2003) The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. *For Ecol Manage* **176**:543–61.
- Shields JM, Webster CR (2007) Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. *Can J For Res* **37**:1797–807.
- Sipe TW, Bazzaz FA (1995) Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology* **76**:1587–602.
- Smith KJ, Keeton WS, Twery MJ, *et al.* (2008) Understorey plant responses to uneven-aged forestry alternatives in northern hardwood–conifer forests. *Can J For Res* **38**:1303–18.
- Stadt KJ, Lieffers VJ (2000) MIXLIGHT: a flexible light transmission model for mixed-species forest stands. *Agric For Meteorol* **102**:235–52.
- Tucker GF, Lassoie JP, Fahey TJ (1993) Crown architecture of stand-grown sugar maple (*Acer saccharum* marsh.) in the Adirondack Mountains. *Tree Physiol* **13**:297–310.
- Tyrrell LE, Crow TR (1994) Structural characteristics of old-growth hemlock-hardwood forests in relation to age. *Ecology* **75**:370–86.
- Uhl C, Clark K, Dezzio N, *et al.* (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology* **69**:751–63.
- USDA NRCS (2009) *The PLANTS Database* (<http://plants.usda.gov>): USDA NRCS, National Plant Data Center. Baton Rouge, LA: USDA NRCS.
- Whitmore TC (1989) Canopy gaps and the two major groups of forest trees. *Ecology* **70**:536–8.