Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function

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ABSTRACT

Recent observations demonstrate that, against expectations, some forests maintain high carbon (C) storage rates for centuries, though the underlying mechanisms remain poorly understood. To test the hypothesis that age-related increases in canopy structural complexity improve resource-use efficiency and to evaluate canopy structural influences on forest C storage over successional timescales, we measured the fraction of photosynthetically active radiation absorbed by the canopy (fAPAR), foliar N_{mass}, and aboveground net primary production (ANPP) in a chronosequence of 39 passively managed stands spanning >160 years of forest development in Northern Lower Michigan, USA. We used ground-based portable canopy LiDAR to quantify canopy structural complexity as rugosity, an integrated metric of 3D heterogeneity in canopy leaf area arrangement. Here, we describe a mechanism capable of maintaining high rates of ANPP over nearly two centuries of forest development. Results support our hypothesis that increasing canopy complexity over the course of forest development mediates greater resource-use efficiency in these forests. Forest stands with more structurally complex canopies had higher light and nitrogen use efficiencies (LUE & NUE) and higher ANPP. LAI was stable across stands older than 50 years, while canopy complexity (rugosity) increased with age through >160 years of stand development. Rugosity had a bigger influence on ANPP across all stands than did LAI, demonstrating the greater long-term influence of leaf area arrangement, rather than quantity within the canopy on forest C storage. We conclude that canopy structural complexity may facilitate greater resource use efficiency (RUE) in aging forests and so increase ANPP compared to structurally simpler canopies in young forests, thus maintaining significant C storage potential in aging forests. We suggest that forest managers should incorporate canopy structural complexity as a robust proxy of stand C storage potential in forests differing widely in age and disturbance history.

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1. Introduction

Forests are an integral component of the Earth's carbon (C) cycle, storing at present 2.4 Pg C annually in biomass and soils (Pan et al., 2011). Considerable uncertainty exists, however, in the future trajectory and magnitude of the terrestrial C sink as globally many aggrading forests approach maturity following clear-cut harvesting a century or more ago (Birdsey et al., 2006). With these regrowing forests advancing beyond the early aggrading phase of succession, an ecologically important transition is underway in which structurally and biologically simple forests dominated by short-lived early successional trees senesce and give way to more complex stands comprised of longer-lived, later successional species (Caspersen and Pacala, 2001; Birdsey et al., 2006). Widespread forest regrowth is leading to a reemergence of later successional forests in many regions, especially the naturally-regenerated, mixed-deciduous forests of North America and Eurasia (Caspersen et al., 2000; Luyssaert et al., 2010; Wang et al., 2011).

Investigations of forest net primary production (NPP) over the course of ecological succession support a general trend of declining production with forest age, but with important knowledge gaps for

late successional, mixed forests (Gower et al., 1996; Ryan et al., 1997; Smith and Long, 2001; Law et al., 2003; Parker et al., 2004a; Pregitzer and Euskirchen, 2004; Gough et al., 2008a). Quantitative syntheses consistently report lower NPP in old-growth rather than young, aggrading forests (Pregitzer and Euskirchen, 2004; DeLucia et al., 2007; Luyssaert et al., 2008). These syntheses provide critical assessments of changes in NPP over time; however, the inference of their findings may not extend to temperate deciduous forests for two important reasons. First, coniferous forests dominate global syntheses and thus drive trends in and conclusions regarding old growth NPP. Secondly, mixed deciduous forests included in these syntheses were less than a century old, highlighting the lack of NPP data from mature mixed deciduous-conifer forests. Single-site empirical studies of mixed deciduous forest NPP from early through late succession have not been conducted; however, decadal studies of NPP in mixed deciduous forests entering mid-succession indicate NPP may increase, contrary to expectations derived from studies of coniferous forests (Urbanski et al., 2007; Gough et al., 2008a, 2010). Moreover, recent modeling studies report considerably different NPP trajectories among forest types, with some temperate deciduous broadleaf forests showing no decline in NPP after 100 years (Wang et al., 2011).

Reported patterns of C storage rates from aging stands are not consistent, showing trends in different directions with different proposed mechanisms (Ryan et al., 1997; Pregitzer and Euskirchen, 2004; DeLucia et al., 2007; Luyssaert et al., 2008). The mechanisms controlling successional trajectories of NPP in mixed-deciduous forests likely depart from those well described for many coniferous-dominated forests. Declines in production by very tall old-growth coniferous forests of the western US (Ryan et al., 1997; Binkley et al., 2006) and in a >100-years-old loblolly pine (*Pinus taeda*) forest reaching maturity (Drake et al., 2011) can be partially attributed to height-related limitations in hydraulic conductivity, but in shorter and more structurally and biologically diverse forests, height-related growth limitations may prove less prominent. Instead, increasing canopy structural complexity, which has been linked to forest production in a narrow range of stand ages, may sustain high rates of production in some mixed deciduous old-growth forests (Luyssaert et al., 2008; Gough et al., 2010; Hardiman et al., 2011) by improving light and nitrogen use efficiency.

Canopy complexity, the vertical and horizontal heterogeneity of leaf area distribution within the canopy, can strongly influence light interception (Walcroft et al., 2005) and light use efficiency (Duursma and Makela, 2007) with significant consequences for NPP as forests age. Canopy structural complexity increases through forest development and succession due to disturbances that rearrange canopy leaf area; these changes are evident in the topography of the outer canopy surface in stands differing in age by more than a century (Ishii et al., 2004; Parker et al., 2004a; Chmura et al., 2007; Ishii and Asano, 2010). In contrast, leaf area index (LAI) tends to saturate early in stand development upon crown closure for many forest types and, barring severe disturbance, remains stable for long periods (Gough et al., 2007; Hardiman et al., 2011; He et al., 2012). Given the insensitivity of LAI to stand age, LAI is not a robust candidate to explain long-term trends in forest NPP, suggesting that leaf area arrangement may be more important than leaf area quantity in determining NPP. Structurally complex canopies have relatively greater canopy surface area exposed to incident radiation (Parker et al., 2004b; Walcroft et al., 2005; Duursma and Makela, 2007) and have lower albedo (Ogunjemiyo et al., 2005) indicating greater light interception. Within-canopy spatial partitioning by the complex assemblages of species and age cohorts often seen in late successional temperate forests can promote high canopy photosynthetic capacity in wide-ranging light conditions (Niinemets, 2007, 2010). Canopy light use efficiency (LUE, the ratio NPP to fAPAR, Haxeltine and Prentice,

1996) is determined by within-canopy spatial, temporal, and physiological differentiation of foliage and canopy structures in response to contrasting light levels (Chapin et al., 2002; Niinemets, 2007) and is known to vary with forest composition (Ahl et al., 2004). We therefore hypothesized that, barring limitation by other resources, increased light availability to foliage in the interior of the canopy resulting from reorganization of canopy structure will increase C assimilation rates. We also hypothesized that nitrogen use efficiency (NUE, the ratio of NPP to canopy N, Finzi et al., 2007) should increase with canopy structural complexity since as more light infiltrates deep into the canopy, low-lying foliage can maximize photosynthetic output relative to foliar N concentrations (Rocha et al., 2004). These hypotheses form the basis for a novel physiological explanation for previously observed linkages between canopy structural complexity and carbon storage rates and may explain sustained high C storage observed in some mid-late successional temperate forests.

To understand changes in canopy structural complexity and NPP, we studied passively managed forest plots in Northern Lower Michigan varying in age over >160 years of development. We evaluated the effects of changing canopy structural complexity on light and nitrogen use efficiencies, and thus on forest C storage potential. To do so, we combined ground-based near-surface remote sensing of canopy structure with biometric C storage accounting methods and chemical analysis of foliage.

2. Materials and methods

2.1. Study area and plots

We conducted this study from 2005 through 2011 at the University of Michigan Biological Station (UMBS) located in northern Lower Michigan (45°35.5′N, 84°43′W). This site in the Upper Great Lakes region is located in the transition zone between Northern mixed deciduous and boreal forests. Forests throughout this region were subject to clear-cutting and slash-fueled wildfires in the early 1900s (Frelich and Reich, 1995; USDA, 2001), with few, mostly small remnants of uncut or selectively cut forest remaining (Albert and Minc, 1987). Vegetation at UMBS is representative of this mix of forest compositions and ages found throughout the region, reflecting a legacy heavily influenced by anthropogenic disturbances of varying intensities (Gough et al., 2010).

We used 39 plots ranging in age from 6 to 172 years at the time of data collection, providing >160 years of perspective on the influence of canopy structural complexity on forest C storage. All plots were located within 10 km of each other and shared a common climate and similar soil type with minimal topographic relief (USDA, 1991). Stand age varies among plots based on severity and frequency of local disturbance.

Thirty-six permanent plots (16 m radius circular, 0.08 ha) were established in the early/mid successional forest type dominant throughout the region. Early successional aspen (*Populus grandidentata* Michx. & *Populus tremuloides* Michx.) and birch (*Betula papyrifera* Marsh) dominate these stands with substantial representation of co- or sub-dominant northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and American beech (*Fagus grandifolia* Ehrh.) in the canopy. Five of these 36 plots were established in areas subjected to a second experimental clear-cut harvest and burn in 1936, 1948, 1954, 1980, or 1998 (thus ranging in age from 6 to 68 years old at time of study). The most recent of these was the youngest stand in the dataset, but ages of the oldest three of these five stands were not different from those of the other early/mid successional plots, which ranged from 54 to 88 years old.

Three plots (12 m radius circular, 0.05 ha) were established in late-successional forest stands (131–172 years old) in 2005 at the

Colonial Point (CP) forest (~9 km southeast of the other plots) and re-sampled in 2010 and 2011. CP is a selectively harvested forest with old growth characteristics and resembles mature forests that dominated the area historically. This stand was subjected only to low-intensity disturbances prior to 1900 with no record of clear cutting (Albert and Minc, 1987). The canopy at CP is dominated by eastern hemlock (*Tsuga canadensis* L.), American beech (*F. grandifolia* Ehrh.), northern red oak (*Q. rubra* L.), and sugar maple (*Acer saccharum* Marsh.).

2.2. Aboveground net primary production (ANPP)

We calculated ANPP as the sum of aboveground net primary production of wood ($ANPP_W$) and leaves ($ANPP_L$). Biometric measurements of $ANPP_W$ were based on repeated measurements of stem diameter at breast height (DBH; 1.37 m height). $ANPP_W$ values were estimated from yearly measurements of dendrometer band diameter on a subsample of trees in each plot (~20% of the population, Gough et al., 2008b) or from repeated censuses of all within-plot stems every 3–5 years. We evaluated and corrected over- or underestimation of $ANPP_W$ from banded subsamples by comparison to values obtained during a complete census of all stems in all plots in 2010. Mass of aboveground wood was calculated from DBH based on exponential allometric equations with site- and species-specific coefficients (Gough et al., 2010). A site-specific C fraction of 0.49 was used to convert from dry wood to C mass (Gough et al., 2008b). The parameterization and evaluation of this method was described by (Gough et al., 2010). To minimize the effects of climate-driven interannual variability in $ANPP_W$ (Curtis et al., 2005; Gough et al., 2008b), we averaged all available leaf and wood production values (minimum 2 years).

Leaf ANPP ($ANPP_L$) was measured annually from litter traps deployed in each plot. Litter was collected weekly during autumnal leaf senescence and monthly otherwise. To determine C content, leaves were dried and weighed and a species- and site-specific leaf C fraction ranging from 0.45 to 0.48 was applied to convert from dry to C mass. $ANPP_L$ for each plot was derived from ⩾2 years of litter trap data to minimize interannual variability due to climate.

2.3. Canopy structural complexity

Complexity of canopy structure was quantified as rugosity, quantified here as the spatial heterogeneity of foliage distribution (Hardiman et al., 2011) using a Portable Canopy LiDAR (PCL) system (Parker et al., 2004a). Rugosity is a stand-level expression of canopy structural complexity, summarizing the 3-D heterogeneity of foliage distribution. The PCL system uses a pulsed, near-infrared laser to sample the canopy directly above it at a rate of up to 2 kHz, allowing it to quantify heights of all vegetative surfaces throughout the canopy with 2.5 cm vertical resolution. Branch area in deciduous forests is a small fraction of total canopy surface area, is not arranged differently from leaf area, and has been demonstrated to be a smaller source of bias in estimation of canopy leaf area using optical methods than stem area (Kucharik et al., 1998). Due to the vertical orientation of the LiDAR beam, stems did not contribute to canopy LiDAR returns. We established transects passing through the center of each plot and with length equal to approximately two times canopy height (canopy height ⩽40 m at CP, ~20 m elsewhere). A 0.25 ha square grid was also established in stands 30, 85, and 131 years old to create high-resolution 3D visualizations of the spatial variation of canopy surface structure.

2.4. Forest age and species richness

Ages of plots in the experimental burn chronosequence stands are known from records of experimental cutting and burning (Gough et al., 2007). Stand age in all other plots was determined by counting annual growth rings of oven-dried cores obtained from 2 to 3 canopy dominant trees. A random subsample of cores was counted multiple times by multiple researchers to ensure accuracy. Species richness was calculated as a simple count of distinct species present in the canopy of each plot.

2.5. Light and nitrogen use efficiency

To calculate LUE and NUE we measured the percent of photosynthetic photon flux density transmitted by the canopy (fAPAR), ANPP, and foliar N_{mass}. Foliar N_{mass} and fAPAR were measured in a subset of 11 plots selected from the 36 early/late succession plots and the three late successional CP plots. These subset plots were selected to represent the full range of rugosity and ANPP present in the complete dataset.

We calculated canopy LUE as the ratio of ANPP to canopy fAPAR (Haxeltine and Prentice, 1996). We quantified fAPAR by comparing above- and below-canopy light intensity during June–August 2011. Above-canopy light intensity was measured at an adjacent meteorological tower equipped with a BF2 sunshine sensor (Delta-T Devices, Cambridge, UK) to measure total and diffuse radiation. We only used data from periods when the diffuse fraction of total radiation was >85% (Kranabetter and Simard, 2008; Tobin and Reich, 2009). Below-canopy light was measured for between 300 and 2170 min over the course of 1–7 daylight periods between 7/24/2011 and 9/28/2011 with a linear array of eight PAR sensors (Li-190 Quantum Sensor, LICOR Biosciences, Lincoln, Nebraska USA & SQ-110 Quantum Sensor, Apogee Instruments, Logan, Utah USA) evenly spaced along the transect used for measuring rugosity of each plot. Data collection periods varied due to variable cloud conditions. Each below-canopy light sensor was calibrated against the above canopy sensor and linked to a central datalogger (CR1000 Campbell Scientific, Inc., USA). Daytime averages across the eight sensors in each plot were averaged over all hours of the day to reduce solar angle influence.

We quantified NUE, as the ratio of ANPP to canopy foliar N_{mass}, modified from Finzi et al. (2007) as below. Within each plot, we collected 2–3 leaves from 2 to 3 trees each of all dominant species at ⩾3 heights throughout the canopy via shotgun and pooled the plot-level samples by species. Species sampled accounted for 60–100% of total plot LAI (mean = 85% of total LAI). Dried, ground samples were analyzed for %N using a CHN analyzer (Costech International, Valencia, CA USA). Following previous methods employed at this site (Dronova et al., 2011; Nave et al., 2011), we calculated foliar N_{mass} (g N per g leaf dry mass) for each of the dominant species in each plot and scaled to canopy N_{mass} (Mg N ha^{-1}) by multiplying by a multi-year average of annual species specific leaf litter production. Specific leaf area (SLA) declined with increasing canopy height for all species, but leaf %N was not consistently related to canopy position, allowing us to estimate canopy N_{mass} as a simple product of litter production and foliar %N. While canopy N_{mass} was quantified as a pool rather than a flux, in these deciduous-dominated forests, the turnover rate of this pool is nearly identical to the time step in our ANPP rate and we treated canopy N_{mass} as a flux when calculating NUE.

2.6. Statistical analysis

We used Spearman's rank correlation coefficients to evaluate interactions between measured variables. Spearman's ρ is a rank transformation which indicates the degree to which the relationship between two variables is monotonically increasing or decreasing and is less sensitive to deviations from bivariate normality and linearity than Pearson's R (Conover and Iman, 1981). Regression analysis and stepwise forward model selection (JMP 8.0.1 SAS

Statistical Institute, Cary, NC, USA) was used to evaluate relationships between rugosity, LAI, LUE, NUE and stand age. Akaike information criterion ($AICc$) was used to justify additional variables in the model to improve overall goodness-of-fit and to select between similar models. Data were evaluated for possible outliers in the relationship between rugosity and ANPP using Mahalanobis distance, Jackknife distance, and Hotelling T^2 statistic. Two plots were identified as outliers in all three tests and were eliminated from further statistical consideration. Relationships between parameters were considered significant when $P \leqslant 0.1$.

3. Results

3.1. ANPP, LAI, and canopy structure

Components of aboveground stand production ($ANPP_W$ and $ANPP_L$) were both normal, unimodal distributions, though $ANPP_W$ was slightly positively skewed and $ANPP_L$ was slightly negatively skewed. Mean leaf to wood production ratio (LWR) was 1.04 for all plots (Table 1). We observed lowest LWR values in late successional plots (between 0.3 and 0.5; Fig. 1). In the five plots established via experimental cutting and burning we observed the highest LWR values (0.7–2.4) and these stands formed a smooth log-linear increase in LWR with stand age ($R^2 = 0.95$, $P = 0.0041$). No other spatial or age-based subset of plots exhibited relationships between LWR and age, but LWR decreased with age across all plots ($R^2 = 0.18$, $P = 0.0097$; Fig. 1).

Stand level canopy structural complexity increased with stand age, as evidenced by increasing fine-scale topographic heterogeneity of the outer canopy surface (Fig. 2). Rugosity (structural complexity of the entire canopy, not just the surface), increased monotonically with stand age (Table 2) until reaching an apparent maximum at 100–120 years ($R^2 = 0.73$, $P < 0.0001$; Fig. 3a). We found no evidence of net change in canopy rugosity in stands older than 120 years ($P > 0.1$). Rugosity was normally distributed and nearly nine times greater in the oldest (>130 years old) than in the youngest (<50 years old) stands. LAI and rugosity were correlated ($P = 0.002$), but LAI explained less than 20% of variance in rugosity (not shown, but see Hardiman et al., 2011).

LAI increased rapidly up to age 50, with considerable inter-plot variability, ranging from <2 to nearly 7 m² m⁻² (Table 1), and then changed slowly in plots >50 years old ($R^2 = 0.24$, $P = 0.0015$, Fig. 3b). The three oldest stands drove the increase in LAI with age seen in stands >50 years old ($n = 31$). These stands averaged
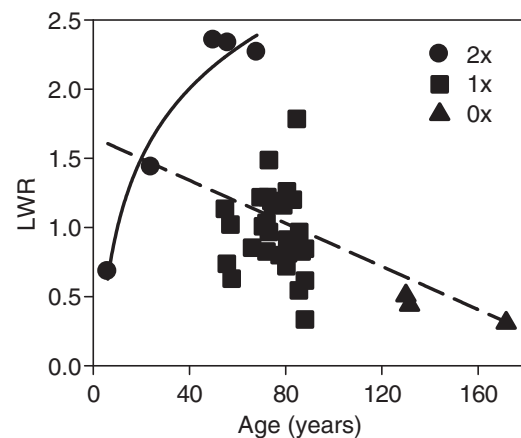
Table 1
Summary statistics describing wood (W), leaf (L), and total aboveground net primary production (ANPP), leaf to wood production ratios (LWR), age, rugosity, leaf area index (LAI), species richness, the fraction of photosynthetically active radiation absorbed by the canopy (fAPAR), light use efficiency (LUE), foliar nitrogen (N) mass, and N use efficiency (NUE) in 39 forest plots (unless noted otherwise) spanning >160 years of forest succession. Standard Errors (S.E.) represent between-plot variability of interannual means.

Variable	Mean ± S.E.	(Min, Max)
[1] $ANPP_W$ (Mg C ha⁻¹ years⁻¹)	1.66 ± 0.15	(0.64, 5.54)
[2] $ANPP_L$ (Mg C ha⁻¹ years⁻¹)	1.44 ± 0.05	(0.68, 2.24)
[3] LWR	1.04 ± 0.08	(0.31, 2.35)
[4] ANPP [(1+2)]	3.11 ± 0.18	(1.68, 7.26)
[5] Age (years)	77 ± 4	(6, 172)
[6] Rugosity (m)	15.53 ± 1.22	(0.95, 32.57)
[7] LAI (m² m⁻²)	4.14 ± 0.17	(1.8, 6.56)
[8] Species richness (n)	4.75 ± 0.21	(2, 8)
[9] fAPAR[a]	0.94 ± 0.01	(0.85, 0.99)
[10] LUE [(4–9)a]	0.04 ± 0	(0.02, 0.07)
[11] Foliar N_{mass} (Mg N ha⁻¹)[b]	0.04 ± 0.01	(0.02, 0.08)
[12] NUE [(4–11)b]	95.73 ± 14.93	(31.47, 176.24)

[a] $n = 12$ plots.
[b] $n = 11$ plots.

Fig. 1. Patterns of biomass allocation in stands clear-cut and burned twice (2×), once (1×), and in stands with no historical records of clear-cutting or stand-replacing fire (0×). Leaf to wood ratio (LWR) is average yearly leaf: wood ANPP for each plot. LWR in plots cut and burned 2x correlated with stand age (solid line; $y = 0.727 * \ln(abs(x)) - 0.678$, $R^2 = 0.95$), but not in other subsets of plots. LWR declined with age across all plots (dashed line; $R^2 = 0.18$).

32% more LAI than the average for all other plots but were not outside the range exhibited by younger plots.

Aboveground NPP showed a positively skewed unimodal distribution with only two plots over 6 Mg C ha⁻¹ years⁻¹. ANPP was higher in older plots (Table 2, $R^2 = 0.81$, $P < 0.0001$, Fig. 3c), and in the late successional plots it was over 4 Mg C ha⁻¹ years⁻¹. In the youngest plots, ANPP was <2 Mg C ha⁻¹ years⁻¹. Despite several significant interactions (Table 2), rugosity was the only significant explanatory variable retained in a stepwise model selection on potential drivers of ANPP that included rugosity, species richness, fAPAR, and foliar N_{mass}. Rugosity correlated positively with ANPP with little difference between linear and quadratic fits (quadratic $R^2 = 0.31$, $AICc = 100.2$, $P = 0.0004$ compared to linear $R^2 = 0.29$, $AICc = 99.9$, $p = 0.001$; Fig. 4).

3.2. Resource use efficiency in subset plots

Both LUE and NUE increased with increasing rugosity ($P = 0.0237$, 0.0607 for LUE and NUE, respectively; Fig. 5 a and b). We observed a threefold difference between highest and lowest LUE among plots, but only 15% variation between plots with highest and lowest fAPAR. Rank order of plot fAPAR did not predict rank order of plot LUE (Wilcoxon Signed Rank Test, $P = 0.75$), but the oldest plots had both the highest fAPAR and LUE. We found that fAPAR was greater than 0.85 in all plots and those with greater LAI had significantly higher fAPAR (Table 2). Rugosity and LAI varied five and threefold, respectively, in the subset of plots in which we measured fAPAR and rugosity did not explain significant residual variability in fAPAR after accounting for LAI ($P > 0.1$). After removing LAI variability associated with rugosity, residual variation in LAI still explained slightly more fAPAR variation than rugosity (LAI $R^2 = 0.69$, LAI vs. Rugosity residuals $R^2 = 0.48$, Rugosity $R^2 = 0.40$).

Similar to LUE and fAPAR, NUE varied fivefold among plots and was more variable than foliar N_{mass}. Rank order of plot foliar N_{mass} was predictive of plot NUE (Wilcoxon Signed Rank Test, $P = 0.002$). NUE increased with stand age while foliar N_{mass} was unrelated to ANPP, rugosity, LAI, age, species richness, or fAPAR (Table 2). Foliar N_{mass} varied threefold in plots between 50 and 100 years of age, but foliar N_{mass} was nearly invariant in the oldest (>100 years old) plots. The three oldest plots did not have the highest foliar
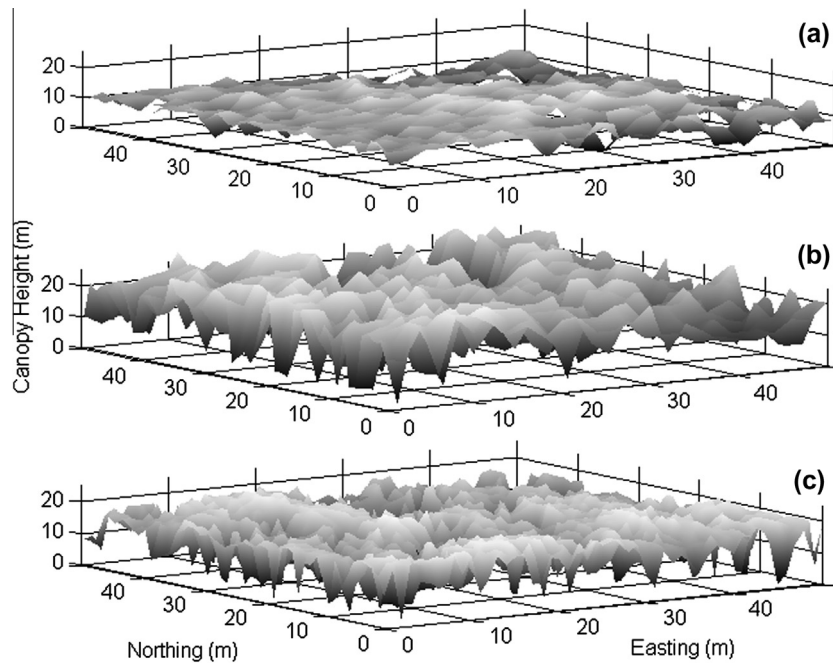
Fig. 2. 3D renderings of canopy-top surface texture are of 0.25 ha forest plots 30 (a), 85 (b), and 131 (c) years old. A curved surface was interpolated between the highest LiDAR data point in each vertical column of 1 m³ bins formed by the transect grid in each plot. All plots are displayed at identical scaling and rotation.

Table 2

Spearman's rank correlation coefficients (ρ) for the subset of plots in which fAPAR and foliar N_{mass} were measured. ρ indicates the degree to which the relationship between any two variables is monotonic. Sign indicates direction of interactions between measured variables. Limited sample size for foliar N_{mass} ($n = 11$) and fAPAR ($n = 12$) necessitate caution when interpreting significance of ρ.

	ANPP	Rugosity	LAI	Species Richness	Age	fAPAR
Rugosity	0.62**					
LAI	0.55**	0.55**				
Species richness	0.37*	0.04	−0.06			
Age	0.70**	0.81**	0.37*	0.17		
fAPAR	0.75**	0.74**	0.82**	−0.04	0.73*	
Foliar N_{mass}	−0.01	0.01	−0.12	0.28	−0.12	−0.21

* $P < 0.05$.
** $P < 0.01$.

N_{mass} values, but were three of the top five most nitrogen use-efficient plots.

The subset of plots in which we measured fAPAR and canopy foliar N_{mass} was representative of all plots in this study and spanned the range of variation of both ANPP and rugosity (Fig. 4, inset). Mean rugosity did not differ between subset plots and the mean for all plots ($P > 0.1$). Mean age was greater in the subset ($P = 0.04$) and the range of ages represented in the subset spanned 116 of the >160 years observed across all plots. Mean (±S.E.) annual ANPP was slightly greater in subset plots relative to all plots ($P = 0.054$) with mean ANPP of 3.71 (±0.48, $n = 12$) Mg C ha⁻¹ years⁻¹ in the subset, compared to 3.11 (±0.18, $n = 39$) Mg C ha⁻¹ years⁻¹ for all plots.

4. Discussion

4.1. Canopy structure and function

The relationships between LUE, NUE, and rugosity reported here provide evidence for a functional linkage between canopy structure and ecosystem carbon storage functioning. Canopies of older forests were more structurally complex, with higher rates of ANPP per unit light absorbed by the canopy and per unit foliar N than stands with structurally simple canopies. While we characterized LUE and NUE in a subset of our study plots, these plots spanned the range of variation in both ANPP and rugosity and the relationship observed in our subset of plots between canopy structural complexity and RUE is robustly representative of that occurring across the broader landscape. Increased canopy structural complexity is known to improve whole-canopy photosynthesis rates (Walcroft et al., 2005) and previous work at this site established a link between canopy structural complexity and wood ANPP (Hardiman et al., 2011). These results indicate greater structural complexity improves RUE in some aging forests, consequently increasing ANPP compared to more structurally simple canopies in young forests.

We observed that while rugosity and ANPP increased significantly with age, LAI did not (Fig. 3). LAI is generally observed to increase as stands age, but this is primarily in stands that are still relatively young (e.g. Humphreys et al., 2005; Gough et al., 2007; McMillan and Goulden, 2008; He et al., 2012). Further, while LAI and rugosity are indeed interrelated features of canopy structure, these variables have been demonstrated at this and other sites to have distinct influences on stand production (Walcroft et al., 2005; Drake et al., 2011; Hardiman et al., 2011). These results support and extend previous observations at this site (Gough et al., 2007; Hardiman et al., 2011) that LAI was largely insensitive to age in stands older than 50 years, making higher leaf area an unsatisfactory explanation for increases in ANPP of aging and old forests.

In contrast, rugosity was the most consistent and effective predictor of stand production in stands not only differing in age by more than a century, but which also varied widely in disturbance histories and biomass allocation patterns. Stands established through a second stand-replacing experimental cutting and burning (including the youngest stands in this study) allocated twice as much to leaf as to wood production and had LWR values twice as large as plots of the same age that were cut and burned only
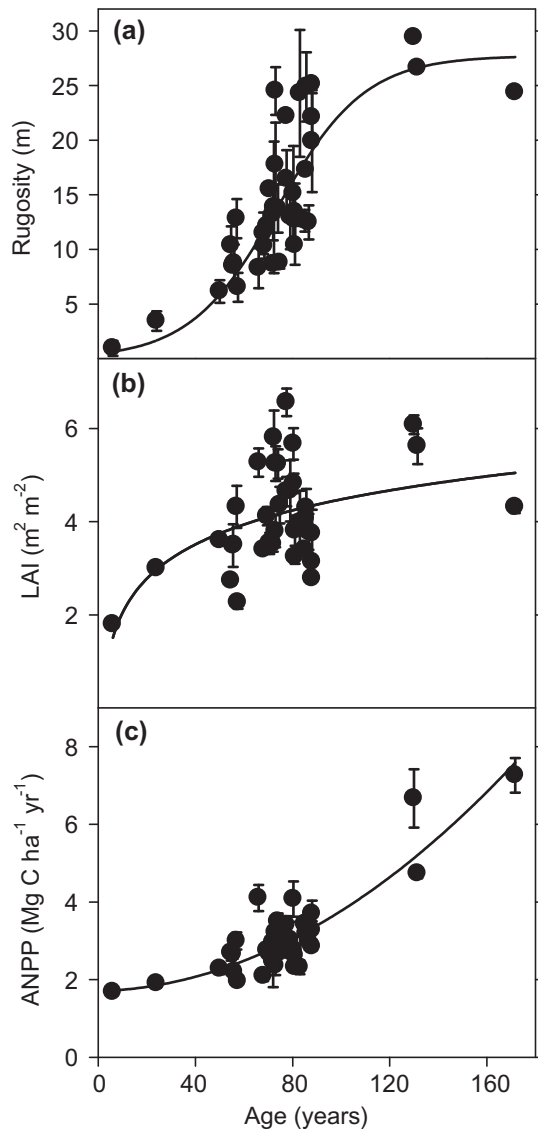
Fig. 3. Relationships of canopy rugosity (a), leaf area index (LAI) (b), and ANPP (c) with stand age ($y = -29.412/(1 + e^{-(x+74.020)/-8.957)}$), $R^2 = 0.73$; $y = -0.379 + 1.044 * \ln(x)$, $R^2 = 0.25$; and $y = -1.706 - 0.002 * x - 1.902 \times 10^{-004} * x^2$, $R^2 = 0.80$, for (a), (b), and (c) respectively). Rugosity and LAI values are mean (±S.E.) among ⩾2 years. ANPP is the yearly production of leaf and aboveground wood biomass averaged over ⩾2 years of data collections to reduce climate-associated interannual variability. AICc supported a quadratic relationship between ANPP and age (AICc = 39.89; compared to linear AICc = 62.45, P < 0.0001 for both models).

Fig. 4. ANPP and canopy structural complexity (rugosity) in forest plots ranging across >160 years of development and encompassing disturbance histories varying widely in severity ($R^2 = 0.34$). Inset illustrates the representative subset of research plots in which fAPAR and foliar N_{mass} was quantified ($R^2 = 0.65$).

Fig. 5. Relationships between Light Use Efficiency (LUE, a), Nitrogen Use Efficiency (NUE, b), and canopy rugosity. $R^2 = 0.60$ and 0.32 for LUE and NUE, respectively. Areas bounded by dotted lines are 95% confidence intervals.

once (Fig. 1). Gough et al. (2007) observed that fine root biomass was unchanged in these stands relative to control sites but soil quality was lower. The larger LWR observed in twice disturbed stands relative to those cut and burned once is consistent with the compensatory response observed in regenerating aspen stands supporting the C requirements of a large and active belowground biomass pool and enhanced root foraging under reduced nutrient availability (DesRochers and Lieffers, 2001; Craine, 2009). The oldest plots, those subject to the least intense disturbance history, allocated twice as much to wood as to leaf production, providing stand-level evidence of a trend generally observed in aging individuals (Niinemets, 2010). Canopy rugosity explained the most variation in stand ANPP despite wide variations in disturbance severity and aboveground biomass allocation patterns. The observed decrease in LWR with stand age among all plots indicates that quantity of leaf area is only a significant correlate with production in
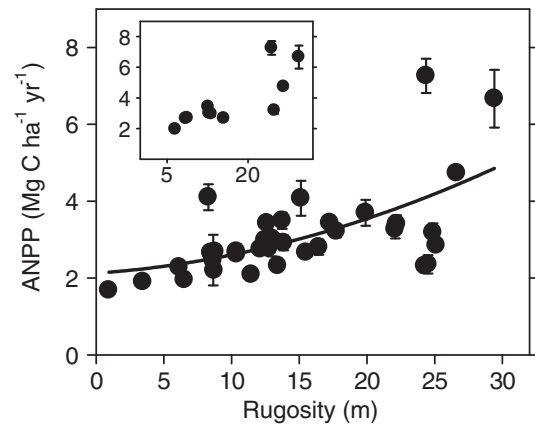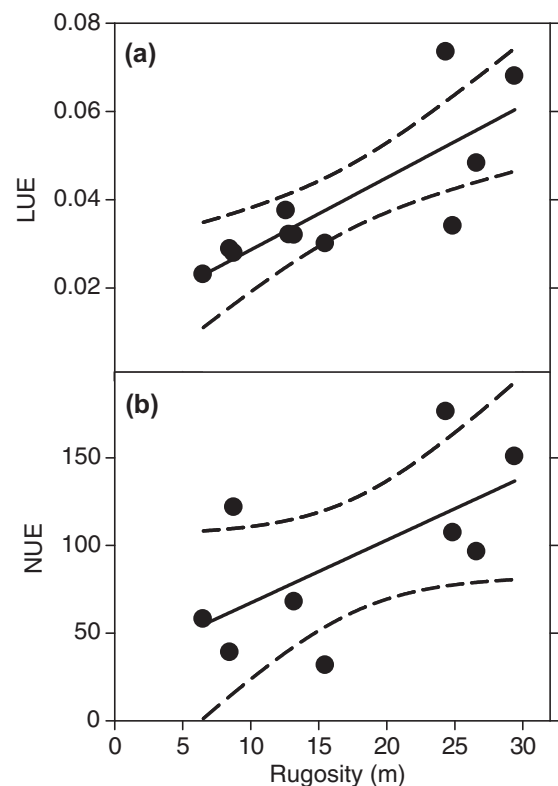
young and twice disturbed forests. The general trend among all plots was a shift toward greater ANPP$_W$ with age, illustrating the increasing contribution of slow-turnover biomass (wood) to total ANPP as stands age, likely contributing to stability of C storage in old forests.

4.2. Rugosity and resource use efficiency

Structural complexity allows more efficient use of available light in canopies and increased C uptake over stand development. Canopy structural complexity increases with stand age (Canham,

1989; Hart and Grissino-Mayer, 2009; Hardiman et al., 2011) due in part to recruitment of later-successional shade-tolerant species which have significantly different crown structures from early successional shade-intolerant species (Niinemets, 2010; D'Amato et al., 2011). The incorporation of a variety of crown geometries increases canopy structural complexity (Horn, 1971). In addition, later-successional species, which recruit under an established canopy, use light more efficiently owing to the necessity to maintain a positive C balance in a reduced light environment (Valladares and Niinemets, 2008). Foliage produced by these trees exhibits a greater increase in photosynthesis rate per unit of increased light availability than does light-adapted foliage (Niinemets, 2007, 2010). As in Gough et al. (2010), we observed an increase in proportion of shade tolerant species with stand age despite no net change in species richness. The gradual incorporation of species with greater shade tolerance and higher LUE shifts over time the way canopies in stands of different ages use available light (Smith et al., 2008; Niinemets, 2010) and contributes to higher LUE in stands with more structurally complex canopies. Indeed, canopy structural complexity explained more variation in stand LUE than LAI did, despite LAI explaining more variation in fAPAR. Further, this suggests that increasing canopy structural complexity could boost whole-canopy photosynthesis rates in addition to increasing stand LUE. These and previous observations of increased rates of woody biomass production in stands with structurally more complex canopies (Gough et al., 2010; Hardiman et al., 2011) are consistent with a mechanism linking forest canopy structure to ecosystem function.

Consistent with previous research at this and other sites (Walcroft et al., 2005; Duursma and Makela, 2007; Hardiman et al., 2011), both arrangement (rugosity) and quantity (LAI) of canopy foliage affected canopy light transmission. Our short-term measurements of fAPAR varied more strongly with LAI than with rugosity. Residual analysis of LAI and rugosity on fAPAR revealed that LAI was still a better predictor of stand fAPAR than rugosity after removing covariation between LAI and rugosity. This indicates that rugosity does not fully account for canopy light interception, which is at least partially driven by LAI as documented in Hardiman et al. (2011). Several previous studies have also noted the dual influences of leaf arrangement and leaf quantity on transmission of light through the canopy (Lefsky et al., 1999; Ishii et al., 2004; Walcroft et al., 2005; Tobin and Reich, 2009). Importantly, mean LAI changed much slower when stand age exceeded 50 years, while rugosity continued to increase rapidly until stands approached late succession (Fig. 3a and b). This observation is supportive of a steady-state canopy in stands where the main source of disturbance is individual mortality and gaps are formed and filled at approximately the same rate (Kneeshaw and Bergeron, 1998; Drake et al., 2011; He et al., 2012). Thus, as LAI stabilized in middle succession, rearrangements in canopy structure, rather than changes in LAI controlled ANPP into later succession. Over the lifetime of a forest, rugosity and LAI each constrain fAPAR at different stages in stand development and succession, with consequent effects on ANPP.

As forest rugosity increases with age, foliar rearrangements effectively redistribute foliar N within the canopy. As increasing structural complexity boosts whole canopy photosynthetic rates, foliar N utilization becomes more efficient. Greater light availability per unit of leaf area increases NUE by facilitating higher photosynthetic output without the need for additional leaf area. Distributing N over greater canopy surface area also increases light absorption and C assimilation more effectively than increasing foliar N concentration (Niinemets, 2007). In canopies with high rugosity, higher leaf-level photosynthetic rates can be realized with existing foliar N concentrations, increasing stand NUE concurrent with increases in stand LUE.

4.3. Conclusions: Rugosity's relevance to models and managers

For several decades, conceptual models of C storage patterns in forests through ecosystem development (e.g. Odum, 1969; Bormann and Likens, 1994) have proven useful as testable hypotheses and are increasingly critical to understanding the interaction between forests and the atmosphere in a global climate change context. When confronted with increasingly available long-term and spatially extensive data from field studies however, models do not reliably reproduce observed patterns of C storage (Luyssaert et al., 2008; Johnson and Abrams, 2009; McMahon et al., 2010). In this study, we observed increasing biomass production rates in stands at ages generally predicted to be C neutral. This mismatch between model output and field observations limits utility of model predictions to forest managers, especially with respect to old forests. Explicit high-resolution models that account for forest structure have large computational-time requirements and thus are limited to simulations of small plots and cannot be used to simulate large-scale environments (Dupont and Brunet, 2008; Bohrer et al., 2009). Recent regional and large-scale ecosystem models (e.g. ED2, BIOME-BGC, FVS) are far more sophisticated, but simplify the complex 3-D structure of forest systems to a small number of leaf layers in a few representative plant functional types per forest to increase computational tractability (Dietze et al., 2011). This approach entails a risk of oversimplifying these complex systems. The present study demonstrates that within-stand, tree-scale 3-D spatial structure of the forest canopy is a robust predictor of ANPP in temperate, mixed deciduous stands varying in age by more than a century (>160 years), with contrasting disturbance histories, and exhibiting divergent biomass allocation patterns. Resource-use efficiency increased with rising canopy structural complexity into late forest succession, demonstrating the increasing importance of rugosity as a driver of ecosystem function as forests age. Updating current-generation models to include the physiological linkage demonstrated here between canopy structural complexity and ecosystem function mediated through canopy light and nitrogen use efficiency will improve estimates of C storage in aging and old forests thereby increasing the value of model predictions to forest managers.

Land managers need accurate estimates of C storage potential in old and aging forests when deciding how to value these systems among a portfolio of forest types and management objectives (Carey, 2006). Many old forests sequester substantial C in biomass (i.e., by maintaining NPP) (Urbanski et al., 2007; Luyssaert et al., 2008; Wang et al., 2011) for much longer than projected (for example, see Birdsey et al., 2006), and therefore the contribution of these old, mixed temperate forests to long-term C storage must be reconsidered. Our results suggest that while ignoring the influence of canopy structure in young forests may have limited consequences, doing so in aging and old forests may lead to increasing underestimation of terrestrial C sink strength as globally many forests recover from historical disturbance (Birdsey et al., 2006). As remote sensing data can now be used to provide plot-level estimates of tree size and age distributions (demonstrated at our site by Garrity et al., 2012), incorporating the influence of canopy structural complexity on RUE to revise predictions of C storage in old forests may reveal that conservation of passively managed aging and old forests is a viable strategy for achieving long-term C storage.

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