Effects of selective tree harvests on aboveground biomass and net primary productivity of a second-growth northern hardwood forest

Jacob H. Dyer, Stith T. Gower, Jodi A. Forrester, Craig G. Lorimer, David J. Mladenoff, and Julia I. Burton

Abstract: Restoring structural features of old-growth forests, such as increased canopy gap sizes and coarse woody debris, is a common management goal for second-growth, even-aged stands. We experimentally manipulated forest structure by creating variable-size canopy gaps in a second-growth northern hardwood forest in north-central Wisconsin following two growing seasons of pre-treatment monitoring. The objectives of this study were to quantify the influence of canopy gaps of different sizes (50–380 m^2) on aboveground biomass and productivity of each vegetation stratum two growing seasons following treatment. Two years after treatment, ground layer biomass in canopy openings increased significantly relative to surrounding undisturbed transition zones. The response of ground layer biomass was greatest in the large versus the medium and small gaps. Sapling aboveground net primary productivity was significantly greater in undisturbed transition zones than within gaps across gap sizes following the second post-treatment growing season. Annual stem diameter increment was greatest for trees along gap borders and was correlated with crown class, percentage of crown perimeter exposed, gap area, and shade tolerance. Total aboveground net primary productivity was significantly lower in the gap addition plots the first year but by the second post-treatment growing season no longer differed from that in the control plots.

Résumé : La restauration des attributs structuraux des vieilles forêts, tels que des trouées de plus grande taille dans la canopée et davantage de gros débris ligneux, est une pratique d'aménagement usuelle dans les peuplements équiennes de seconde venue. Nous avons modifié expérimentalement la structure forestière en créant des trouées de taille variable dans la canopée d'une forêt de feuillus nordiques de seconde venue établie dans le centre-nord du Wisconsin. Ce travail a été précédé d'un suivi prétraitement pendant deux saisons de croissance. Les objectifs de cette étude étaient de quantifier l'influence des trouées de taille variable (de 50 à 380 m^2) dans la canopée sur la biomasse aérienne et la productivité de chaque strate de la végétation après les deux saisons de croissance qui ont suivi l'application du traitement. Deux ans après le traitement, la biomasse de la végétation au sol dans les ouvertures de la canopée avait significativement augmenté par rapport aux zones de transition environnantes non perturbées. La réaction de la biomasse de la végétation au sol était plus forte dans les grandes ouvertures que dans les moyennes et petites ouvertures. La productivité primaire nette aérienne des gaules était significativement plus grande dans les zones de transition non perturbées qu'à l'intérieur des trouées pour toutes les tailles de trouées après deux saisons de croissance. L'accroissement annuel en diamètre des tiges était plus élevé chez les arbres situés en bordure des trouées et était corrélé à la classe de cime, au pourcentage du périmètre de la cime exposé, à la superficie de la trouée et à la tolérance à l'ombre. La productivité primaire nette aérienne totale était significativement plus faible dans les placettes situées dans les trouées que dans les placettes témoins au cours de la première année, mais cette différence disparaissait au cours de la deuxième saison de croissance après l'application du traitement.

[Traduit par la Rédaction]

Introduction

Foresters and ecologists have long been interested in the influence of silvicultural systems or disturbances on ecosystem structure and function. The need for this information has increased as demands for wood fiber, biodiversity, and wildlife habitat have risen in response to increasing populations and a dwindling resource base. In temperate deciduous forests of North America, understanding the role of disturbance in ecosystem structure and function has received much attention (Bormann and Likens 1979; Boring et al. 1981; Phillips and Shure 1990; Elliott et al. 2002). These studies,

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J.H. Dyer. Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, 120 Russell Labs, Madison, WI 53706, USA; Department of Forest Resources, University of Minnesota, 1530 Cleveland Ave. N, St. Paul, MN 55108, USA.
S.T. Gower, J.A. Forrester,[1] C.G. Lorimer, D.J. Mladenoff, and J.I. Burton. Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, 120 Russell Labs, Madison, WI 53706, USA.

[1] Corresponding author (e-mail: jforrester@wisc.edu).

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and many others, have established the importance of disturbance spatial extent (i.e., "patch size"; sensu Pickett and White 1985) and severity on structural attributes of forests such as growth rates of regeneration in patches as well as functional attributes such as net primary productivity (NPP) and nutrient cycling rates. This work has proven integral to informing foresters and ecologists alike on the long-term sustainability of wood fiber as well as water, nutrient, and carbon cycles.

Numerous experiments have quantified the influence of large-scale disturbances (e.g., clear-cutting, wildfire, etc.) on subsequent ecosystem processes, which have increased the knowledge of stand-replacing disturbances on many facets of succession (Gower et al. 1996; Ryan et al. 1997). However, while it is widely recognized that canopy gap formation is one of the primary disturbances in temperate deciduous forests (Runkle 1985; Frelich and Lorimer 1991), relatively little information has been gleaned on the influence of small-scale disturbance on functional characteristics, especially biomass accumulation and NPP, of the recovering stand. There is a need to better understand the influence of small-scale disturbance on biomass accumulation and NPP for Great Lakes forest ecosystems because uneven-aged silvicultural systems such as single-tree selection and group-selection cutting are widely implemented (Crow et al. 1981), and small gaps and windthrows are the major disturbance in these forests (Frelich and Lorimer 1991).

Canopy gap formation alters the forest environment in a distinctly different way than large-scale disturbances, and these changes may affect subsequent recovery of important processes such as NPP. Typically, canopy gaps result from the death of one or a few trees caused by wind, insects, disease, or selective harvest. In old-growth stands in northern hardwood forests in the Great Lakes region, canopy openings typically range in size from 4 to over 1000 m^2 with an average gap size between 30 and 50 m^2 (Dahir and Lorimer 1996). The influence of canopy gap formation on the growth of advance regeneration, seedlings, and released canopy trees has received much attention (Runkle 1982, 1985; Dale et al. 1995; Coates and Burton 1997). However, the influence of these disturbances on biomass accumulation and NPP of the stand is not well understood, especially when considering vegetation other than potential overstory trees. The studies of Phillips and Shure (1990) and Shure et al. (2006) quantified the effects of canopy opening on regrowth and NPP of a southern Appalachian hardwood forest and reported that recovery rates of biomass and NPP decreased from larger to smaller openings. The important early-successional fast-growing species common to their study (e.g., black locust (*Robinia pseudoacacia*) L. and tuliptree (*Liriodendron tulipifera* L.)) are largely absent in the Great Lakes forests; therefore, it is unclear if their results are representative for other temperate forests. Webster and Lorimer (2002) also examined the influence of opening size on tree height growth and basal area increment, but they limited their analysis to woody vegetation. Their results also suggested that as opening size increased, productivity of woody vegetation increased and the relationship was asymptotic, with biomass production slowing at opening sizes over 100 m^2.

Understanding the differences between long-term sustainable systems such as "old-growth" forests and potentially unsustainable systems such as degraded second-growth forests resulting from poor management practices in the past may further aid in future management and restoration of degraded forests. Results from experiments in which a degraded or second-growth stand without characteristics typical of old-growth forests of the region are lacking; it may be necessary to quantify the influence of altering forest structure and processes and understand the linkage between disturbance scale as a result of implementing these management scenarios.

The overall objective of this study was to quantify the influence of canopy gap formation on biomass and productivity of each vegetation stratum. Specific questions that we addressed were how does gap size influence aboveground NPP (ANPP) and biomass of the different vegetation strata, does the hypothesized increased growth of trees bordering the canopy openings offset the loss of productivity in the gaps, and how does the whole-plot (i.e., stand-level) ANPP compare for the manipulated stand relative to the control?

Methods

Study area

This study is part of a larger project designed to quantify the effect of canopy gap formation and coarse woody debris amount on ecosystem processes in northern hardwood forests. The 280 ha study area (45°37′N, 90°47.8′W) is located in the Flambeau River State Forest, Rusk County, north-central Wisconsin. The field site is representative of the Great Lakes forest landscape with even-aged, second-growth hardwood stands that originated after region-wide harvests in the early 1900s. Based on stem cross sections about 30 cm above the ground surface, most of the stems in this stand originated between 1920 and 1940, with a few stems originating before 1900 that were advance regeneration released by the clearcut. Sugar maple (*Acer saccharum* Marsh.) is the dominant overstory tree species. Other important overstory tree species included white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), and bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch). Sugar maple, white ash, bitternut hickory, and ironwood (*Ostrya virginiana* (Mill.) K. Koch) dominated the sapling layer and sugar maple dominated the seedling layer. Tree density averaged 444 trees·ha^{-1} and stand basal area averaged 29.1 m^2·ha^{-1} for trees ≥10 cm diameter breast height (DBH) (1.37 m).

The site is generally mesic with level to gently sloping topography. Soils are silt loam (Glossudalfs) of the Magnor, Ossemer, and Freeon series overlaying dense till (D. Hvizdak, US Department of Agriculture, Natural Resources Conservation Service, personal observation). The median length of the growing season is 105 days (base temperature = 0 °C) (1971–2000). January and July air temperatures (1971–2000) average –13 and 19 °C, respectively. Mean annual precipitation is 84 cm with a mean annual snowfall of 133 cm (1971–2000) (Northeastern Rusk County, Wisconsin, Midwest Regional Climate Center: mcc.sws.uiuc.edu). Mean annual air temperature from dataloggers in the site was 7.4, 6.1, and 4.4 °C and annual precipitation was 558, 618, and 530 mm across the years 2006, 2007, and 2008, respectively.

Experimental design

The large-scale manipulative experiment was established in 2004 at the Flambeau River State Forest. Thirty-five 80 m × 80 m (0.64 ha) experimental plots were established and treatments were assigned within a randomized complete block design. Three blocks that account for moderate natural heterogeneity occurring within the research area were created using ordinations of pre-treatment vegetation data. Plots were assigned to blocks based on the relative importance of white ash and bitternut hickory as codominant species or the presence of eastern hemlock (*Tsuga canadensis* (L.) Carr.). We focused on two of the experimental treatments: gap addition ($n = 15$) or no canopy manipulation/controls ($n = 20$). When assigned a gap treatment, canopy gaps were created within three subplots nested in each 0.64 ha plot (Fig. 1). In the central or "gap" zone (Fig. 1) of each subplot, a canopy gap of 50, 200, and 380 m^2 for the small, medium, and large subplots, respectively, was created. Each gap is surrounded by an unharvested transition zone of 4, 8, and 11 m radius, respectively. Each zone distance is equal to the radius of the respective gap zone (Fig. 1). Control plots followed the identical design, but no manipulation occurred in the gap zones.

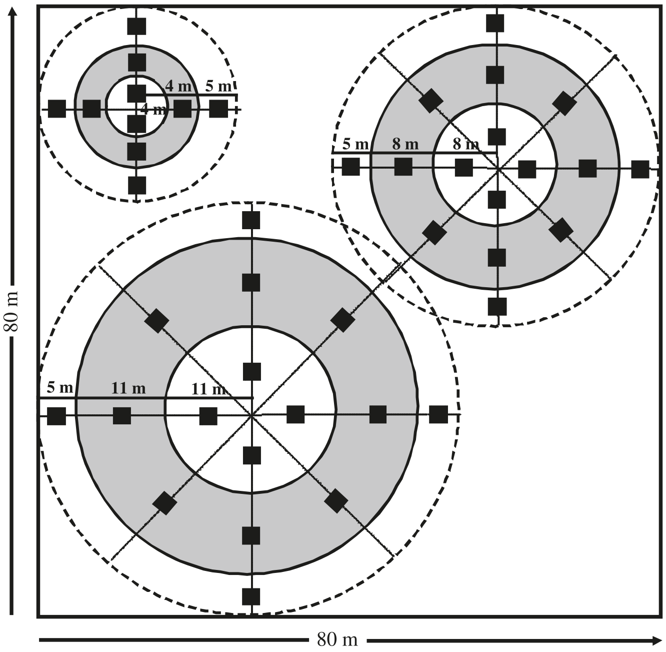
Gap trees were harvested in January 2007 when the soil was frozen and snow covered (depth of 15–20 cm). All stems >5 cm DBH in the gap zones of gap treatment plots were cut using a rubber tire harvester (Ponsse Ergo, Ponsse Oyj, Vieremä, Finland) operated by a certified master logger. All wood cut from each subplot was either removed from the gap area (gap treatment only) using a forwarder (Ponsse Buffalo, Ponsse Oyj, Vieremä, Finland) or left in place (gap plus coarse woody debris treatment). Coarse woody debris treatments were not a focus of this paper and are therefore not discussed any further. Post-treatment sampling was done in the 2007 and 2008 growing seasons.

Woody biomass and productivity

All trees ≥10 cm DBH within a plot were permanently tagged and identified by species in the fall of 2005. DBH was measured to the nearest 0.1 cm with a diameter tape at the end of each growing season (September and October) in 2005–2008. All saplings in the gap and transition zones were measured at DBH with calipers and categorized into one of five DBH classes: 0.5–0.9, 1–2.4, 2.5–4.9, 5.0–7.4, and 7.5–9.9 cm. Starting in 2007, DBH was measured to the nearest 0.1 cm with vernier calipers and saplings in the transition zones of nongap addition plots were no longer remeasured. Sapling heights were measured using either a height pole (to the nearest 0.01 m) or a clinometer and distance tape and recorded from 2005 to 2008.

Species-specific allometric equations were used to calculate stem and branch biomass for each tree and sapling (Jenkins et al. 2003). Allometric equations were selected from the literature based on geographic proximity to our study site and having an appropriate range of diameters for the particular species because these are the two most important factors influencing biomass estimates (Gower et al. 1996). Because we were unable to locate an equation for butternut (*Juglans cinerea* L.), we substituted the bitternut hickory equation due to similarities in structure. All allometric equations had an $R^2 \geq 0.90$ with a range from 0.90 to 0.99 for selected species, locations, and diameter ranges (Jenkins et al. 2003). Woody biomass was calculated as the sum of the biomass of individual trees for each subplot divided by the area of the subplot for small, medium, and large subplot and zones separately. Sapling biomass was estimated using the midpoint of each diameter class for 2005 and 2006 and by using the actual DBH values for 2007 and 2008. For all analyses, saplings were grouped into two DBH classes, 0.5–2.4 and 2.5–9.9 cm, based on the allometric biomass equations used (Brenneman et al. 1978; Young et al. 1980).

Fig. 1. Detail of an 80 m × 80 m treatment plot containing three subplots, each with three concentric zones and permanent vegetation quadrats (squares). The central "gap" zones of subplots have radii of 4, 8, and 11 m, which coincide with the range of canopy gap treatments. The "transition" zones (shaded rings) are 4, 8, and 11 m in width, respectively (undisturbed canopy). The outer buffer (closed canopy) zones are 5 m wide for all subplots. Experimental gaps coincide with central gap zones in gap addition plots; this zone was left undisturbed in control plots.



ANPP was calculated as the sum of biomass increment for one sampling period for the subplot/zone divided by the area of the subplot/zone. Trees dead at the time of remeasurement were assumed to have had no growth between sampling periods, since sampling was conducted annually (Clark et al. 2001; Kloeppel et al. 2007). Ingrowth production for saplings and trees was calculated as the difference between the biomass of the stem in the first sampling period minus the biomass of the smallest stem for that class (i.e., 0.5 cm DBH for saplings and 10 cm DBH for overstory trees) to avoid overestimating production from new stems (Kloeppel et al. 2007).

Gap border tree measurements

Gap border trees, defined as overstory trees with crown perimeter exposed to the gap opening (i.e., release from the side), were identified in June 2007 after the winter harvest.

The DBH and crown class (see Oliver and Larson 1996, p. 153) of all trees were measured annually beginning in 2005 for biomass estimation. Following the gap addition treatment, we measured tree height, percent crown perimeter exposed to the canopy opening, and crown area of each gap border tree. Percent exposed crown perimeter was measured as the angle from where the crown of the subject tree touches the crown of its nearest neighbor(s) using a compass, and the angle was converted to a percentage of 360°. Total height was measured using a clinometer and a distance tape, and angles were measured at a distance of at least one tree height away from the subject tree. Crown area was estimated from crown radii of the four cardinal directions and assuming an elliptical crown shape.

Ground layer biomass and productivity

Ground layer vegetation (all herbaceous and woody species <1.4 m tall) was sampled annually in the spring and midsummer of 2005–2008. Cover classes were assigned to all species occurring in forty-two 2 m × 2 m permanent quadrats located systematically within the zones of each subplot (Fig. 1). When species were observed during both sampling periods, the larger cover class was retained for analysis. In conjunction with the permanent quadrat surveys, we estimated species cover, biomass, and productivity in three 1 m^2 quadrats (clip quadrats) established outside subplot areas within each plot annually from 2006 to 2008 (n = 105). Additional clip quadrats (n = 20) were established in canopy openings created outside the main treatment plots to sample the full range of conditions present in the permanent quadrats. Each year, three new clip quadrats for regular plots and one quadrat from off-plot gaps were established and clipped to avoid the influence of clipping on subsequent growth and species composition.

Quadrats were surveyed and clipped two or three times per growing season. Samples were bagged, returned to the laboratory, dried at 70 °C for 48 h, and weighed to the nearest 0.001 g. Biomass data were regressed with their respective cover data to obtain biomass predictor equations used to calculate biomass from cover estimated from the permanent vegetation quadrats. This approach was used for the regular plots (closed canopy predictors) and for the extra off-plot gaps (gap opening predictors) and avoided destructive harvests in the permanent quadrats. The allometric equations were all significant at $p < 0.05$ and had R^2 values between 0.6 and 0.9 (J. Dyer, unpublished data).

Prior to application of equations, cover data from permanent vegetation quadrats were summed using the midclass percentage of each species within herbaceous and woody vegetation categories separately. Total ground layer biomass was calculated for each quadrat and averaged within each zone within each subplot to estimate mean ground layer biomass in canopy openings, transition zones, and buffer zones. For ground layer vegetation, we assumed that each year's biomass estimates were equivalent to total production; thus, biomass and ANPP were the same.

Litterfall

Nine 0.18 m^2 litter traps (laundry baskets lined with fine-mesh netting and pinned to the ground) were placed randomly within each plot prior to treatments. After the treatments took place, traps were relocated into the subplots. The large subplot contained three traps in the transition zone and two in the gap zone, the medium subplots contained two traps in the transition zone and one in the gap zone, and the small gap contained one trap that was randomly located. Litter was collected seasonally for 2 years pre-treatment and 2 years post-treatment. Samples were sorted into four different categories: leaves, branches and wood (>0.5 cm diameter), twigs and wood (<0.5 cm diameter), and miscellaneous (flowers, fruits, epiphytes, etc.). Sorted samples were dried to constant mass at 50 °C and weighed to the nearest 0.001 g. All four seasons of litter data were summed and averaged across the plot for plot-level litter production.

Plot-level total biomass and ANPP

Total aboveground biomass was calculated as the sum of overstory, sapling, and ground layer biomass and was determined for each zone within each subplot and for the entire plot. In gap addition plots, we used an area-weighted mean to scale the sapling biomass from subplots up to plot-level estimates. The mean sapling biomass of the nongap plots was applied to the buffer zone and matrix (remaining area of plot not within the subplots) of gap addition plots. We did not include litterfall in the biomass calculation because it is not a standing crop. ANPP was calculated as the sum of overstory and sapling ANPP and ground layer and litterfall biomass. We assumed that no overstory litter production occurred within canopy openings after treatment. The remaining saplings undoubtedly produced some foliage; however, because saplings made up generally <2 $Mg \cdot ha^{-1}$, it was assumed that any foliage production was negligible. ANPP was calculated from the periods 2005–2006 (pre-treatment ANPP), 2006–2007 (first season post-treatment), and 2007–2008 (second season post-treatment).

Statistical analysis

We applied ANOVA to pre-treatment overstory biomass and ANPP, sapling, ground layer, and litterfall biomass to test for differences among the plots prior to harvesting of the gaps. The effect of gap size and location (zone) on biomass and ANPP by component was tested using mixed models with fixed (block, gap size, and zone) and random effects (plot nested in block and plot nested in block by gap size interaction) followed by post hoc Tukey multiple comparison tests (α = 0.1). Gap border tree diameter growth was analyzed using ANOVA to compare the relative effect of distance from canopy opening, gap size, shade tolerance class (i.e., shade-tolerant versus mid-tolerant species groups), crown class, and the percentage of the crown perimeter exposed to canopy opening (for gap border trees only). If the ANOVA was significant at the $p < 0.1$ level, Tukey's HSD was used to conduct pairwise means comparisons to detect further significant differences. For total biomass and ANPP, we applied a mixed model with repeated measures to test for differences within treatments and sampling intervals. All statistical tests were conducted using SAS version 9.1 (SAS Institute Inc., Cary, North Carolina) or R software (R Development Core Team 2005).

Table 1. Aboveground live biomass by component in the Flambeau River State Forest prior to gap addition treatments (2006) (standard errors are based on plot-scale variation).

	Gap addition plots (n = 15)		Nongap plots (n = 20)	
	Mean	±SE	Mean	±SE
Woody ($Mg \cdot ha^{-1}$)				
Trees	242.7	5.37	239.2	5.02
Saplings	4.67	0.76	4.38	0.33
Annual ($Mg \cdot ha^{-1} \cdot year^{-1}$)				
Litterfall	6.24	0.12	5.98	0.11
Ground layer	0.25	0.17	0.31	0.16

Results

Pre-treatment aboveground biomass and NPP patterns

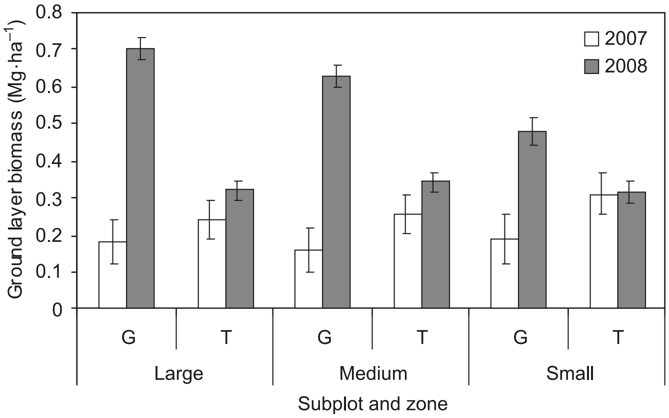
Prior to treatments, overstory trees comprised ~96% of total aboveground biomass, while saplings plus ground layer vegetation comprised ~2% of total aboveground biomass (Table 1). Total aboveground biomass ranged from 254 $Mg \cdot ha^{-1}$ in closed canopy plots to 250 $Mg \cdot ha^{-1}$ in gap plots prior to treatment. Despite wood being the bulk of the standing crop biomass, foliage production, estimated from litterfall, comprised ~70% of ANPP, which averaged 6 $Mg \cdot ha^{-1} \cdot year^{-1}$. Overstory tree wood production was the second largest component of ANPP (~25%, 2.5 $Mg \cdot ha^{-1} \cdot year^{-1}$). Saplings and ground layer vegetation NPP was <0.5 $Mg \cdot ha^{-1} \cdot year^{-1}$.

Overstory biomass was not significantly different among the gap and control plots prior to treatment (p = 0.649), nor was overstory production (p = 0.775). Tree ANPP differed by block (p = 0.028), with ANPP in plots containing eastern hemlock significantly lower than the other blocks where eastern hemlock was not present during this pre-treatment period only. This was the only test where the block effect was significant, so we will not present any additional results for this factor. Neither litterfall or sapling biomass differed significantly between treatment types (p = 0.118 and 0.692, respectively), but ground layer biomass was significantly greater in plots that would remain undisturbed versus pre-treatment gap plots (p = 0.01).

Post-treatment aboveground biomass and NPP patterns within gaps

Within the gap addition treatment, in the first growing season after harvest, ground layer biomass (and productivity) remained lower in gap than in transition zones across gap sizes (0.17 versus 0.27 $Mg \cdot ha^{-1}$, p = 0.0003). However, 2 years after treatment, ground layer biomass in canopy openings increased significantly relative to surrounding transition zones (p < 0.001 for all three gap sizes compared with transition zones) (Fig. 2). Additionally, within the gap zones, ground layer biomass was significantly greater for large than for medium and small gaps (p = 0.04 for medium and p < 0.001 for small gaps).

Fig. 2. Mean ground layer biomass within gap (G) and transition (T) zones in experimental canopy gaps ranging in size from 50 to 200 to 380 m^2. Error bars are ±1 SE.



Our minimum tree diameter for gap harvests was 5 cm; therefore, following the gap treatment, sapling biomass in all gap sizes was significantly less than biomass in the neighboring transition zones (p = 0.029, 0.006, and <0.0001 for small, medium, and large gaps compared with the transition zone, respectively) (Fig. 3). However, the 5–10 cm DBH size class was not completely removed within the gap zones, since the zones delineated on the ground did not match exactly with the opening created based on canopy crowns. A significant zone by subplot interaction (p = 0.084) indicated that the difference between biomass in zones varied with the size of the gap. The biomass of saplings <5 cm DBH did not differ significantly between gap sizes or zones prior to treatment, but following the harvest, biomass was lower within gap than transition zones for all gap sizes (0.9 versus 1.3 $Mg \cdot ha^{-1}$, p = 0.004 in 2007). Patterns in biomass were identical in the second post-treatment growing season (Fig. 3).

Trends in sapling ANPP the first growing season following treatment were not reliable because we were comparing diameter class midpoints with true diameters; thus, the data are not shown. In the second growing season after treatment, sapling ANPP was significantly greater in transition zones than in gap zones across gap sizes (0.22 versus 0.09 $Mg \cdot ha^{-1} \cdot year^{-1}$, p = 0.002) (Fig. 4). This difference was due largely to the remaining larger saplings, since ANPP for stems <5 cm DBH did not differ between gap sizes or zones (p = 0.3 and 0.4, respectively).

Gap border tree growth analysis

Annual diameter growth of the border trees differed among shade tolerance classes. Shade-tolerant trees, such as sugar maple, eastern hemlock, and ironwood, had a signifi-

Fig. 3. Mean sapling biomass among gap sizes and zones (**g**ap (G) or **t**ransition (T)) separated by size class in the Flambeau River State Forest. Many stems $5 < 10$ cm in diameter were cut within gap zones in January 2007. Error bars are ±1 SE based on saplings <10 cm DBH. Differences in biomass were statistically significant between zones for all subplot sizes in both years.

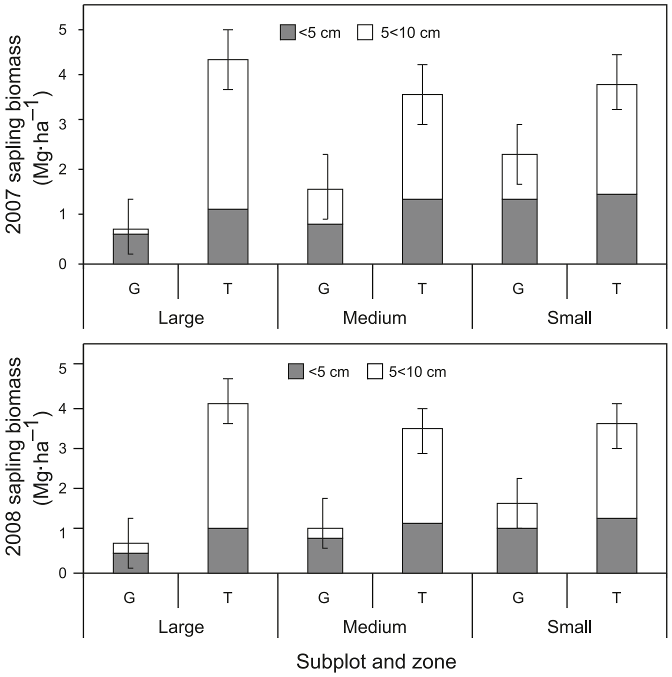


Fig. 4. Mean sapling aboveground net primary productivity among gap sizes and subplot zones (**g**ap (G) or **t**ransition (T)) at the Flambeau River State Forest during 2007–2008. Error bars are ±SE based on saplings $0 < 10$ cm DBH. Many stems $5 < 10$ cm diameter within gap zones were cut in January 2007. ANPP of saplings $0 < 10$ cm is significantly different between zones ($p = 0.002$). No differences in ANPP for stems <5 cm were statistically significant.

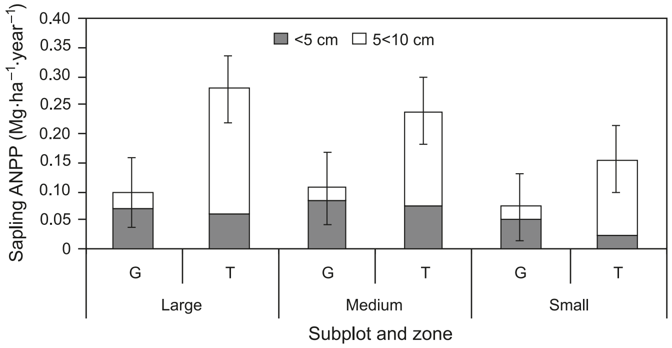
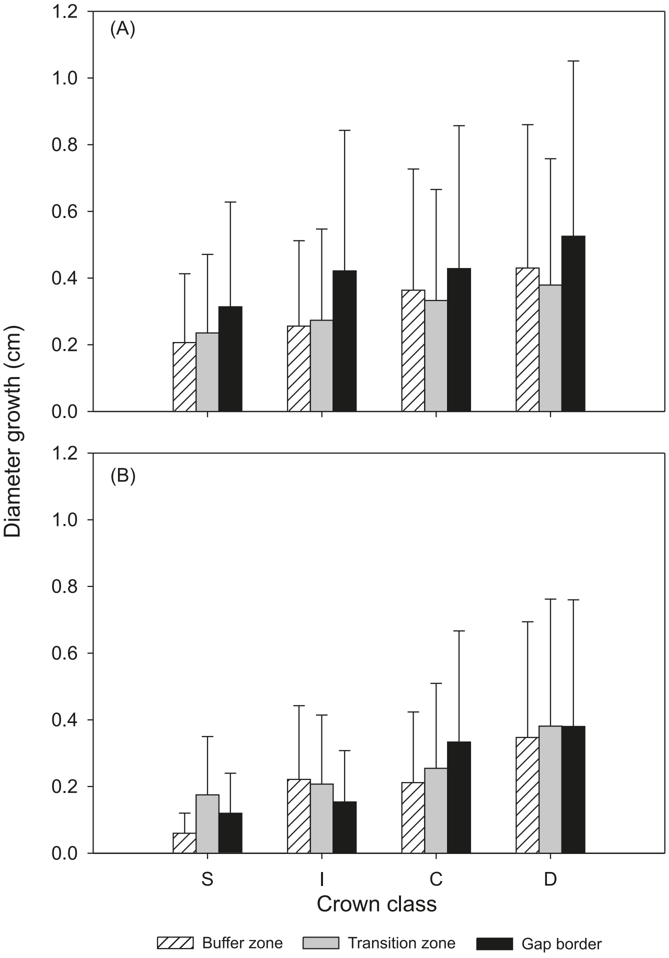


Fig. 5. Mean second-year diameter growth of trees >10 cm DBH by crown class and zone for (A) shade-tolerants and (B) midtolerants. S, suppressed; I, intermediate; C, codominant; D, dominant. See plot schematic for details on zones. Gap border trees are trees with the crown perimeter exposed to the canopy opening. Error bars are 1 SD.



cantly greater diameter growth than midtolerants ($p = 0.009$). To account for the influence of initial differences in diameter and crown exposure on diameter growth response, trees were divided into the four crown classes. For shade-tolerant trees, annual diameter growth was significantly greater for suppressed, intermediate, and codominant gap border than for nonborder trees in the second year after treatment. Annual diameter growth was not significantly different between border and nonborder positions for dominant canopy class trees (Fig. 5). Midtolerant codominant trees on the gap border had significantly greater annual diameter increment than codominant trees in the buffer zones; however, the differences were marginally significant between gap border trees and transition trees 2 years after treatment ($p = 0.001$ and 0.084 for buffer and transition zone comparisons, respectively) (Fig. 5).

Annual diameter growth in both species groups differed significantly among crown class for the trees in the gap borders. Suppressed trees grew significantly slower than intermediate, codominant, and dominant stems ($p = 0.01$, 0.004, and <0.001, respectively) (Fig. 5). For midtolerant trees, dominant stems outgrew intermediate stems in the gap border ($p = 0.04$). Percentage of crown perimeter exposed to the canopy opening significantly explained gap border tree annual diameter growth for both midtolerant and shade-tolerant species. For midtolerants, stems with $>75\%$ crown perimeter exposed were growing significantly greater than stems with $<50\%$ crown perimeter exposed in gaps <200 m^2 ($p = 0.002$ and 0.01, respectively) (Fig. 6). However, annual diameter was not correlated with percent exposed crown perimeter for midtolerant trees in gaps >200 m^2. For shade-tol-

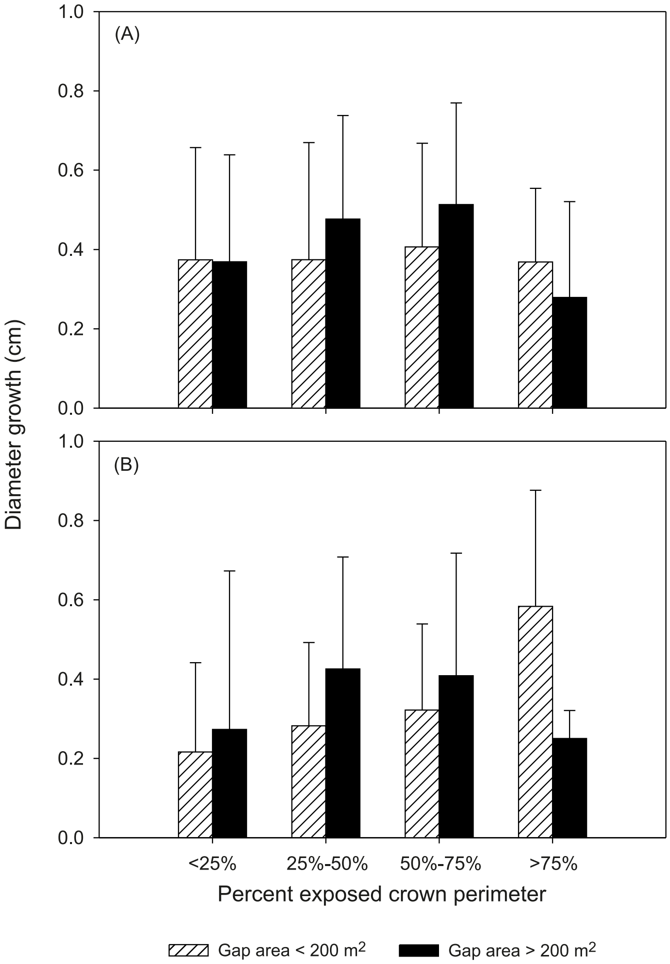


Fig. 6. Mean second-year diameter growth of gap border trees as a function of percentage of crown perimeter exposed to the gap opening by gap area for (A) shade-tolerants and (B) midtolerants in response to gap creation. Error bars are 1 SD.

erant species in gaps <200 m^2, annual diameter growth was not correlated with percent exposed crown perimeter. However, in gaps >200 m^2, annual diameter growth was significantly greater for trees with 25%–75% crown perimeter exposed than <25% ($p < 0.05$) and >75% of crown perimeter exposed ($p < 0.01$) (Fig. 6). Lastly, for stems within a percent exposed crown perimeter class (<25%, 25%–50%, 50–75%, and >75%), there were some differences between gaps <200 and >200 m^2. For midtolerants, trees with 25%–50% crown perimeter exposure in gaps >200 m^2 significantly outgrew stems with 25%–50% crown perimeter exposure in gaps <200 m^2 (p = 0.008, two-sample t test); however, this trend was reversed for stems with >75% crown perimeter exposure (p = 0.04, two-sample t test) (Fig. 6). For shade-tolerant species, stems with 25%–50% and 50%–75% crown perimeter exposure in gaps >200 m^2 significantly outgrew stems in gaps <200 m^2 (p = 0.03 and 0.04, respectively, two-sample t test) (Fig. 6).

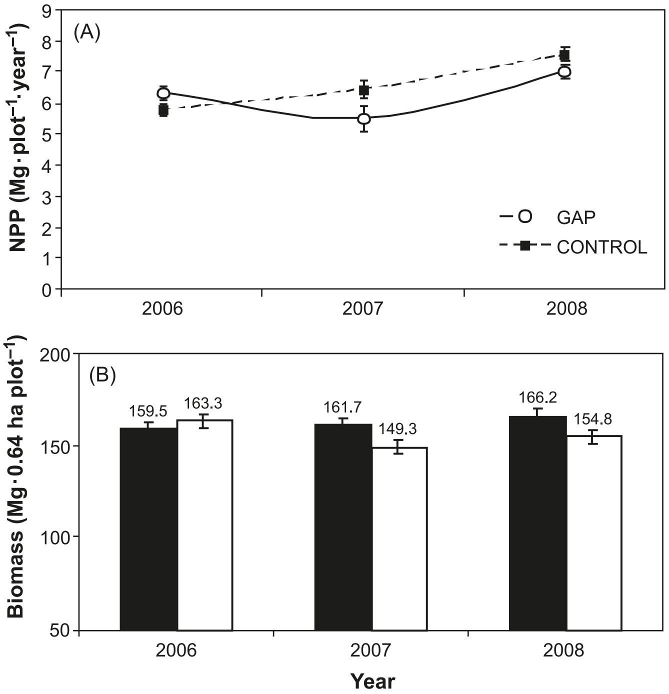


Fig. 7. Average whole-plot (0.64 ha, all zones combined) above-ground (A) net primary productivity and (B) biomass for closed canopy plots (solid bars, n = 20) and gap addition plots (open bars, n = 15), which have three gaps per plot making up ~10% of plot area, by treatment year. Error bars are ±1 SE.

Plot-level comparison of ANPP and total biomass

Plot-level aboveground biomass and ANPP were calculated using data from the entire plot (see Fig. 1). Comparisons were made between gap treatment plots (n = 15) and nongap or control plots (n = 20). Canopy gaps comprised ~10% of total plot area following the gap addition treatment. Pre-treatment total biomass did not differ between plots designated to gap or control treatments (p = 0.41), but ANPP was significantly greater in control plots (p = 0.08) (Fig. 7). In the first growing season following treatment, both biomass (p = 0.07) and ANPP (p = 0.06) were significantly lower in gap addition plots relative to the controls. Biomass remained significantly lower in gap plots relative to controls in the second year following harvest (p = 0.02), although ANPP was no longer significantly different from the controls (p = 0.13).

Discussion

Two years after treatment, both aboveground biomass and productivity remained significantly less in gaps than in closed canopy subplots and transition zones of gap subplots. Gap size had minimal effect on total biomass and productivity per unit area in our study plots 2 years after treatment. Phillips and Shure (1990) found that 2 years after selection harvest in a southern Appalachian hardwood forest, total biomass and ANPP per hectare increased significantly with gap area up to 2 ha. They found that 2 years after cutting, gaps 160 m^2 in area only recovered 14% of ANPP of the surrounding forest whereas gaps 2 ha in area recovered 58% of ANPP of the surrounding forest (Phillips and Shure 1990). The majority of the biomass and ANPP was attributed to stump and root sprouting from early-successional, fast-growing species such as black locust and tuliptree. In our study, ANPP in the smallest gaps (~50 m^2) and largest gaps (~380 m^2) was only 5.2% and 8%, respectively, of that of control plots. The difference in recovery rate may explain the differences between the two studies. Sprouting was a significant source of regeneration in our study gaps (Dyer 2009); however, sprouts were not quite sapling size, and abundance was limited to the number of cut stumps. In the Phillips and Shure (1990) study, species such as black locust sprouted prolifically from stumps and roots and dramatically increased ANPP in experimental openings relative to our northern hardwood ecosystem, which lacked rapidly growing, early-successional tree species.

Webster and Lorimer (2002) studied biomass accumulation in canopy openings and reported that 1–15 years after gap formation in a northern hardwood–hemlock forest, standing tree biomass was 81% less in recent single tree openings (<80 m^2 and <15 years old) compared with multiple tree openings (>80 m^2 and up to 800 m^2). Differences among gap size declined in older gaps. In our study, sapling woody biomass in canopy openings was significantly lower than in transition zones for all gap sizes 2 years after treatment, indicating a slow growth response of existing saplings and little or no recruitment into the sapling layer (stems with DBH > 0.5 cm). It is reasonable to speculate that the trend will change over time as seedlings and stump sprouts grow into the sapling layer and increase total biomass in canopy openings. The apparently slow response of advance regeneration in canopy openings may be due to increased mortality from harvesting, especially across the gradient of gap sizes (Peck and Zenner 2008).

Vegetation recovery after disturbance is important in minimizing the leaching of mineral nutrients (Marks 1974; Bormann and Likens 1979; Fahey et al. 1991; Mou et al. 1993). In northern hardwood ecosystems following large-scale disturbance, vegetation regrows quickly and nutrients are stored in the regrowth (Marks 1974; Mou et al. 1993). Thus, the rate at which vegetation recovers can be important in maintaining nutrients within the stand, which would help maintain stand productivity as growth at the stand level switches from dominance by herbaceous and small woody plants to saplings, which will eventually occupy a space in the canopy layer. In our study, ground layer vegetation (both woody and herbaceous) biomass and productivity were significantly greater in the canopy gaps than in the control plots 2 years after treatment. We expect this trend to continue for a few more years until seedlings and stump sprouts recruit into the sapling layer and eventually shade out ground layer vegetation. Thus, the ground layer vegetation can play an important role in minimizing nutrient loss while woody vegetation recovers and begins to dominate the canopy openings.

We detected a significant increase in annual diameter growth for trees that had some portion of their crown released from the side 2 years after selection harvest. Studies have shown that release from the side can dramatically increase diameter growth in deciduous forests (Lamson et al. 1990; Singer and Lorimer 1997; Jones and Thomas 2004; Jones et al. 2009) as well as in other forest types (York et al. 2004; Wiser et al. 2005). In a study of the response of sugar maple diameter growth to selection harvest, Jones and Thomas (2004) found that annual growth response gradually increased over 2–5 years and stem size was the dominant influence on annual growth response to cutting. In a later study, Jones et al. (2009) reported that shade-tolerant species had a greater annual basal area increment response than midtolerant species and our results are consistent with their study. We found that trees that experienced some release from the side had significantly higher annual diameter growth rates only 2 years after canopy opening. Additionally, corroborating the results of Jones and Thomas (2004) and Jones et al. (2009), we found that stem size had a significant influence on the magnitude of diameter growth increase. However, we found that codominant and dominant individuals exhibited the greatest increase in diameter growth 2 years after harvest, not the smaller stems. This was true for midtolerant species where diameter growth did not differ between the gap border zone and openings for suppressed and intermediate trees.

Selective harvest and ecosystem goods and services

Carbon management has become an important goal in some forests. Net ecosystem production, defined as the difference between NPP and heterotrophic respiration, determines whether a forest ecosystem is a carbon sink or source. The selective harvest removed 10% of stand canopy area and that decreased ANPP by 6%–10% 2 years following treatment. Understory and border trees partially compensated for the loss of leaf and growth of the trees removed in the selective harvests. Halpin (2009) simulated the effects of canopy openings composing 9% of a stand area using the forest growth model CANOPY (Choi et al. 2001) and found that a cutting cycle of 15 years decreased net wood volume production by about 10%. Additional years of data are required to quantify the long-term implications of selective harvest on ANPP for each of the vegetation strata, but it is interesting to speculate how ANPP may change in the near future. It seems plausible that ANPP on the gap plots will recover to pre-treatment levels in the next few years based on how quickly gap border trees occupy the gap and ANPP is positively correlated with leaf area (Landsberg and Gower 1997). Another factor affecting the net ecosystem production is heterotrophic respiration, which is a component of soil surface CO_2 flux. Soil microbial respiration typically comprises just over half of the soil surface CO_2 flux, while field-based forest studies indicate, on average, that roots contribute 48.6% (Hanson et al. 2000). Stoffel et al. (2010) reported that annual soil surface CO_2 flux was not significantly different among treatments prior to the winter 2007 harvest and was not significantly different among treatments 2 years after harvest. Annual (+1 SE) soil surface CO_2 flux averaged 967 + 72 and 1012 + 72 g $C{\cdot}m^{-2}{\cdot}year^{-1}$ in the control and gap treatments, respectively, for the 2-year post-treatment period.

Another worthy forest management objective is to maintain or improve biodiversity. Understory plant species diversity generally increases following silviculture treatments and selective logging (Gilliam et al. 1995; Halpern and Spies 1995; Crow et al. 2002; Scheller and Mladenoff 2002; Smith et al. 2008; Wolf et al. 2008), although new species are typically common or non-native. The increase in diversity is often attributed to greater light availability and heterogeneity (Brosofske et al. 2001; Smith et al. 2008) and coarse woody debris (Scheller and Mladenoff 2002). Gap size or the spatial pattern of retention can also be an important variable for the maintenance of late-successional species that may be more prone to local extirpation in group versus single-tree selection treatments (Smith et al. 2008). Collectively, these studies suggest while selective harvest may temporarily decrease ANPP, it can increase biodiversity. Forests are increasingly managed for multiple resources and it appears there are trade-offs that must be considered between maximizing ANPP and understory biodiversity.

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