

The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest

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Abstract. The even-aged northern hardwood forests of the Upper Great Lakes Region are undergoing an ecological transition during which structural and biotic complexity is increasing. Early-successional aspen (*Populus* spp.) and birch (*Betula papyrifera*) are senescing at an accelerating rate and are being replaced by middle-successional species including northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*). Canopy structural complexity may increase due to forest age, canopy disturbances, and changing species diversity. More structurally complex canopies may enhance carbon (C) sequestration in old forests. We hypothesize that these biotic and structural alterations will result in increased structural complexity of the maturing canopy with implications for forest C uptake.

At the University of Michigan Biological Station (UMBS), we combined a decade of observations of net primary productivity (NPP), leaf area index (LAI), site index, canopy tree-species diversity, and stand age with canopy structure measurements made with portable canopy lidar (PCL) in 30 forested plots. We then evaluated the relative impact of stand characteristics on productivity through succession using data collected over a nine-year period. We found that effects of canopy structural complexity on wood NPP (NPP_w) were similar in magnitude to the effects of total leaf area and site quality. Furthermore, our results suggest that the effect of stand age on NPP_w is mediated primarily through its effect on canopy structural complexity. Stand-level diversity of canopy-tree species was not significantly related to either canopy structure or NPP_w. We conclude that increasing canopy structural complexity provides a mechanism for the potential maintenance of productivity in aging forests.

Key words: canopy structure; carbon sequestration; diversity; forest; lidar; net primary production; rugosity.

INTRODUCTION

Structure and function of forests of the Upper Great Lakes region have been dramatically altered by disturbance over the last century (Karamanski 1989, Frelich and Reich 1995, Friedman and Reich 2005). Intensive harvest and repeated fires have resulted in forests that bear little structural or functional resemblance to their ecological predecessors. Gradually declining aspen (*Populus* spp.) and birch (*Betula papyrifera* Marsh) populations dominate forests throughout the region today (Frelich and Reich 1995, Cleland et al. 2001). These early-successional species inhibit their own regeneration (Frelich and Reich 1999) and current disturbance regimes throughout the region do not permit continued aspen–birch dominance (Caspersen et al. 2000), setting the stage for a region-wide transition in forest type. The current forest understory is more structurally and biotically diverse than the upper canopy

and provides a glimpse of the composition and structure of the future forest.

Odum (1969) hypothesized that net ecosystem production (NEP) increases during early succession before beginning a gradual decline to near zero in older stands, due in large part to declining net primary production (NPP). In a compilation of 33 forested sites with a ≥ 9 -year continuous record of above-canopy C flux data, Gough et al. (2008a) found general support for Odum's prediction of declining annual C storage in aging forests, but documented considerable variability between sites. Furthermore, old-growth forests are poorly represented in C flux studies. Kane et al. (2010a) cite similar limitations in the number of sites in which canopy structural development has been studied. Several recent studies, alternatively, show that older forests maintain significant net C assimilation, and therefore rates of NPP, well beyond the age at which they are expected to begin showing declines in C uptake (Luyssaert et al. 2008, Stoy et al. 2008). The mechanisms sustaining productivity in older forests are undetermined, but these recent studies implicate changes in forest canopy structure as a leading candidate.

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Structurally complex forest canopies are more efficient at harvesting light than structurally simpler ones and thus may contribute to unexpectedly high NPP and C sequestration (Ahl et al. 2004, Ishii et al. 2004, Martin and Jokela 2004, Duursma and Makela 2007). Structural and functional reorganizations in late succession may, then be important in understanding rates of C assimilation over a range of light conditions (Ahl et al. 2004, Chmura et al. 2007, Niinemets 2007). Canopy structural reorganizations are driven by canopy disturbances and successional transitions that alter the distribution of foliage throughout the canopy and that can also increase species diversity (Ishii et al. 2004, Hart and Grissino-Mayer 2009). Cumulative effects of patch-scale canopy disturbances (Canham 1989, Hart and Grissino-Mayer 2009) and recruitment of additional species (McElhinny et al. 2005) as forests age have been proposed as drivers of increasing canopy structural complexity. These changes to canopy structure may improve light harvesting (Lefsky et al. 1999, Ishii et al. 2004) and light-use efficiency (LUE, carbon fixed per unit light absorbed; Leuschner et al. 2009) and consequently increase production (Ishii et al. 2004, Duursma and Makela 2007).

Canopy structures may be increasing in complexity in the forests of northern Michigan, USA. At our regionally representative research site in northern Lower Michigan, Gough et al. (2010) found that plots with increasing mortality of early-successional species exhibited negligible declines in NPP_w , which was 26% of total above- and belowground NPP (Gough et al. 2008b). NPP_w was similarly insensitive to declines in leaf area, suggesting that whole-canopy light harvesting improved with mortality-driven canopy disturbances. The same study also found that plots with increasing representation of mid-successional species over the past decade exhibited a less marked decline in NPP compared to those where early-successional species remained dominant (Gough et al. 2010).

Our objective in this study was to identify the relationship between forest age, canopy structure, species composition, and primary production, thereby providing a mechanistic hypothesis explaining prior results indicating sustained high rates of NPP in maturing forests (Luyssaert et al. 2008, Gough et al. 2010). Specifically, we hypothesized that canopy structural complexity increases with stand age and is positively correlated with stand production. We further hypothesized that as mid-successional species grow into the canopy to replace early-successional species, the resulting, more biodiverse forest with a wider representation of shade tolerances could promote C uptake rates that are robust under variable light conditions. Previous work demonstrates that changes in diversity of canopy species can have significant impacts on NPP (Gough et al. 2010). These changes to canopy structure and composition associated with the ongoing successional transition could thus provide a mechanism by which NPP in maturing forests

is sustained or increased over time. We combined long-term growth and diversity data with lidar scans of canopy structure to quantify both canopy structure and C uptake rate and test these hypotheses.

METHODS

Site description and experimental design

We conducted this study at the University of Michigan Biological Station (UMBS) in northern Lower Michigan (45°35.5' N, 84°43' W). The UMBS forest is a mixed northern hardwood forest representative of a dominant forest type in the region with similar tree-community composition, forest age, and disturbance history (Frelich and Reich 1995, Cleland et al. 2001). Early-successional aspen and birch species became dominant following intensive harvest and fire a century ago, but they are in rapid decline (Gough et al. 2010). Northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and American beech (*Fagus grandifolia* Ehrh.) are co- or subdominant later-successional species in the canopy, and bracken fern (*Pteridium aquilinum* L.) and seedlings of red oak, red maple, white pine, and American beech dominate the herbaceous layer. Mean canopy height is 22 m. Mean annual (1942–2003) temperature is 5.5°C and mean annual precipitation is 817 mm. Soils in the study area are coarse-grained, excessively drained, mixed frigid Entic Haplorthods with minimal relief.

To examine the relationship between structural and biological complexity and NPP, we measured stand age, canopy tree-species diversity, leaf area, NPP_w , and stem mortality rates in 30 0.08-ha plots from 1997–2008. These plots are deployed throughout the footprint of an AmeriFlux eddy-covariance meteorological tower and lay along transects up to 1 km long radiating outward from the tower (Schmid et al. 2003). We assessed canopy structural complexity in these plots in 2008 using ground-based portable canopy lidar (PCL) to generate vertical cross sections of canopy vegetation distribution.

Wood net primary production

Mean annual plot NPP_w was estimated using dendrometer bands on a subset of trees in each plot (~19% of the population, $n = 1140$ trees) and site-specific allometric equations relating bole diameter to above-ground wood mass as described in Gough et al. (2008b, 2010). We calculated plot-specific growth rates using data from complete censuses in 1997–1998 and 2001 of all trees >8.0 cm diameter at 1.37 m height ($n = 6141$ trees) in all plots ($n = 30$ plots). We used these growth rates to adjust calculations of NPP_w to account for over- or underestimation based on yearly subsampling. Previous work at this site has established that NPP is sensitive to interannual climatic variability (Curtis et al. 2005, Gough et al. 2008b), so NPP_w values were averaged across all years (1998–2008) to reduce the influence of short-term climate variation in this analysis. Of the several indices of C uptake quantified at our site, we used

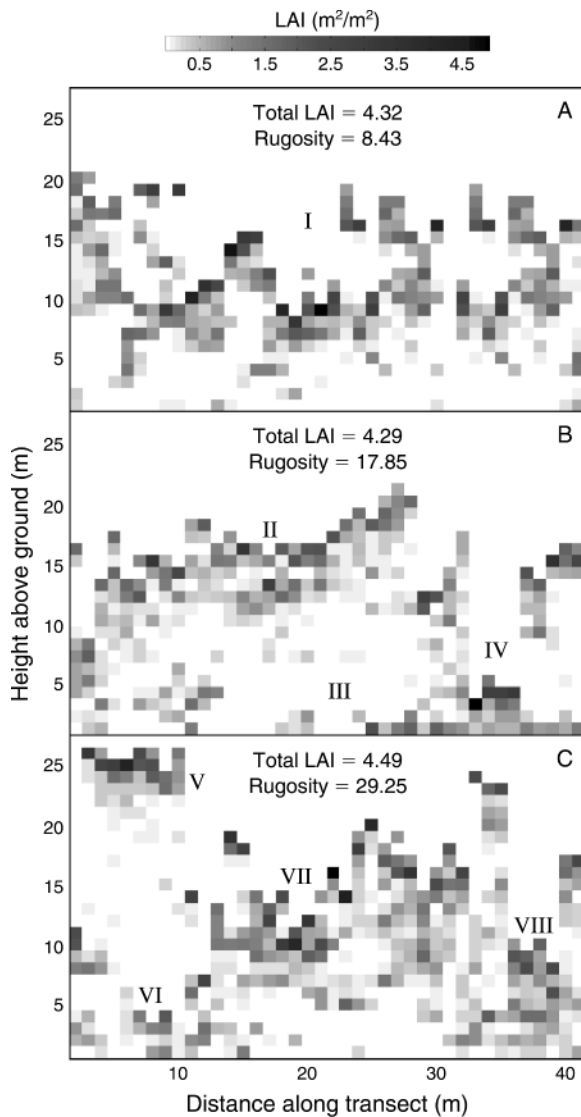


FIG. 1. Bias-corrected distributions of vegetation density in plots of (A) low, (B) intermediate, and (C) high rugosity but of similar total leaf area index (LAI). Each grid section (bin) is 1 m², and darker bins represent areas with greater vegetation density, as indicated by LAI. Features of canopy structure that affect plot-level canopy complexity include: uniform distribution of leaf area density with height and depth (I), variability in canopy height but constant canopy depth (II), lack of understory (III), gaps (IV), individual tree crowns (V), developing understory of later-successional species (VI), variability in canopy height and depth (VII), and canopy gaps with developing understory (VIII).

NPP_W as a gauge of plot-level primary production for two reasons. First, NPP_W contributes to a slow-turnover C pool that dominates long-term C storage in eastern forests of North America (Curtis et al. 2002). Second, NPP_W is measured with high precision (SE = 6%) relative to other components of primary production (Gough et al. 2008b), thereby enhancing confidence that our correlations of primary production and ecosystem structure are of biological significance.

Measurement and definition of canopy structural complexity

We characterized plot canopy structural complexity at peak LAI in summer 2008 using a ground-based portable canopy lidar (PCL) system. The design, operation, and validation of this system is described in Parker et al. (2004a). The PCL is based on an upward looking, near-infrared pulsed-laser operating at 2000 Hz (model LD90-3100VHS-FLP; Riegl USA, Inc., Orlando, Florida, USA). Our system was mounted on a portable frame worn by the operator while walking along a pre-marked 40-m transect passing through the center of each 0.08-ha plot. The high sampling rate relative to the operator's walking speed allows the system to record vegetative surfaces distributed at all heights throughout the canopy with high spatial resolution. We binned the raw data horizontally and vertically at 1-m intervals (Fig. 1). For each 1 m wide vertical column, we calculated vegetation area index (VAI) as the ratio between the number of returns in each bin and the sum of canopy and sky hits in each column. Canopy coverage bias corrections were made following Parker et al. (2004a). This produced 40 vertical columns of VAI values for each plot. PCL-measured VAI was converted to units of LAI using scaling parameters obtained by comparing the mean vegetation density at the site with observed mean LAI. The PCL data correspond to a vertical plane defined by a transect walked by the operator, and as it is impossible to walk through stems, they do not appear in the PCL scans. Branch surface area is small relative to leaf area at our site (Gough et al. 2008b) and its vertical distribution is not significantly different from that of leaf density. This suggests that branch surface area is a small component of our LAI estimates.

We define a parameter for structural complexity, canopy rugosity (R_C), as

$$R_C = \sigma(\sigma[\text{VAI}]_z)_x \quad (1)$$

where z is the vertical axis, x is horizontal axis, and σ is standard deviation. VAI values are obtained along a vertical plane transecting a three-dimensional field of leaf densities. To calculate R_C , we first calculate the standard deviation of the vertical (along the z -axis) leaf density distribution within each column of the VAI data. This results in a horizontal row of values, each representing a vertical standard deviation characterizing a particular 1 m wide column along the forest floor. Finally, R_C is calculated as the standard deviation of the entire row (along the x -axis) of vertical standard deviations. This definition of rugosity is somewhat different from previous uses (e.g., Parker and Russ 2004); we use it as a statistical metric summarizing the full three-dimensional distribution of leaf densities (both vertically and horizontally). Others have used rugosity as a measure of the "wrinkledness" or "rumple" of the general canopy surface only (Parker et al. 2004b, Kane et al. 2010a, b).

Since our site is in successional transition with canopy dominants senescing at an accelerating rate leaving the current understory to replace them in the upper canopy, we decided to evaluate canopy structural complexity throughout the entire canopy thickness, rather than solely at its upper surface. Previous research suggests that woody stems in the understory contribute to forest productivity (Ishii and Asano 2010, Niinemets 2010) and, at our site, juvenile cohorts of eventual overstory species dominate the understory. Rumpel as a metric of outer canopy surface structure is affected primarily by canopy dominant trees and gap saplings and thus would not have provided as much insight into future canopy morphology or function.

Lefsky et al. (2005) found that a combination of mean height of lidar returns, standard deviation of lidar returns, and degree of canopy closure were sufficient to accurately describe canopy structure with strong correlation to coincident field measurements of LAI and aboveground biomass (see also Kane et al. 2010a, b). Our rugosity index of canopy structural complexity, meets these criteria by integrating the variability of foliage density distribution along horizontal and vertical axes, providing sensitivity to canopy height, gaps, and canopy closure.

Site index and plot age

Site index (height at 50 years), a metric of site quality, was calculated using tree height and age data from each of two to three canopy-dominant bigtooth aspen per plot following the procedures of Lundgren and Dolid (1970). We measured height of each tree using a clinometer. Age of each tree was determined by counting annual growth rings on tree cores taken at 1.37 m above ground. Cores were sanded with very fine grit sandpaper and stained to increase contrast of annual rings when necessary. Two individuals independently counted a subset of the cores to verify ring count accuracy. We calculated plot age and site index from tree cores obtained in 2005 and 2008. This parameter, which expresses the effect of edaphic and microclimatic site variables on potential stand production after normalizing for age, allows inter-plot comparisons of overall site quality (Long and Shaw 2010).

Leaf area index

We estimated annual LAI from measurements of overstory leaf mass in years 1997 to 2007–2008, as described in Gough et al. (2010). We quantified plot leaf mass using a single litter trap (0.179 m² or 0.264 m²) placed in the center of each 0.08-ha plot. We emptied litter traps weekly during autumn leaf abscission and monthly otherwise. Leaf litter was dried, separated by species, and weighed. We calculated LAI from individual species-specific leaf area (SLA) determined from measurements of area and mass (four replicate sets of 20 leaves/species). As with NPP, we averaged values across the entire study period, 1998–2008.

Canopy tree diversity

We assessed plot-scale species diversity (D) of canopy trees using Simpson's index of diversity. We calculated Simpson's reciprocal index as

$$D = \frac{1}{\sum_i^n p_i^2} \quad (2)$$

where p is the proportion of LAI contributed by species i to a litter trap located in the center of each 0.08-ha plot and n is the number of species in the plot. We based estimates of plot diversity on canopy LAI to capture potential variation in physiological functioning that could constrain NPP. Diversity estimates based on stem counts would have included many small trees likely to have considerably less impact on plot NPP. Higher Simpson's reciprocal index values indicate greater diversity of trees in the canopy of the plot.

Statistical analysis

We used linear regression and path analysis (JMP 8.0.1; SAS Institute, Cary, North Carolina, USA) to evaluate interactions between rugosity, LAI, site index, plot age, and canopy tree diversity and to determine how these forest characteristics might contribute to prediction of NPP_w over decadal time scales. Relationships between parameters were considered significant when $P \leq 0.05$. Path analysis weighs relative influence of several interrelated candidate explanatory variables which may have both direct and indirect effects on the response variable of interest (Hosokawa et al. 2009, Jonsson and Wardle 2010). The contribution of each explanatory variable to prediction of the response variable is proportional to its path coefficient. Variability in stand NPP_w not explained by relationships between parameters included in the path model is indicated by the variable U , defined as

$$U = \sqrt{1 - R^2} \quad (3)$$

where R^2 is the coefficient of determination for the whole model explaining NPP_w.

Jackknife analyses and Hotelling's T^2 statistic identified one plot as a consistent outlier and we excluded it from pairwise correlations and path analyses. This plot was heavily vegetated and had an NPP_w value well outside the 1.5 inter-quartile range of the other 29 plots. This plot's status as an outlier was consistent with field observations of its unique ecological features on the landscape, including low-lying topography and soil properties that result in periodic seasonal inundation.

RESULTS

Stand characteristics

Mean decadal NPP_w rates varied by more than an order of magnitude among plots (Table 1) and the distribution of values skewed slightly rightward, with

TABLE 1. Growth, structural, and compositional characteristics of study plots.

Parameter	\bar{x}	σ	Range
NPP _w (Mg C·ha ⁻¹ ·yr ⁻¹)	1.57	0.83	0.38–4.30
Rugosity (m)	16.86	6.90	7.13–31.47
Total LAI (m ² /m ²)	4.15	0.96	2.27–6.65
Aspen and birch LAI (m ² /m ²)	2.04	0.84	0.24–3.46
Age (yr)	76	9.4	55–88
Site quality (50-yr site index; m)	21.4	3.9	16.3–32.1
Tree-species diversity (Simpson's index)	2.6	0.6	1.3–4.1

Note: Values are averaged across all years for which data were available. Mean (\bar{x}) and standard deviation (σ) values are among all plots ($n = 29$ plots).

only three plots over 2.5 Mg C·ha⁻¹·yr⁻¹ and one over 4 Mg C·ha⁻¹·yr⁻¹. Canopy rugosity showed a fourfold range among plots with values uniformly distributed within that range. Aspen and birch species together comprised on average 50% of total leaf area across all plots, but with substantial variation among plots. Total LAI for each plot was positively related to non-aspen/birch LAI in the plot ($R^2 = 0.50$), but not to aspen and birch LAI values ($P > 0.1$), which varied by an order of magnitude across all plots (Table 1). Only one plot had more than 6.0 m²/m² of leaf area. Mean stand age was 76 years and more than two thirds of the plots were ≥ 70 years old, consistent with the disturbance history of this site. Site quality, quantified as site index, of the most fertile plots was double that of the least fertile plots. The distribution of site index values for all plots skewed slightly right indicating generally low site quality in the study area. Plots had an annual average of six species represented in litter traps from which we calculated diversity, though some plots had as many as nine or as few as three species contributing litter in any given year. Trees of each of the six main species were present at some point during the study period in each of the plots with the exception of *F. grandifolia* and *P. strobus* which were completely absent in one and twelve of the 29 total plots, respectively. Mean Simpson's Index of species diversity of canopy trees across years varied substantially (Table 1). Simpson's Index, accounting for both species composition and abundance, of the most diverse plot was three times that of the least diverse plot.

At our site, low, intermediate, and high rugosity plots had distinct canopy structural features that gave rise to variation in complexity (Fig. 1A–C). Note that all three plots had similar LAI despite varying widely in rugosity. In the low-rugosity stand, trees showed little variability

in canopy height. Leaf area density was distributed uniformly across height, with no evident canopy stratification, and canopy thickness was relatively constant across the plot. The stand with intermediate canopy structural complexity showed some development of distinct canopy strata and, while canopy thickness was still relatively uniform, leaf area density was more variable than in the low-rugosity plot. This plot also exhibited a canopy gap with attendant proliferation of LAI in the understory. In the high rugosity plot, canopy structure was more complex due to the emergence of distinct crowns of individual canopy trees, gaps in the upper canopy with obvious, developing understory, and high variability of both canopy height and thickness. Leaf area density was also highly variable across both horizontal and vertical axes.

Drivers of stand production

Our objective was to evaluate the potential role of canopy structural complexity in the context of other known and potential drivers, as a predictor of stand production. Many of the variables measured correlated significantly with each other and with NPP_w (Table 2). NPP_w increased strongly with rugosity, site quality, total LAI, and stand age. For example, the most productive plots ($\geq \bar{x} + \sigma$; $n = 3$ plots) were 28% older, 38% more fertile, had 91% more LAI which was composed of nearly three times as much aspen and birch, and were more than twice as rugose as the least productive plots ($\leq \bar{x} - \sigma$; $n = 3$ plots). Rugosity correlated significantly with all other plot characteristics except species biodiversity. The most rugose plots ($\geq \bar{x} + \sigma$; $n = 5$ plots) were on average 11 years older than the least rugose plots ($\leq \bar{x} - \sigma$; $n = 7$ plots) and had 32% more LAI, 85% more of which was

TABLE 2. Pearson's correlation coefficients for all pairwise correlations of model parameters.

Parameter	Simpson's index	Aspen and birch LAI	Total LAI	Site index	Age	Rugosity
Aspen and birch LAI	-0.16					
Total LAI	-0.08	0.18				
Site index	-0.08	0.36 [†]	0.43*			
Age	0.21	0.16	0.27	0.26		
Rugosity	-0.11	0.32 [†]	0.41*	0.59*	0.48*	
NPP _w	-0.14	0.47 [†]	0.56*	0.66*	0.45*	0.66*

* $P < 0.05$; [†] $P < 0.1$.

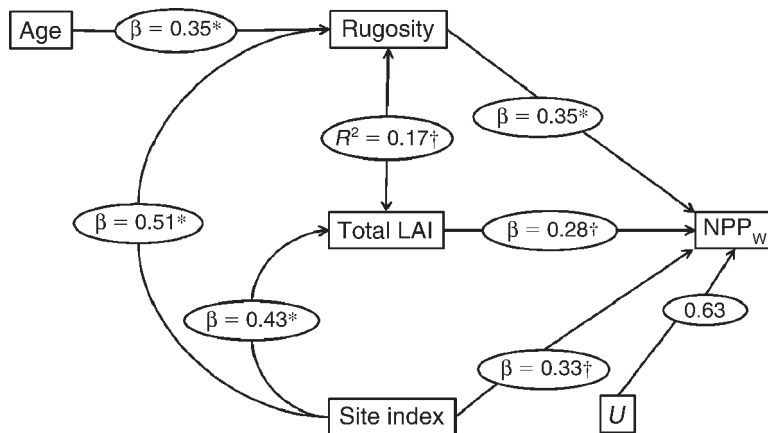


FIG. 2. The relative contributions of stand age, site index, total leaf area index (LAI), and rugosity on annual wood net primary production (NPP_w). Unidirectional arrows indicate significant and direct effects with path strength indicated by standardized partial regression coefficients (β). Bidirectional arrows indicate correlation with path strength indicated by a coefficient of determination (R^2). U indicates the contribution of unmeasured variables.

* $P < 0.05$; † $P < 0.1$.

aspen and birch, and were 30% more fertile. Plot-level species biodiversity of canopy tree species, quantified as Simpson's index, did not correlate significantly ($P > 0.1$) with any other variable measured. The addition of canopy height to the analysis did not explain significantly more variation in NPP_w than the parameters already considered ($P > 0.1$, data not shown).

Inclusion of all variables with significant cross-correlations to other terms in a single multivariate standard least squares (SLS) path analysis model with NPP_w as the response variable revealed that only rugosity (canopy structural complexity), LAI (total photosynthetic surface area), and site index (site quality) had significant direct effects on NPP_w (Fig. 2). The structure of this path diagram is well supported by the data ($R^2 = 0.60$). As indicated by standardized partial beta coefficients, rugosity was nominally stronger as a driver of NPP_w than was site quality and both were much stronger than LAI. Rugosity was among the strongest plot-level drivers of NPP_w and equal to site quality in effect strength, an indication that rugosity is at least as important as LAI and fertility in regulating primary production. Site quality correlated positively with both LAI and rugosity. Rugosity and LAI are weakly autocorrelated ($R^2 = 0.17$), but retention of both in the model suggests that while these parameters supply some redundant information, rugosity provides additional meaningful explanatory power to the model. Stand age interacted significantly only with canopy rugosity, suggesting that stand age may be indirectly affecting NPP_w primarily through its influence on canopy rugosity (Fig. 2).

Plot NPP_w was nonlinearly related to rugosity (Fig. 3) with low rugosity plots (<10 m; e.g., Fig. 1A) having 33% of the predicted NPP_w of high rugosity plots (>25 m; e.g., Fig. 1C). The pairwise relationship between NPP_w and canopy rugosity was best described by an

increasing second order polynomial curve ($R^2 = 0.48$). However, we cannot rule out a simpler linear relationship ($R^2 = 0.43$) as both empirical models produce nearly identical AIC values (polynomial AIC = 61.1, compared to linear AIC = 60.9). We preferred the better fitting model (second-order polynomial) to illustrate the relationship between NPP_w and rugosity (Fig. 3). Rugosity increased with stand age at a greater rate than did LAI across the 30-year range in stand age among plots (Fig. 4). The regression of LAI with stand age in Fig. 4 is best fitted as a logarithmic curve based on previous work at our site that demonstrated that LAI saturates early in stand development and changes little in subsequent years (Gough et al. 2007). We suggest that

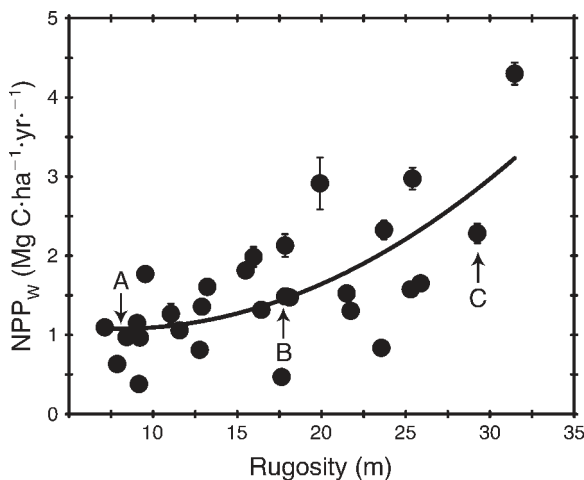


FIG. 3. The relationship between canopy rugosity and decadal wood net primary production (NPP_w, 1999–2008). Lettered arrows correspond to plots illustrated in Fig. 1A–C. Values are mean \pm SE. $NPP_w = 0.004 \times (\text{Rugosity})^2 - 0.062 \times (\text{Rugosity}) + 1.324$ ($R^2 = 0.48$, $P < 0.01$).

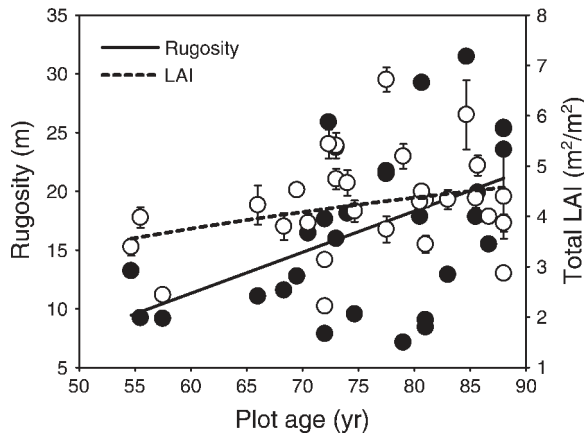


FIG. 4. The relationship between plot age, rugosity (solid circles), and leaf area index (LAI; open circles) in a northern mixed hardwood forest. Rugosity = $0.35 \times \text{Age} - 9.69$ ($R^2 = 0.23$, $P < 0.01$). LAI is not significantly related to stand age ($P > 0.1$). LAI values are depicted as means \pm SE ($n = 29$ plots).

this accounts for the poor correlation between stand age and LAI ($P > 0.1$) in the range of ages observed in this study. Notably, rugosity continues to increase past the LAI saturation point ($\sim 4.5 \text{ m}^2/\text{m}^2$) with no evidence of a slowing rate of increase.

DISCUSSION

Wood NPP and canopy structural complexity

We examined whether variation in canopy structural complexity, or rugosity (the variability of three-dimensional arrangement of photosynthetic surface area within the canopy) could help explain differences in wood NPP across a successional forest landscape in the Upper Great Lakes region. Our results indicate that rugosity is as important as other well-known stand-level drivers of aboveground production including LAI, site quality, and stand age (Fig. 2). Indeed, rugosity was a better predictor of variation in plot-level NPP_W than was LAI (Table 2, Fig. 2). The relative contributions of rugosity and LAI to NPP_W , and the weak correlation between rugosity and LAI, together suggest that the arrangement of leaf area within the canopy is as important to NPP_W as the total quantity of leaf area. This increase in NPP_W with increasing rugosity (Fig. 3) suggests that the same amount of photosynthetic surface area in a canopy, deployed differently in space, can have significant consequences for plot-level NPP_W . Early work considering the interaction of canopy structure and forest productivity came to similar conclusions regarding the importance of structural complexity based on sophisticated conceptual models, but little data was available at the time (Horn 1971). Contemporary models similarly underscore the importance of a complex and heterogeneous canopy structure in driving forest productivity and coexistence of both canopy and sub-canopy species (as reviewed in Ishii and Asano 2010). This study is the first to provide empirical support

for models using first principles to predict an increasing relationship between canopy structural complexities and stand productivity. Our analysis showed that canopy structural complexity was as important to NPP_W as site quality. In addition, site quality directly contributed to NPP_W and indirectly influenced NPP_W through its contribution to both LAI and rugosity.

Canopy rugosity may affect NPP_W through effects on light transmission and interception by photosynthetic tissues (Funk and Lerdau 2004, Ishii et al. 2004, Parker and Russ 2004, Bartemucci et al. 2006, Niinemets 2007). More rugose stands transmit a greater proportion of incoming radiation as direct light to leaves deeper in the canopy, improving light availability to internal canopy foliage (Parker et al. 2004b). Changes to canopy structure that increase overall structural heterogeneity can increase the proportion of total leaf area exposed to direct radiation and increase intensity of light that penetrates beneath the upper-canopy surface (Canham 1988a, b, Parker and Russ 2004, Ishii and Asano 2010), improving light harvesting without an increase in LAI. Aspen and birch were among the oldest and tallest trees in our plots, with their leaf area generally confined to a shallow band in the upper canopy. However, the developing understory and non-aspen/birch canopy codominants were more structurally complex. Increased access to more intense light by the developing understory and canopy co-dominant species may thus be responsible for the higher rates of wood production in more rugose plots. The increase of rugosity with increasing stand age despite no corresponding age-related increase in LAI suggests that, over time, canopy rugosity becomes increasingly important as a driver of stand-level differences in wood NPP while the influence of increasing LAI on production saturates. Indeed, in forests where LAI plateaus early in succession and remains stable for an extended period, increasing canopy rugosity may be the primary mechanism driving NPP_W , thus contributing to the stand's status as net C sink.

Changing canopy rugosity over time

Our results show clearly that canopy structural complexity continues to increase through time with significant consequences for annual wood production. Increasing canopy structural complexity with stand age has been documented in other forests (Ishii et al. 2004, Parker and Russ 2004, Duursma and Makela 2007, Hart and Grissino-Mayer 2009). Kane et al. (2010a, b) found increases in canopy structural complexity with stand age in secondary coniferous forests but emphasized that development of canopy structure was not linearly related to age alone. This was especially true in stands of intermediate age, due to the influence of other edaphic variables such as site quality and disturbances that affect the rate of canopy development (Kane et al. 2010a). Plots at our site represent a narrower age range and uniform successional status relative to other studies of forest age and canopy structural complexity, and

show a clear relationship between age and canopy structure. Similar to Kane et al. (2010a), we observed substantial variability of canopy structural complexity values among plots of similar age. Previous studies provide support for our suggestion that canopy structural complexity increases significantly across a much greater range of ages (e.g., Parker et al. 2004b, Parker and Russ 2004). Future investigations should evaluate the relationship between canopy structure and forest productivity across a greater range of forest successional statuses.

While canopy structural complexity generally increases with stand age, other drivers affect the rate of increase. Stands of similar ages may be subject to widely varying influences on canopy structure including site quality, topography, and geography that will affect the rate of stand development and stand vulnerability to stochastic disturbance events such as wind or ice storms. Thus, age alone provides limited insight into the mechanisms affecting forest development, but rather is a proxy for events that affect the development of stand structure over time at varying rates. In our study, canopy structural complexity was greater in plots with higher site quality, regardless of stand age. In higher-quality sites, trees allocate more to aboveground biomass production, accelerating stand structural development (Litton et al. 2007, Ryan et al. 2008). In spite of varying rates of change in canopy structural complexity, we observed a clear increase in rugosity with age, underscoring the convenience of age as a proxy, but emphasizing how little understanding of underlying mechanisms it provides.

Both total leaf area and the complexity of leaf area distribution throughout the canopy, quantified here as rugosity, are essential to forest C assimilation. These features of canopy structure are correlated but not identical, responding differently to plot age and site quality (Figs. 2 and 4). In turn, leaf area and rugosity have complementary, but unique, influences on plot production (Fig. 2). Considering these characteristics of canopy structure independently seems unrealistic because of their interrelated influences on stand structure and function (Parker and Russ 2004, Weiskittel et al. 2010). Studies have shown that incorporation of detailed canopy structural parameters into growth prediction models is necessary to accurately evaluate stand production potential and improve overall model performance (Duursma et al. 2007, Weiskittel et al. 2010). Toda et al. (2009) found that changes in vertical leaf area distribution had a greater effect on modeled NPP than did changes to above- vs. belowground biomass allocation. Weiskittel et al. (2010) showed that stand LAI was more accurately predicted in models using canopy structural parameters than by using traditional allometric and empirical approaches alone. These results are consistent with our findings, which suggest that changing the distribution of leaf area can affect wood production more than changes in leaf area quantity

alone. As leaf area saturates in these forests, structural complexity continues to increase becoming the important variable driving NPP_W .

Species diversity and canopy structural complexity

Species diversity may be an important ecosystem characteristic affecting primary production (Tilman 1982, 2007, Jonsson and Wardle 2010). In a path analysis on data from a burn chronosequence in a Swedish boreal forest, Jonsson and Wardle (2010) found that plant diversity, stand composition, and stand age all significantly influenced total ecosystem C storage. At our site, Gough et al. (2010) found that plots with significant increases in diversity of canopy tree species over the past decade were more resistant to declines in NPP_W , with evidence that a change in composition toward later-successional species was responsible for this effect. Our results indicate that tree-species diversity was not a significant contributor to prediction of NPP_W or canopy structural complexity. The effects observed by Gough et al. (2010) were for a subset of eight (of 30) plots in which canopy diversity changed significantly over decadal time. Though the same result was not observed in the present study, our examination of NPP_W and canopy diversity included all plots, more than two-thirds of which have not exhibited significant changes in canopy diversity. However, we expect that as the influence of canopy-dominant aspen and birch declines following senescence, and a more species-diverse understory develops broadly across all plots into a mature canopy with higher rugosity and a significantly different light-use regime, the diversity of canopy tree species will impose a more widespread influence on variation in NPP_W (Canham et al. 1999, Parker et al. 2004a, b). Taken together, our results and those of Gough et al. (2010) suggest that canopy species diversity at our site is indeed becoming more important as the forest succeeds, but its overall effect on NPP_W is presently limited to only a few plots and is not yet significant across the entire landscape. Ongoing experiments at our site will determine whether the effects of species diversity on forest production become and remain important as succession proceeds.

Implications for regional forest productivity

Our results indicate that as the forest ages, NPP_W is being progressively more strongly influenced by increases in canopy structural complexity rather than increases in photosynthetic surface area (i.e., LAI). The conceptual models of canopy development proposed by Parker and Russ (2004) and Ishii et al. (2004) suggest that our study site, which is representative of a type covering up to 100 000 km² in the Upper Great Lakes (Cleland et al. 2001), is shifting from an expansion to an erosion phase of canopy development (sensu Parker and Russ 2004). The aspen and birch that currently dominate the canopy are senescing at an accelerating rate, which will produce myriad canopy gaps and facilitate recruitment of canopy

subdominants, greatly increasing canopy structural complexity. We have shown that canopy structural complexity increasingly affects stand production as stands age. Our findings suggest that a more structurally complex canopy will drive higher rates of forest production in similar forest types despite mortality of large numbers of early-successional canopy trees. Recruitment of shade-adapted subdominant cohorts into the canopy may have additive effects on forest productivity with canopy structural complexity by increasing total leaf area and LUE at low light levels. While many factors interact to influence NPP trajectories during succession, canopy structural complexity may merit inclusion in models that simulate forest carbon exchange over stand development (Mitchell et al. 2009, Sierra et al. 2009). Given the extent of forests undergoing this successional transition in the Upper Great Lakes, an increase in NPP caused by increasing canopy structural complexity will have significant implications for regional C storage by allowing forests to remain net C sinks as they mature.

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